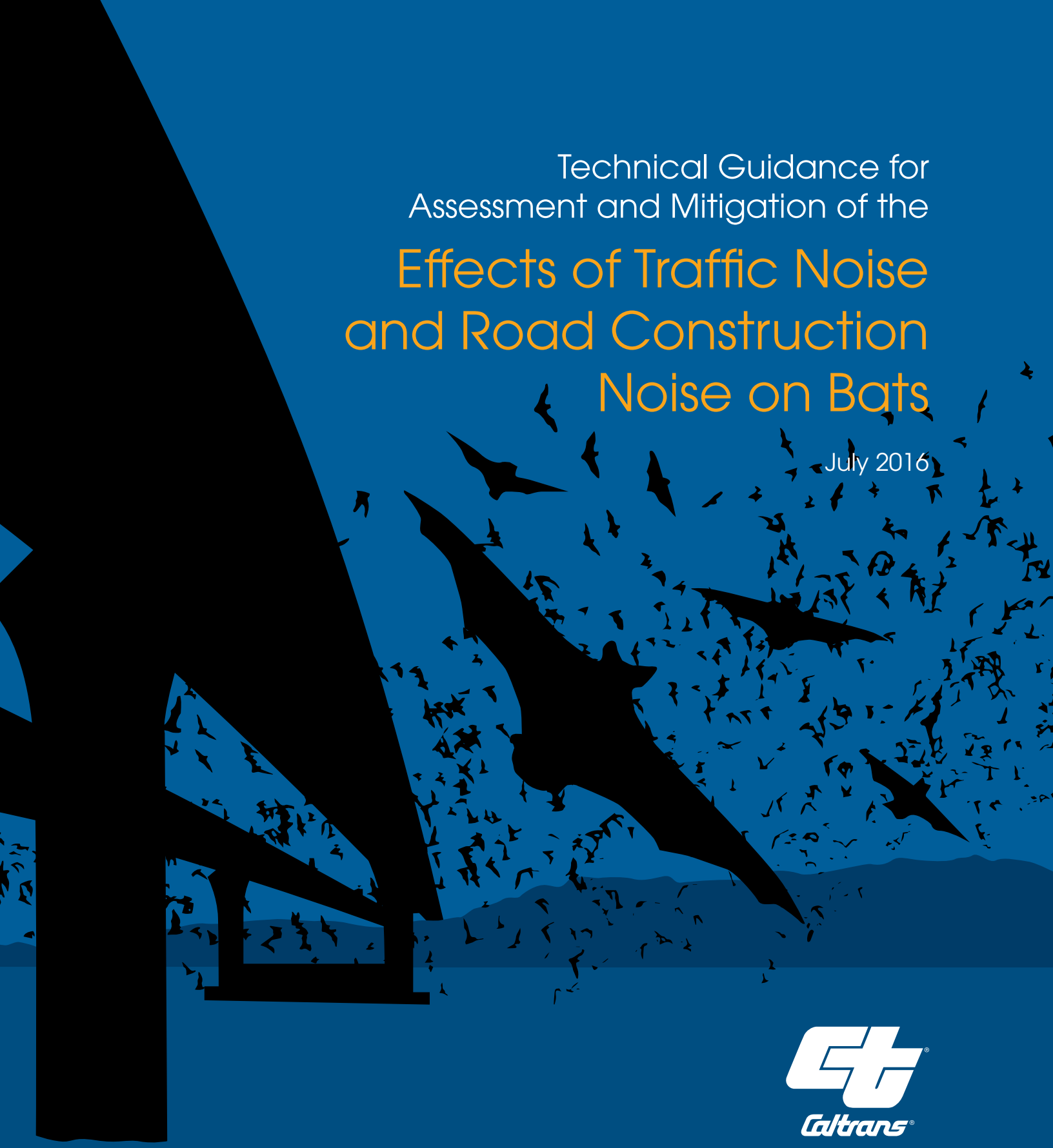
Technical Guidance for
Assessment and Mitigation of the

Effects of Traffic Noise and Road Construction Noise on Bats

July 2016



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15. Abstract

The purpose of this report is to provide Department engineers, biologists, and consultants with guidance related to the effects of traffic noise and road construction noise on bats. This manual covers the sound environment, bat hearing, echolocation and communication, effects of highway noise on bats, and presents guidelines for project noise assessment and management. Literature citations and abstracts have been included in Appendix C and constitute a significant portion of this document.

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TECHNICAL GUIDANCE FOR THE ASSESSMENT AND MITIGATION OF THE EFFECTS OF TRAFFIC NOISE AND ROAD CONSTRUCTION NOISE ON BATS

California Department of Transportation
Division of Environmental Analysis
1120 N Street, Room 4301 MS27
Sacramento, CA 95814

July 2016

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Executive Summary

Increasing levels of anthropogenic noise in natural, rural, and urban areas are creating new sound environments that have the potential to adversely affect many species of wildlife. Noise produced by the construction and operation of highways is of particular concern due to the large areas and diversity of wildlife it can affect, including bats. Because bats commonly roost in bridges and culverts and forage along highway rights-of-way, there is concern regarding how traffic noise may affect bat species. There is also concern regarding effects on bats resulting from highway construction projects, which can often create loud, potentially disturbing noise environments in areas where bats occur.

The California Fish and Game Code (Section 4150) prohibits take of bats. Noise disturbance and displacement of bats from roosts or important foraging areas can potentially result in reduced survivability of individuals from increased susceptibility to predation, reduced quality of thermal and social environments, and reduced foraging efficiencies. Accordingly, bats need to be considered during the environmental review process as per the California Environmental Quality Act (CEQA) (Section 15380).

This report provides technical guidance for the assessment and mitigation of the effects of traffic and road construction noise on bats.

Potential Effects

The principal potential effects of traffic noise and highway construction on bats are acute acoustic trauma, disturbance and displacement from important food and shelter resources, and signal masking. Acoustic trauma is potentially a very serious effect because bats are fully dependent on echolocation and passive listening for both immediate and long-term survival. They do not have the luxury of time for recovery from almost any level of hearing system damage. However, because of the multiple behavioral and physiological defensive mechanisms they have developed to prevent noise overexposure, most bats are likely effectively shielded from most trauma events that would result from highway noise.

Disturbance is likely to be the most pervasive and significant effect associated with highway projects. Potential adverse effects include roost abandonment, avoidance of foraging areas, dysfunctional allocation of time and energy resources to vigilance behaviors, and degradation of physiological condition and social order. Some level of tolerance and habituation to noise does occur in some species that colonize bridges in large numbers.

Signal masking can be significant if highway noise substantially interferes with information transfer during echolocation, communication, or passive listening. However, because the spectra of traffic and construction noise do not appreciably overlap with most bat echolocation calls or their hearing of them, echolocation in most species of bats is likely not affected by highway noise.

Some level of masking of low frequency communication signals likely occurs within bridge roosts due to the proximity of the bats to the highways. However, it is unknown to what extent such masking interferes with communication or how effectively bats use acoustic adaptations to avoid and minimize information loss. These adaptations include elevated signal amplitude (Lombard

effect), frequency shifts (both within and between signals), increased signal length and redundancy, temporal spacing of calls between noise events, and spatial maneuvering to optimize signal transmission. If sufficient avoidance/compensatory conditions cannot be met, some bats may suffer the social consequences of miscommunication, including disconnected communication between parent and offspring, degradation of mate choice enticements, miscues on aggressive intent or alarm signals, and misaligned communication during social events such as emergence and mating.

Masking of important environmental sounds, particularly those of ground dwelling insects targeted by gleaning bat species (e.g., pallid bat [*Antrozous pallidus*], California leaf-nosed bat [*Macrotus californicus*]) can potentially occur in close proximity to highways. However, it is yet to be definitively determined that noise, specifically noise masking, is the principal causal factor as to why bats avoid highway areas.

The Significance of Bat Responses to Noise

Bats are highly evolved and specialized species. They are uniquely and precisely adapted to their nocturnal environment—morphologically, physiologically, and behaviorally. Creating imbalances in these adaptations through noise disturbance or trauma can potentially result in rapid and significant changes in individual and colony viability or more moderate disruptive shifts in habitat use patterns, species distribution, and community structure.

Bats occupy a wide range of habitats that are precisely defined by their physical and thermal properties. These include the many surrogate crevices and thermal refuges in bridges (Erickson et al. 2003) and other highway structures. Displacement from these sites, whether temporary or long-term, may have significant physiological and biological costs (e.g., exposure to predation) if similar resources are not available nearby.

In terms of energy expenditure, bats operate on the edge of optimality. Foraging by flight and homeostatic maintenance of thermal balance in small bodies at night is energetically expensive. Redirecting limited energy reserves to finding new roosts, meeting higher thermoregulatory expenses in suboptimal roosts, and increased vigilance behaviors comes with costs to their ability to grow, maintain, and reproduce. A significant immediate or protracted negative balance in their energy reserves due to noise disturbance may jeopardize survival and reproductive success of both individuals and colonies.

Acoustic trauma can potentially have immediate severe consequences. Bats have evolved highly specialized vocalization and auditory systems to maximize their ability to detect, locate, track, and capture aerial prey and avoid predators. The behavioral, morphological, and physiological mechanisms that have evolved to achieve this end dramatically increase their hearing sensitivity to all sounds, particularly the soft echoes of their echolocation calls. But these specializations also potentially expose the bats to noise shock and acoustic damage from loud anthropogenic noise. However, bats have also evolved very effective compensatory protective measures to prevent undue noise overexposure, specifically from their own very loud echolocation calls. While these mechanisms are effective in achieving the needed protection from auto-exposure, it is unknown whether they also can prevent overexposure from sudden, unexpected anthropogenic noise shocks (e.g., blasting, pile driving); This adaptive mechanism is likely, in theory, but additional studies are needed to verify it and identify the specific mechanisms involved.

Guidelines for Assessment and Mitigation

This report draws on applicable information from several recent documents (e.g., Erickson et al. 2003; Johnston et al. 2004) that provide excellent guidance on the general needs and working protocols for the avoidance, minimization, and mitigation of highway project impacts on bats in California. The strategies presented in these reports include recommended methods for determining bat presence and use patterns in project areas, determining the noise environments of the projects, assessing the level and nature of potential noise effects, and developing effective mitigation measures to avoid and minimize site-specific noise effects on bats. Mitigation strategies include both temporal and spatial impact avoidance methods and possibly the use of acoustic deterrents to temporarily exclude bats from occupied sites. These approaches can be augmented with installation of off-site artificial bat roosts to partially mitigate for loss of extant surrogate roosts on bridges or other highway infrastructure.

Future Research

This report identifies future studies that are needed to address key questions related to emergent issues discussed in the technical analysis, including noise effects thresholds and criteria, natural and evoked adaptations used by bats, the efficacy of current mitigation and conservation measures, important logistics needs necessary to improve our understanding of bat sensory ecology, and how best to build and operate highway projects with minimal impacts on wildlife, including bats.

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Acronyms and Abbreviations

ABR	auditory brainstem response
BLM	Bureau of Land Management
Caltrans	California Department of Transportation
CDFW	California Department of Fish and Wildlife
CEQA	California Environmental Quality Act
CF	characteristic frequency or constant frequency
CT	California Threatened
dBA	weighted decibels
E	Federally Endangered
f@max	frequencies with maximum energy
FM	frequency modulated
Hz	hertz
kHz	kilohertz
L,M,H	Western Bat Working Group Low, Medium and High species ranking
L_{eq}	background noise levels
m	meters
mph	miles per hour
ms	milliseconds
NIHL	noise-induced hearing loss
PTS	permanent threshold shift
S	BLM/USFS Sensitive
SPL	sound pressure level
SSC	California Species of Special Concern
TTS	temporary threshold shifts
USFS	USDA Forest Service
USFWS	U.S. Fish and Wildlife Service
vph	vehicles per hour
WBWG	Western Bat Working Group

Section 1: Introduction

Increasing levels of anthropogenic noise in natural, rural and urban areas are creating new sound environments that have the potential to adversely affect many species of wildlife (Patricelli and Blickley 2006; Warren et al. 2006; Barber et al. 2010; Barber et al. 2011; Knight and Swaddle 2011; Naguib 2013; Read et al. 2014). Noise produced by the construction and operation of highways is of particular concern due to the large areas and diversity of wildlife it can affect (Ortega and Capen 1999; Dooling and Popper 2015; Lengagne 2008; Parris and Schneider 2008; Fahrig and Rytwinski 2009; Arévalo and Newhard 2011; Halfwerk et al. 2011; Herrera-Montes and Aide 2011; Siemers and Schaub 2011; Inglesias et al. 2012; Shier et al. 2012; Francis 2014). Because bats commonly roost in bridges (Wolf and Shaw 2002; Johnston et al. 2004) and culverts and forage along highway rights-of-way, there is concern regarding how traffic noise may affect bat species (Jones 2008b; Schaub et al. 2008; Siemers and Schaub 2011; Hage et al. 2014; Kitzes and Merenlender 2014). There is also concern regarding effects on bats resulting from highway construction projects, which can often create loud, potentially disturbing noise environments in areas where bats occur. Many bat species roost in tree cavities, foliage and bark crevices - sites that can potentially be close to construction work, particularly on single lane roads in large forested habitats (Lacki et al. 2007).

Very little information is currently available that details how bats respond to anthropogenic noise (Jones 2008b; Schaub et al. 2008; Siemers and Schaub 2011; Lou et al. 2014). Bats are known to abandon roosts in caves, mines, and some buildings when directly disturbed by human activities (Humphrey and Kunz 1976; Keeley and Tuttle 1999). Loud ultrasonic noise (i.e., having frequencies above the range of human hearing >20 kilohertz [kHz]) can deter bats from accessing and using known bridge roosts (Szewczak 2011) and wind turbines (Arnett et al. 2013). Traffic noise can potentially deter some bats from feeding alongside and crossing over highways (Schaub et al. 2008; Siemers and Schaub 2011). In contrast, large colonies of bats (e.g., the Brazilian free-tailed bat) commonly roost in very large numbers in bridges with a high level of traffic, suggesting traffic noise does not bother the colonies roosting there (Taylor 2013).

Studies of other species with similar hearing apparatus (e.g., mice) also suggest that chronic loud noise can potentially lead to noise-induced stress, and sudden extremely loud noise can result in auditory system damage and hearing loss (Le Prell et al. 2012; see also Dooling and Popper 2015; Rasmussen et al. 2009; Schroeder et al. 2012). Noise can also potentially mask echolocation signals and important acoustic communication signals and other biologically relevant sounds, such as those made by approaching predators (Ryals et al. 1999; Dooling and Blumenrath 2013; Brumm and Slabbekoorn 2005; Bee and Swanson 2007).

Regulatory Status of California Bats

The California Fish and Game Code Section 4150 prohibits incidental or deliberate take of bats. *Take* means to hunt, pursue, catch, capture, or kill, or attempt to hunt, pursue, catch, capture, or kill designated wildlife (Fish and Game Code Section 86). Noise disturbance and displacement of bats from roosts and important foraging areas can potentially result in reduced survivability of individuals from increased susceptibility to predation, reduced quality of thermal and social environments, and reduced foraging efficiencies. Displacement during the breeding season can also potentially result in reduced reproductive success of affected colonies. Accordingly, bats need to be

considered during the environmental review process as per the California Environmental Quality Act (CEQA)).

Twenty-five species of bats occur in California (Table 1). Bats are found in every county of the state, and many roost on bridges, in culverts, and on other infrastructure associated with or near highways (Table 1). Twelve of these species are classified as Species of Special Concern (SSC) by the California Department of Wildlife (CDFW), one (Townsend's big-eared bat [*Corynorhinus townsendiiI*]) is identified as a candidate species for state listing as Threatened (CT) and also listed as a 'sensitive' species by U.S. Bureau of Land Management and U.S. Forest Service, and one (Lesser long-nosed bat [*Leptonycteris yerbabuenae*]) is federally listed as Endangered (E) (Table 1).

Contents and Organization of This Report

This report provides technical guidance for the assessment and mitigation of the effects of road construction noise and traffic noise on bats; it presents background information on bat biology, ecology, and bioacoustics to frame the assessment protocol. Section 2 describes the sound environments that bats are likely to experience, both under natural conditions and in situations in which highway noise (construction and operation) is prevalent. Section 3 details the important aspects of bat biology that are relevant to understanding how bats may be adversely affected by noise. Section 4 integrates and analyzes the information in Sections 2 and 3 to identify and assess the potential effects of highway noise on bats. Section 5 then provides guidelines on how to determine the level and extent of highway noise for different construction projects and traffic noise scenarios and best management practices for avoiding, minimizing, and mitigating noise impacts on bats. Finally, Section 6 provides recommendations for future research and studies needed to address unanswered questions about potential noise impacts on bats.

This report contain three appendices:

- Appendix A—Glossary of Terms. Definitions of a variety of technical biological and acoustic terms and metrics used in this report.
- Appendix B— Bats in California. A detailed description of bats that occur in California.
- Appendix C—Compilation of the Research Citations and Abstracts.

Terminology and Metrics

This report uses a variety of technical biological and acoustic terms and metrics that may be unfamiliar to the reader. A glossary is provided in Appendix A. Detailed information on the fundamental concepts and analysis of highway noise is available in several documents published by the California Department of Transportation (Caltrans). These include the *Technical Noise Supplement to the Traffic Noise Analysis Protocol* (California Department of Transportation 2013) and *Traffic Noise Analysis Protocol* (California Department of Transportation 2011). Online training on the fundamentals of highway traffic noise and noise measurements is also available at: http://www.dot.ca.gov/hq/env/noise/training.htm. Figure 1 shows general bat anatomy and key structures.

Table 1. Bats of California, Their Regulatory Status, and Bridge Use Patterns

Family and Common Name	Scientific Name and Code	Status[a]					Bridge Use[b]
		CDFW	USFWS	BLM	USFS	WBWG	
Phyllostomidae (Leaf-nosed bats)							
Mexican long-tongued bat	*Choeronycteris mexicana* (CHME)	SSC				H	3
Lesser long-nosed bat	*Leptonycteris yerbabuenae* (LEYE)		E			H	4
California leaf-nosed bat	*Macrotus californicus* (MACA)	SSC		S	S		3
Vespertilionidae (Vesper bats)							
Pallid bat	*Antrozous pallidus* (ANPA)	SSC		S	S	H	1
Townsend's big-eared bat	*Corynorhinus townsendii* (COTO)	CT, SSC			S	H	2
Big brown bat	*Eptesicus fuscus* (EPFU)						1
Spotted bat	*Euderma maculatum* (EUMA)	SSC		S		H	3
Silver-haired bat	*Lasionycteris noctivagans* (LANO)					M	3
Western red bat	*Lasiurus blossevillii* (LABL)	SSC				H	5
Hoary bat	*Lasiurus cinereus* (LACI)					M	5
Western yellow bat	*Lasiurus xanthinus* (LAXA)	SSC				H	5
California myotis	*Myotis californicus* (MYCA)						2
Small-footed myotis	*Myotis ciliolabrum* (MYCI)			S		M	2
Long-eared myotis	*Myotis evotis* (MYEV)			S		M	2
Little brown bat	*Myotis lucifugus* (MYLU)					M[b]	2
Arizona myotis	*Myotis occultus* (MYOC)	SSC				M	3
Fringed myotis	*Myotis thysanodes* (MYTH)			S	S	H	2
Cave myotis	*Myotis velifer* (MYVE)	SSC		S		M	2
Long-legged myotis	*Myotis volans* (MYVO)					H	2
Yuma myotis	*Myotis yumanensis* (MYYU)					LM	1
Canyon bat	*Parastrellus hesperus* (PAHE)						3
Molossidae (Free-tailed bats)							
Western mastiff bat	*Eumops perotis* (EUPE)	SSC		S		H	4
Pocketed free-tailed bat	*Nyctinomops femorosaccus* (NYFE)	SSC				M	4
Big free-tailed bat	*Nyctinomops macrotis* (NYMA)	SSC				MH	3
Brazilian free-tailed bat	*Tadarida brasiliensis* (TABR)						1

CDFW = California Department of Fish and Wildlife; USFWS = U.S. Fish and Wildlife Service; BLM = Bureau of Land Management; USFS = USDA Forest Service; WBWG = Western Bat Working Group

[a] Status: E = Federally Endangered; CT = California Threatened; SSC = California Species of Special Concern; S = BLM/USFS Sensitive; L, M, H = Western Bat Working Group Low, Medium and High species ranking.

[b] Bridge use ranking: 1=commonly found on bridges; 2 = sometimes found; 3= rarely found; 4 = possibly use; 5 = do not use.

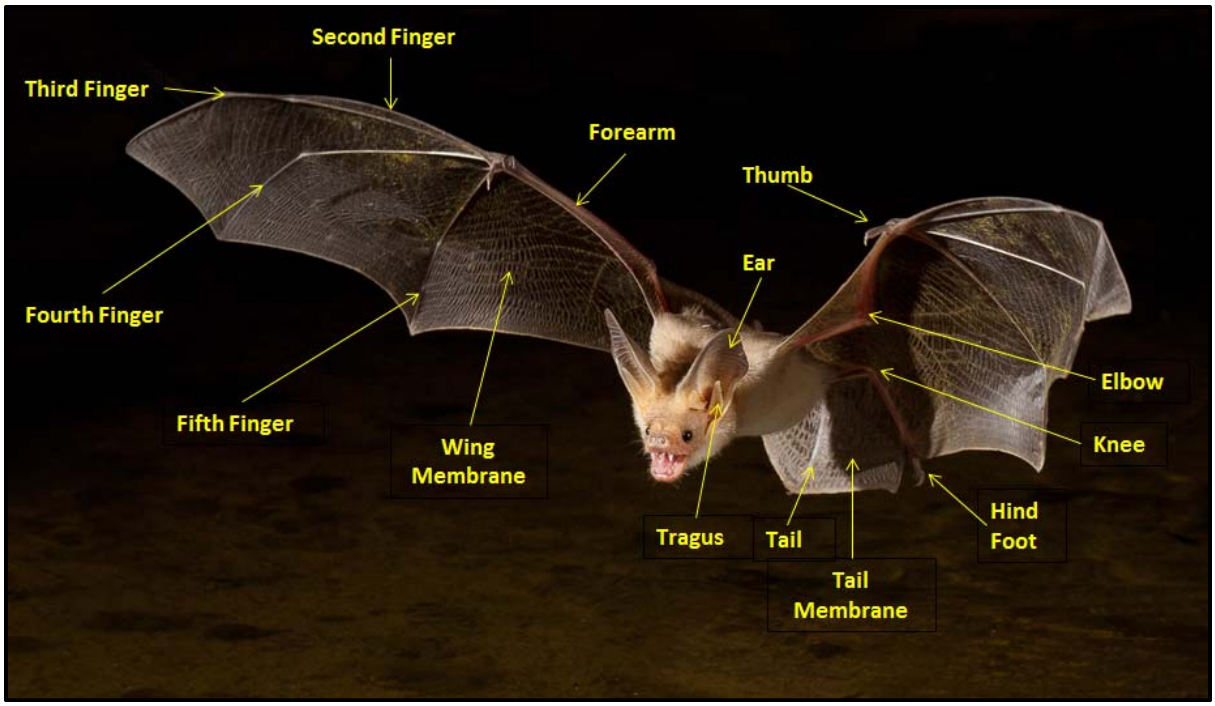

Figure 1. Anatomy of a Bat

(Source: Photo of the pallid bat (*Antrozous pallidus*) by Jared Hobbs. Adapted and used with permission.)

Section 2: The Sound Environment of Bats

Bats live in a complex sound environment (Figure 2) that includes the natural sounds of their environment; their own and other species' echolocation calls; acoustic communication signals from other bats; the sounds of potential prey species on the ground, on vegetation, and in the air; the movement sounds of potential predators and other wildlife; and the sounds of familiar and unfamiliar disturbance factors, including anthropogenic noise, such as traffic and highway construction. Highway sounds, both from construction and operation, can create a loud noise environment that may potentially interfere with the bats' abilities to hear and respond to the many other biologically important sounds that surround them.

Project Sounds and Noise

Highway project sound environments will include sounds of the preproject environment coupled with the add-on sounds that the project generates. The preproject environment may include only natural sounds (birds, wind, insects, etc.) if located in a wilderness setting, or more commonly will include a mix of these sounds and site-specific anthropogenic sounds (e.g., sounds associated with rural or urban human activity). Sounds that are not wanted (i.e., interfere with reception of natural sounds by wildlife or are annoying to humans) are referred to as *noise*. *Background noise* is the combined total of natural sounds and anthropogenic noise. Highway noise includes traffic noise and construction noise distinct from site-specific background noise. However, where preproject sites include an existing highway, the noise from that highway would be considered as part of the background noise for any new projects in the area.

Natural Sounds and Background Noise

Table 2 lists a variety of natural sounds typical of wilderness areas and their typical amplitudes. These sound levels are often used as baseline values for evaluating impacts on wildlife in natural settings. However, because most project study areas do include some anthropogenic noise, background noise levels are more commonly used for baselines. Most noise sources vary temporally and by location, but the sound pressure level (SPL) values listed provide a relative index of background sounds in natural settings. Table 3 lists background noise levels (L_{eq}) associated with urban and developed areas with different population densities.

Traffic Noise

Highway noise includes both traffic noise and road construction noise. Traffic noise varies with traffic volume (vehicles per hour [vph]), vehicle speeds, vehicle mix (percent of cars and trucks), road grade, and the type and condition of both tires and pavement. Generally noise levels increase when traffic volume and/or speeds increase and are proportionally higher when more trucks are included in the traffic flow. A traffic volume of 5,000 vph sounds twice as loud (i.e., 10 A-weighted decibels [dBA] higher) as a traffic volume of 500 vph (Table 4). Traffic at 75 miles per hour (mph) sounds twice as loud as traffic of the same volume at 35 mph. One semi-trailer truck traveling at 55 mph sounds as loud as 28 cars at 55 mph.

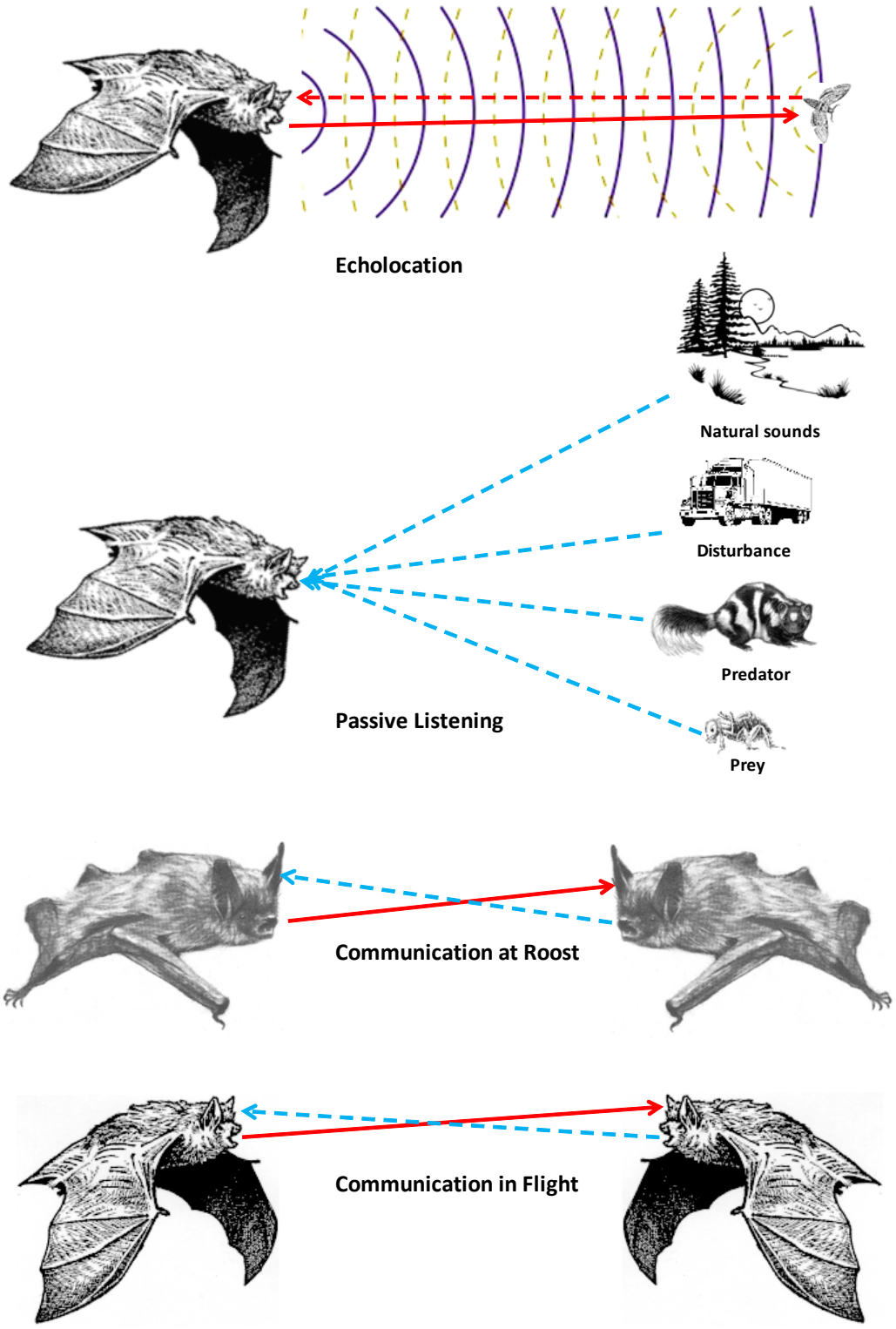

Figure 2.The Bat Sound Environment

Table 2. Natural Background Sounds

Sound	dBA
Thunderclap	120
Thunder	110
Stream, water flowing	73
Surf, pounding	70
Wind, breeze through trees	62
Birds, singing	60
Wind, gusty with rustling tree foliage	55
Rainfall, moderate	50
Rainfall, light	40
Rustling leaves	40
Olympic National Forest	40
Mountaintop	35
Wilderness ambient	35
Lake, quiet	30
Meadow, low wind conditions	30
Insects	25
Mountain slope, open	23
Rustling leaves	20
Grand Canyon, remote trail	15
Grand Canyon at night	10
Haleakala volcano crater, no wind	5

Source: Federal Highway Administration 2011.
dBA = A-weighted decibels

Table 3. Background Noise (L_{eq} Exclusive of Traffic Noise) Associated with Urban Areas of Different Population Densities

Population Density (people/sq. mi.)	dBA
30,000 +	65
10,000–30,000	60
3,000–10,000	55
1,000–3,000	50
300–1,000	45
100–300	40

Source: Federal Transit Administration 2006.
L_{eq} = background noise level
dBA = A-weighted decibels

Table 4. Traffic Noise Levels (dBA L_{eq} [h]) at 50 feet at Different Vehicle Speeds and Traffic Volumes)

Traffic Volume (vph)	Vehicle Speed (mph)									
	30	35	40	45	50	55	60	65	70	75
125	53	55	57	58	60	61	62	64	65	66
250	56	58	60	61	63	64	65	67	68	69
500	59	61	63	64	66	67	68	70	71	72
1,000	62	64	66	67	69	70	71	73	74	75
2,000	65	67	69	70	72	73	74	76	77	78
3,000	67	69	71	72	74	75	76	77	78	79
4,000	6,8	70	72	73	75	76	77	79	80	81
5,000	6,9	71	73	74	76	77	78	80	81	82
6,000	7,0	72	74	75	77	78	79	80	81	82

Note: Noise calculations are based on the total acoustic energy generate by traffic on a straight roadway on flat, acoustically hard terrain with 100% automobiles and no trucks. Typical freeway lanes are limited to about 2,000 passenger cars per lanes per hour. These calculations do not take into account the effect of traffic on multiple lanes.
dBA =A-weighted decibels
L_{eq} = Background noise level
vph = vehicles per hour
mph = miles per hour

Spectral Profile

Figure 3 shows the spectral profile of representative traffic noise (Highway US 101 at Lynch Creek, Petaluma California). The solid red line gives the noise levels for an estimated traffic load of 3,458 vehicles per hour. Measurements were taken 25 feet from the near lane. The dashed line shows the noise spectra for measurements taken in an underpass underneath the freeway. The microphone for the latter measurements was located approximately 1 foot below the surface of the underdeck. Interestingly, the noise levels for the underpass up to 200 hertz (Hz) exceed those measured beside the freeway (up to a maximum of approximately 17 dBA). Above 200 Hz the noise levels average about 12 dBA less. The quieter environment under the freeway is what the bats experience at and near their roost.

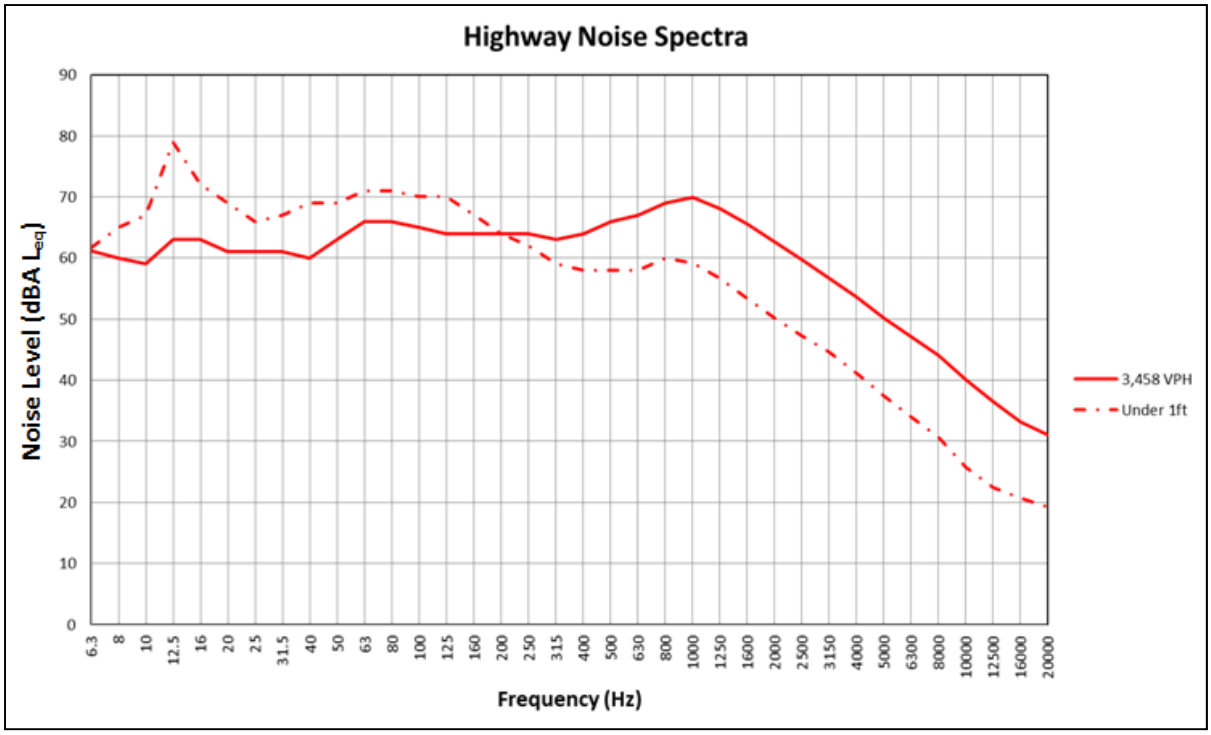

Figure 3. Traffic Noise Spectra for Highway US 101 at Lynch Creek, Petaluma California

(Source: Reyff, J. 2015)

Construction Noise

Construction projects are usually implemented in a series of steps or phases. The noise associated with each phase can vary greatly. Different types of equipment are used for different tasks (individually and in combination), which vary in noise production, duration, and frequency of use. Table 5 lists the average maximum noise levels (L_{eq} at 50 feet) for common construction equipment. The spectral profiles of construction noise are often similar to that of traffic noise (Roberts 2009).

Table 5. Construction Noise (L_{eq} at 50 Feet)

(Colors indicate relative sound level: red = extreme, orange = very high; yellow = high; green = moderate; blue = low; purple = very low; mauve = background. Asterisks show impact noise sources.)

	Noise (dBA)		
	Low	High	Impact[a]
Explosives	94	162	*
Rock Blast	112	112	*
Pneumatic Tools, Jackhammers & Pile Driver	101	110	*
Track Hoe	91	106	*
Impact Pile Driver	96	106	*
Guardrail Installation and Pile Driving	95	105	*
Truck Horn	104	104	*
Pile Driving	74	103	*
Rock Drill and Diesel Generator	80	99	
Rock Drill	85	98	
Dump Truck	82	98	
Rock Drills and Jackhammers	82	97	*
Pneumatic Wrenches, Rock Drills	86	97	*
Vibratory (Sonic) Pile Driver	95	96	*
Diesel Truck	85	96	
Pneumatic Chipper	91	95	*
Hydromulcher	87	94	
Clam Shovel	93	93	
Slurry Machine	82	91	
Pneumatic Riveter	91	91	*
Circular Saw (hand held)	91	91	
Mounted Impact Hammer Hoe-Ram	85	90	*
Concrete Saw	90	90	
Compressor	80	90	
Scraper	85	89	
Paver	80	89	
Large Truck	84	89	
Jackhammer	74	89	*
Drill Rig	85	88	
Dozer	84	88	
Crane	85	88	
Pumps, Generators, Compressors	81	87	
Front-end Loader	80	87	
Large Diesel Engine	86	86	
Gradall	85	86	
Chain saws	75	86	
Road Grader	83	85	

	Noise (dBA)		
	Low	High	Impact[a]
Pump	77	85	
Impact Wrench	85	85	*
Concrete Truck	81	85	
Concrete Mixer	80	85	
Auger Drill Rig	85	85	
Flat Bed Truck	84	84	
Backhoe	80	84	
Generator	52	84	
Ground Compactor	80	82	
Concrete Pump	82	82	
Cat Skidder	81	81	
Roller	74	80	
Horizontal Boring Hydraulic Jack	80	80	
Concrete Vibrator	76	76	
Welder	73	73	
Pickup Truck	55	71	
Yelling	70	70	
Background Sound Level—Forest Habitats	25	44	
Speech (normal)	41	41	

Source: U.S. Fish and Wildlife Service 2006.
[a] Impact noise = sudden, loud impulsive sound
dBA =A-weighted decibels

Bat Sounds

Bats produce a variety of sounds both for echolocation and communication. Echolocation calls are generally in the ultrasonic frequency range (>20 kHz), above human hearing, but a few species (e.g., spotted bat [*Euderma maculatum*] and western mastiff bat [*Eumops perotis*]) emit calls that are audible and marginally within the spectral range of traffic noise (Figure 4). Some bat communication calls are also, at least partially, in this lower frequency range. When bats emerge in large numbers from their roosts, they must contend with a cacophony of calls from all the bats exiting at the same time. In contrast, when foraging in the open, they need to move in a sound environment that permits clear reception of the echoes from their calls. Communication calls are most commonly emitted at close range in the roost, but bats also use contact calls while in flight. More detailed descriptions of both of these call types are presented in Section 4, *Bat Echolocation and Communication*.

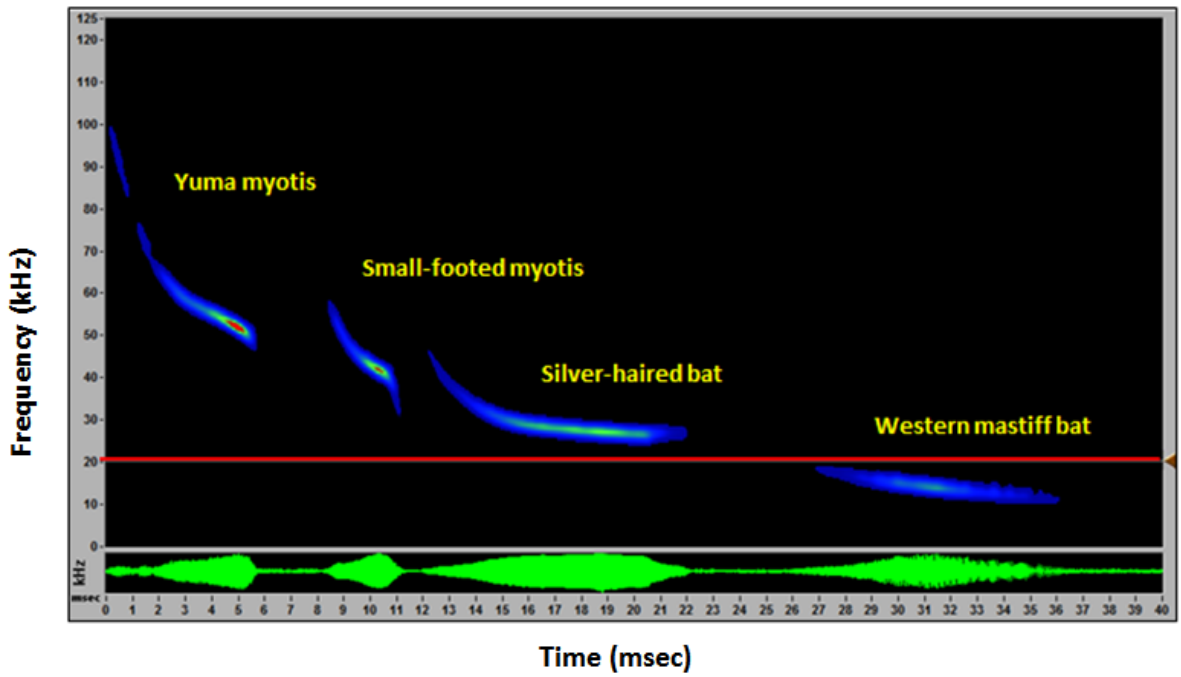

Figure 4. Echolocation Calls of Four Species of Bats in California

(The red line at 20 kHz indicates the upper range for human hearing) (Source: Call sonograms from Sonobat ©3.2.2)

Determining the Extent of Project Noise

The extent of project noise is a direct function of noise levels at the different project source(s) (operation and construction) relative to background noise levels within the project area. Three different project scenarios need to be considered when evaluating the effects of highway noise on wildlife, especially bats.

1. Highway traffic/operation only—no construction. This scenario is typical of when there is no construction and only traffic noise is being analyzed relative to the background noise levels. An example of this scenario would be analyzing traffic noise that can potentially interfere with the passive listening for prey of ground gleaning bats that feed alongside highways (Schaub et al. 2008; Siemers and Schaub 2011, Lou et al. 2015).

2. Highway construction only—no traffic. This scenario is typical of when highway construction-related activities from equipment operation occur away from established highways. An example of this scenario would be analyzing blasting and borrow pit operations for extracting road materials; these project sites are often located in rocky terrain where bats may roost in rock face crevices or cavities.

3. Highway traffic and construction together. This scenario is typical of most highway projects for which the construction is located within established highway corridors. Both traffic noise and construction noise must be analyzed together to determine the extent of project noise. Both traffic and construction noise can affect bats roosting on existing highway infrastructure or

nearby building, tree, or rock outcrop roost sites. Traffic noise is often a part of background noise in these projects.

In this section, quantitative methods are presented to estimate the extent of project noise under each scenario. Fundamental to this analysis is an understanding of noise attenuation.

Noise Attenuation

All noise attenuates (diminishes) with distance from the source (see California Department of Transportation 2013 for technical analysis procedures). This occurs through geometric spreading and signal reduction from ground and atmospheric absorption. Attenuation also varies with source type—point sources (e.g., construction equipment) or linear sources (e.g., highway traffic). Noise from point sources traveling over a hard site (e.g., bare soil or rock substrate) attenuates at approximately 6 dBA for each doubling of distance. Noise from linear sources traveling over the same site attenuates at approximately 3 dBA per doubling of distance. If the noise travels through a soft site (e.g., a forest or meadow), these values are reduced further by 1.5 dBA, giving standard attenuation rates of 7.5 dBA and 4.5 dBA, respectively, for point and linear sources.

Point-Source Attenuation

To determine noise levels at specific distances from a point source (e.g., construction), the following equation is used.

$$\boldsymbol{dBA_2 = dBA_1 + 10 * \log_{10}(D_0/D)^{2+\alpha}} \qquad \textbf{Equation 2.1}$$

Where:

dBA_1 = Noise level at reference distance (usually 50 feet)
dBA_2 = Noise level at specific distance from source
D = the distance from the noise source measurement is being taken
D0 = the reference measurement distance (50 feet for construction noise)
α = 0.5 for a soft site and 0 for a hard site

Example: the noise level at a bat tree hollow roost (entrance) in a forest (soft site; 40 dBA background) (Table 2) 250 feet from a project generating construction-related noise of 84 dBA (**L_{max}**) would be:

$$\boldsymbol{dBA_2 = dBA_1 + 10 * log_{10}(D_0/D)^{2+\alpha}}$$

Where:

$dBA_1 = 84$; $D = 250$; $D_0 = 50$ and $\alpha=0.5$
$dBA_2 = 84 + 10 * \log_{10}(50/250)^{2+0.5}$
$dBA_2 = 84 + 10 * \log_{10}(0.2)^{2.5}$
$dBA_2 = 84 + 10 * \log_{10}(0.02)$
$dBA_2 = 84 - 17.474$
$dBA_2 = \mathbf{66.526}$

To determine the distance the same construction noise will travel before it attenuates to the background sound level, the following equation is used.

$$D = D_0 * 10^{\left(\frac{Construction\ Noise - Background\ Sould\ level\ in\ dBA}{\alpha}\right)}$$ **Equation 2.2**

Where:

Construction noise = highest A-weighted sound level (**L_{max}**) occurring during a noise event during the time that noise is being measured (at **D_0**)

D = the distance from the construction noise source

D_0 = the reference measurement distance (50 feet for construction noise)

α = 25 for soft ground and 20 for hard ground (Note: The alpha [α] values assume a 7.5 dBA reduction per doubling distance over soft ground and a 6.0 dBA reduction per doubling distance over hard ground)

$$D = D_0 * 10^{\left(\frac{Construction\ Noise - Background\ Sould\ level\ in\ dBA}{\alpha}\right)}$$

Where:

$D_0 = 50$ feet (the reference measurement distance)

$D = 50 * 10^{\left(\frac{84-40}{25}\right)}$

$D = 50 * 10^{\left(\frac{44}{25}\right)} = 50 * 10^{(1.76)} = 50 * 57.54$

$D = \mathbf{2,877}$ feet (=0.54 miles)

Figure 5 shows the modeled attenuation pattern of construction noise at a hypothetical project site.

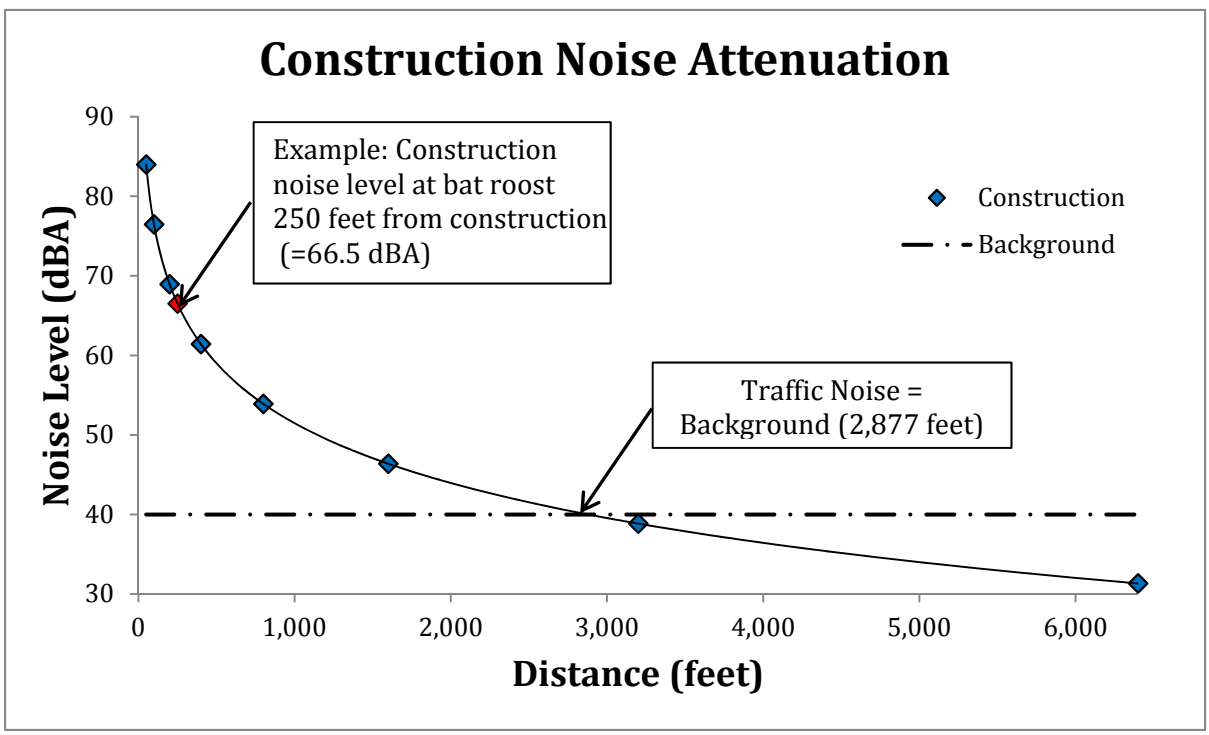

Figure 5. Modeled Attenuation of Construction Noise (84 dBA [Lmax] at 50 feet) through Forest (Soft Site) with a Background Sound Level of 40 dBA

(Note: The blue markers show progressive doubling of distances.)

Linear Source Attenuation

To determine noise levels at specific distances from a linear source (e.g., traffic), the following equation is used.

$$\boldsymbol{dBA_2 = dBA_1 + 10 * \log_{10}(D_0/D)^{1+\alpha}} \qquad \textbf{Equation 2.3}$$

Where:

dBA_1 = Noise level at reference distance (usually 50 feet)
dBA_2 = Noise level at specific distance from source
D = the distance from the noise source
D_0 = the reference measurement distance (e.g. 50 feet)
α = 0.5 for a soft site and 0 for a hard site

Example: the noise level at the same bat tree hollow roost (in forest at 40 dBA background) 250 feet from traffic at 66 dBA would be:

$$\boldsymbol{dBA_2 = dBA_1 + 10 * log_{10}(D_0/D)^{1+\alpha}}$$

Where:

dBA_1 = 66; D = 250; D_0 = 50 and α=0.5
$dBA_2 = 66 + 10 * \log_{10}(50/250)^{1+0.5}$
$dBA_2 = 66 + 10 * \log_{10}(0.2)^{1.5}$
$dBA_2 = 66 + 10 * \log_{10}(0..09)$
$dBA_2 = 66 - 10.484$
$dBA_2 = \mathbf{55.515}$

To determine the distance traffic noise at 66 dBA will travel before it attenuates to background sound level, the following equation is used.

$$\boldsymbol{D = D_0 * 10^{\left(\frac{Traffic\ Noise - Background\ Sould\ level\ in\ dBA}{\alpha}\right)}} \qquad \textbf{Equation 2.4}$$

Where:

D = the distance from the traffic noise
D_0 = the reference measurement distance (e.g. 50 feet)
α = 15 for soft ground and 10 for hard ground (Note: The alpha (α) values assume a 4.5 dBA reduction per doubling distance over soft ground and a 3.0 dBA reduction per doubling distance over hard ground.)

$$\boldsymbol{D = D_0 * 10^{\left(\frac{Traffic\ Noise - Ambient\ Sould\ level\ in\ dBA}{\alpha}\right)}}$$

Where:

$D_0 = 50$ feet (the reference measurement distance)
$D = 50 * 10^{\left(\frac{66-40}{15}\right)}$
$D = 50 * 10^{\left(\frac{26}{15}\right)} = 50 * 10^{(1.733)} = 50 * 53.703$
$D = \mathbf{2,685}$ feet (=0.51 mi.)

Figure 6 shows the modeled attenuation pattern of traffic noise at a hypothetical project site.

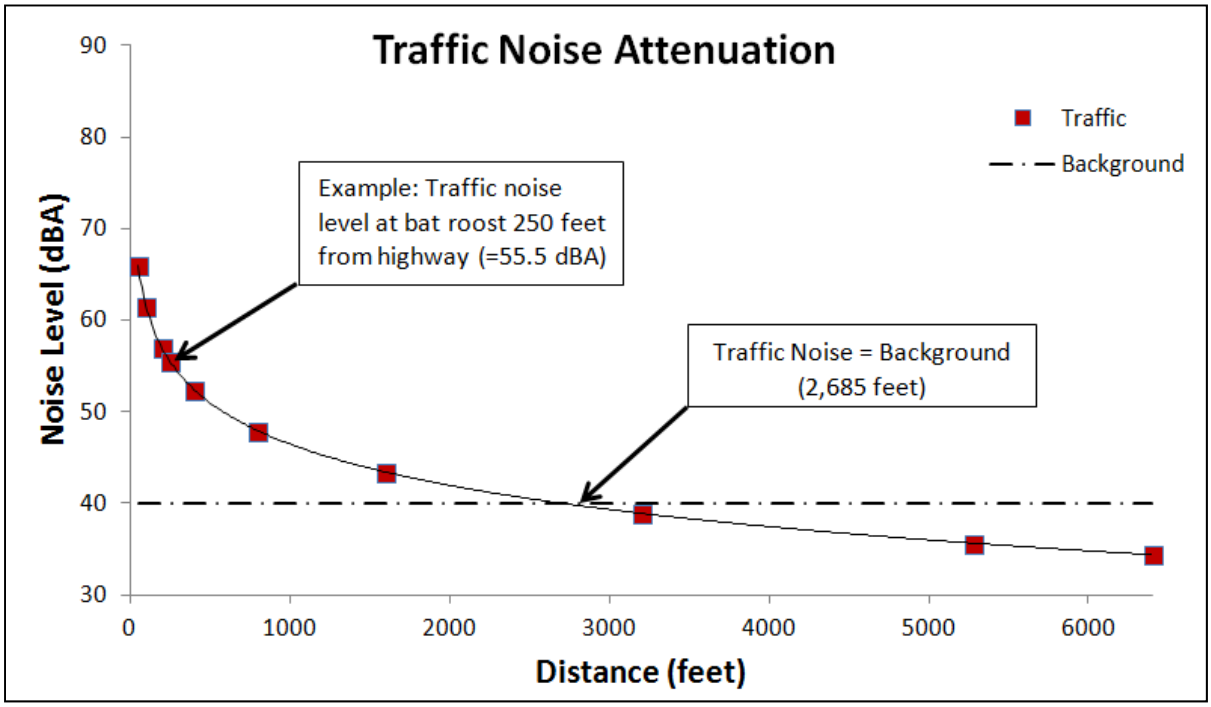

Figure 6. Modeled Attenuation of Traffic Noise (84 dBA at 50 feet) through Forest (Soft Site)

To determine the distance the construction noise would travel before it attenuates to traffic noise level (Figure 7), the following equation is used.

$$\boldsymbol{D = D_0 * 10^{\left(\frac{Construction\ Noise - traffic\ noise}{\alpha}\right)}} \qquad \textbf{Equation 2.5}$$

Where:

D = the distance from the traffic noise

D_0 = the reference measurement distance (e.g. 50 feet)

α = 10 (Note: The alpha [α] values assume a 4.5 dBA reduction per doubling distance over soft ground and a 3.0 dBA reduction per doubling distance over hard ground.)

$$\boldsymbol{D = D_0 * 10^{\left(\frac{Construction\ Noise - traffic\ noise}{\alpha}\right)}}$$

Where:

$D_0 = 50$ feet (the reference measurement distance)

$D = 50 * 10^{\left(\frac{84-66}{10}\right)}$

$D = 50 * 10^{\left(\frac{18}{10}\right)} = 50 * 10^{(1.8)} = 50 * 63.096$

$D = \mathbf{3,154}$ feet (=0.51 mi.)

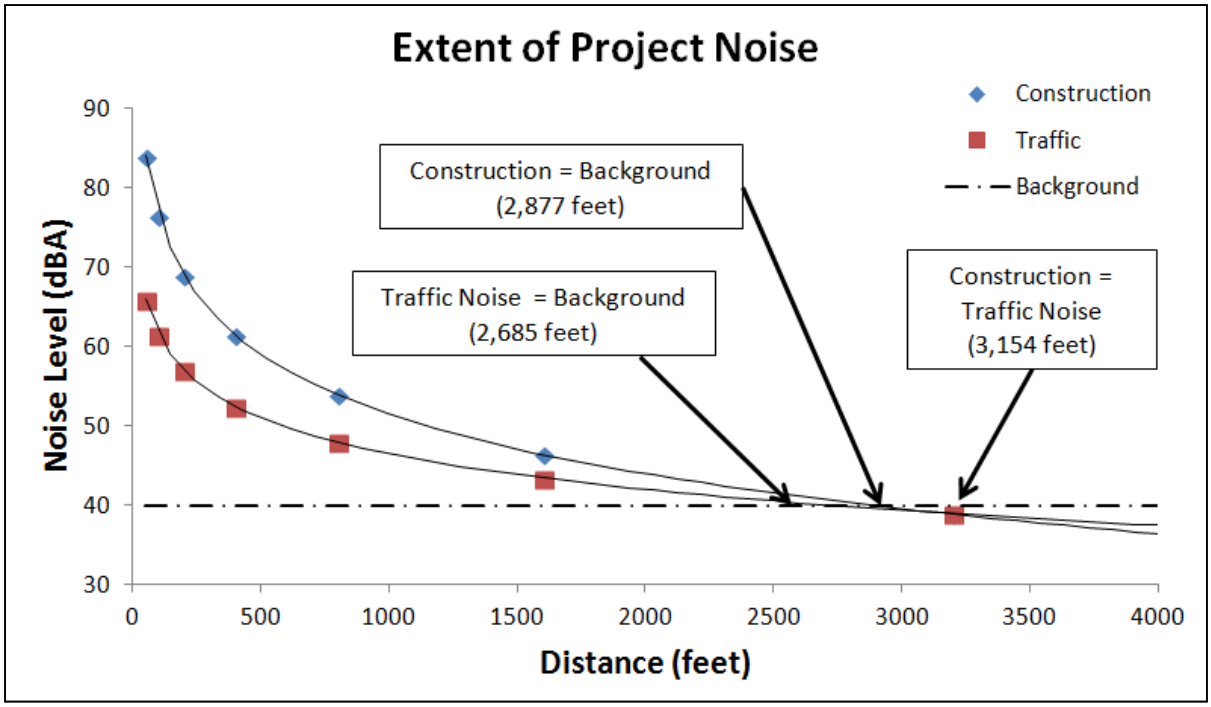

Figure 7. Modeled Attenuation of Traffic and Construction Noise to Estimate Extent of Project Noise

Determining the Extent of Project-related Noise

The extent of project noise is determined by the distance project-related noise travels to the point where it attenuates to background levels. However, because construction noise (a point source) attenuates at a faster rate than traffic noise (a linear source) (7.5 vs 4.5 dBA per doubling of distance) and background noise levels can vary significantly between project sites (e.g., 40–80 dBA), determining the extent of project noise requires analysis of all variable combinations. There are four basic scenarios that define condition states for determining the extent of project noise.

1. Construction noise exceeds highway noise from source to background noise levels (Figures 7 and 8). The extent of project noise equals the distance at which construction noise attenuates to background levels.
2. Highway noise exceeds construction noise from source to background levels (Figure 9). Project noise is always below highway noise, which is part of the background noise. Therefore, under these conditions there is generally no acoustic effect from construction noise unless the summed values (background + construction) exceed the background noise level.
3. The distance at which traffic noise attenuates to ambient or background level is greater than the distance at which construction noise attenuates to background levels (Figure 10). The extent of construction noise is then equal to the distance at which construction noise attenuates to traffic noise levels. In this scenario, traffic noise from the roadway extends farther than construction noise. The extent of project noise is then calculated to determine at what point it attenuates to traffic noise level, which is the dominant background sound. In this case, traffic noise is louder than background levels, and construction noised is audible until it attenuates to the same level as traffic noise.

4. The distance at which traffic noise attenuates to background levels is less than the distance at which construction noise attenuates to background levels (Figure 11). The extent of construction noise is then equal to the distance at which construction noise attenuates to background levels. In this case, construction noise extends father than traffic noise from the roadway. The extent of project noise is then calculated to determine at what point it attenuates to the surrounding background levels. In this case, construction noise dominates until it attenuates to the same level as the surrounding background sound.

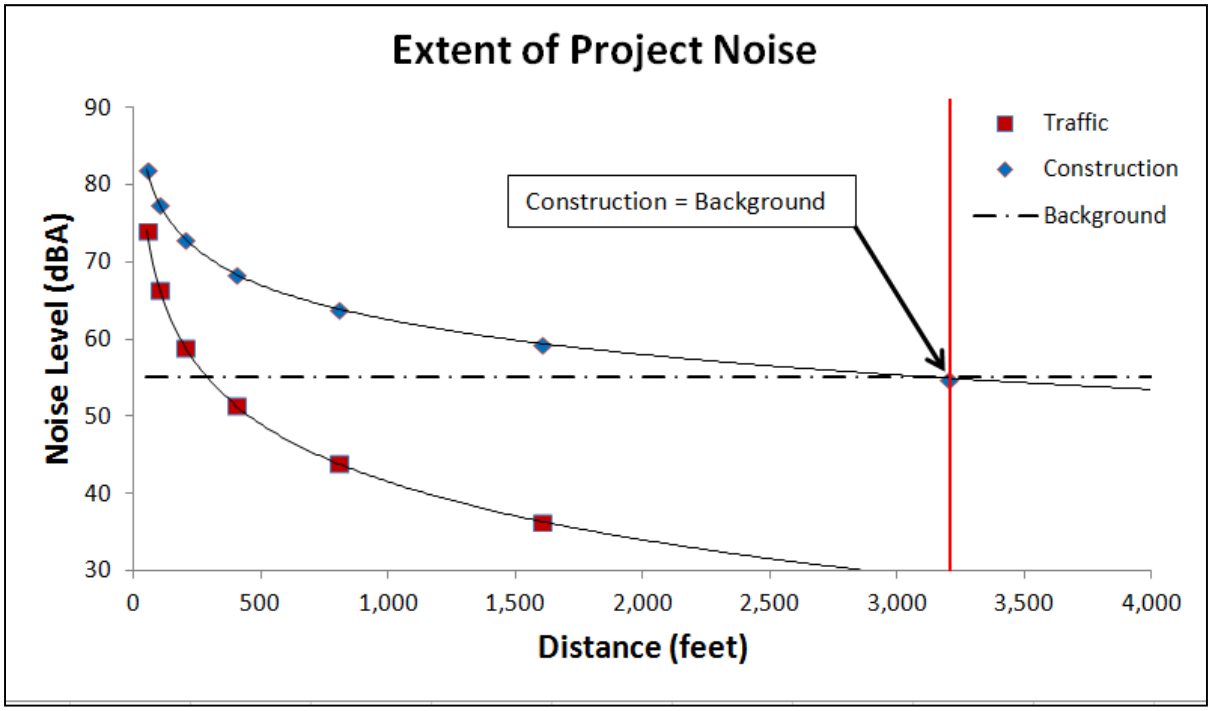

Figure 8. Construction Noise Always Exceeds Traffic Noise

(The extent of project noise here is the point at which construction noise attenuates to background noise level.)

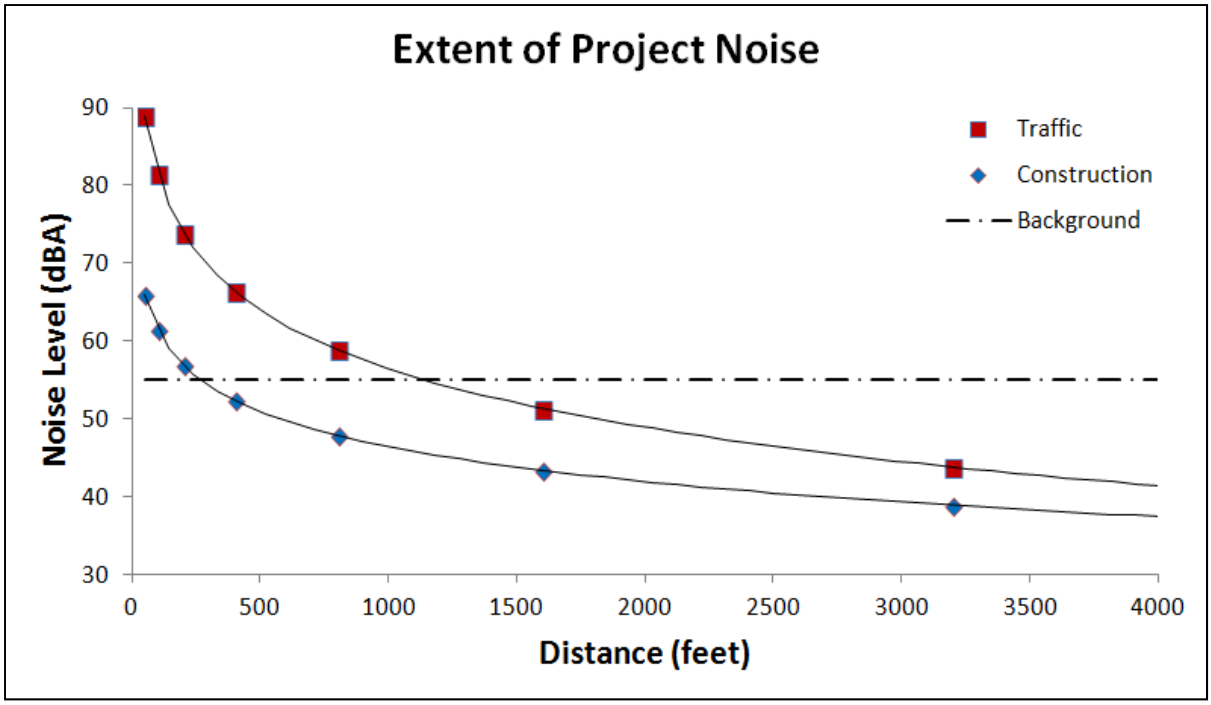

Figure 9. Traffic Noise Always Exceeds Construction Noise—No Effect

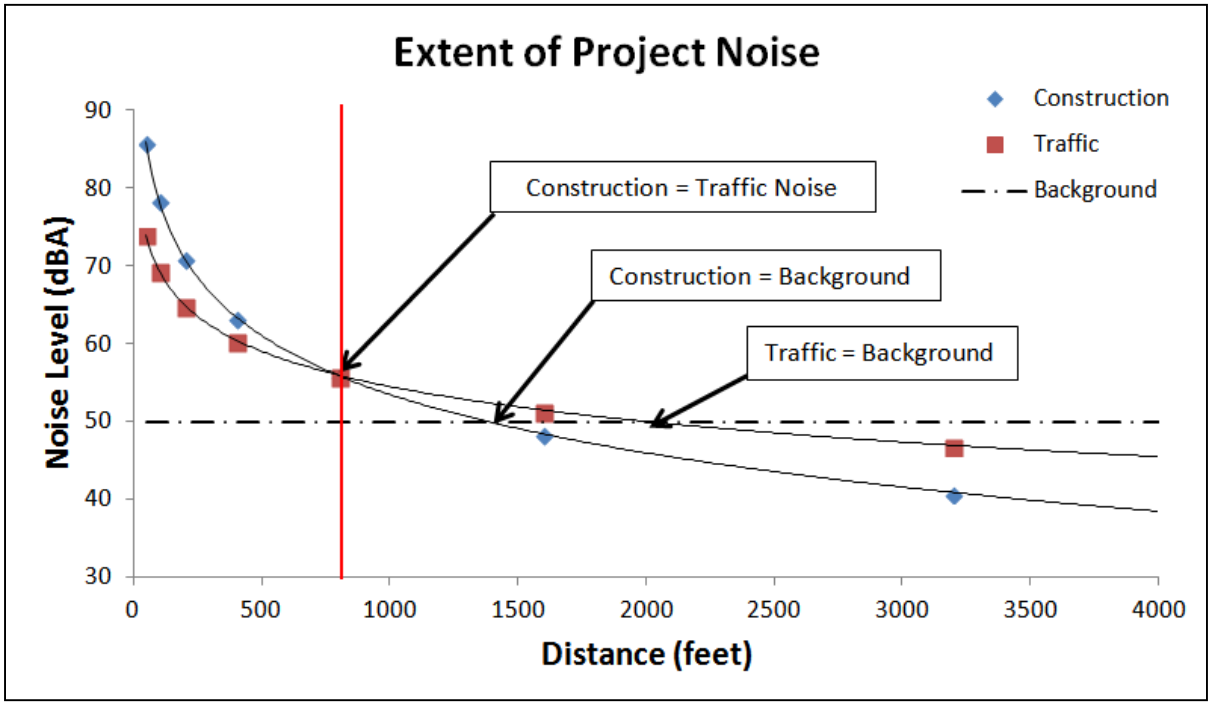

Figure 10. Extent of Project Noise at Attenuation Point where Construction Noise Equals Traffic Noise

(The extent of project noise here is the point at which construction noise attenuates to traffic noise level.)

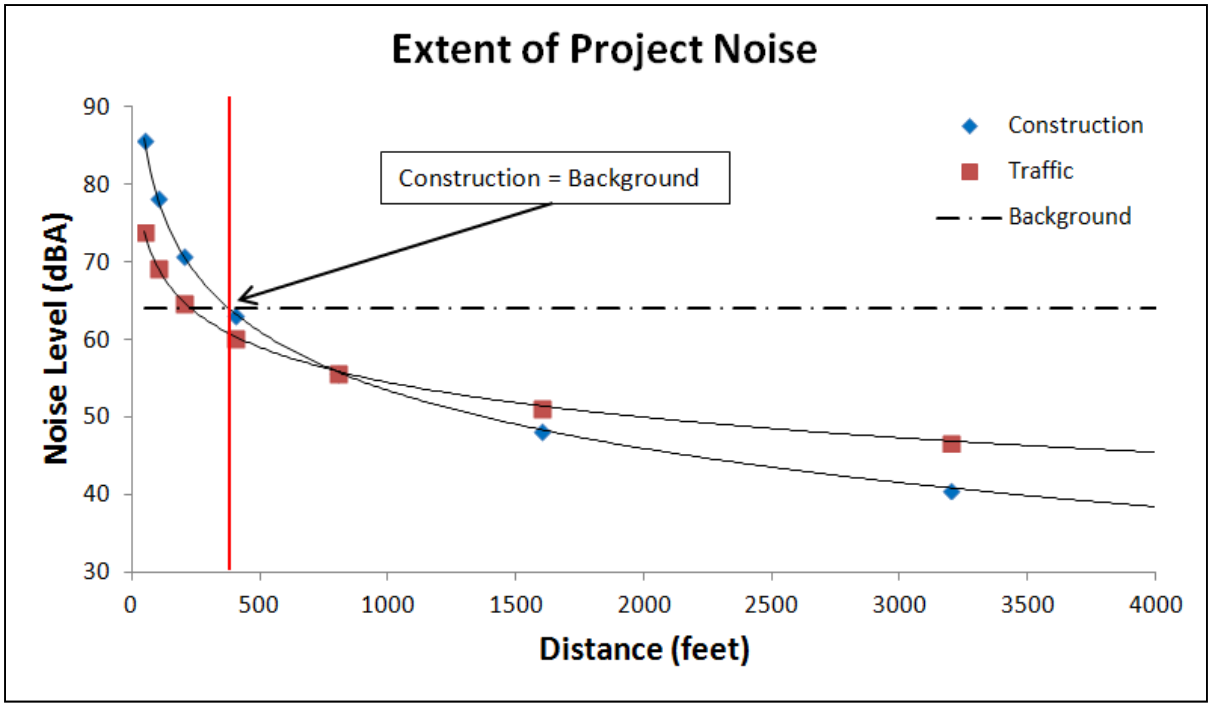

Figure 11. Construction Noise Exceeds Traffic Noise to Background Noise Level

(The extent of project noise here is the point at which construction noise attenuates to background noise level.)

Effects of Wind, Temperature, Humidity and Vegetation

Additional factors can influence the actual noise level that reaches a receiver. Physically blocking the line of sight between the noise source and the receiver can result in a 5 dB reduction. Dense vegetation can reduce noise levels by as much as 10 dB over 200 feet (U.S. Department of Transportation 2011). Atmospheric conditions can have a profound effect on noise levels within 200 feet of a highway (California Department of Transportation 2011, 2013). Vertical air temperature gradients have increasing effects with distance. Noise travels farther during periods of higher humidity and also in colder temperatures (Harris 1991, Washington Department of Transportation 2015). Wind can reduce or increase noise levels by as much as 20 at long distances (Harris 1991).

Because these factors can vary greatly at any location on a project-specific basis, they are difficult to include in a general analysis. Therefore, they are identified but generally not taken into account in environmental noise analyses over short distances. As a result, such analyses are conservative and likely to predict noise levels that are higher than actual levels. When threshold criteria are critical in the project decision process, fine-tuned analyses can be done to provide more precise determinations.

Section 3: Bat Hearing

Bats monitor the acoustic structure and dynamics of their sound environment through echolocation and passive listening. In the dark, the echoes of their calls paint clear neurological pictures of their habitat that allow them to precisely navigate through cluttered vegetation; locate, pursue, and capture elusive prey; find mates; avoid predators; track the activities of other bats; and find safe routes back to their roosts. They also actively and passively listen for and respond to the social communication calls from other bats, both within and outside the roost; the sounds of ground prey scuttling through the litter; and "unnatural" (e.g., anthropogenic) sounds that portend potentially adverse disturbance (Figure 2).

The Bat Auditory System

Among the potential adverse effects that highway noise can cause in bats (see Section 6, *Effects of Highway Noise on Bats*) is noise-induced hearing loss (NIHL) resulting from acoustic trauma and damage to the bat auditory system. It is important, therefore, to have a working understanding of the structure and function of this system to better understand the potential severity of these effects and how bats have developed strong morphological and physiological mechanisms to protect against these effects (Section 6).

The bat auditory system is structurally typical of most mammals (Figure 12), with some specializations. It consists of an outer ear (pinna), a middle ear with three small bones (incus, malleus, and stapes), and an inner ear, which includes the coiled cochlea.

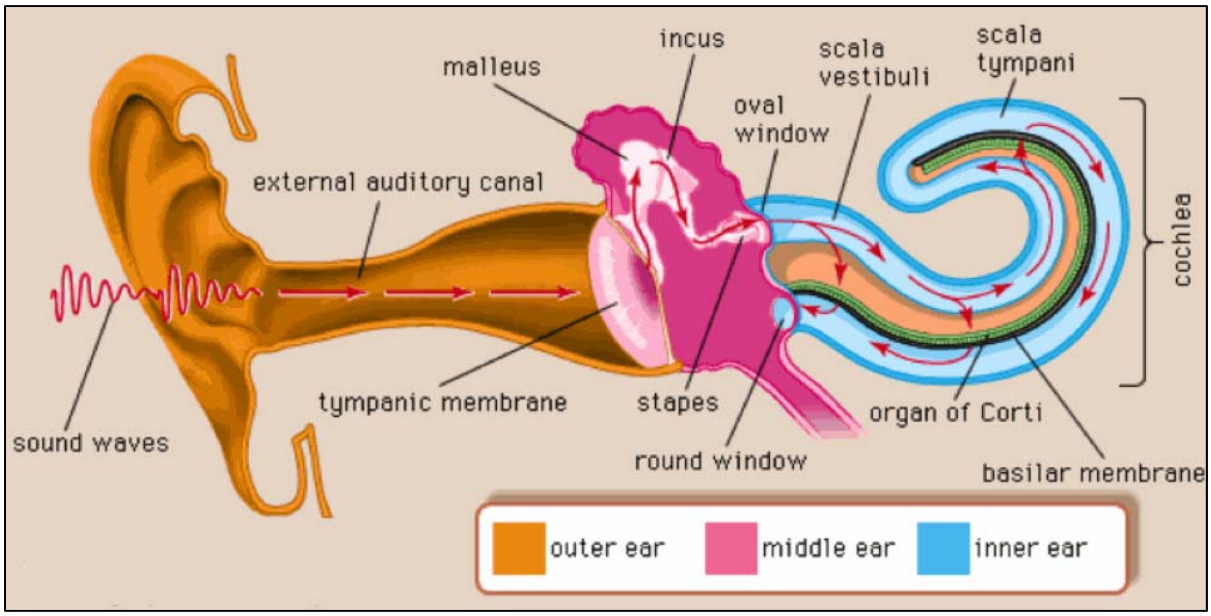

Figure 12. The Mammalian Auditory System

(Source: The Encyclopedia Britannica 1997)

The Outer Ear

The outer ears (pinnae) of bats vary considerably in size and shape (Figure 13). Depending on the species, they may be simple or complex, large or small. The principal function of the pinnae in bats is sound localization and processing (Griffin 1958; Griffin and Grinnell 1958; Lawrence and Simmons 1982; Jen and Sun 1984; Xinde and Jen 1987; Jen and Chen 1988; Obrist and Fenton 1993; Chiu and Moss 2007; Kuc 2009, 2010). During echolocation, bats need to determine not only the distance of their prey, but also their size and type (e.g., large or small; moth or mosquito); angular position (azimuth and elevation); movement direction; and speed (Suga 1990). The shape, size, and movement of the pinnae are coevolved to provide detailed information on these variables. The range of a bat's target can be determined from the time delay between the emitted pulse and the returning echo. Target size is determined by the frequency of the echo; velocity by the frequency change, and location by between-ear differences in echo amplitude. Scanning movements of the pinnae allow the bat to precisely locate the target (Pye and Roberts 1970). Signal strength can be amplified by large ears which allow bats that have them to detect softer echoes returning from prey at greater distances. The parabolic shape of the pinnae enables frequency differentiation that can structurally diffract incoming signals to allow time-delay analysis.

The Middle and Inner Ear

Figure 14 shows the structure of the middle and inner ear of the big brown bat (*Eptesicus fuscus*). The middle ear consists of three small bones—the incus, which attaches to the tympanic membrane (eardrum); the malleus, an intermediate bone; and the stapes, which attaches to the oval window on the cochlea.

The cochlea consists of three membranous tubes coiled in the form of a snail (Figures 15a and 15b). Two of the tubes, the scala vestibule and scala tympani, are filled with perilymph. The third, the scala media, lies between the scala vestibule and scala tympani, is filled with endolymph, and contains the Organ of Corti.

Figure 13. Variation in the Size and Shape of Bat Pinnae

(First row [left to right]: Hoary bat, Townsend's big-eared bat, Yuma myotis. Second Row: spotted bat, western long-eared bat, western red bat. Third row: Mexican long-tongued bat, silver-haired bat, pocketed free-tailed bat. Fourth row: Fringed myotis, Lesser long-nosed bat, western small-footed myotis. All photos ©Merlin D. Tuttle. Merlin Tuttle Bat Conservation (http://www.merlintuttle.com/). Adapted with permission.

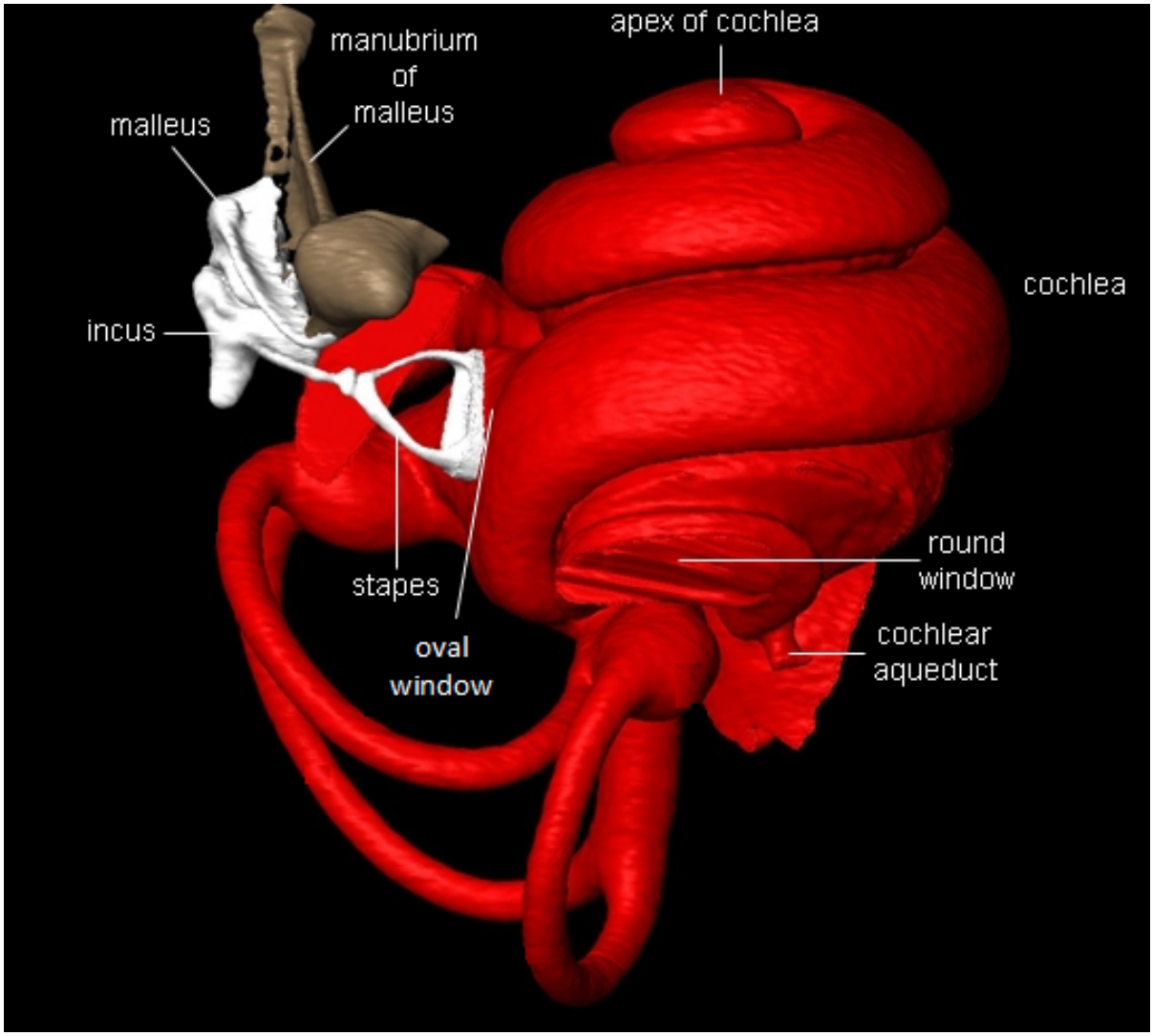

Figure 14. The Middle and Inner Ear of the Big Brown Bat

(Source: CSI, 2015. CT Scan by Woods Hole Oceanographic Institution, Computerized Scanning and Imaging Facility. Used with permission.)

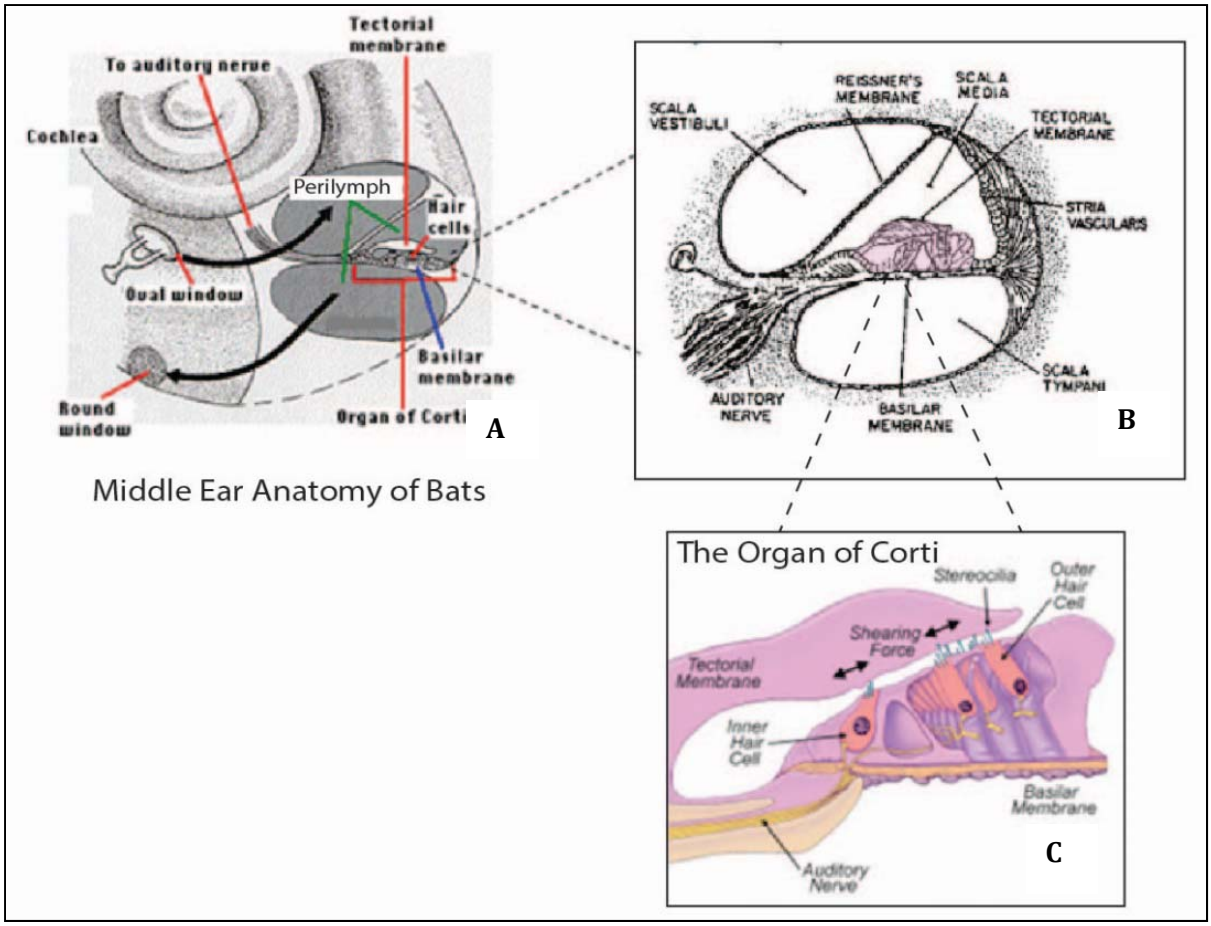

Figure 15. The Mammalian Inner Ear

(Sources: A: Kimball 2011; B: Clopton and Spelman 2015; C: Oghalai 1997)

The Organ of Corti (Figure 15C) is supported by the basilar membrane and contains four rows of delicate mechano-sensory hair cells: three rows of outer hair cells and one row of inner hair cells. Motion of the stapes at the oval window generates motion waves in the perilymph within the cochlea (Figure 15A). That motion causes a shearing force between the top of the Organ of Corti and the tectorial membrane, displacement of the basilar membrane, and deflection of the inner and outer hair cell stereocillia (Figure 15C). When the stereocilia are deflected, the inner hair cells generate neural impulses that are transmitted along the auditory nerve to the brain. The outer hair cells respond to the motions of the basilar and tectorial membranes and feedback signals from the brain by changing their shape and stiffness. These changes are believed to effect frequency amplification in the cochlea.

Figure 12 shows that the basilar membrane extends from the base of the cochlea (where the stapes is attached [Figures 14 and 15A] to the apex. The mechanical properties of this membrane vary along its length, from high stiffness at the base to lower stiffness at the apex. This graded flexibility results in a linear frequency-dependent vibration pattern along the membrane with the inner hair cells near the base responding best to high frequencies and those at the apex responding best to lower frequencies (Figure 16). At any location along the membrane, the hair cells are most sensitive to signal frequencies that cause maximum vibration amplitude in the membrane. Those cells are said to be "tuned" to a specific frequency, called the characteristic frequency ($\mathbf{f_c}$). Hair cells closest to

the base, therefore, have higher characteristic frequencies than those at the apex. This mechanism effectively creates an auditory filter in the cochlea.

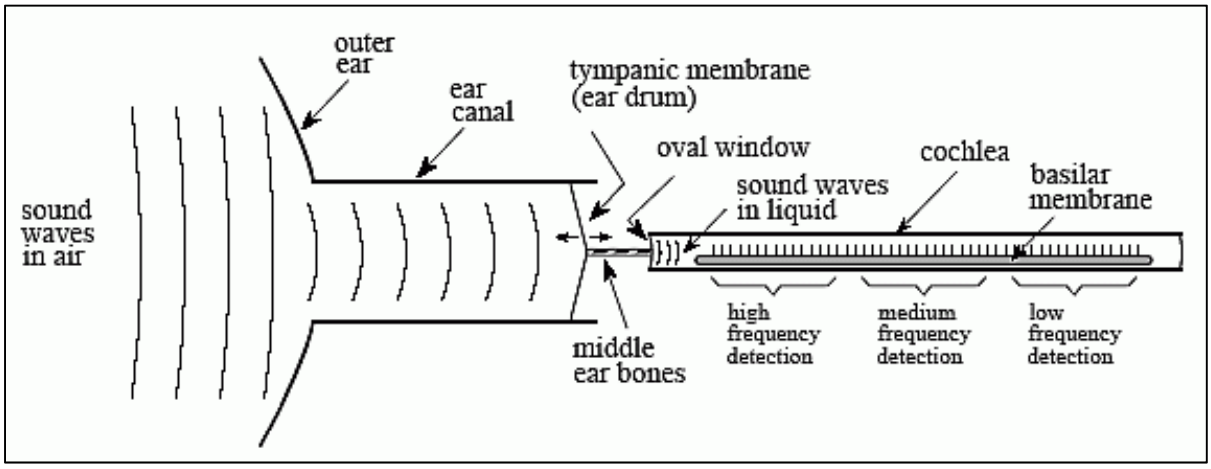

Figure 16. Diagrammatic Representation of the Bat Auditory System, Showing the Linear Sensitivity Zones along the Basilar Membrane

(Source: Batts 2006)

What Bats Hear: The Audiogram

Audiograms (audibility curves) are graphic representations of what animals can actually hear. They show the minimum audible sound pressure that an animal can detect across all frequencies within its range of hearing. With animals, audiograms are most usually determined through behavioral testing. Test animals are trained to give a recognizable response to a given stimulus that they can detect (e.g., a noise pulse at a specific frequency). The amplitudes of the test signal are varied from high to low for each test frequency, and the minimal amplitude at which a response is recorded is the threshold amplitude (Figure17). Audiograms (Figure 17) are usually U-shaped, meaning that very low and very high frequencies require a high amplitude stimulus to evoke any response. The frequency range at which the animal can detect test signals at the lowest intensity is commonly referred to as the *best hearing range*. For species that show lowest sensitivity values at a specific frequency, not over a range, the lowest intensity is identified as the *best hearing frequency*. The amplitude at that frequency is commonly cited as the sensitivity of the auditory system. The bandwidth of the system is the difference between the highest and lowest frequencies at a specified threshold amplitude (e.g. 60 dB is a common standard value). The frequency range of the system is the difference between the upper threshold frequency at which the bandwidth is taken and the auditory system sensitivity level. Figure 18 shows the audiograms of a human, bird, and four species of North American bats (little brown bat [*Myotis lucifugus*] [MYLU], pallid bat [ANPA], eastern red bat [*Lasiurus borealis*] [LABO], and big brown bat [EPFU]). The audibility curves show the hearing capability of these bats extends far beyond that of human and bird hearing into the ultrasonic. Notably, the curves also show that the bats' hearing extends down into the audible range (<20 kHz). The big brown bat (Figures 18 and 19) shows a hearing range from 0.85 kHz at 106 dB and to 120 kHz at 83 dB (Koay et al. 1997; see also Dalland 1965) with two distinct regions of best hearing: (1) a broad range around 20 kHz, and (2) a more sharply tuned region at 60–64 kHz. The highest sensitivity levels (best threshold values) for these regions were 7 dB and 15 dB, respectively. Hearing sensitivity then quickly decreases for frequencies above 60 kHz and below 10 kHz. The 60-

dB low frequency limit for this species was 3.7 kHz; the bandwidth was approximately 89 kHz. The two areas of highest sensitivity in this species align closely with the characteristic frequency (**f_c**; 28.2 kHz) and slightly above the second harmonic (54.2 kHz) of its echolocation call (Figure 20). The lower broad range of best hearing also aligns well with the frequency range of social communication calls use by this species (Figure 19) (Monroy et al. 2011; Gadziola et al. 2012; Wright et al. 2014)

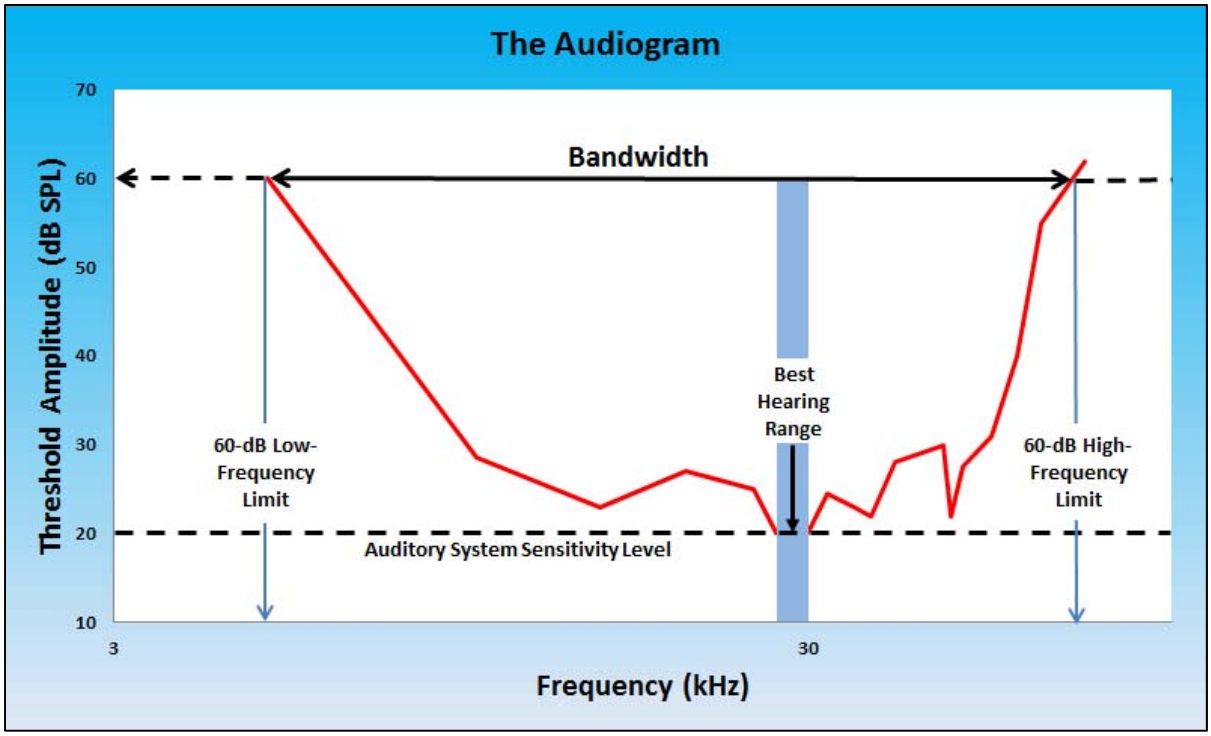

Figure 17. Representative Audiogram of the Eastern Red Bat (*Lasiurus borealis*).

(Sources: Audiogram: data from Obrist and Wenstrup 1998; figure adapted from Heffner and Heffner 2007.)

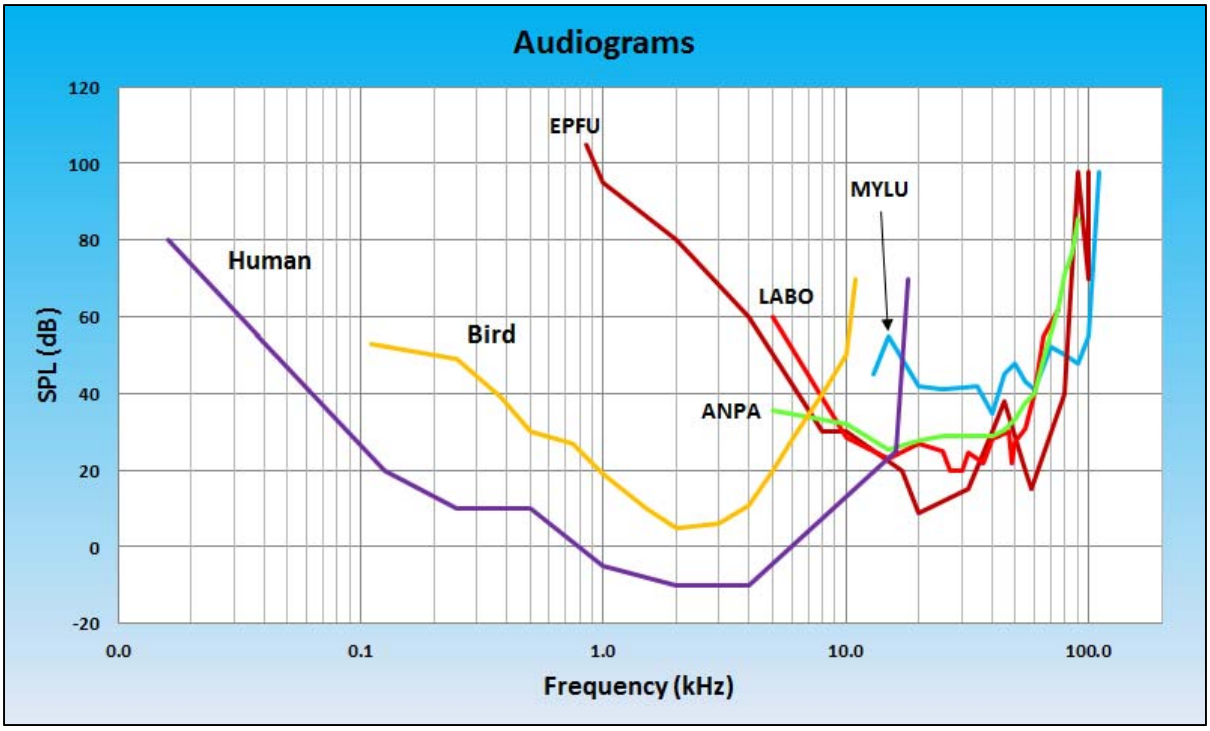

Figure 18. Audiograms of Human, Bird and Four Species of Bats

(Data Sources: Human (Heffner and Heffner 2007); Bird (Dooling 2002); EPFU (Dalland 1965; Koay et al. 1997); ANPA (Brown et al. 1978); LABO (Obrist and Wenstrup 1998); MYLU (Dalland 1965)

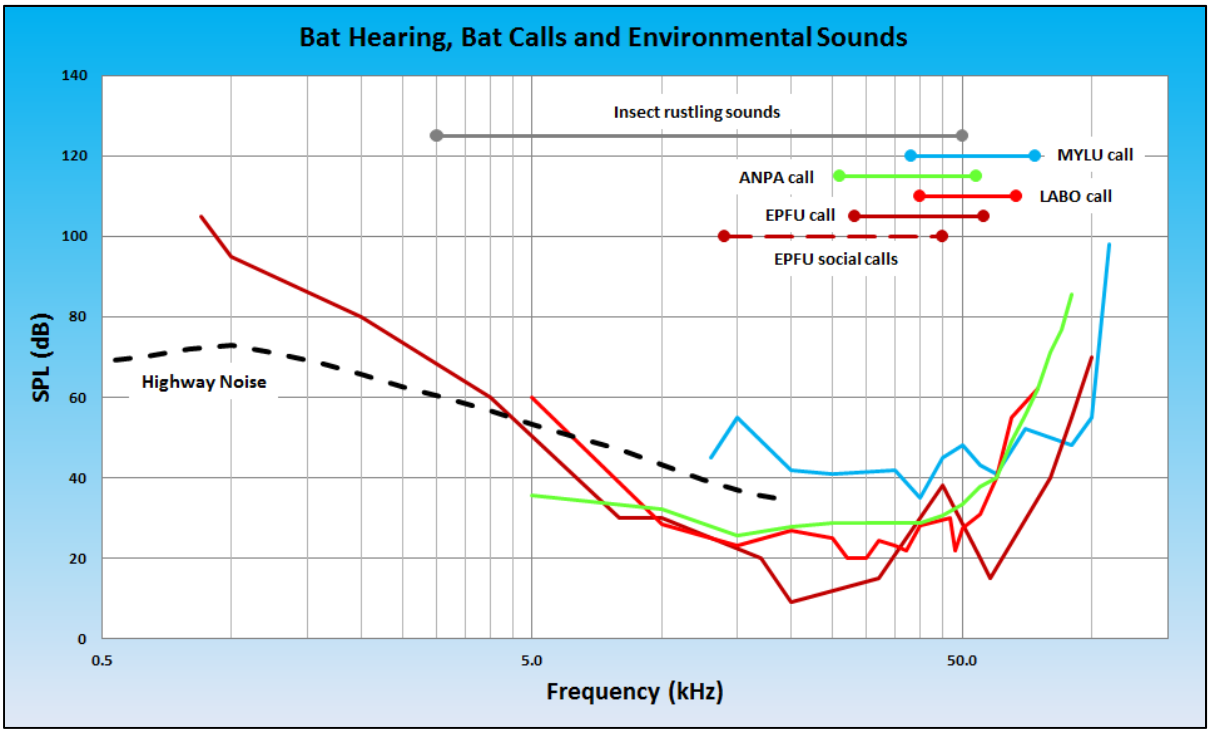

Figure 19. Audiograms of Four Species of Bats with Frequency Ranges of Their Calls and Other Environmental Noises, Including Road Noise

(Sources: Audiograms same as Figure 18; road noise data from Figure 3)

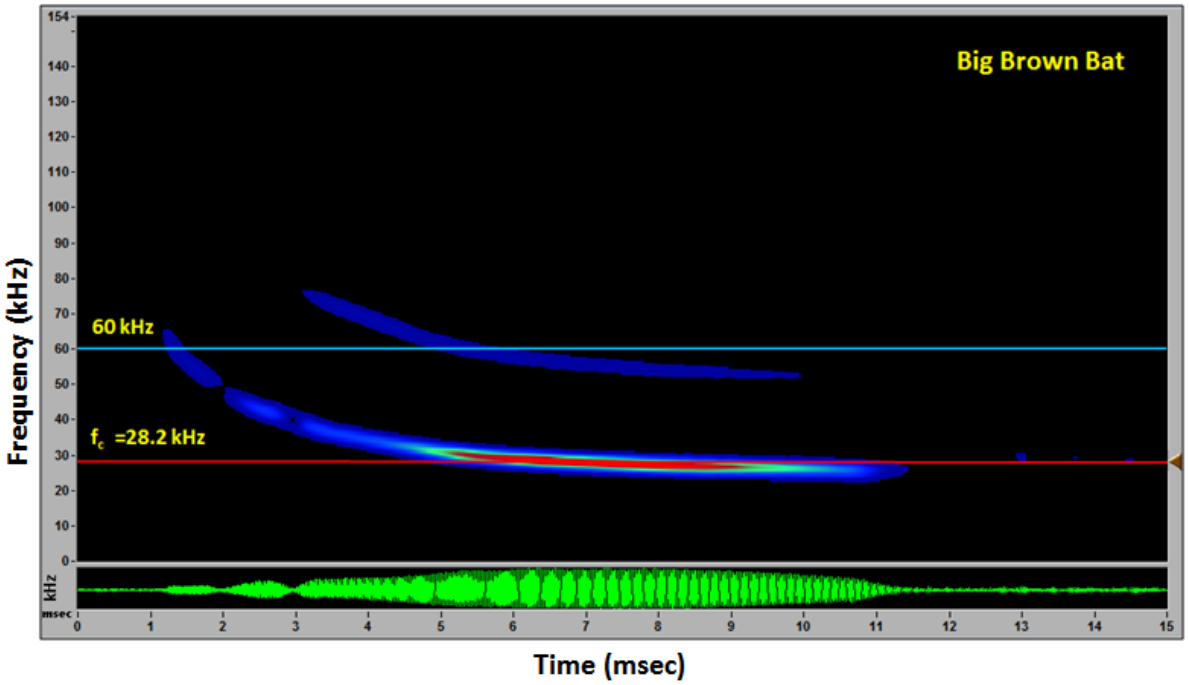

Figure 20. Echolocation Call of the Big Brown Bat

(Call sonograms from Sonobat ©3.2.2)

The audiogram of the eastern red bat (Figures 17, 18, 19) is very similar to that of the big brown bat with a slightly narrower bandwidth (70 kHz at 60 dB) and lower sensitivity. The most sensitive region of the audiogram extended from 10 kHz to 45–50 kHz, with a maximum sensitivity of 20 dB between 25 and 30 kHz (Obrist and Wenstrup 1998). This sensitivity range aligns well with the spectral range of its echolocation calls (f_c = 40.4 kHz). The good sensitivity in the 10–30 kHz range suggests that, like the big brown bat, the eastern red bat may use this band for social communication and monitoring environmental sounds (Obrist and Wenstrup 1998).

It should be noted that the red bat audiogram was developed using evoked potential auditory brainstem response (ABR) methods, not behavioral testing (e.g., Koay et al. 1997). Frequency-dependent ABR thresholds usually provide a valid predictor of the shape of the audibility curve (Shaw 1988; Obrist and Wenstrup 1998) but not the absolute auditory sensitivity (Belknap and Suthers 1982). Thresholds from behavior tests generally are 20 dB or more lower than measured ABR thresholds (Wenstrup 1984). If this is the case for the eastern red bat, it's best behavioral sensitivity would be near 20 dB lower and comparable, if not slightly better, to that of the big brown bat (Figure19).

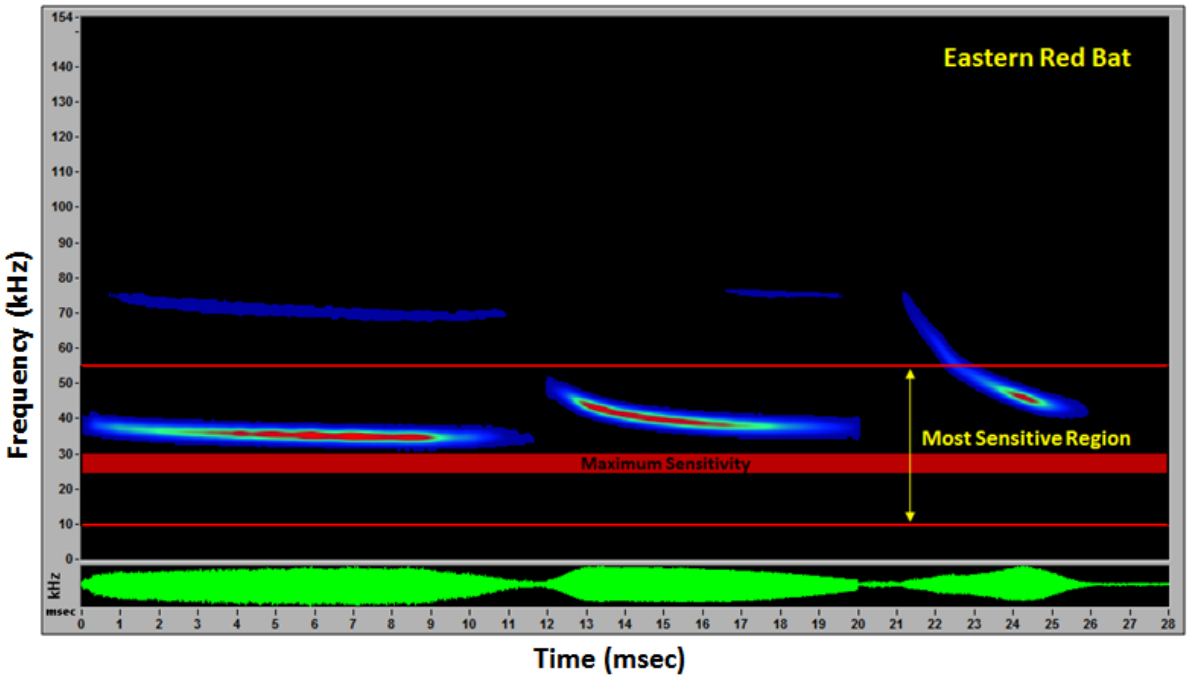

Figure 21. Three Echolocation Calls of the Eastern Red Bat (*Lasiurus borealis*) with Auditory Sensitivity Region

(Call sonograms from Sonobat ©3.2.2)

The hearing range of the little brown bat extends from approximately 10 kHz to 120 kHz (Figures 18 and 19) (Dalland 1965). The best hearing thresholds are at 40, 60 and 90 kHz (Figures 18 and 19), each progressively less sensitive than the former. Each of these high sensitivity areas aligns with the frequencies with maximum energy (f@max) in the species echolocation calls (Low: f@max = 40.1, Higher: f@max = 62.1, Figure 22). Figure 22 shows two echolocation calls: the call on the left is a typical 40 kHz call of the little brown bat. The call on the right is a higher frequency call. Note that the energy distribution in this latter call occurs at two frequency locations—60 kHz and approximately 90 kHz. Some bats can shift the energy allocation of their calls from lower frequencies to higher frequencies to broaden their bandwidth to allow them greater capacity for fine-tune tracking of their prey, particularly during the approach and capture phases of their foraging runs (Jung et al. 2007; Sümer et al. 2009; Fenton et al. 2011; Jakobsen et al. 2012)

Finally, the audiogram of the pallid bat shows a hearing range of 5–100 kHz (Figures 18 and 19 [ANPA]) with a region of greatest sensitivity between 5 and 15 kHz (Brown et al. 1978). Thresholds increase sharply above 50 kHz but remaining fairly low below 15 kHz. This audiogram was developed using evoked potential measurements (Brown et al. 1978). The behavioral thresholds are estimated to be about 15 dB lower than the neurophysiological values shown here.

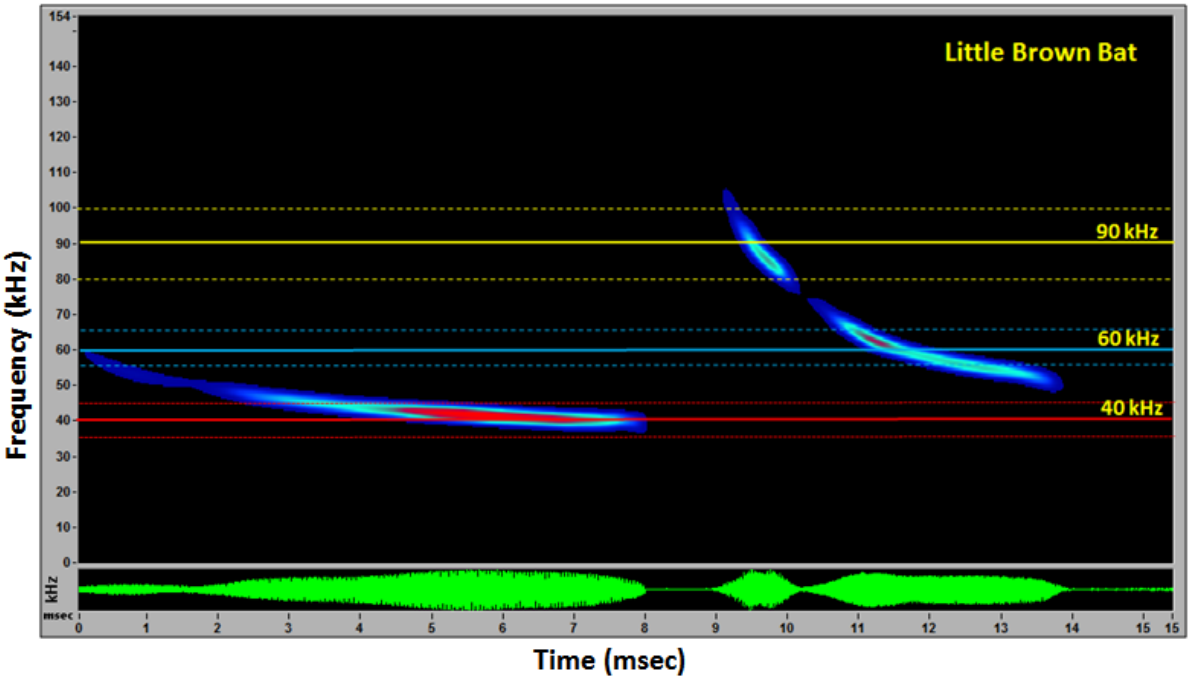

Figure 22. Two Echolocation Calls of the Little Brown Bat (*Myotis lucifugus*) with Auditory Sensitivity Regions

(Call sonograms from Sonobat ©3.2.2)

The pallid bat audiogram (Brown et al. 1978) shows unusually low thresholds in the range of 5–15 kHz, with a best hearing frequency at 15 kHz. This range of best hearing coincides with the frequency range of the pallid bat's echolocation and communication calls and important environmental sounds, including those of ground insects (Figure 19), the species' principal prey. Interestingly, the best hearing frequency aligns with the f@max for some of its social calls (Figure 23), highlighting the apparent importance of these calls in their communication

The audiograms of these four species show that the hearing ranges of bats generally coincide with the frequency ranges of their own echolocation and communication calls, as well as those of other species. Also, in most bats, the hearing ranges coincide with those of environmental sounds the bats need to monitor. The latter is generally done through passive listening (e.g., Koay et al. 1997; Barber et al. 2003)

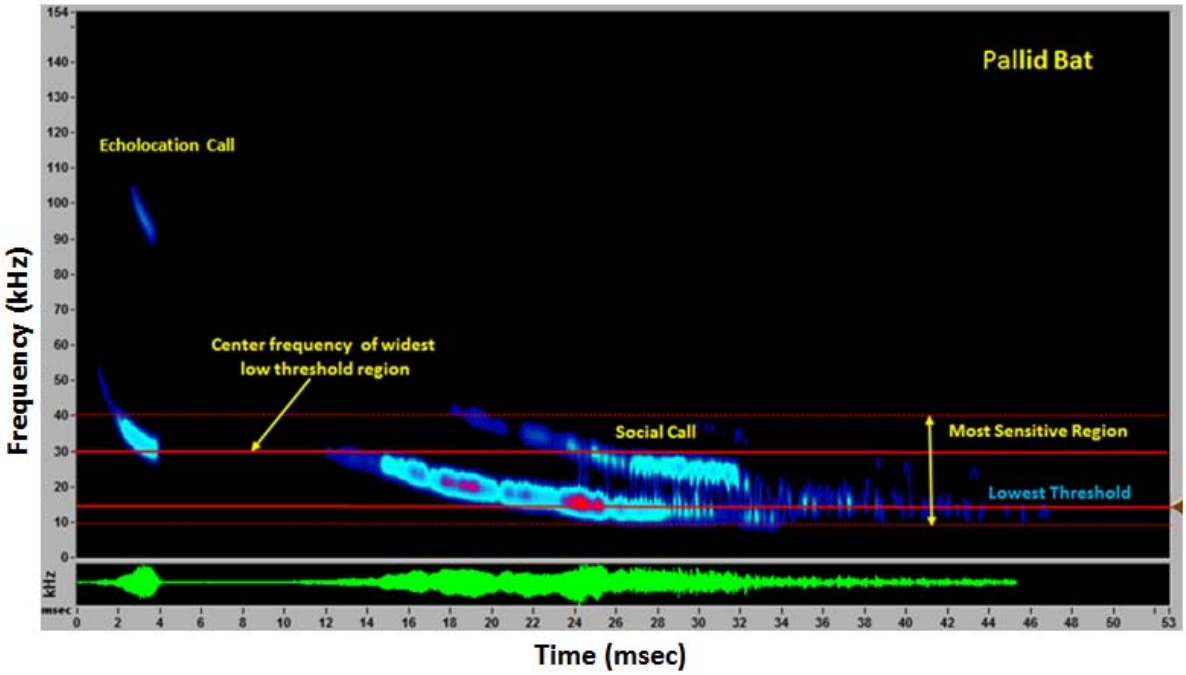

Figure 23. Echolocation Call and Social Call of the Pallid Bat (*Antrozous pallidus*) with Auditory Sensitive Region

(Call sonograms from Sonobat ©3.2.2)

Bat Hearing and Highway Noise

Figure 19 shows the sound spectra of highway noise overlain on the audiograms of the 4 bat species described above. All species, except possibly the little brown bat, potentially would hear road noise under very quiet background conditions (20 dB), at least down to 5 kHz. The big brown bat potentially would hear road noise down to 0.8 kHz if the noise was very loud (80 dB). However, the audiograms presented here were developed in exceptionally quiet conditions of a test lab and are not likely to show what a bat can actually hear in field situations with varying levels of background noise (see Section 2, *The Sound Environment of Bats*). When animals are exposed to background noise that exceeds the best threshold hearing levels, new elevated hearing thresholds are established that reflect how much louder a stimulus sound must be for that species to just detect the sound (Dooling and Popper 2015). This relationship (ratio) between the power of the stimulus sound and the power of the background noise (per Hertz; i.e., the spectrum level) is called the *critical ratio*.

The median critical ratio function typical of most mammals, including humans, shows an approximate 2–3 dB/octave increase in signal:noise ratio. Bats in North America (mostly species using frequency modulated (FM) echolocation signals (refer to Section 4 Bat Echolocation and Communication below) show similar functions. When exposed to different levels of background noise, the test stimulus signal for the typical mammal must be about 27 dB above the spectrum level of noise in order to be detected. Bats using FM echolocation vary somewhat in their critical ratios (Long 1977).

The shapes of the baseline audiograms are unique to the quiet testing conditions of the lab and do not represent actual hearing in natural settings containing noise. However, the critical ratio provides a reasonable metric for estimating the effect of noise on the audiogram because it shows the level (in dB) the test stimulus (representing natural sounds) must be above the spectrum level of the noise to be heard (Dooling and Popper 2015). Figure 24 shows the estimated changes in the audibility curve of the mouse, (*Mus musculus*), another mammal species that hears and use ultrasonic signals, with increasing noise levels. These adjusted audibility curves are only approximate estimations of what the mice likely hear—in field situations, the spectrum of natural background noise is not likely to be flat.

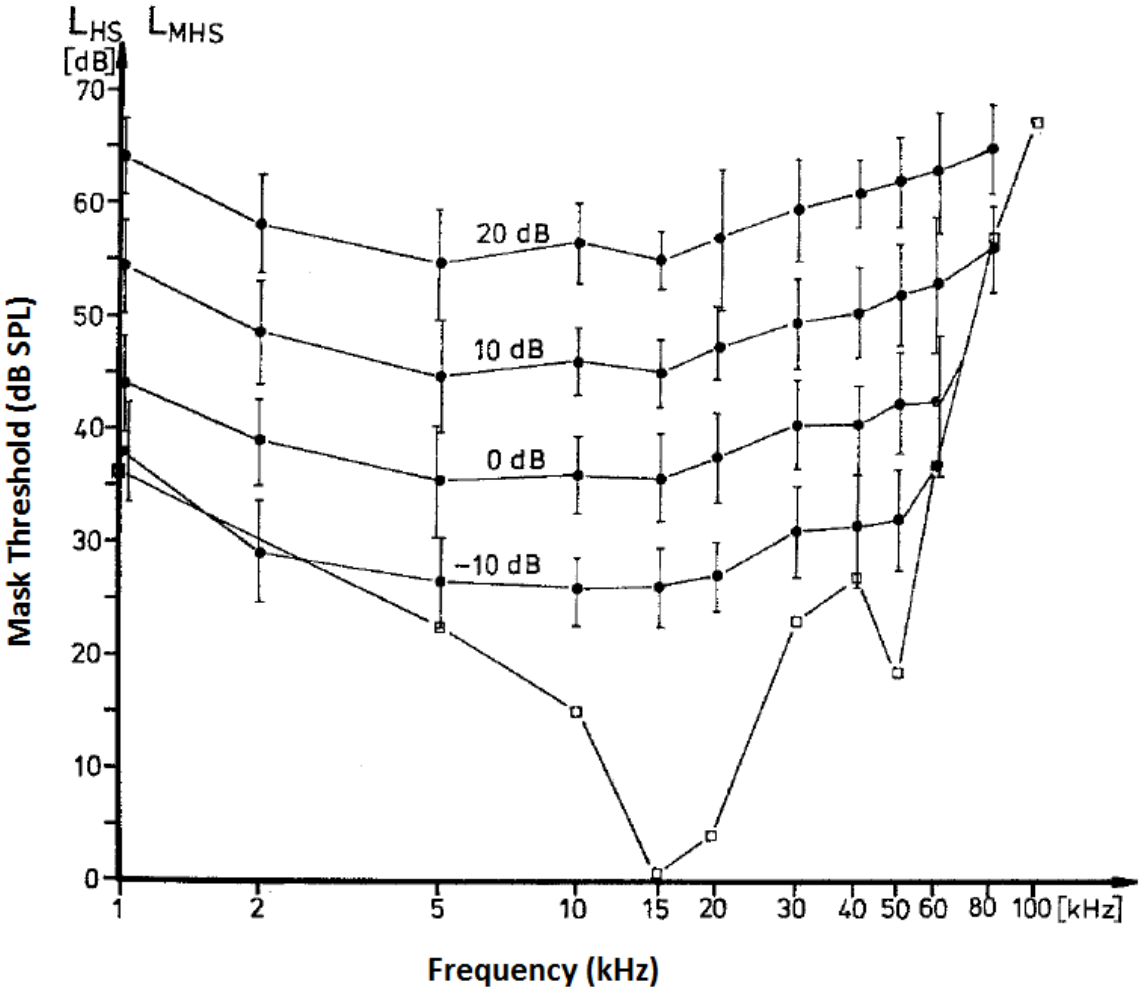

Figure 24. Masked Thresholds (L_{MHS}) at Four Spectrum Levels of White-Band-Pass Noise and the Absolute Threshold Curve of the House Mouse (*Mus musculus*)

(Source: Ehret 1975.)

However, these threshold shifts can be used to reasonably assess the magnitude of change that will occur relative to different background noise levels and the consequential effect that noise will have on masking incoming signals and the actual functional level of sensitivity in the bat auditory system (see Section 3, *Bat Hearing*). It should also be noted that bats that primarily use CF-FM signals (these species do not occur in North America) notably diverge from this pattern in part due to unique

structural features of the cochlea, particularly the coiled length of the basilar membrane (Davies et al. 2013) that focus and amplify signals at the characteristic frequency (Long 1977; Suthers and Summers 1980). Their adjusted thresholds tend to track the best frequency pattern of the baseline audibility curves with notable parallel increased sensitivities at the characteristic frequencies. This extra fine-tuned response capacity is due in part to specialized modifications of the basilar membrane that create acoustic fovea at strategic locations along the membrane (Neuweiler et al. 1984; Fenton et al. 1995). Similar analog features have been found in the Brazilian free-tailed bat (*Tadarida brasiliensis*) (Vater and Siefer 1995), an North American species, but it does not appear to be typical of most species that primarily use FM signals (vs. CF-FM calls). The cochlea morphology of the latter species typically resemble non-echolocating mammals with good high frequency hearing (Pye 1966, 1970; Ramprashad et al. 1979) in having fairly uniform graded dimensions along the basilar membrane.

Section 4: Bat Echolocation and Communication

Bats emit specific sounds that they use to navigate in the dark, find prey, and communicate with other bats. All vocal signals of North American bats, including echolocation and communication calls, are produced by the larynx (Novick 1977). Most bats emit these sounds through their open mouths, but some, in particular leaf-nosed bats, can emit echolocation calls through their nostrils (Pedersen 1998). The structure of these sounds varies significantly between species and within each species' repertoire depending on their function and the nature of the acoustic environment in which they are used.

Echolocation is auto-informatory—the bat sends out a signal that immediately comes back to it with information in the form of an echo (Figure 25). Vocal communication is binary—information is transmitted out by an individual, but return signals are from another individual and are often significantly delayed in time and content. This subtle difference is important when evaluating how noise may interfere with the function of these two processes.

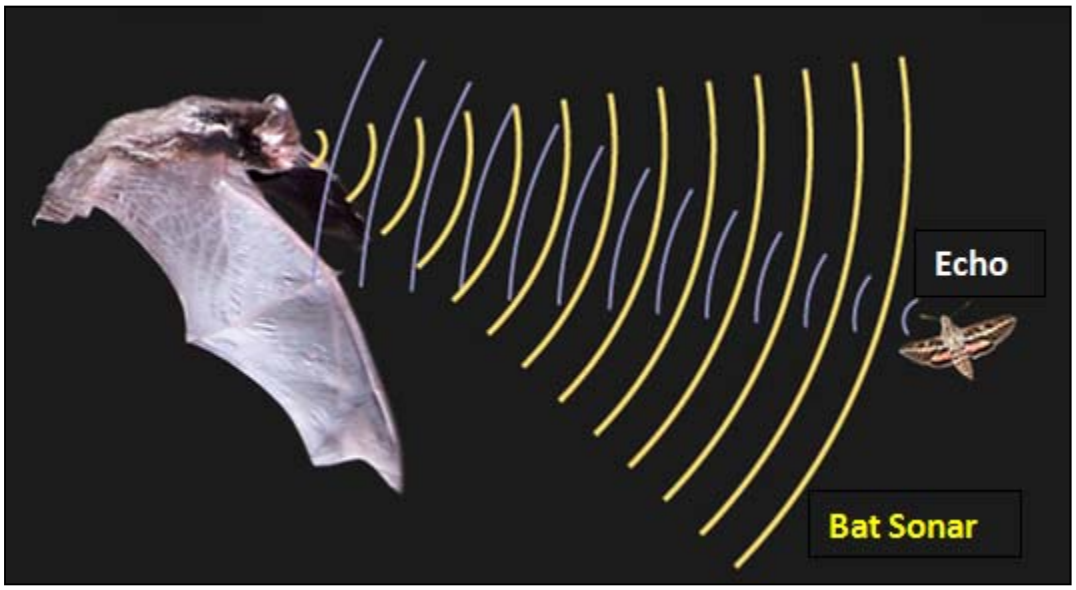

Figure 25. Echolocation (Sonar) by a Bat

(Figure adapted from Hagen 2009)

Echolocation

Echolocation, also called bio sonar, is the use of acoustic signals to determine where objects are in space. It is used by bats, toothed whales and dolphins, some shrews, and a number of cave-dwelling birds (Brinklov et al. 2013). In bats, the key functions of echolocation signals are to generate echoes that provide precise information about a bat's 3-dimensional environment and the location of prey (Figure 26) (Neuweiler 1989, 1990; Schnitzler et al. 2003; Jones and Siemers 2011). To locate, track, and capture aerial prey, bats must obtain immediate and precise information on its angle and distance and angular location, (azimuth, and elevation) relative to the bat. This information flow (auditory stream) (Barber et al. 2003; Moss et al. 2006; Chiu and Moss 2009) is rapid and complex

and must be accurately captured, filtered, and processed by the bats auditory system. The sonar signals also produce echoes from vegetation and other objects in the environment by which bats must be able to navigate. These signals often come back to the bat as a cacophony of sound, commonly referred to as *clutter signals* (Warnecke et al. 2012) (Figure 26) that the bat must detect, recognize, and differentiate from the important information on its prey.

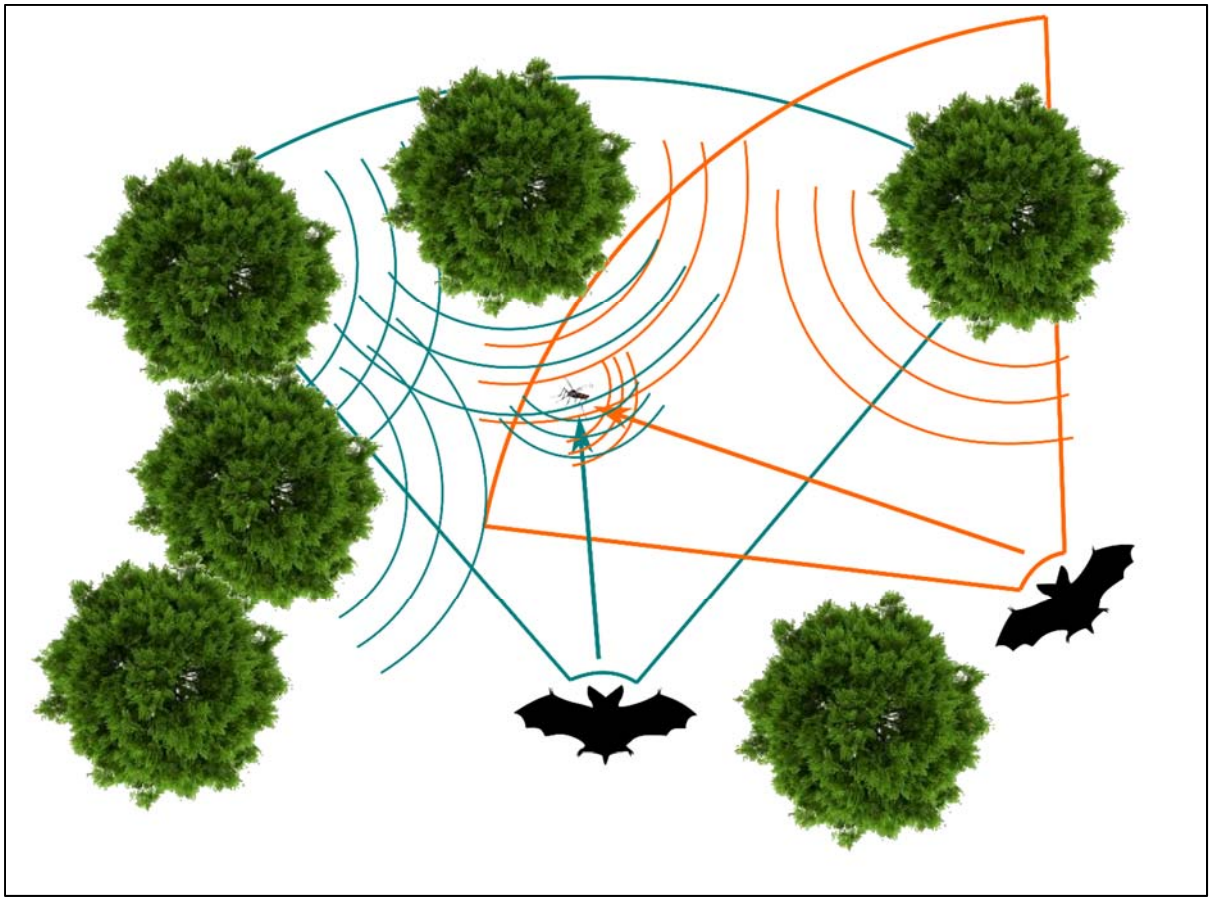

Figure 26. The Acoustic Environment of Bats Searching for Prey in a Cluttered Habitat

(Source: Micaela Warnecke n.d.) Used with permission.

Bats use the differences in the structural and temporal characteristics of the emitted signal and the returning echoes to detect, identify, and characterize (size, shape, movement, etc.) their physical environment (Figure 26) and to determine the location, type, and movement patterns of prey and other species (e.g., other bats and potential predators). Using echolocation, bats can detect objects as thin as a human hair in complete darkness.

Bat echolocation pulses are usually quite loud (>100 dB SPL 10 centimeters [4 inches] in front of the bat) (Holderied and Von Helversen 2003; Surlykke and Kalko 2008) and are emitted at rates of about 2 to 20 pulses when bats are in search mode or during commuting flight (Jones and Siemers 2011). During the approach and terminal buzz phases of prey capture (Figure 27), the call repetition rate and FM bandwidth is increased significantly to provide fine-tuned details on the exact location of the prey.

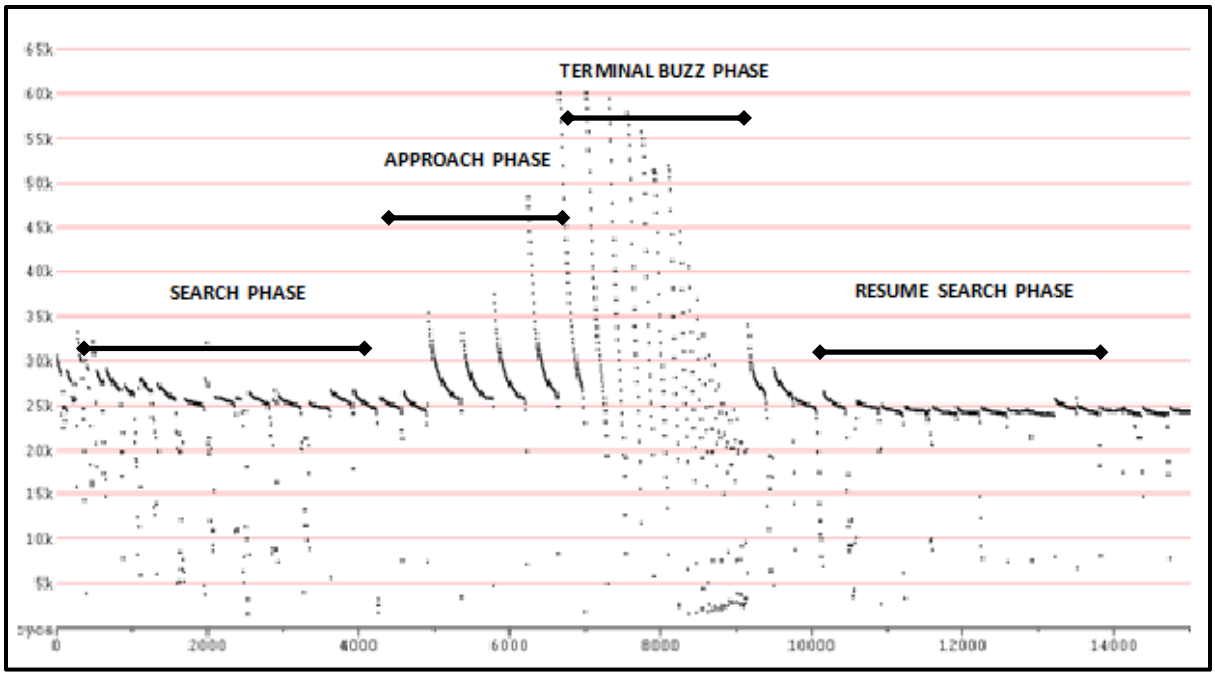

Figure 27. Search, Approach and Terminal Buzz Phases of Echolocation by a Brazilian Free-Tailed Bat

Signal Structure

The majority of North American bat echolocation calls are ultrasonic (Figure 28). The best human ear can detect sounds with frequencies up to 20 kHz; bat echolocation calls generally range from 20 to 120 kHz. However, a number of bats (e.g., spotted bat and western mastiff bat; Figures 28 and 29) produce calls with characteristic frequencies between 7 and 16 kHz—calls that can be readily heard by humans. Also, a variety of other bats produce audible calls that are used for social communication (see *Vocal Communication* section, below).

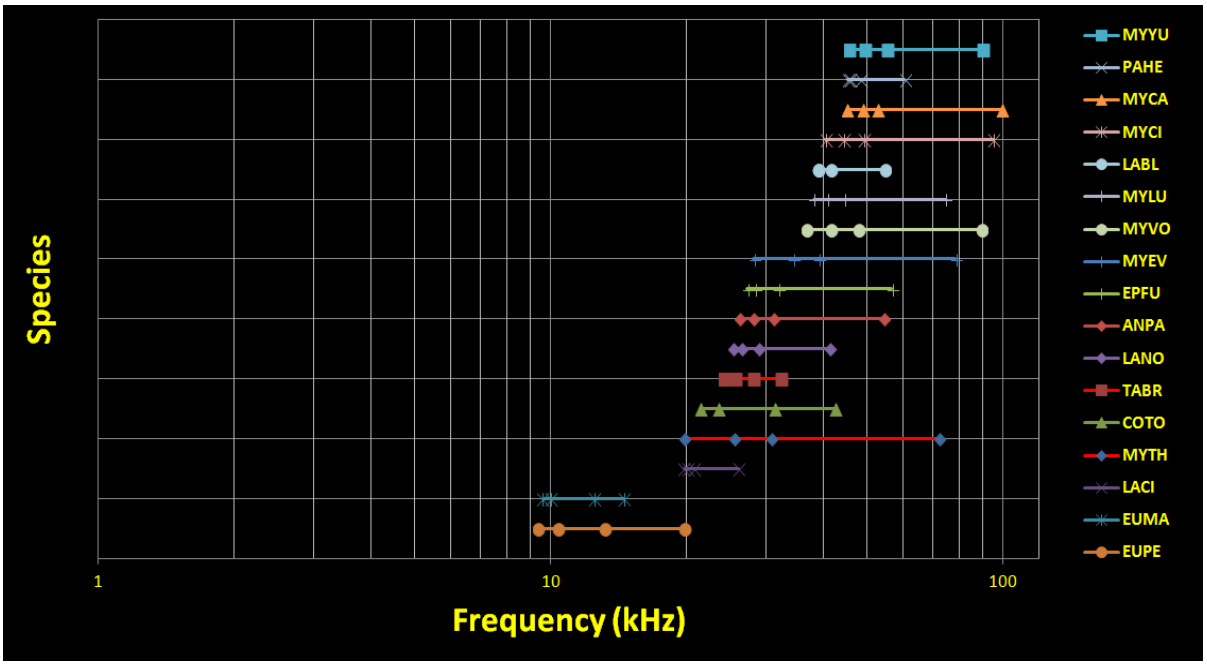

Figure 28. Frequency Ranges of California Bat Echolocation Calls

(See Table 1 for species names and codes.) - The markers on each species line show from left to right: lowest apparent frequency (f_{lo}), characteristic frequency (f_c), frequency with greatest power (f_{maxE}), and highest apparend frequency (f_{hi}). (Source: Echolocation call characteristic data from Humboldt State University Bat Lab 2011)

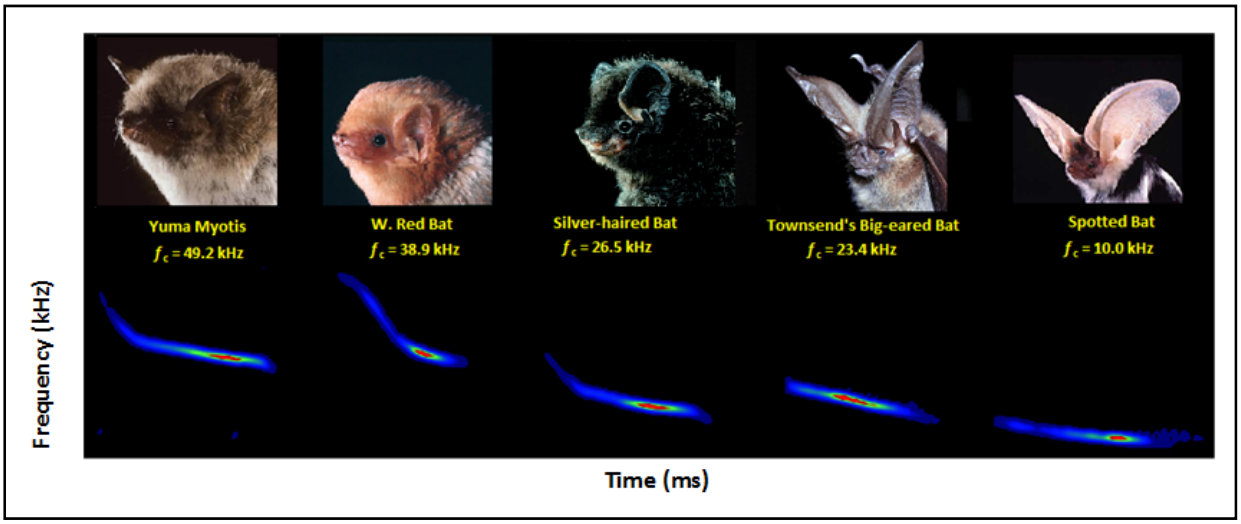

Figure 29. Echolocation Calls of Five California Bats Showing Frequency Differences

(Call sonograms from Sonobat© 3.2.2) Photos of Yuma myotis, western red bat, silver-haired bat and spotted bat ©Merlin D. Tuttle, Merlin Tuttle Bat Conservation (http://www.merlintuttle.com/). Townsend's big-eared bat photo provided by J. Aliperti.

Bat echolocation calls consist of either FM components or CF components, or various combinations thereof (Neuweiler 1989, Fenton 1990; Schnitzler and Kalko 2001; Schnitzler et al. 2003) (Figures 29 and 30). FM signals can be broadband (steep modulation) (Figure 30, Call A) or narrowband (shallow modulation) (Call C), and are generally of short to moderate duration (Call B). CF calls (Figure 30c, insert) are generally long calls of constant or near constant frequency. Many bats use calls comprised of integrated elements of these different signal types (e.g., Figure 30b). All of these signals can vary greatly in absolute frequency, bandwidth, duration, harmonic structure, and sound pressure level. This broad structural diversity allows exacting application of specific signals to the time and site-varying echolocation needs of each bat.

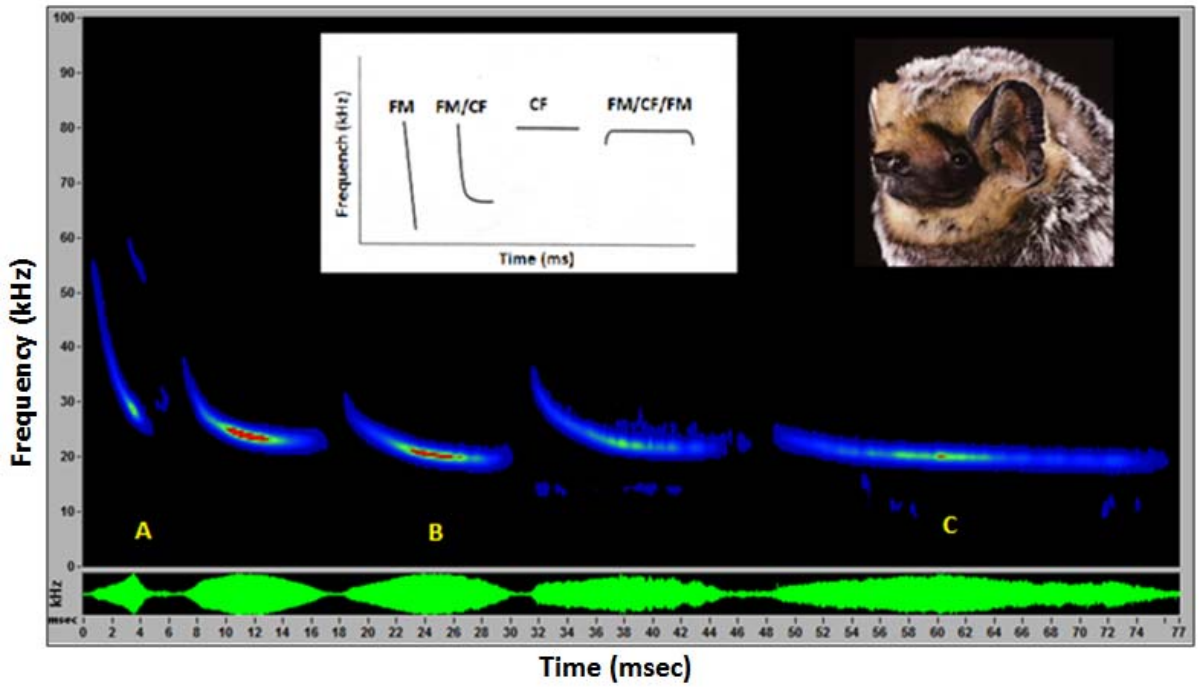

Figure 30. Echolocation Calls of the Hoary Bat (*Lasiurus cinereus*) Showing Variation in Calls from FM to CF

(Call sonograms from Sonobat ©3.2.2) Photo ©Merlin D. Tuttle, Merlin Tuttle Bat Conservation (http://www.merlintuttle.com/).

Higher frequency sounds attenuate faster than lower frequency sounds. Because most bat calls are high frequency (ultrasonic), they attenuate quickly as they travel through air (Jones and Siemers 2011). The range over which a bat can be heard by other bats and other animals, including prey and predators, assuming a detection threshold of 20 dB SPL (see Section 3, *Bat Hearing*), is approximately 281 meters (m) for a 12 kHz pulse, 128 m for a 20 kHz pulse, 35 m for a 50 kHz pulse, and 16 m for 100 kHz pulse (Hoffman et al. 2007; Jones and Siemers 2011). However, echolocation calls must travel twice the distance between the bat and its prey or environmental feature (i.e., emitted call distance to prey+ echo return distance). Because of this double attenuation distance, the detection distances for a large insect would be only 14, 11, 6, and 3 m, respectively, for 12, 20, 50 and 100 kHz signals (Jones and Siemers 2011). These distances define the active acoustic space of echolocating bats where they can find their prey (Shimozawa et al. 1984).

Signal Function

Foraging bats must detect, classify, and localize their prey and discriminate between the echoes of the prey and the echoes of the background environmental "clutter," such as nearby trees, branches, the ground and other bats (Figure 26) (Schnitzler and Kalko 2001). Different characteristics of the calls and echoes provide critical information that facilitates these determinations. Time delays between the emitted signals and returning echoes encode a target's range. Temporal comparison of the time arrival of echoes at each ear (binaural analysis) provides information on the horizontal angle of the prey. Monaural assessment of spectral patterns of the echoes provides information on vertical angle.

Different echolocation calls have evolved in response to strong selection pressures on signal design for optimizing spatial information in returning echoes. Narrowband signals (e.g., Figure 30C), particularly those of long duration, are well designed for echo detection and target classification because they activate neuronal filters in the bat's auditory system which are tuned to the narrowband frequency signal during the entire echo. When a signal hits the wings of a fluttering insect at the moment the nearest wing is perpendicular to the incident signal, a short but high amplitude peak (an acoustic *glint*) characterizes the echo (Simmons 1989; Fenton 2012). Glints can be up to 20-30 dB stronger than the echo from the body of the insect. The inherent amplitude modulation pattern generated by the fluttering insect during the CF echo readily distinguishes the insect from the unmodulated clutter echoes of surrounding vegetation. Some bats also can lower the frequency of their CF calls on approach to compensate for Doppler shifts caused by their own flight movement (Metzner et al. 2002; Smotherman and Metzner 2003).

Broadband FM signals (e.g., Figure 30A) are better suited for target localization in cluttered environments because they activate more neuronal filters for very short periods, providing precise time markers needed for accurate range and angle determination. FM signals with large bandwidths also provide fine-tuned spectral cues that that allow acoustic characterization of prey based on differences in texture and 3-dimensional structure (Neuweiler 1989, 1990).

Often bat species need to perform several echolocation tasks at once, acoustically combining signals needed for both detectability and accuracy of localization. Bats generally accomplished this using integrated signals that contain both FM and CF/shallow FM components (e.g., Figures 30). For example, little brown bat (*Myotis lucifugus*), flying in the open, likely use search calls with an initial steep FM section, followed by a shallow FM section (Figure 22). The initial FM section generates echoes that best provide information on prey localization; the shallow FM section generates echoes with information best used for prey detection and classification.

Signal Masking

Bats use different call types in different habitats depending on where and how they forage and the cluttered conditions of their use areas. All echolocating bats must be able to separate the target echo from interfering signals, such as echoes from vegetation and even the bats' own emitted signals. When target echoes and clutter echoes evoke neuronal activity at the same time, the bat's ability to evaluate the target echoes is hampered. This process is referred to as *signal masking*.

During echolocation, masking can occur in two ways—forward masking and backward masking. *Forward masking* occurs when an interfering signal, usually the bat's own call, precedes the target echo (Figure 31). This occurs when the bat flies too close to an insect, and the returning echoes

overlap with the bat's emitted signals. The width of this signal overlap zone depends on the emitted signal duration. A signal of 10 milliseconds (ms) would create an overlap zone of approximately 1.7 m (Schnitzler and Kalko 2001). Each ms of signal duration adds 17 cm to this zone width. *Backward masking* occurs when bats fly too close to vegetation and echoes from the background clutter interfere with returning target echoes (Figure 31). The width of the clutter-overlap zone is also determined by signal duration. Only when the prey targets are far away from the bat and from background clutter (i.e., in the overlap-free zone) will the bat be able to detect signals without interference.

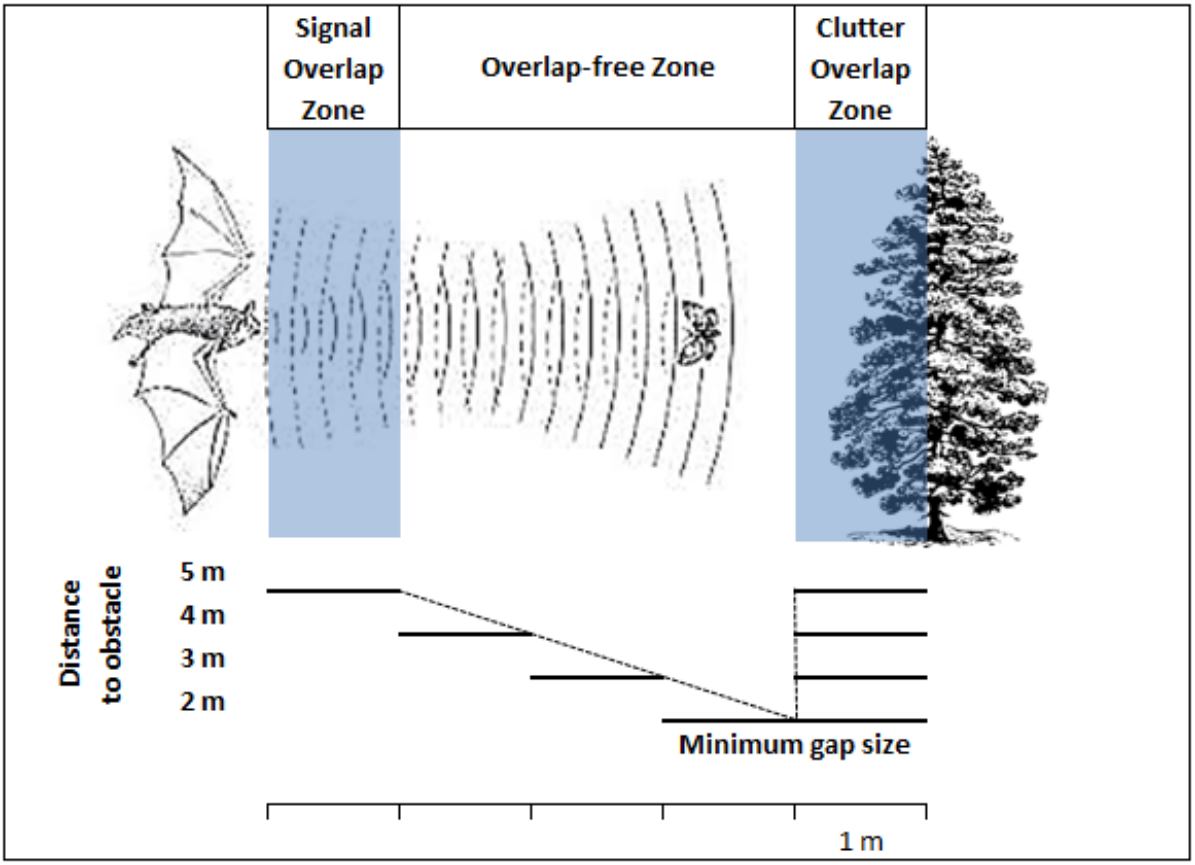

Figure 31. Forward and Backward Masking Conditions for Echolocating Bats

(Source: Adapted from Schnitzler and Kalko 2001.)

The actual effects that these masking situations have on prey echo reception and interpretation depend largely on signal structure, the strength of the prey echo, and interfering signals and their temporal relationship. Bats using loud, long, and low frequency calls close to their prey and near dense vegetation will experience wider overlap zones than species using softer, short interval FM signals under the same conditions (Schnitzler and Kalko 2001). The types of calls used by bats in different habitats (e.g., open versus cluttered), therefore, depends largely on which best minimize masking interference (Simmons et al. 1979; Neuweiler 1989; Fenton 1990; Schnitzler and Kalko 2001).

Call Type and Foraging Areas

Bats forage in a mixed variety of habitats depending on their preferred prey, their flight agility, and the design of their echolocation calls (Neuweiler 1989; Fenton 1990). Bats that forage close to, between, and within the foliage of trees (Figure 32, numbers 4, 5 and 6) tend to be highly agile and have calls that are strongly FM, allowing the bat to precisely locate prey amongst the clutter of the forests. By contrast, strong, fast-flying bats that catch insects in the open above the forest canopy (Figure 32, number 1) or in large meadows Figure 32, number 7) and open fields (Figure 32, number 2) commonly use high intensity, long, narrowband calls of lower frequency (Fenton 1990). These calls propagate long distances and allow bats to detect prey farther out and then approach and track them without the interference of clutter echoes from woodland vegetation. Figure 33 shows the general shape and frequency patterns of calls on a gradient from those used by bats in clutter (e.g., MYCI, MYCA MYTH etc.) to the open area foraging species (e.g., EUPE, TABR, LACI etc.).

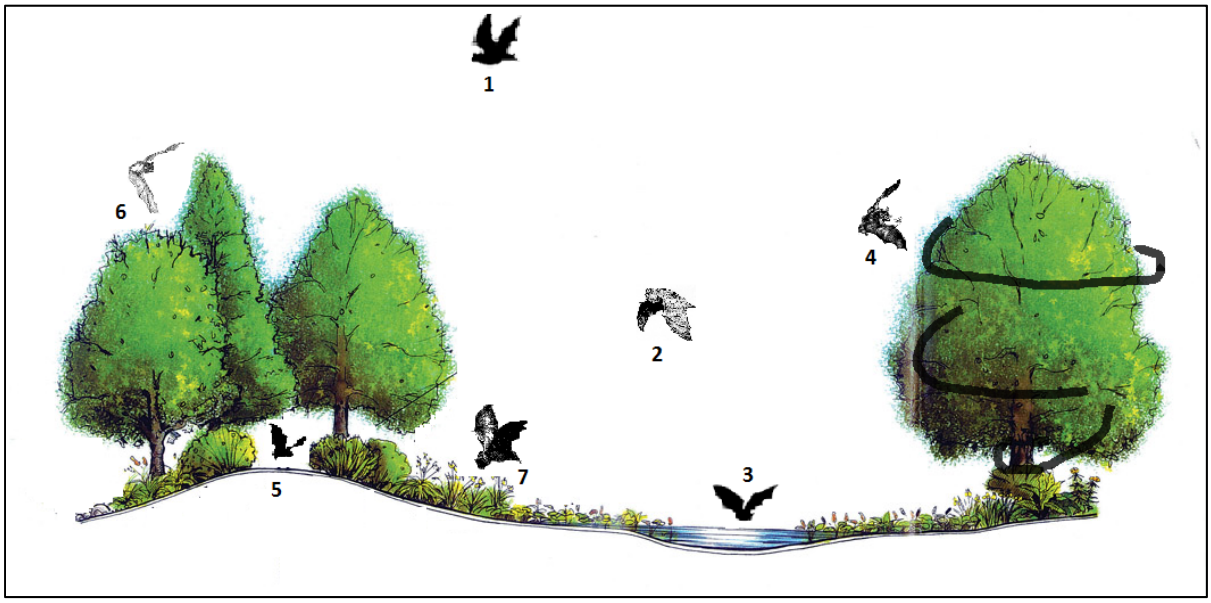

Figure 32. Spatial Areas Used by Bats while Foraging

(1= above canopy; 2 = open spaces between canopies; 3= over open water; 4 = close to and within foliage; 5 = between trees; 6 = amongst foliage; 7 = ground foraging) (Source: Adapted from Neuweiler 1989.)

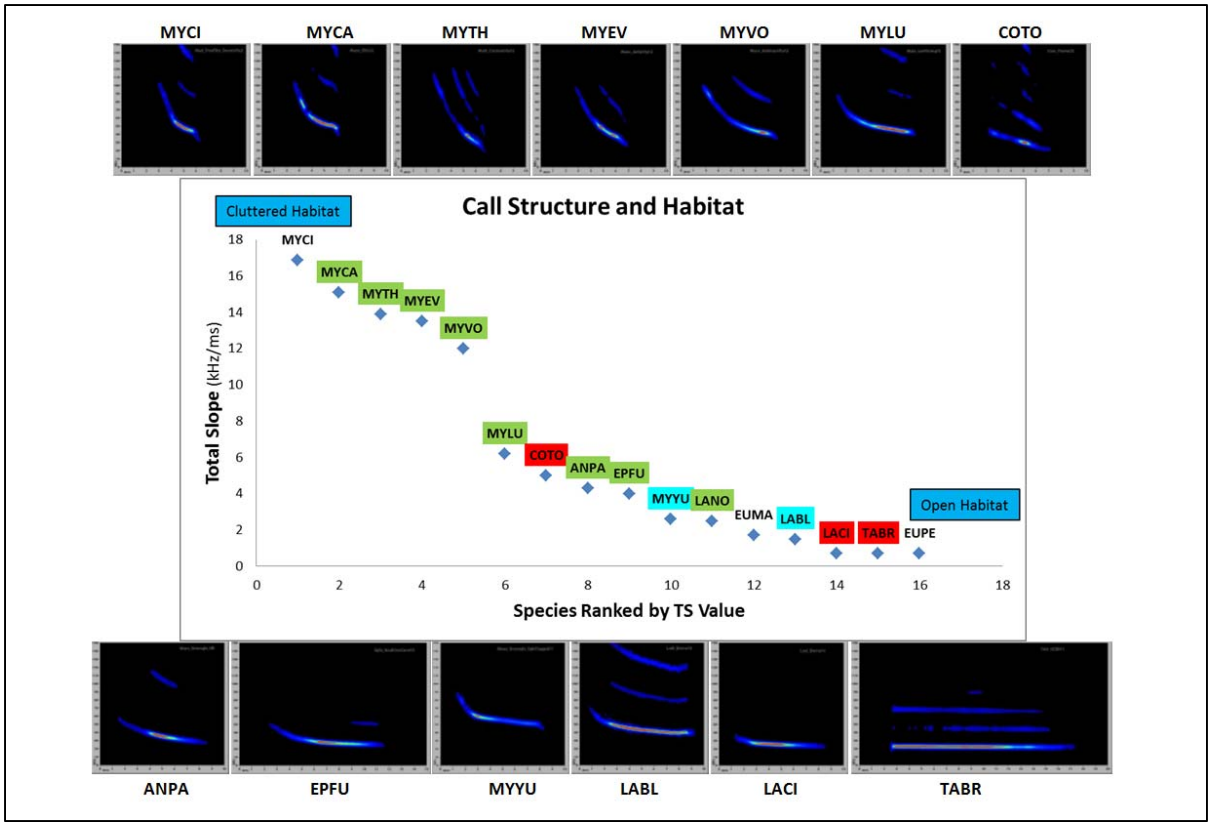

Figure 33. Echolocation Call Structure in Bats Using Different Habitats

(Call sonograms from Sonobat ©3.2.2) The species codes are color coded to identify different flight foraging behaviors of each species as described in Norberg and Rayner (1987): red indicates fast fliers that forage primarily by open-air hawking; blue identifies fast fliers that forage in cluttered habitats; green identifies slow, highly maneuverable fliers that forage in cluttered habitats; no color identifies species for which no data was available.

Vocal Communication

Vocal communication in bats consists of transmitting one-way signals to other bats, most commonly in the roost, but also during flight. Vocalizations transfer information about the caller that is intended to evoke a response in the receiver. That response may or may not be a return call. Nevertheless, information is mutually and communally shared in most roosts, generally in close quarters. Figures 34–37 show a few of the more interesting calls in some California bat species. The functions of these calls are poorly known and are only beginning to be studied.

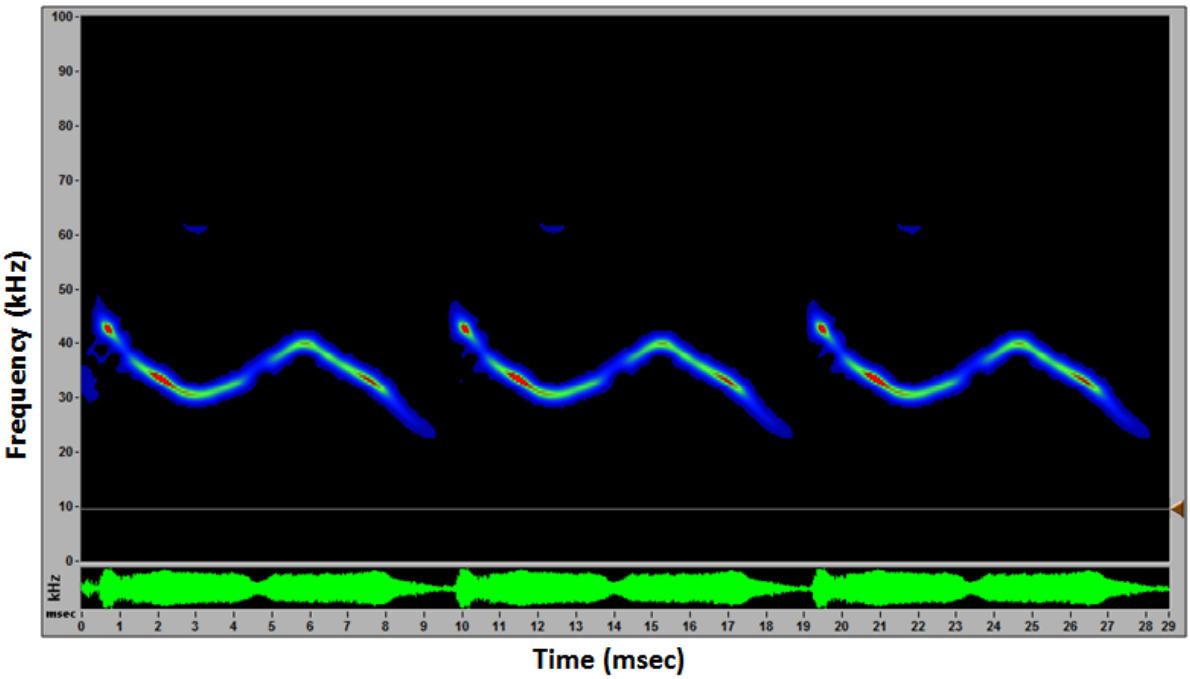

Figure 34. Townsend's Big-Eared Bat Triplet Social Call (*Corynorhinus townsendii*)

(Call sonogram from Sonobat ©3.2.2)

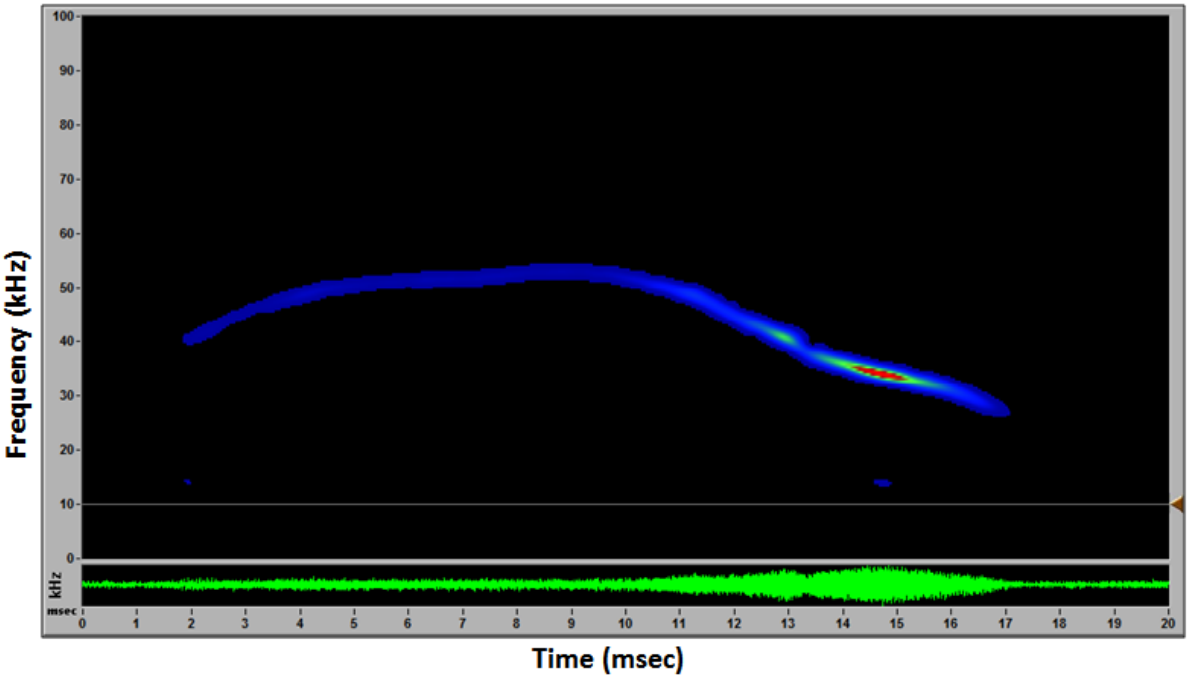

Figure 35. Brazilian Free-Tailed Bat (*Tadarida brasiliensis*) Social Call

(Call sonogram from Sonobat ©3.2.2)

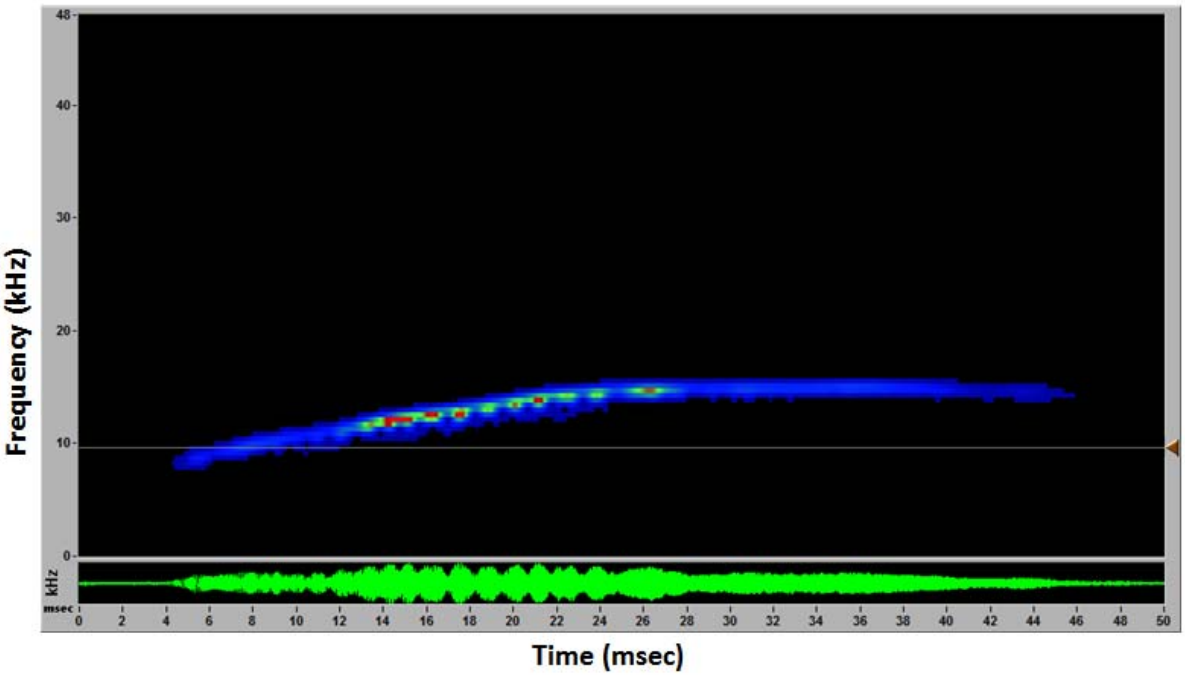

Figure 36. Hoary Bat (*Lasiurus cinereus*) Social Call

(Call sonogram from Sonobat ©3.2.2)

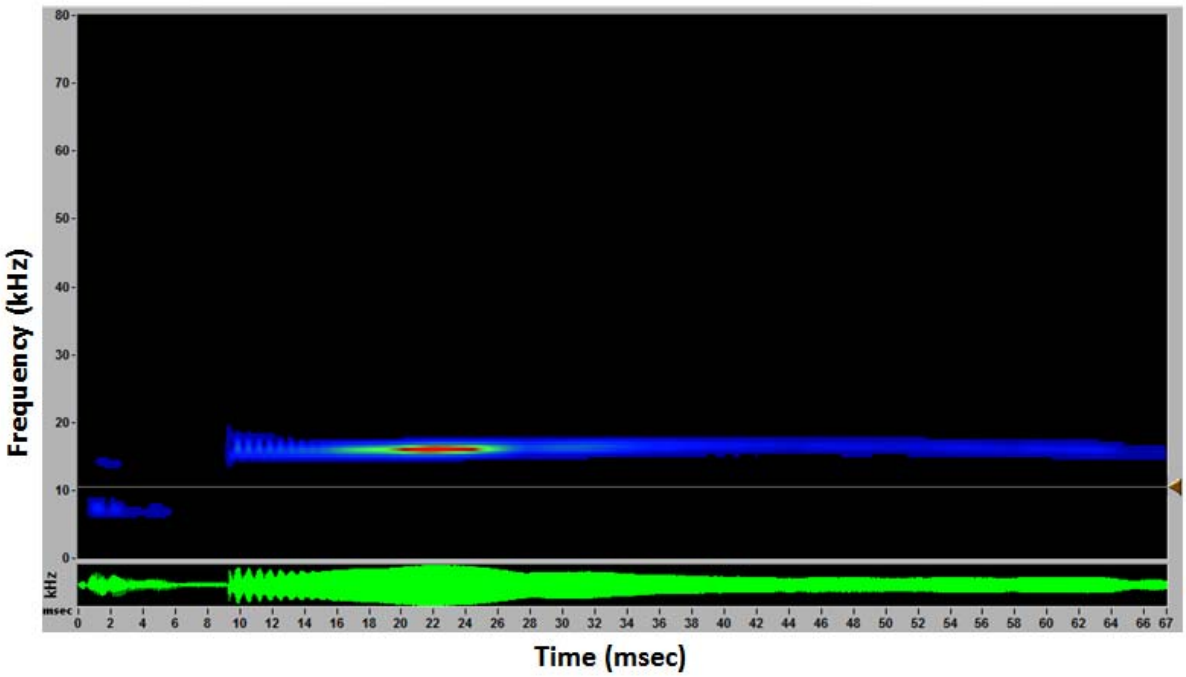

Figure 37. Very Long Social Call of the Brazilian Free-Tailed Bat (*Tadarida brasiliensis*) Recorded in its Roost at the I-80 Yolo Causeway between Davis and Sacramento, California

(Call sonogram from Sonobat ©3.2.2)

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Section 5: Noise Exposure in Bats

A bat's noise exposure level depends on its proximity to the source, the time it spends within the noise space (Figures 38 and 39), and the flight path it takes. Bats that roost close to highways or construction sites may be exposed to chronic noise for long periods during the day while they are in the day roost but much less at night when they are out foraging. During the night, bats may only infrequently fly through a noise space or may remain in it longer if they forage along vegetated rights-of-way paralleling a highway (Figure 39). Most fly-throughs are near instantaneous and inconsequential with regard to noise exposure, unless they are unfortunately timed to coincide with a bat being very close to a very loud piece of equipment. However, that scenario is likely to be quite rare in that bats would likely hear the noise from afar and avoid it.

The shapes of these noise spaces—or noise envelopes—are neither hemispherical around a point source (such as a construction site), nor are they lineally hemispherical (such as along a highway). Because of marked differences in the sound attenuation rates along the vertical versus horizontal axes, the shapes of the noise envelopes are elongated vertically (Figure 38). Because ground absorption affects sound transmitted horizontally (e.g., an added 1.5 dBA per doubling distance for a soft site) but not vertically (only attenuation by spherical spreading), the shapes of the 3-dimenstional noise volumes are elongated along the vertical axes and diminish proportionally to shorter distances defining the surface plane over the ground (Figure 40). The result of this acoustic geometry is the creation of an acoustic cone over construction sites and an elongated linear hemisphere over highways.

Effect Space

Effect space is the 3-dimensional area around the noise source that bats use or potentially use. This space may not be all encompassing, particularly along highways where habitats vary widely, but includes only those areas that bats use for specific reasons—foraging, roosting, commuting, etc. Areas outside these use zones are essentially no effect zones. However, because it is exceptionally difficult, if not impossible, to physically differentiate these areas, the geometric volume surrounding a noise source out to a radius where the source noise attenuates to background noise levels should be considered the effect space. This spatial estimate is conservative and overestimates actual effect space, but it is a very reasonable starting point for avoidance and mitigation planning.

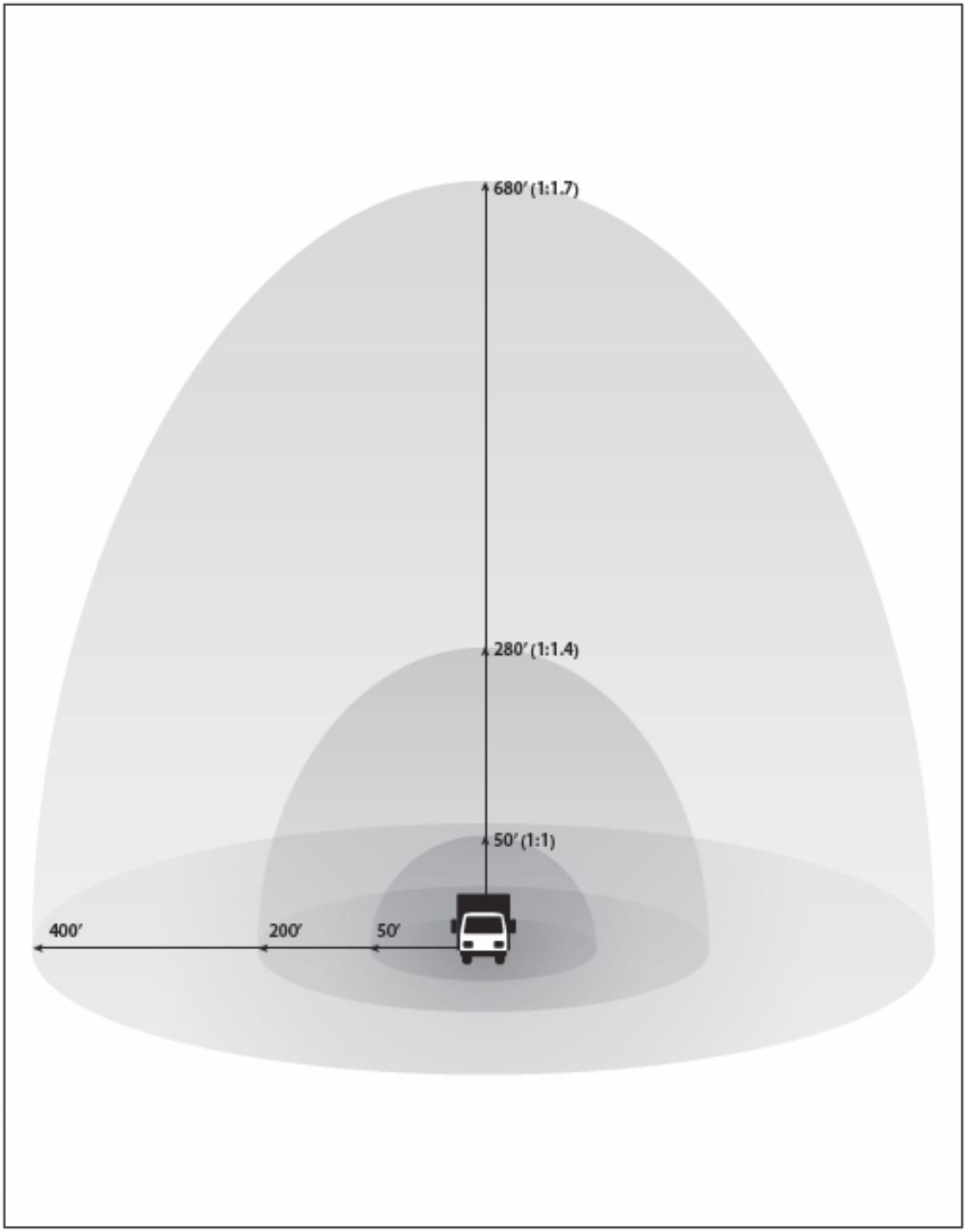

Figure 38. Diagrammatic Representation of Noise Envelopes Surrounding a Point Noise Source (Construction Site)

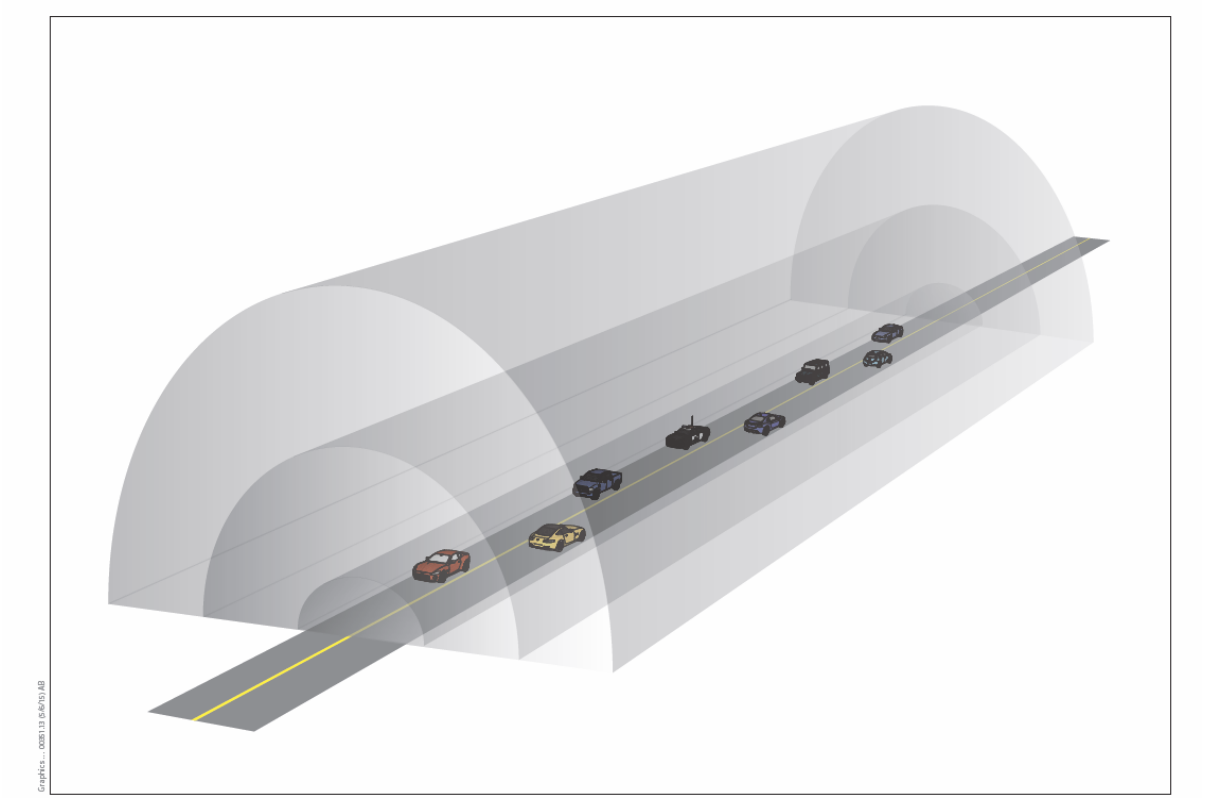

Figure 39. Diagrammatic Representation of Noise Envelopes Surrounding a Linear Noise Source (Highway)

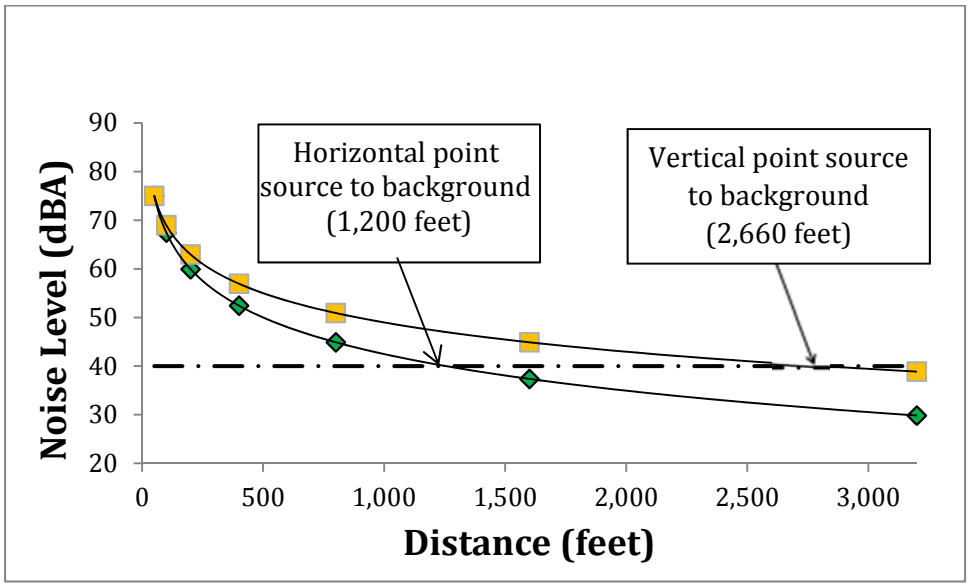

Figure 40. Comparison of the Vertical and Horizontal Attenuation Distances for a Point Noise Source

Critical Exposure Periods

Bats are more sensitive to noise effects at certain times of the year. Figure 41 shows the annual reproductive cycle of the Townsend's big-eared bat, a species considered to be very sensitive to disturbance. Reproductive females and their young are particularly vulnerable during the maternity season (mid-March through mid-August). During this period, disturbance can potentially cause these bats to abandon their roosts and young (Humphrey and Kunz 1976; Pierson and Rainey 1998; Sherwin et al. 2000). In cold regions, bats may also be vulnerable during hibernations periods (October through mid-March) if noise disturbances cause arousal from hibernation. Bats may be less vulnerable during this period in regions with milder temperatures that allow them to emerge periodically to forage. The periods of least vulnerability are after the pups become volant (fly) and before hibernation (late August through early/mid-October) and after hibernation but before maternity colonies are established (mid-March).

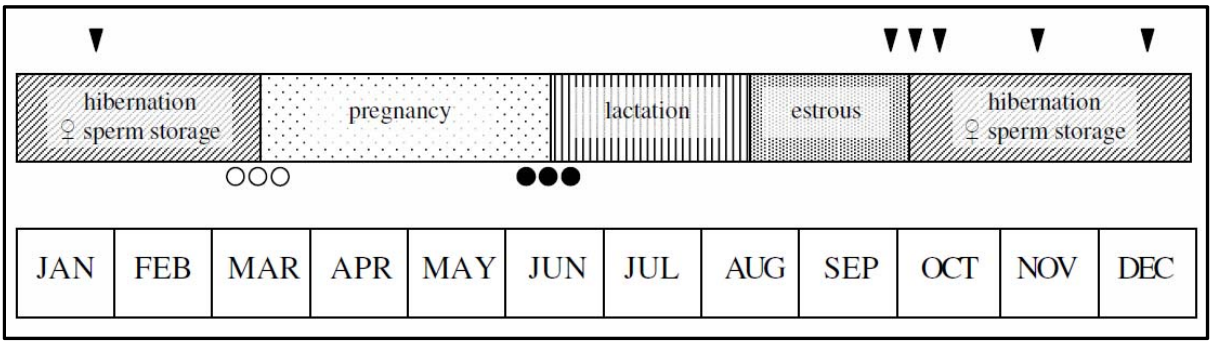

Figure 41. Generalized Timing of Reproductive Events for Female Townsend's Big-Eared Bats (*Corynorhinus townsendii*)

Annual and Geographic Variation in Timing is Likely (inverted triangles = probable copulatory periods; open circles = ovulation; closed circles = parturition) (Source: Gruver and Keinath 2006.)

Section 6: Effects of Highway Noise on Bats

Overview

The effects of highway noise have been studied in many animal groups including birds (Leonard and Horn 2005; Parris and Schneider 2008; Slabbekoorn and Ripmeester 2008; Francis et al. 2009; Nemeth and Brumm 2010; Halfwerk et al. 2011; McClure et al. 2013; Nemeth et al. 2013), mammals (Rasmussen et al. 2009; Benítez-López et al. 2010; Iglesias et al 2012), amphibians (Bee and Swanson 2007; Lengagne 2008; Sun and Narins 2005; Holderegger and Giulio 2010; Herrera-Montes and Aide 2011), and fish (Dooling et al. 2015; Radford et al. 2014). These studies clearly show that wildlife near highways respond, often negatively, to the presence of roads. However, because many factors other than noise can also potentially affect wildlife presence and activity near roads (e.g., moving cars, substrate vibrations, different microclimate, vegetation and food availability, pollution) it is often difficult, if not impossible, to differentiate among them and identify the principal causal factors.

Emerging studies have shown that some bats, particularly slower moving, ground gleaning species (i.e., species that passively listen for and prey on terrestrial beetles), forage less frequently near highways and often balk at crossing over the roads, even along established travel routes (Bennet and Zurcher 2013; Bennett et al. 2013). Playback studies of highway noise in the lab show these bats actively avoid noisy areas, and search times for prey dramatically increase when the bats do forage in such areas (Schaub et al. 2008; Siemers and Schaub 2011; Luo et al. 2015; Bunkley and Barber 2015). Because the sounds of the ground beetles that the bats use to detect their prey fall within the spectra of highway noise, it is hypothesized that this avoidance behavior/reduced foraging efficiency may be due to acoustic masking of these important signals. However, other factors, such as reduced prey availability near roads, differences in microclimate, and vehicle and light disturbance need to be examined in the field to more fully clarify the contributory role of traffic noise in these responses (Dooling and Popper 2015; Luo et al. 2015).

Highway construction noise (e.g., heavy equipment, blasting, and pile-driving) can also potentially affect bats, particularly those species that roost in bridges, culverts, or other highway infrastructure or in nearby buildings, trees, or rock outcroppings. Sudden, loud noises can potentially disturb bats and cause abandonment of roosts (Pearson et al. 1952; Humphrey and Kunz 1976; Kunz 1982; Fenton 1997; Ferrara and Leberg 2005). If loud enough and sudden, such noise can also potentially cause temporary or permanent hearing loss in bats, but this has yet to be tested. Chronic disturbance may also alter important colony activity patterns, particularly during the breeding season (Shirley et al. 2001; Mann et al. 2002) and disrupt critical torpor cycles of hibernating/overwintering bats, forcing them to overuse critical energy resources (Speakman et al. 1991; Thomas 1995; Fenton 1997; Johnson et al. 1998).

Some well-defined experimental lab studies on noise effects (e.g., Siemers and Schaub 2011; Bunkley and Barber 2015) show clear effects of playback road noise on species' behaviors that likely represent probable causal responses in the field. However, the independent or synergistic effects of other roadside variables may also be important (Luo et al. 2015).

The primary objective of this section is to use the information provided in Sections 2 through 6 of this report to examine the biology, behaviors, and sensory ecology of bats to determine if, how,

where, and when they might be affected by highway noise. Unlike birds (except oilbirds and swiftlets) (Konishi and Knudsen 1979; Brinklov et al. 2013), bats use echolocation to navigate, find prey, communicate socially (Knörnschild et al. 2012; Melendez et al. 2006; Gadziola et al. 2012; Wright et al. 2014; Jones and Siemers 2011) and acoustically monitor (e.g., eavesdrop) (Gilliam 2007; Dechmann et al. 2009; Fenton et al. 2003, Jones et al. 2011), and compete with other bats (e.g., engage in acoustic jamming) (Corcoran and Conner 2014; Masters et al. 1995). Most echolocation signals and many communication calls are ultrasonic, but some are lower in frequency such that they overlap with the spectral profile of highway noise and, therefore, are potentially subject to masking.

Approach

Dooling and Popper (2007, 2015) (see also Dooling and Blumenrath 2014) developed an analytical process for systematically assessing the effects of highway noise on birds. This approach is based on four overlapping types of effects: (1) hearing damage from acoustic shock or chronic extreme noise, including permanent hearing loss (permanent threshold shift [PTS]); (2) temporary hearing loss due to temporary threshold shifts (TTS) from acoustic overexposure; (3) masking of communication signals and other important environmental sounds; and (4) changes in behavior and other physiological responses to noise (Figure 42). This analytical framework keys on the proximity of noise recipients to the noise source which, with additional consideration for the unique acoustic features of echolocation, is equally applicable for identifying and analyzing highway noise effects on bats. Accordingly, it is used in this report for that purpose.

Figure 42 summarizes the general potential effects of highway noise on bats. A noise-induced *threshold shift* (PTS or TTS) is a reduction in auditory sensitivity following a noise exposure. Masking, as discussed in section 4, is the reduction in the ability to hear a sound caused by the presence of another sound. Both masking and threshold shifts have the effect of reducing an animal's auditory sensitivity over some frequency bandwidth, with the key distinction between the two being that masking essentially occurs during the noise exposure, while a threshold shift persists after cessation of the noise.

Noise levels are generally highest close to highways and construction sites, and auditory trauma (PTS, TTS), signal masking, and behavioral and physiological effects can all potentially occur simultaneously in some taxa.

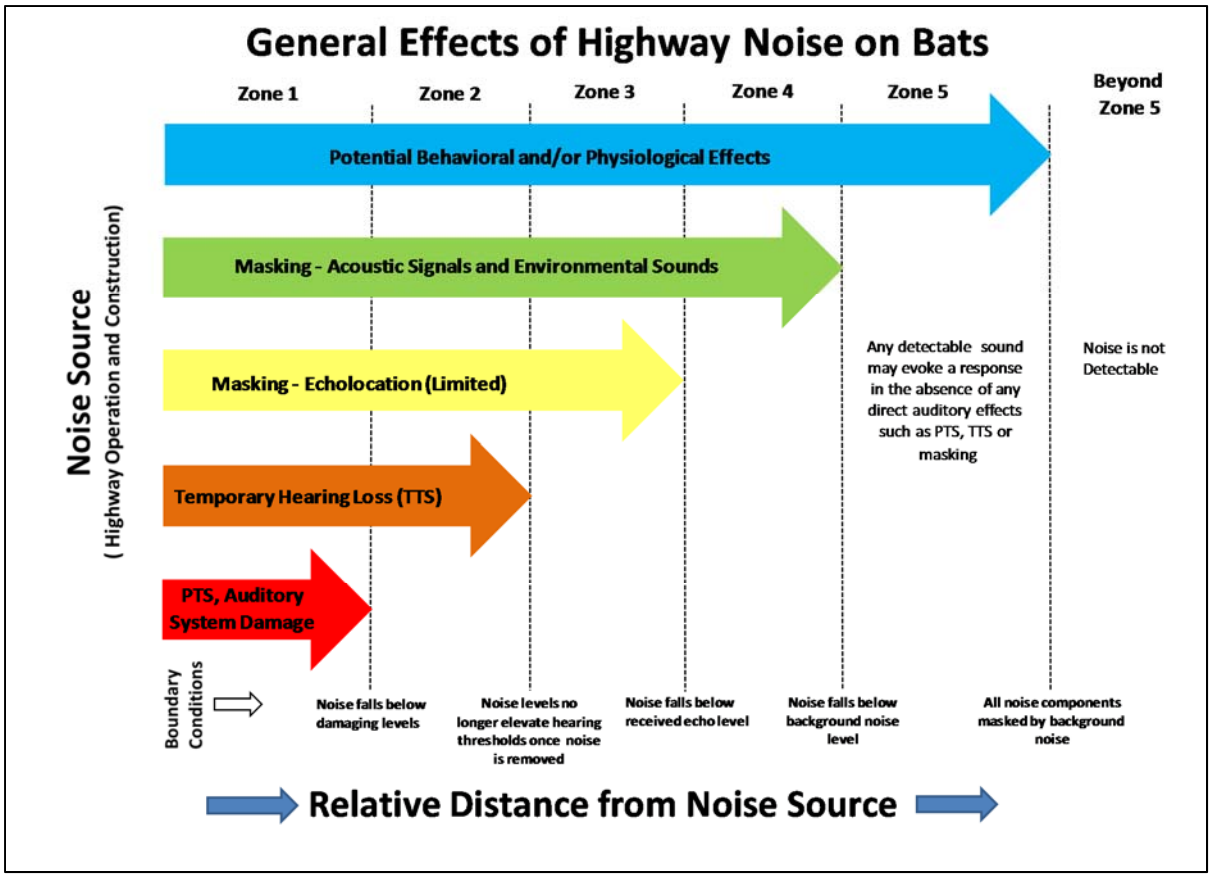

Figure 42. Conceptual Format for Analysis of Highway Noise Effects on Bats

(Source: Adapted from Dooling and Popper 2015.)

At greater distances, noise levels are lower and trauma events are less likely, although TTS can still occur beyond the PTS zone when noise exposure is of sufficient duration and intensity. At even farther distances, hearing loss is no longer likely to be a problem, but noise above background levels can potentially cause signal masking, therein disrupting normal communication or detection of other important environmental sounds (e.g., approaching predator; movement sounds of prey species). Masking of echolocation signals is likely rare and limited to species having low frequency calls that significantly overlap with the spectral range of the highway noise. Additionally, the range of effect is differentially affected by the position and flight pattern of the echolocating bat; the power and shape of the calls (FM versus CF); the size, distance, and texture of the prey; the amount of acoustic clutter; and the adaptive strategies the bat uses to fine-tune and enhance reception of the echo. Masking of low frequency communication calls may also potentially occur in flight or within a bat roost if the noise is loud enough. Interestingly, a growing number of studies indicate that echolocation calls have information that is also important in communication; this suggests that a blending of the masking effects (on echolocation and communication) is possible when there is sufficient spectral overlap between the calls and the noise.

Hearing Loss

When exposed to sudden or chronic loud (90 - 120 dB SPL) noise, mammals generally respond with a shift in hearing sensitivity, either temporarily (TTS), lasting from seconds to days depending to the level of exposure, or permanently (PTS), if the noise is sufficient to damage the structure and function of the inner ear (Dooling and Popper 2015, Hom et al. 2015). No studies on NIHL have been conducted on bats. However, many studies have been conducted on other mammals (e.g., cats, rats, and chinchillas) that have very strong similarities in structure and function of the inner and middle ears. It is reasonable that the results of these studies, at least in general, can be applied to analysis of similar conditional situations in bats. This assumption was made for the following assessment.

Permanent NIHL is primarily due to the destruction of the sensory hair cells and supporting cells within the cochlea (Figure 15C), either mechanically or metabolically (Liberman and Dodds 1984; Kujawa and Liberman 2009). Loud noises induce strong energy fluxes in the cochlear fluid of the inner ear that can result in mechanical trauma to the basilar membrane and the complete or dysfunctional loss of the sensory cells of the Organ of Corti (Figure 43). Under severe conditions, there can be progressive degeneration and complete loss of the Organ of Corti (Figures 43c and 43d).

The functional consequences of these effects include partial to complete impairment of the auditory system. The location of the damage along the cochlear spiral (Figures 14 and 16) generally relates to the frequency of the noise exposure and the sensitivity pattern of the sensory cells along the basilar membrane. The most dramatic loss of hair cells is likely to occur at the locations on the membrane that are most sensitive to the predominant frequencies of the noise. Figure 16 shows that cells near the base of the cochlea are most sensitive to high frequencies and those at the apex are more sensitive to lower frequencies. Therefore, lower frequency noise, like that from highway noise, may affect apical cells more than basal cells. However, it also has been shown with broadband noise that basal cells are inherently more susceptible to damage than apical cells. The composite outcome of damage may therefore be a mix of degraded sensitivities depending on the relative effects of the intensity versus the frequency of the noise.

In bats, damage to high frequency cells would likely result in impaired echolocation. Damage to the lower frequency cells would likely result in impaired capacity for passive listening. Either effect could potentially be life threatening. Failure to accurately assess the locations of trees, branches, and other obstacles in their flight path could result in fatal collisions or debilitating injury. Failure to accurately detect and determine the precise location and movement patterns of prey (both aerial and ground) would likely result in significantly diminished capture success. Similarly, failure to detect the approach of a predator could be fatal. Because bats simply do not have the luxury of extended recovery time, even temporary shifts in hearing abilities have the potential to result in negative effects on affected individuals. Young in maternity colonies are particularly susceptible to noise induced hearing loss during sensitive development periods (Brown et al. 1978).

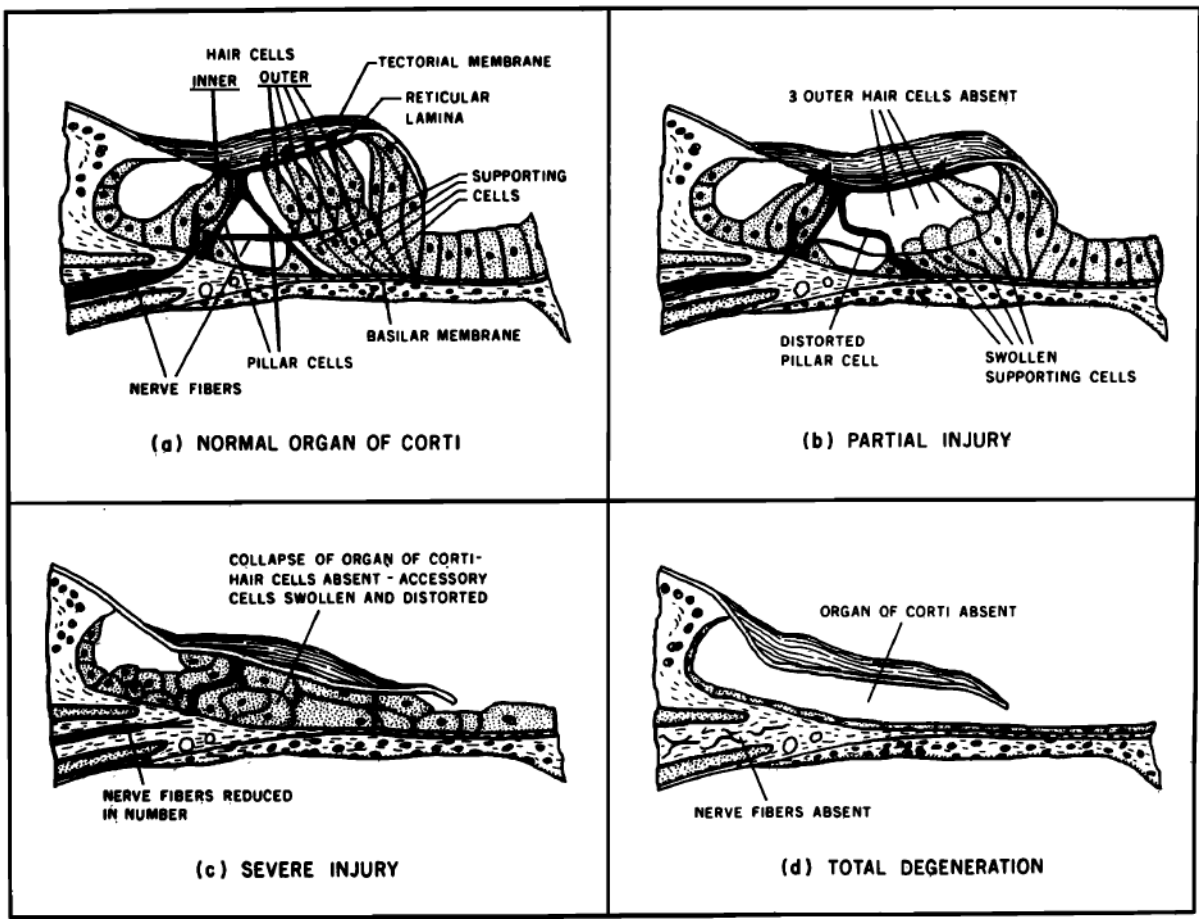

Figure 43. Normal Structure and Damage Injuries to Organ of Corti from Noise Overexposure

(Source: Saunders et al. 1985.)

Signal Masking

Echolocation

Masking occurs when noise overlaps with acoustic signals to the extent that the information content of the signal is degraded or lost. Echolocation masking could potentially occur if the noise interferes with a bat's clean reception of echoes. Bats naturally adapt to forward and backward masking of their own signals (Figure 31) by adjusting their signal duration and flight position while foraging. Noise masking of echolocation signals is acoustically equivalent to extending the "clutter overlap zone" out from the noise source to the bat at a threshold distance where the noise level equals the signal strength of the returning echo.

Because bat hearing is extremely sensitive, bats can detect echoes at low amplitudes. Consequently, the threshold distance for masking may be quite far from the noise source (i.e., the noise will attenuate to the low value of the echo amplitude at large distances). For example, Lawrence and Simons (1982) calculate that if a bat directs a 30 kHz sonar signal towards a small insect at 3 m, attenuation due to spherical spreading on the outward path and atmospheric attenuation on the outward and return paths would be about 34 dB (30 dB for spreading loss over 3 m and 4 dB for

atmospheric attenuation of 6 m). Additional spreading losses on the echo's return would amount to about 30 dB, for a total reduction in echo sound pressure of 64 dB due to all the effects of propagation. Additionally, attenuation would occur due to the signal energy being scattered elsewhere or absorbed by the target's shape during echo formation, resulting in an estimated total attenuation of about 90 dB. Given that most bats emit outgoing signals at approximately 110 dB (Griffin 1958; Lawrence and Simmons 1982), the returning echo from a small insect at 3 m will be in the range of 20–46 dB (i.e., [110 dB–64 dB] – [110–90]) at the bat's ear. Minimally, the effects threshold distance—the distance highway noise would attenuate to 46 dB—would therefore be approximately 2,600 feet (Figure 57) for a construction site with a noise level of 84 dB.

However, masking can only occur if the noise spectrum overlaps with that of the bat's echoes. For most bat species in California, echolocation calls are in the ultrasonic range beyond the upper frequency limits of highway noise (Figure 44). For these species, there is effectively no echolocation masking effect from highway noise.

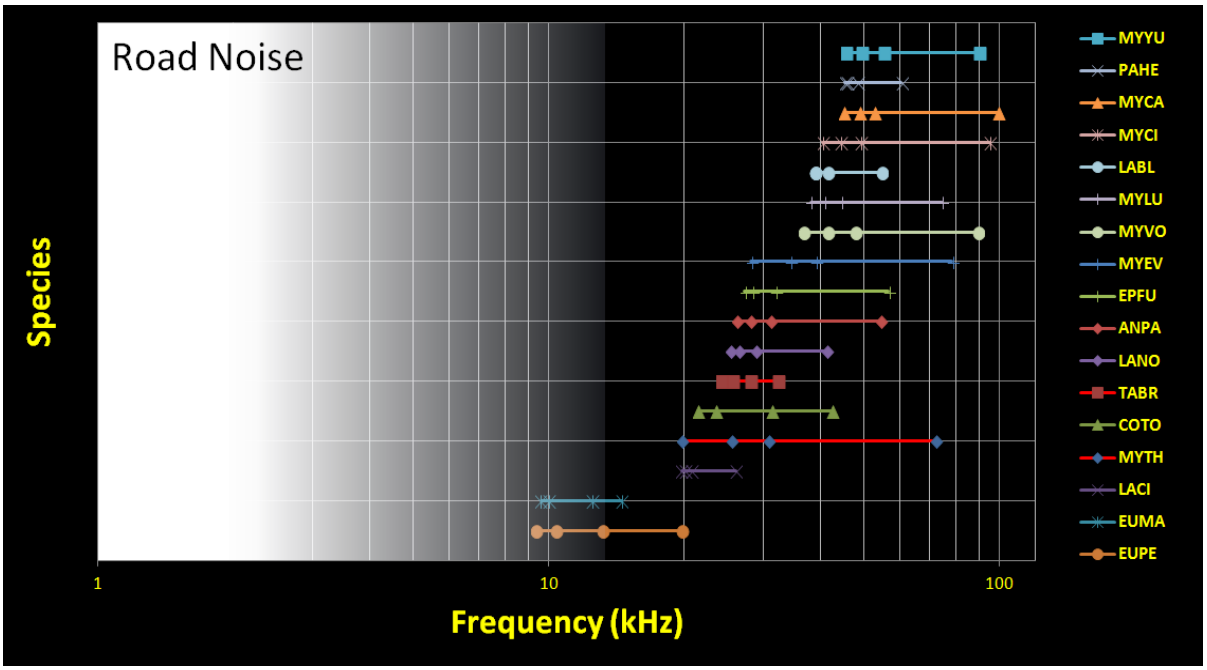

Figure 44. Spectral Range of Bat Echolocation Calls Showing Overlap of Road Noise

The markers on each species line show from left to right: lowest apparent frequency (f_{lo}), characteristic frequency (f_c), frequency with greatest power (f_{maxE}), and highest apparend frequency (f_{hi}). The graded white shading on the left side of the figure graphically approximates the spectral change in traffic noise shown in Figure 3. (Source: echolocation call characteristic data from Humboldt State University Bat Lab 2011)

However, two species, the spotted bat (EUMA) and the western mastiff bat (EUPE), use echolocation signals with frequencies low enough to be potentially masked, at least partially, by highway noise (Figure 44). Figure 45 shows the spectral overlap between highway noise and the echolocation call of the spotted bat. The highway noise will vary in amplitude with traffic load and speed as will the spotted bat echolocation call (Figure 46) with relative distance. But the overall pattern shows that above quiet background sound levels (e.g., 40 dBA), there is only partial overlap between the noise and the echolocation signal and the overlap occurs at the frequency band where the intensity of the highway nose is near background levels. It is likely that with its large ears, the spotted bat can amplify the incoming echo sufficiently to allow it to readily detect the echo in the highway noise.

Passive Listening

Passive listening involves listening for biologically important sounds in the environment. These sounds include natural sounds (e.g., wind and vegetation), the sounds of insect prey rustling in ground litter, communication and echolocation calls of other bats, and the sounds of potentially approaching predators or other possible threats. For bats that glean prey off the ground (e.g., pallid bats and California leaf-nosed bats, echolocation searches for litter-dwelling species is often impeded by the litter reflecting back their search signals. To adapt, these species commonly use a combination of passive listening, vision, and echolocation to find their prey (Fuzessery et al. 1993; Bell and Fenton 1986 These species often have good low frequency hearing, large ears, and highly maneuverable flight (Brown et al. 1978, Fuzessery 1996)

A growing number of studies are showing that bats, particularly passive listening species, tend to avoid areas with a high level of anthropogenic noise, notably near highways (Jones 2008b; Schaub et al. 2008; Siemers and Schaub 2011; Berthinussen and Altringham 2012; Kitzes and Merenlender 2014; Bunkley and Barber 2015). While the causal factors for this behavior have not been definitively established, it is reasoned that next to highways, traffic noise can potentially mask the sounds gleaning bats use to find their prey. In a set of experimental studies, Schaub et al. (2008) and Siemers and Schaub (2011) tested the hypothesis that bats will avoid foraging areas with high background noise. Using a combination of playback trials with recorded traffic noise, vegetation noise, and computer-generated broadband noise, Schaub et al. (2008) found that foraging efficiency of the mouse-eared bat (*Myotis myotis*), a ground-gleaning species, dropped significantly when the bats were exposed to each of the different noise sources. Interestingly, the digital computer generated broadband noise (i.e., a sound foreign to the bats) had the greatest effect, followed by vegetation noise (wind through a reed bed), and then traffic noise. This study shows that these bats are clearly responsive to a variety of environmental sounds, including highway noise, which they typically monitor through passive listening.

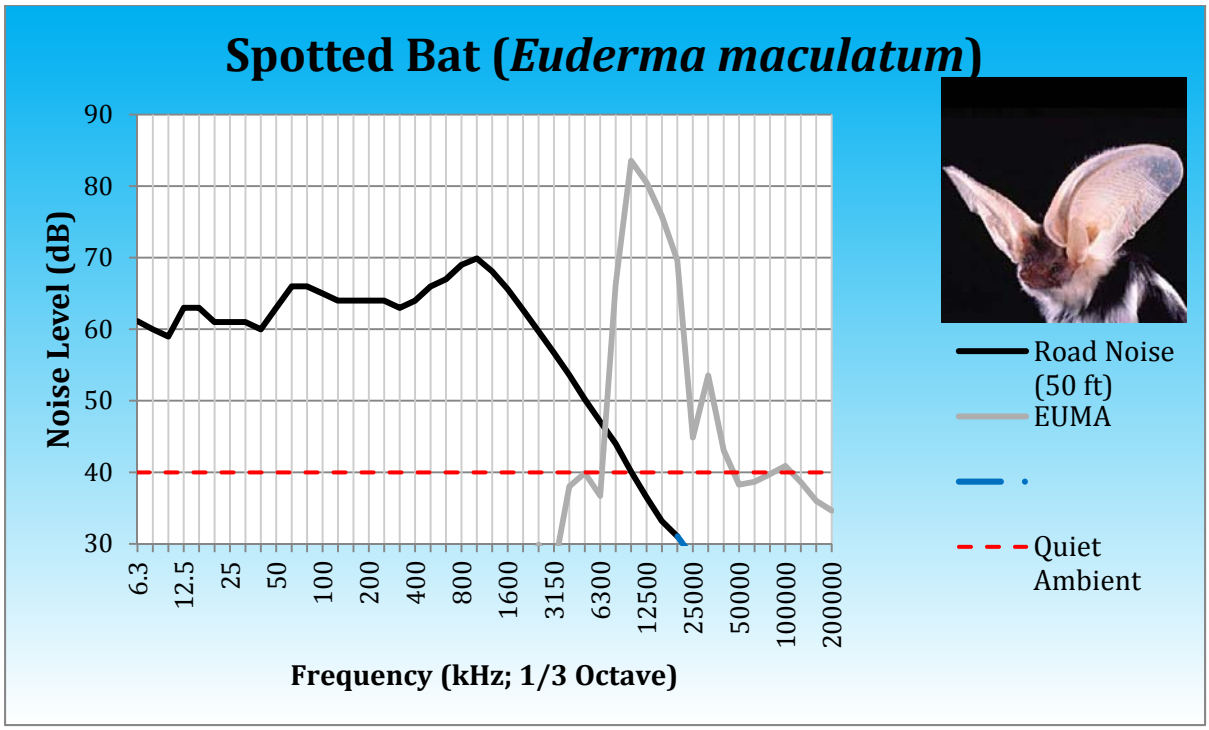

Figure 45. Spectra of Spotted Bat Echolocation Call and Traffic Noise

Photo ©Merlin D. Tuttle, Merlin Tuttle Bat Conservation (http://www.merlintuttle.com/).

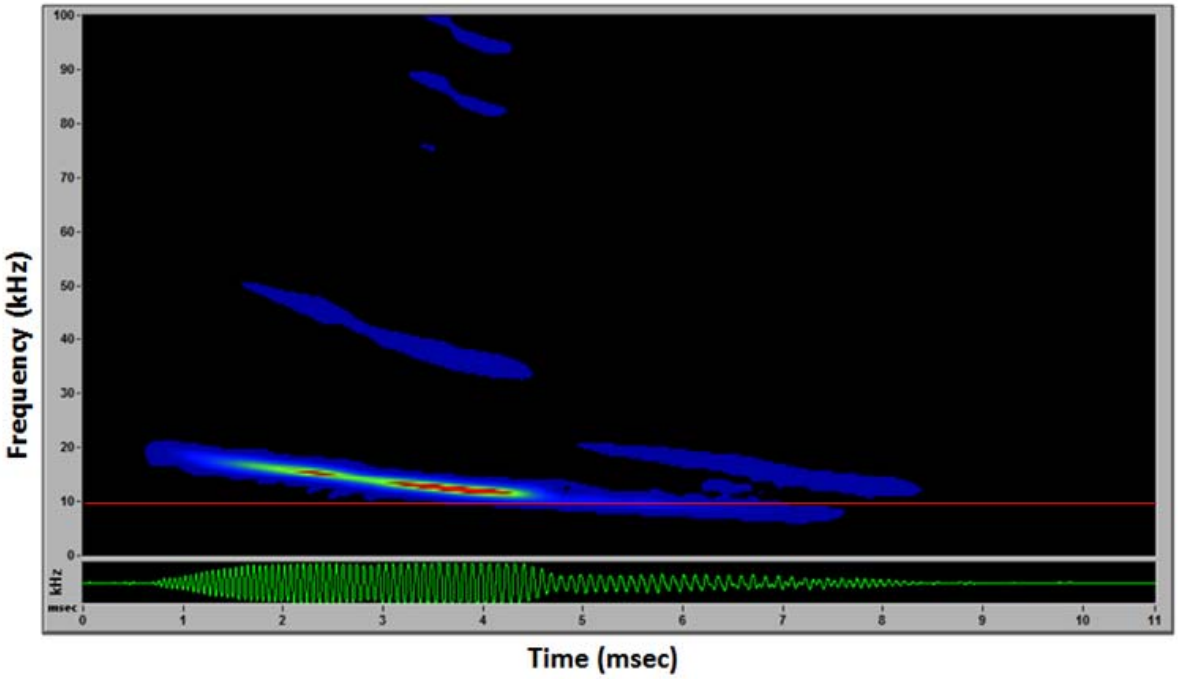

Figure 46. Low Frequency Echolocation Call of Spotted Bat (*Euderma maculatum*)

Red line provide 10 kHz reference point. (Source: Call sonogram from Sonobat 3.2.2.)

In a follow-up study, Siemers and Schaub (2011) exposed captive foraging bats to playbacks of different types of road noise (continuous and transient) and different amplitudes simulating noise levels with increasing distances from a highway (7.5–50 m). They found that foraging efficiency in the bats decreased proportionally with increasing proximity to the simulated highway. Search times increased by a factor of five in trials simulating noise conditions closest to the highway. The study authors estimated that effect of the highway noise on foraging efficiency was equivalent to a 25-fold decrease in available foraging area for the bats.

However, Siemers and Schaub (2011) also determined that even close to the highway, the bats were still able to detect and localize prey by their rustling movement sounds in about 50% of the trials. These results show that bats may be impeded, but not prevented, from foraging effectively next to highways. The studies suggest that the bats' acute and highly directional sense of hearing allow them to differentiate and localize the high frequency components of the click-like sounds of the prey from the lower frequency road noise.

Vocal Communication

Section 4, *Bat Echolocation and Communication*, describes the various low frequency communication calls used by bats. Some of those calls, at least in part, overlap acoustically with the spectral profile of highway noise and can potentially be subject to masking. Between Davis and Sacramento, California, there is a 3-mile long causeway along Highway I-80 (Yolo Causeway) that supports over 250,000 Brazilian free-tailed bats. They roost in gaps between concrete girders under the causeway (Figure 47). When the bats are within the crevices, they are within inches of the highway road surface above and can potentially experience fairly high levels of traffic joint "slap" noise created by cars and trucks driving over the expansion joints into the roosts. However, there appears to be substantial shielding from airborne road noise under the causeway (Figure 3) and in the crevices

To assess whether road noise masking does occur during communication within the roost, a series of recordings were made of the all sounds in the roost during normal mid-day traffic conditions. A Pettersson M500 microphone was attached to an extension pole and positioned at gap openings at several locations under the road (Figure 47). All recordings were made onto a Dell Venu Pro 8 laptop using Pettersson BatMicRecorder. Figure 48 shows a series of typical low frequency communication calls (in compressed mode—i.e. the intervals between calls have been removed). Figure 49 shows a series of calls in real time. The frequencies with maximum energy (red) of all of these calls fall within the typical frequency range of the highway noise.

Figure 50 shows bat calls recorded during traffic with the Pettersson M500 microphone at the bottom of the girder gaps (Figure 47). The overlap of the highway noise with the bat calls is evident.

Figure 47. Roost Sites used by Brazilian Free-Tailed Bats (*Tadarida brasiliensis*) under the Davis–Sacramento Causeway

(Arrows show urine deposits marking bat concentrations.)

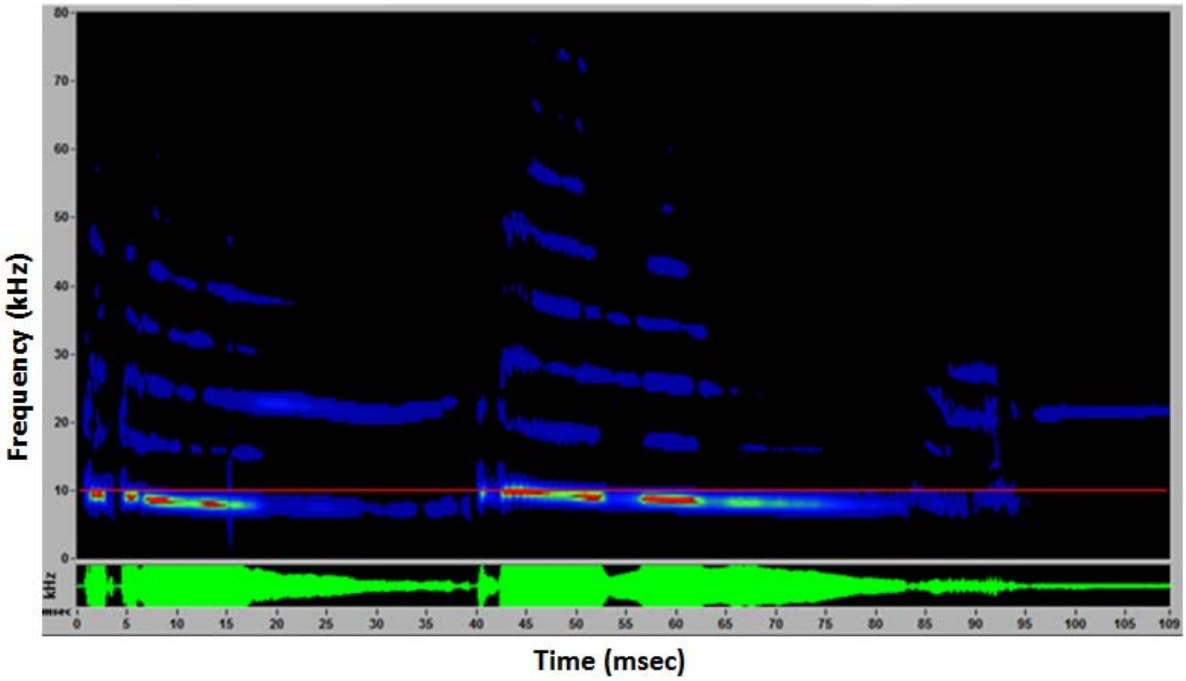

Figure 48. Social Calls of Brazilian Free-Tailed Bats Located in Roosts Shown in Figure 47

(Calls are shown in compressed mode where the intervals between calls have been removed. Red line is at 10 kHz for reference.)

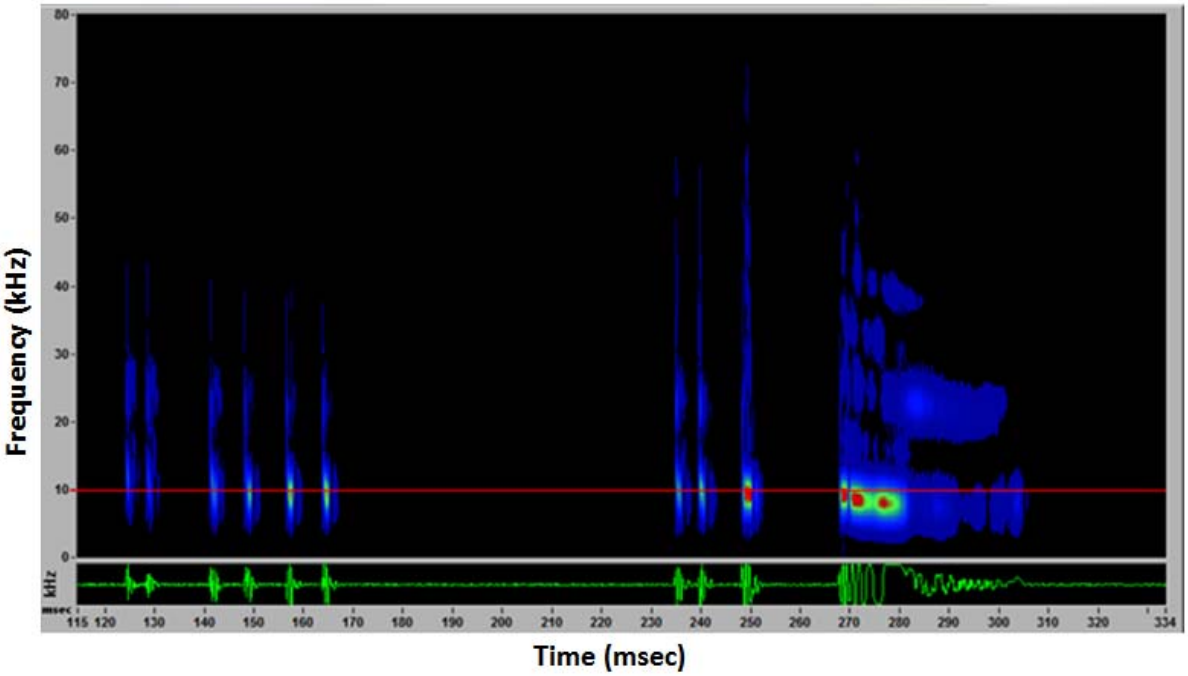

Figure 49. Real-Time Recordings of Brazilian Free-Tailed Bat (*Tadarida brasiliensis*) Calls in Causeway Roosts without Traffic Noise

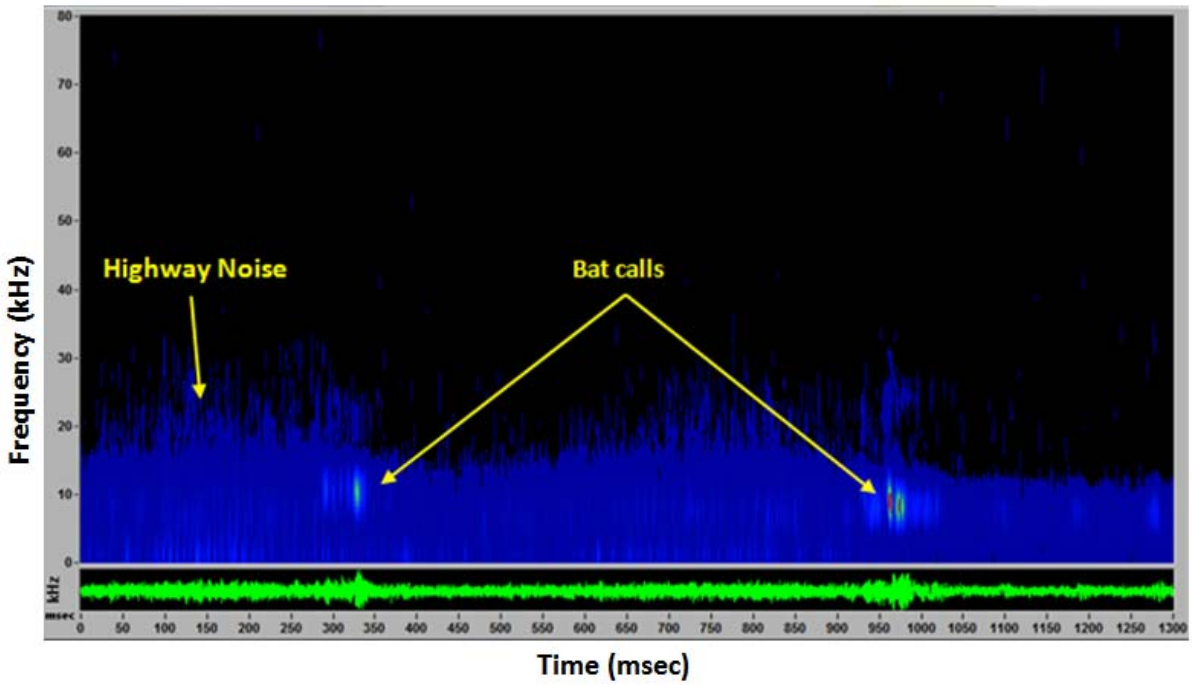

Figure 50. Real-time Recordings of Brazilian Free-Tailed Bat (*Tadarida brasiliensis*) Calls in I-80 Causeway Roosts with Traffic Noise Showing Acoustic Overlap with the Calls.

The effect(s) of this apparent masking on bat communication in the causeway roost is unknown. Clearly the large colony size shows that the bats are well adapted to the causeway environment. It is evident that while there are periods when road noise can potentially mask bat signals, there are also periods when clear communication is possible. Even during periods of apparent masking, it is likely that the bats can readily detect most calls through differentiation of recognizable signal profiles (many with harmonics above road noise) (e.g., Figure 47). Additionally, within the small confines of the roost crevices, communication is usually over very short distances. Many of these presumptive communication calls were low frequency and of long duration such that attenuation over those distances would be minimal. Figures 19, 45 and 48 also show that the overlap of traffic noise with bat hearing occurs marginally at the spectral regions of declining energy in the traffic noise. This effect may be accommodated by a number of behavioral and physiological adaptations, described below.

Behavioral and Physiological Effects

The different sections of this report and the references cited herein readily show that bats are attuned to their acoustic environment. Through constant acoustic scene analysis (Moss and Surlykke 2010), bats continually monitor their environment and develop, through experience and learning, dynamic acoustic pictures of what is normal, different, or possibly threatening. Generally, potentially threatening conditions or situations require constant vigilance and monitoring of different threat levels to prepare for appropriate responses.

At perceived high levels of potential threat, bats may abandon their roosts (Pearson et al 1952; Kunz 1982; Sherwin et al. 2000), be it a day roost or night roost, and move to locations less threatening. These threats may be associated with close proximity to human activity, chronic high noise, and

sudden and repeated high level impulse noise that is not part of the common background noise. The consequences of this action can be severe if young are abandoned at a maternity roost, predation exposure increases, or there is loss of access to important nearby foraging or alternate roosting areas. At lower levels of perceived threat, the bats may stay in place but invest moderate to high amounts of time and energy in vigilance behavior—time and energy often redirected from other critical behaviors such as care of young, foraging, rest, and proper thermoregulation (Schaub et al. 2008; Barber et al. 2010). This vigilance is also normally accompanied by varying levels of stress that can potentially result in dysfunctional behaviors and/or changes in important physiological and hormonal conditions that may directly and indirectly affect the survival and well-being of individuals and colonies.

Bat Avoidance and Minimization of Loud Noise Effects

Bats are well adapted morphologically, physiologically, and behaviorally to avoid acoustic trauma. Because they are often aurally confronted with exceptionally loud sounds from their own and other bats' echolocation signals (e.g., 110 dB) they have evolved very fast protective mechanisms to prevent sensory overload and damage to the auditory system (Wever and Vernon 1961; Henson 1965; Braun 1994). These mechanisms include those described below.

- **Behavioral avoidance.** Bats can immediately leave an area when disturbance levels rise beyond their comfort level or move deeper into roost crevices where noise exposure is less. Generally, it is possible that before exceptionally loud equipment (e.g., pile driver) is used for a project, the noise from staging operations can potentially raise the disturbance level high enough that the bats would leave the area. But it is important to note that this graded avoidance behavior has not yet been documented. Blasting is another very loud and sudden noise-generating activity and it may be more likely to impact bats, especially if drilling noise is moderate and at a distance from active roosts. The shock wave from the blasts could arrive suddenly at a time the bats would be physically unprepared to actively block such impacts. Sudden jackhammering immediately above or near a bridge roost could have similar consequences.
- **Changing the shape and orientation of the pinnae.** Wever and Vernon (1961) note that a forward folding of the pinnae tip in the little brown bat can result in a 20 dB attenuation in cochlear response. Realignment of the pinnae out of alignment with intense incoming sound beams can also help to avert noise overexposure. Many large eared bats, such as Townsend's big-eared bat and spotted bat, frequently curl their ears while roosting. This mechanism is adaptive for conserving heat but also is effective in reducing excessive noise exposure.
- **Closing the cartilaginous fold in the outer ear canal.** This mechanism allows direct physical blocking of loud noise and can result in a 20 to 40 dB attenuation (Wever and Vernon 1961).
- **The tympanic reflex.** The tympanic reflex is the contraction of muscles in the inner ear, primarily the stapedius, which disconnect the three middle ear bones in response to loud noise. This mechanism reduces the transmission of sound along the bones and can result in an attenuation of up to 23 dB in the little brown bat (Wever and Vernon 1961). Henson (1965) found that in the Brazilian free-tailed bat this mechanism resulted in an attenuation of 22 dB from 4 to 10 ms prior to vocalization of orientation pulses by the bat and up to 30 ms before communication calls. Between the single orientation pulses the muscle relaxed fast enough to permit unattenuated reception of pulse echoes up to a pulse rate of 80/s just before the bat

reaches its target. Up to that point, the attenuation is continuous. Braun (1994) interpreted Henson's results to mean the stapedius is under central nervous system control and is linked to the neural interface between vocalization and hearing.

- **Resonance absorption.** Braun (1994) presents a model of cochlear function in which he asserts that the basilar membrane is a tuned vibration absorber that can reduce excessive kinetic energy in perilymph waves produce by loud noise. This mechanism would effectively protect the delicate sensory hair cells in the Organ of Corti and help prevent damage to the auditory system.

Notably, a recent study on the effects of noise exposure on echolocation behavior in flying big brown bats (Hom et al. 2015) shows that noise exposure (20 - 100 kHz, 116 db SPL for 1 hour) had little or no influence on echolocation behavior in individual bats. The mechanisms for this acoustic accommodation are not specified, but potentially include some or all of the above physiological responses during exposure.

Within limits, as has been demonstrated in other vertebrate taxa, bats may be able to acoustically compensate for noise by: (1) changing the amplitude of their calls (Lopez et al. 1988, Brumm et al. 2004), (2) shifting their signal frequencies out of the noise band (Lopez et al. 1988; Slabbekoorn and Peet 2003, Gillam and McCracken 2007), (3) changing the duration of the calls (Leonard and Horn 2005, Penna et al. 2005) , or (4) waiting to signal until noise is reduced (Ulanovsky et al. 2004, Gillam et al 2007, Fuller et al. 2007). Similarly, receivers have specific strategies to improve detection and recognition of sounds in noise by co-modulation masking release, precise frequency tuning, and temporal and spatial release from masking (Hubner and Wierebe 2003; Warnecke et al. 2012, Sümer et al. 2009; Siemers and Schaub 2010).

Synthesis and Summary

The principal potential effects of highway noise on bats are acute acoustic trauma, disturbance, and displacement from important food and shelter resources and signal masking. Acoustic trauma is potentially a very serious effect, should it occur, because bats are fully dependent on echolocation and passive listening for both immediate and long-term survival. They do not have the luxury of time for recovery from almost any level of acoustic damage. However, because of the multiple behavioral and physiological defensive mechanisms they have evolved to prevent noise overexposure (Section 3), most bats are likely effectively shielded from most trauma events that would result from highway noise.

Disturbance is likely to be the most pervasive and significant effect associated with highway projects. Bats are acutely sensitive to changes in their sound environment and can respond to even quiet noise if it is foreign to them and stimulates stress. Potential adverse effects include roost abandonment, avoidance of foraging areas, dysfunctional allocation of time and energy resources to vigilance behaviors and finding alternate roosts, and degradation of physiological condition and social order. Some level of tolerance and habituation does occur in some species (e.g. e.g., Brazilian free-tailed bats), that by choice colonize bridges and other highway structures. It is unknown if anthropogenic roost availability differentially favors one species over another that could result in shifts in natural community diversity patterns.

Signal masking can potentially be significant if highway noise substantially interferes with information transfer during echolocation, communication, or passive listening. Because the spectrum of highway noise does not appreciably overlap with most bat echolocation calls or their

hearing of them, highway noise does not likely affect echolocation in most species of bats is likely not affected by highway noise for most species. Some level of masking of low frequency communication signals likely occurs within bridge roosts due to the proximity of the bats to the highways. However, it is unknown to what extent such masking interferes with communication or how effectively bats use acoustic adaptations to avoid and minimize information loss. These adaptations include elevated signal amplitude (Lombard effect), frequency shifts (both within and between signals), increased signal length and redundancy, temporal spacing of calls between noise events, and spatial maneuvering to optimize signal transmission. If sufficient avoidance/compensatory conditions cannot be met, some bats may suffer social consequences of miscommunication including, but not limited to disconnect communication between parent and offspring, degradation of mate choice enticements, miscues on aggressive intent or alarm signals, and misaligned communication during social events such as emergence, and mating. When acoustic conditions erode to the point where critical communication is ineffective, the bats generally will leave.

Finally, masking of important environmental sounds, particularly those of ground dwelling insects targeted by gleaning bat species can potentially occur in close proximity to highways. However, it is yet to be definitely determined that noise, specifically noise masking, is the principal causal factor for highway aversion by bats. Schaub and Siemers (2008) nicely show that bats avoid noisy environments while when foraging under simulated highway noise conditions. But the results also show that bats are more averse to the sounds of wind in the reeds than highway noise. While their results show up to 25% reduction in foraging efficiency in lab conditions, it is unknown what the actual effects would be in the field. Bats are generally wide-ranging in their search for food and adapt to locally available prey whether it be near the highway or in patches away from the influence of highway noise. In some locations the availability of insects within the highways may be higher than other regions of their foraging range, and species that forage optimally in open areas may benefit overall from the vegetation management programs along the highways.

The Significance of Bat Responses to Noise

Bats are highly evolved and specialized species. They are uniquely and precisely adapted to their nocturnal environment—morphologically, physiologically, and behaviorally. Creating imbalances in these adaptations through noise disturbance or trauma can potentially result in rapid and significant changes in individual and colony viability or more moderate disruptive shifts in habitat use patterns, species distribution, and community structure.

Bats occupy a wide range of habitats with specific limitations defined by their physical and thermal properties. These include the many surrogate crevices and thermal refuges in bridges (Erickson et al. 2003) and other highway structures. Displacement from these sites, whether temporary or long-term, may result in significant physiological and biological costs (e.g., exposure to predation) if similar resources are not available nearby. In terms of energy expenditure, bats operate on the edge of optimality. Foraging by flight and homeostatic maintenance of thermal balance in small bodies at night is energetically expensive. Redirecting limited energy reserves to finding new roosts, meeting higher thermoregulatory expenses in suboptimal roosts, and increased vigilance behaviors comes with costs to their ability to grow, maintain, and reproduce. A significant immediate or protracted negative balance in their energy reserves due to noise disturbance may jeopardize survival and reproductive success of both individuals and colonies.

Acoustic trauma can potentially have immediate severe consequences if it occurs. Bats have evolved highly specialized auditory sensory systems to maximize their ability to detect, locate, track, and capture aerial prey. The behavioral, morphological, and physiological mechanisms that have evolved to achieve this end dramatically increase their hearing sensitivity to all sounds, particularly the low amplitude echoes of their echolocation calls. But these specializations also expose the bats to noise shock and acoustic damage from loud noise. However, to avoid this they also have coevolved very effective compensatory protective measures to prevent undue noise over exposure, specifically from their own very loud echolocation calls. While these mechanisms are very effective in achieving the needed protection from auto-exposure, it is unknown whether these mechanisms also can prevent over exposure from sudden, unexpected anthropogenic noise shocks (e.g., blasting, pile driving). While it seems likely bats have the capacity to do so (e.g. Henson (1965), found Brazilian free-tailed bats could initiate the tympanic reflex very quickly (4-10 milliseconds) before giving echolocating), additional studies are needed to determine this and to identify the mechanisms involved.

Section 7: Guidelines for Project Noise Assessment and Management

Several recent documents (Erickson et al. 2003; Johnston et al. 2004) provide excellent guidance on the general needs and working protocols for the avoidance, minimization, and mitigation of highway project impacts on bats in California. This section presents applicable information from these reports and other relevant publications, with focus on effective strategies for avoiding, minimizing, and mitigating potential construction and traffic noise impacts on bats. These strategic measures include those listed below.

- Define the project.
- Determine if bats are present.
- Conduct a construction and traffic noise assessment.
- Evaluate the level and nature of potential noise effects.
- Identify and implement appropriate avoidance, minimization and mitigation measures.

Project Definition

To define the project, identify and characterize the following elements of the project.

- The spatial footprint of the project and surrounding area that could potentially be within the project noise envelope. This area should include all areas utilized by the project, including ingress and egress routes and equipment staging areas, etc.
- The project phases, duration, and scheduling (day, night, month[s]).
- The equipment that will be used in each phase and the expected frequency of use.

Bat Presence Assessment

Have a qualified (CDFW permitted) bat biologist conduct a site assessment to determine if bats, and which species, are likely to occur within the project area and in offsite areas that might be affected by project noise. Review the Western Bat Working Group bat distribution maps to determine what species are likely to occur in the area. Check the California Natural Diversity Database for reported records of bats and contact CDFW regional biologists and other knowledgeable bat biologist (e.g. Western Bat Working Group) for any additional occurrence information. Conduct visual and acoustic surveys where necessary to document species presence and site use patterns, including roost sites. Bat presence in a project area may vary seasonally and annually. Therefore, depending on the nature of the site surveys may need to be conducted during the spring, summer, fall, and winter and for more than one year to fully assess the use of the site by bats. Surveys should be conducted in a manner to detect the presence of hibernating or torpid bats, reproductive colonies and migratory stop-over roosts. Multiple nights of surveys may be necessary to detect all species. Multiple types of surveys may also be necessary to determine species

use of the site, including mist netting, exit surveys, and both active and passive acoustic surveys. Areas directly and indirectly impacted by the project should be surveyed.

Site and Project Noise Assessment:

Due to the technical requirements for estimating background and project noise levels it is important that environmental planners and biologists coordinate with District noise engineering specialists when conducting highway/project noise assessments and making the noise calculations presented in Section 2. The following details the main steps required for completing the site and project noise assessments and determining appropriate avoidance, minimization and mitigation measures.

Baseline Site Noise Assessment

1. **Estimate the background noise level.** Based on known noise levels for environmental settings similar to the project site (e.g., Tables 2 and 3), estimate the background noise level for preconstruction conditions.
2. **Estimate the normal operation traffic noise level**. Based on the existing speed limits and traffic volume at the project site, estimate the current background traffic noise level. Based on the expected reduced speed limits (or lane closures) during construction, calculate the project period background traffic noise level. Develop a timeline of estimated normal operation traffic noise levels for each phase of the project.
3. **Determine if the project area is a hard or soft site**. Hard sites are those with open, bare soil or rock surfaces with very little or no vegetation. Soft sites are those with notable vegetation ground cover such as grass, meadows and forests. Construction noise traveling over a hard site attenuates at approximately 6 dBA for each doubling of distance. Traffic noise traveling over the same site attenuates at approximately 3 dBA per doubling of distance. If the noise travels through a soft site these values are reduced further by 1.5 dBA, giving standard attenuation rates of 7.5 dBA and 4.5 dBA respectively for construction and traffic noise sources.

Project Noise Assessment

1. **Estimate the construction noise level for the project**. Based on known noise levels and use projections for each type of equipment (e.g., Table 5), estimate the mean and maximum hourly noise levels for each project phase. Determine if any impact equipment will be used and determine the maximum impulse noise output for each type being used.
2. **Determine whether the noise is a point source or linear source.** All construction noise at most project sites is generally considered a point source with a 7.5 dBA per doubling distance attenuation rate. All traffic noise from highways is considered a line source which will attenuate at 4.5 dBA per doubling distance. Some projects may have several widely separated noise sources in which case each should be considered a separate point source. Also if two or more highways pass through the project area each should be considered a separate linear noise sources (e.g. convergence location of merging highways).
3. **Determine project noise extent distances using the equations in Section 2, *The Sound Environment of Bats*, or develop an attenuation table to estimate the distances**. Dooling and Popper (2015) suggest that the attenuation distance for project noise to 60 dBA is a

reasonable starting point for estimating the effects distance for communication in birds. This level would likely result in underestimates of effect distance for highway noise impacts on passive listening in bats but would likely overestimate the effect distance for roost displacement and acoustic trauma effects. In most situations, the distance at which project noise attenuates to background noise levels will be the minimum noise level criterion for assessing potential adverse effects in bats. This value may be reduced if foraging areas for passive listening bats do not occur in the project area or the structural nature of the roost significantly augments project noise attenuation at the sites. Each project will require site-specific evaluations to determine the most applicable effects distance.

Avoidance, Minimization and Mitigation Assessment

1. **Evaluate the level and nature of potential noise effects on bats at the project site.** Bats may or may not be responsive to project noise depending on the amplitude and spectra of the noise. Determine the spectral profiles of all noise sources and determine whether the expected noise can be heard by bats or overlap with bat acoustic activities. Evaluate the potential for adverse effects, including acoustic trauma, disturbance, displacement from important food and shelter resources, and acoustic masking of bat signals or important environmental sounds, including ground prey sounds. The minimal baseline noise level for evaluating potential effects, particularly disturbance at bat roosts, is the existing background noise level. It is assumed that bats using the project area are adapted to existing conditions, to the extent possible. Project-related effects will be associated with noise conditions that exceed those levels whether they be cumulative or independent. Also, when evaluating noise impacts on bats at the project level, consider the project's schedule and timing and whether it will coincide with any portion of the critical exposure periods or influence a bat's effect space (see Section 5, *Noise Exposure in Bats*).
2. **Based on site baseline and project noise levels and estimated potential effects of the noise on bats using the project site, determine applicable avoidance, minimization and mitigation measures**. Johnston et al. (2004) present general mitigation strategies for avoiding disturbance to bat roosts, but do not directly consider noise effects. This section focuses specifically on avoidance, minimization and mitigation opportunities for offsetting potential highway project noise effects. Detailed information on the technical aspects of traffic and construction noise analysis and mitigation is available in the *Technical Noise Supplement to the Traffic Noise Analysis Protocol* (California Department of Transportation 2013) and *Traffic Noise Analysis Protocol* (California Department of Transportation 2011).

Avoidance

Avoidance of noise effects can be completely or partially achieved through either scheduling project activities so that they do not impact active roosts or implementing humane exclusion measures to keep bats away from noisy sites. Avoidance should always be considered first with any project, when feasible. The best avoidance measure is to work when the bats are not present. In many locations where bats roost in bridges, they do so only seasonally and will leave the roost sites during the fall and winter. This behavior provides an opportunity to schedule work while they are absent. However, in areas like the Central Valley and near the coast, where temperatures are mild, bats may overwinter in bridge roosts, going into torpor during cold periods and arousing to forage during warm spells. In these situations, consideration must be given to noise disturbance of torpid and active bats (e.g., Luo et al. 2014) and effective avoidance by project scheduling may not be possible.

The Bat Presence Assessment, described above, should be conducted in a manner to detect the presence of hibernating or torpid bats, reproductive colonies and migratory stop-over roosts.

When bats cannot be avoided during a project, they will need to be excluded from the site when possible. Exclusion of bats from roost sites should only be done after August 15 and prior to April 15 to avoid impacts on maternity colonies. Exclusion may be done by using physical exclusion methods (Erickson et al. 2003), acoustic exclusion (Szewczak 2011), or a combination of both. Physical exclusion methods include temporarily filling the small openings and crevices in structures with expanding foam or other materials or covering sections of the structures with plywood or screens (e.g., netting, plastic). However, physically complex structures such as those found in old wooden bridges and projects where access to the structure is difficult, physical exclusion can be problematic, costly, and unlikely to succeed. An alternate, new method is biotic exclusion using acoustic deterrents (Arnett et al. 2010; Arnett et al. 2011; Arnet et al. 2013; Szewczak 2011).

It is also important to make sure that materials used during various phases of the project don't create suitable roosting habitat and attract bats. For example, piles of boards or debris creating crevices suitable for roosting.

Biotic exclusion has been experimentally tested at open ponds (Szewczak and Arnett 2008), wind farms (Szewczak and Arnett 2006; Arnett et al. 2010; Arnett et al. 2011, 2013) and at bridges (Szewczak 2011) with varying levels of success. This method involves playback of loud ultrasound to acoustically deter bats from approaching former roost sites. Bats notably respond to these ultrasound playbacks by avoiding the noise envelope radiating out from the playback speaker. However, because high frequency ultrasound attenuates rapidly, the effective broadcast distance is limited to 5–15 m, depending on the power output of the signal generator. While notable avoidance behaviors were observed in the test studies (Szewczak and Arnett 2008; Arnett et al. 2010, 2011; Szewczak 2011) the method was partially successful in excluding bats from bridges Szewczak 2011). In this study, bats were apparently deterred from establishing maternity colonies on bridges in the spring when these colonies typically form. However, midsummer surveys revealed bats had established a maternity colony at one of the bridges, surprisingly, comprised of females with pups. Continued broadcasting or ultrasound, augmented with the low frequency social calls of hoary bats (*Lasiurus cinereus*), a predatory species, was followed by gradual decrease in colony size and complete abandonment of the site in late summer.

The reasons for the limited success of this method are not fully clear. Bats are highly adept at moderating their acoustic environment, including the behavioral and physiological exclusion of loud ultrasonic sounds from other bats. The mechanisms they use to do this (see Section 3, *Bat Hearing*) may allow them to strategically exclude, or reduce, the playback ultrasounds, at least for brief periods they may be exposed while approaching the roost. This may be automatic, a reflex jamming avoidance response, or a learned acoustic avoidance behavior. The basilar membrane in the cochlea is innervated with efferent fibers from the bat's brain that can control the stiffness of the membrane that regulates its flexibility and sensitivity to acoustic stimuli. Braun (1994) has identified this feature as a defensive mechanism for absorbing excess energy from loud sounds. This could also be a mechanism by which chronic irritating sounds can be moderated and allow the bats to at least momentarily reduce and tolerate the playback sounds. If the bats are intimately familiar with the flight path to the roost, they possibly could gain access with brief, intense echolocation calling as they approach the entrance that exceeds the masking effect of the playback ultrasound. Once inside the roost, the acoustic shielding effect of the structure walls likely would reduce the deterrent sounds to tolerable levels. Additional studies are certainly needed to determine if this type of

habituation or avoidance behavior occurs in bats as it does in birds when responding to noxious sounds and predator call playbacks.

Minimization

Johnston et al. (2004) recommend a buffer distance of 100 feet between work activities and active roosts. For a project with a noise levels of 84 dBA (at 50 feet), the noise attenuation at 100 feet would only be to about 76 dBA (using Equation 2.2 , Section 2, *The Sound Environments of Bats*) which is still loud enough to exceed most background noise and be a source of potential disturbance for bats in an active roost. Greater avoidance distances (TBD based on project noise level) are recommended to allow noise to attenuate to approximately background levels to achieve optimal noise avoidance. These values should be adjusted for the reduction in effective noise based on the spectral profile of the prevailing noise (e.g., Figure 3). Measured dBA values at the project site are likely overestimates of the actual dBA for the noise within the spectral range of hearing of bats (usually >5kHz.

Noise minimization at project sites would require installation of some type of sound shielding in the vicinity of the bat roosts. There are a variety of systems commercially available (e.g., Quickwall http://www.modularwalls.com.au/quikwall, temporary event sound walls http://www.environmental-noise-control.com/noise_control_entertaiment.php) that can be used. In addition, innovative methods using hay bales or other sound absorbing materials that can be adaptively crafted to specific site conditions may be needed. When installing these structures, it is very important to maintain clear airspace access for the bats to and from the roost. In some cases, this may conflict with optimal placement of the sound barriers. Each project area will undoubtedly have unique features that will require some level of customization in building and installing these structures. Where possible, these should be designed by an acoustic sound engineer and monitored following installation to insure the sound reduction level objectives are being met.

Mitigation

Good mitigation measures for providing replacement habitat (e.g., artificial roosts) for bats are readily available (e.g., Erickson et al. 2003; Johnston et al. 2004). Many of these structures are designed to maintain optimal thermal conditions that are needed by the bats (Erickson et al. 2003). However, few, if any, consider the acoustic properties of these structures or the environment in which they are placed. Not all structures are appropriate for all bat species. The different species and their different acoustic and physical roosting requirements need to be fully considered. It is generally the case that the quieter the site, the better. When evaluating the design of the structures and their final placement information on the acoustics should be used to determine the best design and site location. Concrete structures are generally better for replacement roosts, both thermally and acoustically, compared with plywood. The orientation of the opening is also important, as is the required flight path the bats must take to access and leave the structure. Excess noise may deter use of some structures if they are placed too close to high or chronic noise sources.

Because each project generally will have unique site-specific features that influence the noise environment, the need for and nature of project mitigation should be determined on a project-by-project basis to ensure effective implementation.

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Section 8: Future Research

This section identifies and describes areas that could benefit from further studies in the future that could address key questions related to the emergent issues identified in the technical analysis. Such issues include noise effects thresholds and criteria, natural and evoked adaptations used by bats, the efficacy of current mitigation and conservation measures, important logistical needs necessary to improve our understanding of both bat sensory ecology, and how best to build/operate highway projects with minimal impacts on wildlife. Following are possible topics regarding the effects of highway noise on bats that would benefit from further research.

The regulatory environment for project noise control is largely cued to human hearing needs and conditions. Because bats are responsive to a much broader hearing range than humans, it is important to learn more about their sensitivities within the current domain of noise monitoring (i.e., < 20 kHz) to determine specific noise effects thresholds and criteria, if any, for different species. Potential masking of low frequency communication signals and some echolocation calls can potentially occur in this acoustic zone, but it is unknown if bats readily use compensatory mechanisms (e.g., frequency and amplitude shifts) to neutralize those effects. Also, it is unknown whether such adaptive behavior might be detrimental to some populations in establishing acoustic patterns not aligned with evolved optimal responses. For example, females may favor traditional call patterns and frequencies when selecting male breeding partners. Males using calls adjusted to accommodate noise may be less effective (e.g., lower transmission distance; different call patterns) in attracting females than males with traditional calls. This potential problem is referred to as an *evolutionary sink* (Francis and Barber 2013).

Alternately, the new adjusted calls may be highly adaptive in maintaining clear communication, albeit modified, for bats chronically exposed to noise. The bats in roosts under bridges and causeways are a good example. Over a period of 40 years, the Brazilian free-tailed bat population under the Yolo Causeway between Davis and Sacramento, California has grown from approximately 70,000 bats to over 250,000. Obviously, the causeway environment, even with increasing highway noise over four decades, has not adversely affected this population. Research is needed on how these and other bat populations in such noisy environments adapt acoustically to maintain clear communication and how they differ from populations of the same species in quiet environments. Information acquired on what adaptations have been made and whether they are causally related to highway noise levels will be important in assessing the long-term effects (negative or positive) on affected populations. Also, understanding the acoustic dynamics of various highway structures can provide better information on how to design and locate artificial roosts when needed to optimize the bat's sound environment.

Different bat species are known to occupy bridges and other highway structures. Preliminary information on what species occur in different bridge types is provided by Erickson et al. (2003). Further information and analysis is needed to assess how these structures, and the associated highway noise might be affecting bat community structure if they are differentially beneficial to different species. Additional studies looking at bat use patterns of highway structures under different traffic noise levels could provide much needed information on what impact different levels of effect highway noise may be having on different species and whether there is a long-term benefit to some species and possible adverse effect to others.

The question of whether highway noise directly masks passive listening in gleaning bats (e.g., pallid bat, California leaf-nosed bat) needs to be further examined. Alternate explanations with regard to possible effects of road-side air turbulence on transmission quality of environmental sound and echolocation need to be examined. Also, how foreign sounds and large numbers of passing vehicles actually affect bats possibly more than loud noise requires more research. Further, whether acoustic noise zones exist -in the space above highways due to differential vertical versus horizontal sound attenuation rates that might affect bats willingness to cross highways needs to be investigated to determine if movement corridors (e.g., commute routes, migration corridors) are being blocked.

The question of whether bats are naturally adapted to withstand loud acoustic shock from some construction projects without permanent or temporary hearing damage is critical to determining specific effects thresholds and proper avoidance protocols. While current research indicates most bats are able to behaviorally and physiologically manage the loud calls of close conspecifics or other bats, it is not known whether they also employ those mechanisms to effectively respond to sudden, unexpected noise that would result from blasting, pile driving, or other high intensity impulsive sound activities. Controlled lab studies on this question would be very important in providing a better understanding of this potentially very significant effect.

Finally, additional studies on the use of acoustic deterrents are warranted, particularly in concert with traditional physical exclusion methods. At sites where netting or other screening can be applied to some portions of a structure but not others, installation of ultrasonic acoustic devices in the uncovered areas could possibly augment the process sufficiently to result in complete exclusion.

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Appendix A: Glossary

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Appendix A: Glossary

Absorption—The process by which sound energy is converted into heat in the water or air.

Acoustic clutter—Echoes of unwanted targets such as twigs, foliage, or the ground, referred to as *clutter echoes,* or simply *clutter*.

Acoustic fovea—In constant frequency (CF) bats, the section of the basilar membrane within the cochlea that responds to the frequency of returning echoes is much larger than the region of response for any other frequency. This area of high sensitivity to a specific, narrow range of frequency is known as an *acoustic fovea*.

Acoustic glint—When a echolocation signal hits a fluttering insect and the insect's wings are perpendicular to the impinging sound wave, a short and very prominent amplitude peak, an acoustic *glint,* is defined in the echo. This glint, which can be up to 20–30 dB stronger than an echo from the body of the insect, reveals the fluttering insect target and increases a bat's probability of detecting it.

Acoustic space—The acoustic environment in which sound is heard.

Acoustic trauma—An injury to the inner ear that is often caused by exposure to a high decibel (dB) noise.

Amplitude—The strength or magnitude of the pressure of a sound wave.

Anthropogenic—Changes in nature caused or influenced by humans.

Acoustic attenuation—The reduction in sound intensity with distance as it propagates through air or other media. **Audiogram—**A measure of hearing sensitivity, or a threshold of hearing, at each frequency in the hearing range of an animal.

Audible (frequency) spectrum—The frequency range normally associated with human hearing, usually between 16 kHz and 20 kHz.

Auditory masking—The acoustic process wherein the perception of one sound is affected by the presence of another sound. Auditory masking in the frequency domain is known as *simultaneous masking*, *frequency masking*, or *spectral masking*. Auditory masking in the time domain is known as *temporal masking* or *non-simultaneous* masking

A-weighted sound level (dBA)—The frequency weighted sound pressure level (SPL) approximating the frequency response of the human ear. It is the sound level, in dB, measured with a sound level meter having the metering characteristics and a frequency weighting specified in the American National Standards Institute Specification for Sound Level Meters. The A-weighting de-emphasizes lower frequency sound sounds below 1000 Hz (1 kHz) and higher frequency sounds above 4 kHz. It emphasizes sounds between 1 kHz and 4 kHz. A-weighting is the most generally used measure for traffic and environmental noise throughout the world.

Auditory brainstem response (ABR)—A physiological method to determine hearing bandwidth and sensitivity of animals without behavioral training. Electrodes (wires) are placed on the head of the animal just outside of the base of the brain (brainstem) to record electrical signals emitted by the brain in response to sounds that are detected by the ear. These signals are averaged and used to

determine if the animal has detected the sound. It is possible to determine auditory thresholds for fishes using this method.

Auditory streaming—In many acoustic environments segregated sound elements can be linked together in time by the listener, producing an auditory stream. This ability can be demonstrated by the so-called cocktail party effect. Up to a point, at a gathering with a number of people speaking at the same time or with background sounds such as moderately loud music, one can follow a particular voice even though other voices and background sounds are present. The ear acoustically segregates this voice from other sounds and the mind aligns these segregated sounds into a distinctive auditory stream. This skill is highly developed in bats that need to identify and segregate echoes from prey from echoes returning from vegetation or other objects.

Acoustic scene analysis (ASA)—A model of auditory perception that proposes the auditory system organizes sound into perceptually meaningful elements

Auditory threshold—The lowest detectable sound, usually at a specific frequency. Most often, thresholds are the level at which a signal is detected some percent of the time—often 50% or 70%. Absolute thresholds are the lowest level of signal that is detectable when there is no background (masking) noise.

Azimuth—the angle of horizontal deviation, measured clockwise, of a bearing from a standard direction, as from north or south.

Background noise—The composite of sounds from all sources near and far at a given place and time.

Bandwidth—The range of frequencies over which a sound is produced or received.

Basilar membrane—The stiff structural element within the cochlea of the inner ear that separates two liquid-filled tubes that run along the coil of the cochlea, the scala media, and the scala tympani.

Binaural analysis—The acoustic comparison of signal inputs at both ears**.**

Broadband—Noise that covers a wide range of frequencies relative to which the ear is sensitive. In contrast, **narrowband** noise covers only a limited number of (contiguous) frequencies. In relation to bat or human hearing, for instance, a broadband noise might contain sound energy from 10 kHz to 70 kHz, whereas a narrowband noise may contain sound energy from 20 kHz to 25 kHz.

Characteristic Frequency (fc)—The frequency at which a given neuron responds to the smallest sound intensity.

Cochlea—A spiral-shaped cavity of the inner ear containing the nerve endings that transmit sound vibrations from the middle ear to the auditory nerve.

Constant frequency (CF)—A CF component of the echolocation call is often used by bats hunting for prey while flying in open, clutter-free environments. The success of the former strategy is due to two aspects of the CF call, both of which confer excellent prey-detection abilities. First, the greater working range of the call allows bats to detect targets present at great distances—a common situation in open environments. Second, the length of the call is also suited for targets at great distances; in this case, there is a decreased chance that the long call will overlap with the returning echo.

Critical ratio—The ratio of the intensity of a pure tone to the intensity per Hertz (Hz) of a signal or noise (i.e., the spectrum level) at a listener's threshold. For example, if a listener can just hear a 60 dB pure tone against a background of noise whose spectrum level is 40 dB, the listener's critical ratio is said to be 20 dB.

Decibel (dB)—A standard scale commonly used for reporting levels of sound. A difference of 10 dB corresponds to a factor of 10 in sound power.

dBA—A-weighted decibels - an expression of the relative loudness of sounds in air as perceived by the human ear. In the A-weighted system, the decibel values of sounds at low frequencies are reduced, compared with unweighted decibels, in which no correction is made for audio frequency. This correction is made because the human ear is less sensitive at low audio frequencies, especially below 1000 Hz, than at high audio frequencies.

Doppler Effect—The change in observed frequency of a sound wave caused by a time rate of change in the effective path length between sound source and receiver. If the path length rate of change causes the source and receiver to approach each other, the observed frequency shifts upward. If the source and receiver recede relative to each other, the frequency shifts downward. The frequency shift is called the *Doppler Shift*, and the unit is Hz.

Echolocation—Using reflected sound, usually ultrasonic, to locate objects.

Endolymph—The fluid contained in the membranous labyrinth of the inner ear.

Evoked potential—An electrical **potential** recorded from the nervous system of an animal following presentation of a stimulus.

Excess attenuation—Sound attenuation in addition to that caused by geometric spreading. This measure is usually used as a measure of attenuation due to ground effects and sometimes also the atmospheric effects.

Existing noise levels—Noise resulting from natural and mechanical sources and human activity present in a particular area.

Frequency modulation (FM)—A broadband signal that contains a downward sweep through a range of frequencies**.** FM calls are excellent for hunting prey while flying in close, cluttered environments because the broadband signal enable the bat to resolve their prey from large amounts of background noise. The short duration of the FM call is also good in close, cluttered environments because it enables the bat to emit many calls extremely rapidly without overlap, providing an almost continuous stream of information on the dynamic location of the prey.

Geometric spreading—Referring to the shape of sound pressure wave fronts and the manner in which they propagate. Geometric divergence or spreading is a generic term used for specific types of divergence, such as cylindrical or spherical divergence.

Hair cell stereocillia—The mechanosensing organelles of hair cells in the inner ear that respond to fluid motion induced by sound waves.

Hard Site—The reflective characteristics of the ground surface between a noise source and receiver. The term is most often used in traffic noise prediction models, where it is associated with a 3 dB per doubling of distance line source attenuation (i.e., due to geometric spreading only, without excess attenuation).

Harmonic—A component of a bat call having a frequency that is a whole-number multiple of the fundamental frequency of the wave. If a component has a frequency twice that of the fundamental frequency, it is called the *second harmonic*.

Hertz (Hz)—the unit of frequency defined as one cycle per second.

Kilohertz (kHz)—a unit of frequency equal to 1,000 hertz.

Larynx—The upper part of the trachea that contains the vocal cords.

Leq—The equivalent steady state sound level which in a stated period of time would contain the same acoustical energy as the time-varying sound level during the same period.

Lmax—The highest sound pressure level of a call in a specific time period.

Lombard effect—The involuntary tendency of species to increase their vocal effort when communicating amid loud noise to enhance the audibility of their voice.

Noise—Sound that is loud, unpleasant, unexpected, or otherwise undesirable.

Noise envelope—The physical space in which noise is heard.

Noise induced hearing loss (NIHL)—Hearing impairment resulting from prolonged exposure to high levels of noise.

Noise level—The noise power, usually relative to a reference level, usually measured in dB.

Octave—An octave is any frequency band where the highest included frequency is exactly two times the lowest included frequency.

One-third (1/3) octave band—A frequency band in which the interval between the upper and lower cut-off frequencies is one third of an octave. A one-third octave band is usually described by its center frequency; three contiguous octave bands make up one octave band

Passive listening—Acoustic monitoring of natural and anthropogenic sounds without the use of echolocation.

Perilymph—The extracellular fluid located within the cochlea (part of the inner ear) in two of its three compartments: the scala tympani and scala vestibuli.

Permanent threshold shift (PTS)—Permanent hearing loss caused by some kind of acoustic trauma (such as frequent exposures to noise of high intensities) or drug trauma. PTS results in irreversible damage to the sensory hair cells of the ear, and thus a permanent loss of hearing.

Pinna—The largely cartilaginous projecting portion of the external ear.

Point source—A noise source essentially concentrated at a single point, from which noise propagates outward in all directions.

Roost—A place where winged animals, especially birds or bats, rest or sleep.

Scala media—The middle division of three divisions of the spiral cavity of the cochlea in the inner ear. It is situated between the scala vestibuli and scala tympani, filled with endolymph, and houses the Organ of Corti.

Scala vestibule—The lymph-filled, spirally arranged canal in the bony canal of the cochlea that is separated from the scala media below by the vestibular membrane, connected with the oval window, and receives vibrations from the stapes.

Scala tympani—The lymph-filled spirally arranged canal in the bony canal of the cochlea that is separated from the scala media by the basilar membrane, communicates at its upper end with the scala vestibuli, and abuts at its lower end upon the membrane that separates the round window from the middle ear.

Sensory hair cells—The cells in the basilar papilla and other end organs of the ear that are responsible for converting (transducing) mechanical energy of sound waves to signals that can stimulate the nerve from the ear to the brain.

Soft Site—Types of ground (such as normal earth and most grounds with vegetation) that are absorptive to sound energy.

Sonar—echolocation in bats.

Sound—A vibratory disturbance created by a moving or vibrating source, in the pressure and density of a gaseous, liquid medium or in the elastic strain of a solid which is capable of being detected by hearing organs.

Sound Intensity—The average rate of sound energy transmitted in a specified direction through a unit area normal to this direction at a point considered.

Sound pressure level (SPL)—An expression of the sound pressure using the dB scale and the standard reference pressures 20 μPa for air and other gases.

Spectrum level—The intensity level of a sound within a 1 Hz band.

Spectrum (Spectra)—The range of frequency content within a signal.

Spectrogram—A graphical display of the contribution of each frequency component contained in a sound.

Stapedius—A small skeletal muscle in the middle ear of mammals that dampens the vibrations of the stapes by pulling on the neck of that bone. It prevents excess movement of the stapes, helping to control the amplitude of incident sound and protects the inner ear from high noise levels.

Stapes—The third bone of the three small sound transmitting bones in the middle ear. It is stirrup-shaped and rests on the oval window.

Tectorial membrane—One of two acellular gels in the cochlea of the inner ear, the other being the basilar membrane.

Temporary threshold shift (TTS)—Temporary loss of hearing resulting from of exposure to loud sound over time. The mechanisms underlying TTS are not well understood, but there may be some temporary damage to the sensory hair cells. The duration of TTS varies depending on the nature of the stimulus, but there is generally recovery of full hearing over time. Exposure to high levels of sound over relatively short time periods will cause the same amount of TTS as exposure to lower levels of sound over longer time periods.

Threshold—The lowest signal level an animal will detect in some statistically predetermined percent of presentations of a signal. Most often, the threshold is the level at which an animal will

indicate detection 50% of the time. Auditory thresholds are the lowest sound levels detected by an animal at the 50% level.

Ultrasonic—Sound frequencies above the human audible sound spectrum (in general higher than 20,000 Hz).

Appendix B: Bats in California

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Appendix B: Bats in California

Throughout the world there are approximately 1,240 species of bats—20% of all classified mammals. They are incredibly diverse in their morphology, diet, and ecology. About 70% are insectivores, feeding primarily on insects, spiders and other invertebrates. The remaining species feed variably on fruit (frugivores), pollen and nectar (nectivores), rodents, amphibians, reptiles, and other bats (carnivores), fish (picivores), and blood (sanguivores). Most, but not all bats use echolocation for flight orientation and foraging. Vision and smell are also used to find food and shelter. Bats are primarily nocturnal, emerging from their day roosts near sunset, but some are active earlier.

Twenty-five species of bats occur in California (Table B1), representing three taxonomic groups: Leaf-nosed bats (Phylostomatidae; 3 species), evening bats (Vespertilionidae; 18 species), and free-tailed bats (Molosidae; 4 species). Annotated accounts of each species are provided below summarizing their distribution, habitat preferences, diet and foraging strategies, bioacoustics, and conservation status. For those readers unfamiliar with bats, this appendix provides a primer on their biology, describing their general form and functions and highlighting important aspects of their ecology relevant to analyses and discussions presented in this report. All photos except cave myotis ©Merlin D. Tuttle, Merlin Tuttle Bat Conservation (http://www.merlintuttle.com/). Cave myotis photo by C. Wade (http://www.batsoftexas.com/species/myotis-velifer/).

Leaf-nosed bats are named for the distinctive leaf shaped appendage on their nose which is believed to be used to direct echolocation signals the bat sends through its nostrils. Primarily tropical, three species occur in California (Table 1); two are Species of Special Concern and one is federally listed as Endangered.

California leaf-nosed bat (*Macrotus californicus*) occurs in the Lower Sonoran life zone in the deserts of southern California. They roost primarily in abandoned mines, caves, and rock crevices, but are occasionally found on bridges. These bats are substrate insectivores, feeding on moths and immobile diurnal insects such as butterflies and katydids that it gleans off vegetation. While foraging, they uses vision to locate its prey in low light, but switches to multi-tonal high frequency (95–50 kHz [2nd harmonic]) FM echolocation calls in total darkness. The California leaf-nosed bat is a Species of Special Concern in California.

Table B1. Roost sites used by bats in California

Common Name	Scientific Name	Species Code[a]	Bridges	Buildings	Tree Foliage	Snags/Hollow Trees	Under Bark	Cliffs/Rock Crevices	Caves/ Mines	Status[b]
Phyllostomidae (leaf-nosed bats)										
California leaf-nosed bat	*Macrotus californicus*	MACA	3	X				X	X	SSC
Mexican long-tongued bat	*Choeronycteris mexicana*	CHME	4	X				X	X	SSC
Lesser long-nosed bat	*Leptonycteris yerbabuenae*	LEYE	4							E
Vespertilionidae (Evening bats)										
Pallid bat	*Antrozous pallidus*	ANPA	1	X		X		X	X	SSC
Townsend's big-eared bat	*Corynorhinus townsendii*	COTO	2	X					X	CT
Big brown bat	*Eptesicus fuscus*	EPFU	1	X		X	X	X	X	
Spotted bat	*Euderma maculatum*	EUMA	3	x				X	X	SSC
Silver-haired bat	*Lasionycteris noctivagans*	LANO	3	X		X	X	X	X	
Western red bat	*Lasiurus blossevillii*	LABL	5		X					SSC
Hoary bat	*Lasiurus cinereus*	LACI	5	X	X	X				
Western yellow bat	*Lasiurus xanthinus*	LAXA	5		X					SSC
California myotis	*Myotis californicus*	MYCA	2	X		X			X	
Western small-footed myotis	*Myotis ciliolabrum*	MYCI	2	X		X	X	X	X	
Western long-eared myotis	*Myotis evotis*	MYEV	2	X		X	X	X		
Little brown bat	*Myotis lucifugus*	MYLU	2	X		X		X	X	
Arizona myotis	*Myotis occultus*	MYOC	3							SSC
Fringed myotis	*Myotis thysanodes*	MYTH	2	X				X	X	
Cave myotis	*Myotis velifer*	MYVE	2						X	SSC
Long-legged myotis	*Myotis volans*	MYVO	2	X		X	X	X	X	
Yuma myotis	*Myotis yumanensis*	MYYU	1	X				X	X	
Canyon bat	*Parastrellus hesperus*	PAHE	3	X				X	X	
Molossidae (Free-tailed bats)										
Western mastiff bat	*Eumops perotis*	EUPE	4					X		
Pocketed free-tailed bat	*Nyctinomops femorosaccus*	NYFE	4					X		SSC
Big free-tailed bat	*Nyctinomops macrotis*	NYMA	3							SSC
Brazilian free-tailed bat	*Tadarida brasiliensis*	TABR	1	X				X	X	

[a] 1=commonly found on bridges; 2 = sometimes found; 3= rarely found; 4 = possibly use; 5 = do not use.
[b] SSC = California Species of Special Concern; CT = California Candidate species (Threatened); E = federally Endangered.

Mexican long-tongued bat (*Choeronycteris mexicana*) occurs in oak-conifer woodlands and semi desert grasslands of southern California. They roost in abandoned mines, caves, and rock crevices, but may occur on bridges in some locations. They are primarily nectivorous, feeding on pollen and nectar from agaves and night blooming cacti, but occasionally will take insects. They use high frequency (125–75 kHz [2nd harmonic]) multi-tonal FM/CF echolocation calls primarily for finding and maneuvering around their food plants. The Mexican long-tongued bat is a Species of Special Concern in California.

Lesser long-nosed bat (*Leptonycteris yerbabuenae*) inhabits of the Sonoran desert scrub, semi- desert grasslands and lower oak woodlands in Arizona and New Mexico; only two occurrences have been documented in California (Erickson et al. 2003). They roost in caves and mine tunnels, but like the Mexican long-tongued bat, could potentially occur on bridges. They are also nectivorous, feeding mainly on nectar from night blooming cacti, agave, and the century plant, but may also eat cactus fruits and pollen when the opportunity arises. Echolocation calls are largely indistinguishable from those of the Mexican long-tongued bat (Western Bat Working Group 2015). The lesser long-nosed bat is federally listed as Endangered but has been recorded in California only a few times and is considered a vagrant species in the state.

Vesper Bats (Family Vespertilionidae)

Pallid bat (*Antrozous pallidus*) commonly occurs foraging over open shrub-steppe grasslands, oak savannah grasslands, open Ponderosa pine forests, talus slopes, gravel roads, lava flows, fruit orchards, and vineyards throughout California (Western Bat Working Group 2015). They roost in rocky outcrops and cliffs, caves, mines, and trees (e.g., basal hollows of coast redwoods and giant sequoias, bole cavities of oaks, exfoliating Ponderosa pine and valley oak bark, deciduous trees in riparian areas, and fruit trees in orchards). They are also frequently found on bridges and other human-made structures (e.g., barns, porches, bat boxes, and human-occupied and vacant buildings). Roosts may include single bats, small groups (2–20 bats) or large colonies (100s of individuals).

Pallid bats are opportunistic insectivores/carnivores that glean prey from the ground and vegetation, but they also hawk insects on the wing. Prey species include antlions, beetles, centipedes, cicadas, crickets, grasshoppers, Jerusalem crickets, katydids, moths, praying mantis, scorpions, termites, and occasionally geckos, lizards, skinks, even small rodents. Pallid bats forage largely by passive listening for prey generated sounds (e.g., movement in leaf litter) and vision, but also use short, mid frequency (60–25 kHz) FM calls, to orient within and maneuver through the vegetation. The pallid bat is a Species of Special Concern in California.

Townsend's big-eared bat (*Corynorhinus townsendii*) is distributed throughout California in coniferous and mixed meso-phytic forests, deserts, native grasslands, riparian communities, active agricultural areas, and coastal habitat types (Western Bat Working Group 2015). They roost mainly in caves and abandoned mines, but also is found in buildings, bridges, rock crevices, and hollow trees. They forage primarily on moths which include over 90% of its diet. Preferred foraging areas include edge habitats along streams adjacent to and within a variety of woodlands (Western Bat Working Group 2015). They use short, mid-frequency (60–21 kHz) FM calls to locate and capture prey. The Townsend's big-eared bat is currently a Candidate species (Threatened) under the California Endangered Species Act (CESA). (Photo courtesy of Joe Szewczak)

Big brown bat (*Eptesicus fuscus*) occurs in most habitats throughout California, roosting in buildings, mines, and bridges, and other human-made structures, but also in caves, rock crevices, tree and cactus hollows, and even abandoned swallow nests (E. West, pers. obs.). They feed mainly on hard-bodied insects including beetles, bugs, aphids, flies, moths, bees, and wasps. They use mid-to-high frequency (80–27 kHz) FM/CF calls while hawking insects in tree canopies, over meadows, or along water courses.

Spotted bat (*Euderma maculatum*) has a scattered distribution throughout California from low desert to high elevation coniferous forests. They roost primarily in crevices in cliff faces, but has also in mines, caves, and occasionally on bridges. Foods include a variety of insects, but moths comprise its primary diet. In the desert, they forage in canyons, in the open, and over riparian vegetation. In montane regions they feed over meadows, along forest edges, and in open coniferous forests. Flight heights are generally at or above treetop level. They use low frequency (20–6 kHz) FM calls while foraging. The spotted bat is a Species of Special Concern in California.

Silver-haired bat (*Lasionycteris noctivagans*) is a forest-associated species distributed in California primarily in the northern counties of the state and at higher elevations in the southern and coastal mountain ranges. It occurs primarily in mature and old growth coniferous and mixed coniferous forests with Douglas fir, ponderosa pine, and black oak. They roosts almost exclusively in trees, but winter roosts also include rock crevices, abandoned mines, caves, buildings, and infrequently bridges. The diet of this species includes a variety of insects, but is primarily comprised of moths. It uses mid frequency (55–26 kHz) FM/CF calls to find and capture its prey and maneuver through the forests.

In California, the **western red bat** (*Lasiurus blossevillii*) is found most commonly in low elevation riparian and woodland habitats scattered throughout the state, but a few records have been documented at higher elevations (up to 8000 feet) in the Sierra Nevada. They roost exclusively in trees, within the foliage. Insect prey includes true bugs, beetles, bees and wasps, flies, and moths that are captured in aerial pursuit over ponds and waterways. They use mid frequency (60–40 kHz) FM/CF calls for prey capture and maneuvering. The western red bat is a Species of Special Concern in California.

Hoary bat (*Lasiurus cinereus*) is a tree associated species found primarily in forested habitats from sea level to 13,200 feet in California. They roost almost exclusively within the foliage of coniferous and deciduous trees. Infrequently, they may roost in caves, beneath ledges in woodpecker holes, and in squirrel's nests. Moths comprise this bat's principal diet, but it may also take other insects, including dragonflies and beetles. Foraging occurs mostly over the tree canopy. They use mid-to-low variable frequency (41–18 kHz) FM/CF calls to maneuver through their forested habitat and to locate and pursue insects at long distance in open habitat above the trees.

Western yellow bat (*Lasiurus xanthinus*) occurs mostly in fan palm oases and associated riparian habitats in the Colorado Desert and Los Angeles Basin. They roost mainly under the shag of palm trees, but also in the foliage of sycamores and hackberry trees. They feed mostly on moths but include other insects in their diet, including beetles. Mid-frequency (60–32 kHz) FM/CF calls are used by these bats in pursuit of prey in open areas above the canopy. The western yellow bat is a Species of Special Concern in California.

California myotis (*Myotis californicus*) inhabit the drier area of California, usually below 6,000 feet, but usually near water. They commonly roost in mines, caves, buildings, rock crevices, hollow trees, under bark, and occasionally on bridges. Their diet includes small flying insects, commonly flies, moths, spiders, and beetles that they capture using slow maneuverable flight (Adams 2003) along the margins of vegetation clumps, tree canopies, and in the open high above the ground. They use short high frequency (100–50 kHz) FM echolocation calls.

Small-footed myotis (*Myotis ciliolabrum*) occurs throughout California, at mid-to-high elevations (6,000 feet), favoring mesquite scrub, grasslands, oak, and pinyon juniper woodlands and pine forest habitats. They roost in cavities including rock crevices in mines and tree hollows. Their diet includes small moths, flies ants, and beetles. Like California myotis, they have slow maneuverable flight and short, high frequency (100–40 kHz) FM calls to locate and capture prey. They typically forage 1–3 m off the ground along cliffs and rocky slopes.

Long-eared myotis (*Myotis evotis*) is primarily a forest-associated species found in mixed hardwood/conifer forest and montane conifer forest in northern California and in pinyon-juniper, mesquite scrub, and pine/oak woodlands in southern California. They roost in caves, mines, trees, rock crevices, buildings, and bridges, usually close to forested habitat. They use both substrate gleaning and aerial pursuit to capture prey, foraging in forest-edge habitats along rivers and streams, over ponds, and within cluttered forest environments. Their diet includes moths, small beetles, and flies. They use short, broad bandwidth (120–35 kHz) FM echolocation calls.

Little brown bat (*Myotis lucifugus*) occurs in the higher elevation and more northern portions of California and is generally associated with coniferous forests. They commonly roost in buildings, but also are found in trees, under rocks, in rock crevices, caves and mines, and on bridges. They forage preferentially in open areas among vegetation and along water margins, and sometimes over water. Their diet consists of a variety of small aquatic insects, including caddis flies, midges, mayflies, and mosquitos, but also lacewings, flies, small moths, and small beetles. They use medium frequency (70–35 kHz) FM echolocation calls.

Arizona myotis (*Myotis occultus*) occurs only along the Colorado River between Nevada and Mexico borders. They are found associated with low desert areas with permanent water available amongst cottonwood, sycamore, and willow vegetation. Roosts include buildings, mines, bridges, trees, and caves. Information on diet is limited but likely similar to little brown bat as they feed close to water in riparian areas. Echolocation calls are similar to those of little brown bat. The Arizona myotis is a Species of Special Concern in California.

Fringed myotis (*Myotis thysanodes*) occurs throughout California from low desert scrub to high elevation coniferous forest. Roost sites include mines, caves, trees, buildings, and bridges. They forage in and among vegetation, along forest edges, and over the forest canopy and use both aerial capture and gleaning. Beetles, moths, spiders, crickets, and other insects are taken. They use short mid-to-low frequency, high bandwidth (110–13 kHz) echolocation calls with variable start frequencies.

Cave myotis (*Myotis velifer*) is restricted to the lower Colorado River Valley in California. They roost in caves, mines, buildings, and bridges in arid lands dominated by creosote bush, palo verde, and cactus and in desert riparian habitat. They forage in open areas near the edges of and over vegetation. The diet includes mostly moths and beetles. Cave myotis use high frequency (97–42 kHz) QFM echolocation calls to maneuver along the vegetation edges and locate distant prey in open habitats. The cave myotis is a Species of Special Concern in California.

Long-legged myotis (*Myotis volans*) occurs throughout California from the coast to high elevation in the Sierra Nevada. However, it is absent from the Central Valley and the lower desert regions in the southeastern parts of the state. They roost largely in hollow trees, but also in rock crevices, mines, buildings and on bridges. Moths comprise the principal food, but beetles, flies, termites and other insects are included. Foraging usually occurs in open area, frequently above the canopy. Long-legged myotis use meadium broadband (90–35 kHz) FM echolocation calls while foraging.

Yuma myotis (*Myotis yumanensis*) typically occurs in a wide variety of habitats, but mostly in association with lower-to-mid elevation ponds, reservoirs, and open areas in streams and rivers where they feed on emergent aquatic insects such as caddis flies and midges. They roost in buildings, trees, mines, caves, bridges and rock crevices. They use moderate-length, mid-range broadband (72–45 kHz) calls to their insect prey almost exclusively over water.

Canyon myotis (*Parastrellus hesperus*) bats inhabit the deserts and dryland regions of California in lower and upper Sonoran desert and coastal sage scrub habitats, usually in association with canyon and rocky terrain. Roosts are found primarily in rock crevices, mines, caves buildings, and, infrequently, on bridges. Their food includes small moths, leafhoppers, flies, gnats, mosquitos, and flying ants, which they capture on the wing in open areas. Their flight is usually slow and agile. Canyon bats use strong, high frequency (100–45 kHz) FM/CF calls to locate and accurately track their prey.

Free-Tailed Bats (Family Molossidae)

The **western mastiff bat** (*Eumops perotis*) is distributed largely in southwestern California, along the coastal range and the foothills of the Sierra Nevada and eastern Trinity Alps. These bats inhabit a variety of habitats from desert scrub to chaparral and mixed conifer forest. Roost sites are located in crevices at least 6 m above the ground in cliff faces and cracks in large boulders, and occasionally in buildings. It is possible they could use bridges, but that has yet to be verified. Mastiff bats are fast flying bats that feed mainly on moths in open areas over desert washes, grasslands, meadows, and above the forest canopy. They use low frequency (13–9 kHz) narrowband FM/CF calls well adapted for open aerial foraging using straight line pursuit. The western mastiff bat is a Species of Special Concern in California.

The **pocketed free-tailed bat** (*Nyctinomops femorosaccus*) occurs in the arid lowland areas and desert canyons of the lower Colorado Desert and coastal areas in southern California. Like western mastiff bats, they roost mainly in crevices in cliff faces and boulders but have also been found in caves and buildings. Bridge use is not documented, but possible. Moths and beetles are the principal prey for this species. Their echolocation calls are narrowband mid–to-low frequency (59–16 kHz). The pocketed free-tailed bat is a Species of Special Concern in California.

The **big free-tailed bat** (*Nyctinomops macrotis*) has scattered distribution throughout California, with most of the records in San Diego County. They are mainly inhabitants of rugged, rocky habitats in arid landscapes, roosting in crevices of rocks and cliffs, in buildings, caves, and tree cavities. They forage mostly on moths but also will take other insects including grasshoppers, beetles, crickets, leafhoppers, and flying ants. Their echolocation calls are similar to those of the mastiff bats, but are at a slightly higher frequency beginning at 18 kHz and ending about 12 kHz. The big free-tailed bat is a Species of Special Concern in California.

The **Brazilian free-tailed bat** (*Tadarida brasiliensis*) occurs throughout California from low desert to over 12,000 feet in the White Mountains. It is the most common species in the Central Valley, with a colony of up to 250,000 inhabiting the Yolo Causeway between Davis and Sacramento. Besides bridges, this species roosts in cliff faces, bridges, buildings, mines, and caves. Prey species mainly include moths, but other open air insects may also be taken. Brazilian free-tailed bats are primarily open area aerial predators using straight line pursuit. They use a variety of echolocation calls that change from mostly long flat CF components (approximately 28 kHz) during the search phase to short broadband FM calls (60–25 kHz) during the terminal buzz contact phase.

Appendix C: Compilation of the Research Citations and Abstracts

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Overview

Increasing levels of anthropogenic noise in urban, rural and natural areas are creating new sound environments that can negatively affect the social behaviors and viability of many vocal wildlife species (Patricelli and Blickley 2006; Warren et al. 2006, Dooling and Popper 2007, Naguib 2013; Proppe et al. 2013). Recent studies on the effects of highway and other anthropogenic noise on birds (Leonard and Horn 2005, Parris and Schneider 2008, Slabbekoorn and Ripmeester 2008, Francis et al. 2009, Nemeth and Brumm 2010, Halfwerk et al. 2011), amphibians (Herrera-Montes and Aide 2011, Lengagne 2008) and small mammals (Rasmussen et al. 2009) show that sounds that acoustically interfere with normal hearing and communication can alter behaviors important in mate selection, pair bonding, parent-offspring communication, song learning and predator/prey detection and can potentially induce stress that can alter reproductive and other important hormone levels (Warren et al. 2006, Naguib 2013). Similar studies on the effects of highway noise on bats (Schaub and Siemers 2008, Siemers and Schaub 2011, Hage et al. 2014, Jones 2008, Bennett and Zurcher 2013, Kitzes and Merenlender 2014) are also beginning to show comparable results, at least with regard to degraded prey detection ability in some insect gleaning species. However, because bats commonly echolocate and communicate using ultrasonic signals that are beyond the normal spectra of most highway noise it is unclear whether those and associated behaviors are being affected in any way. Also, most bats can hear in the audible range and monitor natural sounds to detect potential disturbances, including predators. Some bats also passively listen for the movement sounds of ground dwelling insect prey to locate them.

This compendium provides a working compilation of the research citations and abstracts that were used to evaluate the potential effects of highway noise on bats and prepare the final analysis report: *Technical Guidance for the Assessment and Mitigation of the Effects of Traffic Noise and Road Construction Noise on Bats* (*Caltrans 2016*). It includes studies that detail the hearing capacity of bats and the critical acoustic, morphological and physiological requirements for effective echolocation and social communication. Information on the spectral/amplitude range of highway noise and how it can potentially interfere with these behaviors were also acquired and reviewed. The final report endeavors to identify all apparent real and emerging biological and regulatory/conservation issues regarding the affects of noise on bats that are important to consider during planning and implementation of Caltrans highway maintenance, construction and operation projects.

Citations and Abstracts

Abbott, I.M., Butler, F. & Harrison, S., 2012. When flyways meet highways – The relative permeability of different motorway crossing sites to functionally diverse bat species. *Landscape and Urban Planning*, 106(4), pp.293–302.

Abstract: Bat populations are potentially vulnerable to the barrier effects of roads. However, empirical data on how road features facilitate or impede bat movements are scarce and essential for planning mitigation measures. We investigated bat movements across a motorway where it intersects with potential bat commuting routes along prominent linear landscape elements (treelines along hedgerows, minor roads, and rivers). Bat activity was recorded acoustically at

four types of potential crossing routes; two under-motorway routes (river bridges and underpasses) and two over-motorway routes (overbridges and severed treelines), while simultaneously recording activity in the adjacent habitat. Bat activity above and below motorway structures and the timing of crossing flights with respect to motorway vehicles were also recorded. All bat species recorded in the adjacent landscape crossed the motorway. Bats used under motorway routes, particularly river bridges, more than over-motorway routes. Contrary to expectations, many species flew across motorway gaps in treelines despite the lack of a guiding structure, including clutter-adapted species (*Myotis* spp., *Plecotus auritus*). Furthermore, bat passes were also recorded for the more collision-prone flight route at crossing structures (2% and 6.4% recorded above motorway level at river bridges and underpasses respectively, and 50% recorded on the underside of overbridges). In a subset of 10 nights of motorway-edge recordings, 18.3% of bat passes coincided with, and 17.1% were within 1–5 s of, passing vehicles. Our results highlight the prevalence of bat flyways along motorway-disrupted landscape features, and also the challenge in locating and designing crossing structures to minimize the risk of collision mortality.

Abbott, I.M., Harrison, S. & Butler, F., 2012. Clutter-adaptation of bat species predicts their use of under-motorway passageways of contrasting sizes - a natural experiment N. Bennett, ed. *Journal of Zoology*, 287(2), pp.124–132.

Abstract: Bat populations may be vulnerable to the barrier impacts of roads, including habitat restriction and traffic mortality. Under-road passageways may reduce these impacts, but little is known about the ecological factors influencing their use by bats. The study area provided a natural experimental design, in that adjacent under-motorway passageways had contrasting dimensions (two long, narrow drainage pipes within <1 km of a large underpass for a minor road), and local bat species had contrasting functional and morphological adaptations. We predicted that inter-species differences in flight capability and sensory perception would influence bat use of passageways. All-night acoustic recordings of bat activity inside passageways (52 nights) indicated clear guild-specific responses to passageway dimensions. Only *Rhinolophus hipposideros*, *Myotis nattereri* and *Plecotus auritus* flew through the narrow drainage pipes. These species are adapted for flight and foraging in cluttered airspace, in terms of wing morphology and echolocation signal design. Edge-space species (*Pipistrellus*, *Pipistrellus pygmaeus*) were highly active in the area but never flew through the narrow pipes. All species, except the open-adapted *Nyctalus leisleri*, flew through the large underpass. Simultaneous recordings made above and below this underpass (16 nights) also indicated that species' tendency to cross over, rather than under, the structure was inversely related to the degree of clutter-adaptation. If motorways are built through bat habitat, trade-offs between optimal mitigation of impacts on protected bats and cost/engineering practicality are inevitable. Large underpasses are advisable where possible as they accommodate a wider range of species, and bats are less likely to fly over them. However, their construction is costly and is dependent on landscape topology. If the target species for mitigation are clutter adapted bats, our findings indicate that incorporation of a greater number of suitably located small tunnels into new roads may facilitate safe passage more effectively than fewer large underpasses.

Adams, M.D., Law, B.S. & French, K.O., 2009. Vegetation structure influences the vertical stratification of open- and edge-space aerial-foraging bats in harvested forests. *Forest Ecology and Management*, 258, pp.2090–2100.

Abstract: Heavy logging leads to regrowth of dense forest, which may adversely affect the flight and foraging activities of bats. We compared insectivorous bat activity and insect abundance at three heights (understorey, subcanopy and canopy), two locations (forest and track) and three time periods (evening, night and dawn), in old and young regrowth sites in south-eastern Australia (456 detector-hours). We measured activity levels of all bats and four echolocation guilds—one open-space and three edge-space aerial-foraging guilds. Mean bat activity in the subcanopy and canopy was up to 11 times that in the understory of forests, a pattern opposite to that of insect abundance. However, bat activity in the two upper strata was lower in young regrowth than in old regrowth. Vegetation was more cluttered in young regrowth at these upper heights (closer stems and less vertical space in the subcanopy). Mean activity on the track was 2–5 times higher than in the forest, particularly at understorey level (17 times higher for all bats), where vegetation was less cluttered (more distant understorey trees and shrubs, and less cover of ground vegetation). Time of night had little effect on bat activity. The negative response of bat guilds to increased clutter was strongest in the open-space guild and weakest in the edge-space guild with the highest frequency calls. There was an interaction between insect abundance and an index of vegetation openness, with high values of both variables producing high bat activity levels for all bats and the two highest frequency call guilds. Our results highlight the need for management practices in logged forests that increase or preserve the amount of flight and foraging space available to bats.

Adams, R.A., 1996. Size-specific resource use in juvenile little brown bats, *Myotis lucifugus* (Chiroptera: Vespertilionidae): Is there an ontogenetic shift? *Canadian Journal of Zoology*, 74(7), pp.1204–1210.

Abstract: This paper correlates shifts in habitat use and diet with morphological transitions occurring during postpartum growth and development (ontogenetic niche) in little brown bats, *Myotis lucifugus*. Juveniles were captured in mist nets as they foraged in different microhabitats that were defined and quantified using "clutter indices" ranging from 0 (least cluttered) to 5 (most cluttered). I analyzed fecal samples from captured individuals to assess diet. Chi-squared analyses showed that there was a significant difference in habitat use and diet among juveniles captured in early, mid, and late July. Juveniles with smaller wings foraged in the least cluttered habitats, whereas juveniles with larger wings foraged in habitats with a high degree of clutter. Juveniles with larger wings were captured in all microhabitats, whereas those with smaller wings were captured predominantly in open microhabitats. Juveniles with relatively higher aspect ratios and lower wing loadings used a greater diversity of habitats than those with lower aspect ratios and higher wing loadings. In addition, differences in diet were significant and correlated with wing size. My results suggest resource partitioning between juveniles as a function of wing size. These data have important implications regarding how relative size among juveniles may effect intraspecific structuring of populations.

Adams, R.A., 1997. Onset of volancy and foraging patterns of juvenile little brown bats, *Myotis lucifugus*. *Journal of Mammalogy*, 78(1), p.239.

Abstract: In this paper I quantify and compare patterns of use of habitat and diet of adult and juvenile little brown bats (*Myotis lucifugus*). Individuals were captured in mist nets as they foraged. Clutter indices (CIs) ranging from 0 (least cluttered) to 5 (most cluttered) were used to categorize feeding microhabitats based on density of vegetation. A total of 378 *M. lucifugus* was banded over a 2-year period and dietary analysis was performed on fecal samples from 90

individuals. Foraging patterns of juveniles and adults differed significantly, and patterns of adult were density dependent. When population density was high, adults moved from foraging primarily in open areas close to the ground (CI1) to semiclutter and heavy clutter microhabitats (CI3, CI4, and CI5). Adults shifted foraging areas in mid-July when juveniles developed volancy. When density of the population was low (the result of a population crash at the site), adults foraged in CI1 throughout summer and did not shift habitats. Juveniles foraged predominantly in the least-cluttered microhabitat (CIO) in both years independent of density of population.

Adams, R. A., 2003. Bats of the Rocky Mountain West. Natural History, Ecology, and Conservation. The University Press of Colorado. 289 pp.

No Abstract

Adams, R. A. & Hayes, M. A., 2008. Water availability and successful lactation by bats as related to climate change in arid regions of western North America. *The Journal of Animal Ecology*, 77, pp.1115–1121.

Abstract: 1. Climate change in North America is happening at an accelerated rate, reducing availability of water resources for bats and other wildlife that require it for successful reproduction. 2. We test the water-needy lactation hypotheses directly by tracking the drinking habitats of individual lactating and non-reproductive female fringed myotis at an artificial water source located near a maternity roost. 3. We used a submerged passive integrative transponder (PIT) tag reader system designed to track fish to instead record numbers of water source visitations by tagged bats. 4. Of 24 PIT-tagged adult females, 16 (67%) were detected repeatedly by the plate antenna as they passed to drink between 18 July and 28 August 2006. 5. The total number of drinking passes by lactating females (n = 255) were significantly higher than those of non-reproductive adult females (n = 22). Overall, lactating females visited 13 times more often to drink water than did non-reproductive females. On average, lactating females visited six times more often per night. Drinking bouts occurred most frequently just after evening emergence and at dawn. 6. Drinking patterns of non-reproductive females correlated significantly with fluctuating ambient temperature and relative humidity recorded at the water source, whereas lactating females drank extensively regardless of ambient conditions. 7. We provide a mathematical model to predict the rate of decline in bat populations in the arid West in relation to climate change models for the region.

Akasaka, T., Nakano, D. & Nakamura, F., 2009. Influence of prey variables, food supply, and river restoration on the foraging activity of Daubenton's bat (*Myotis daubentonii*) in the Shibetsu River, a large lowland river in Japan. *Biological Conservation*, 142, pp.1302–1310.

Abstract: To conserve the foraging habitat of Daubenton's bat (*Myotis daubentonii*) in a large lowland river, we investigated the influence on this bat of prey variables (number or biomass) and insect origin (aquatic or terrestrial). We tested the hypothesis that river restoration (re-meandering) conducted in the Shibetsu River, northern Japan, enhances foraging habitat quality by increasing the abundance of aquatic insects. From June to September 2004, flying insects were collected using Malaise traps in restored and channelised reaches in the Shibetsu River. Bat activity was recorded by bat detectors placed near the Malaise traps in each of the two reaches.

Foraging activity of Daubenton's bat was more strongly related to the number of insects than to biomass, and to adult aquatic insects than to terrestrial insects. The high dependence of Daubenton's bat on aquatic prey was attributed to the fact that aquatic insect numbers were always higher than those of terrestrial insects. Contrary to the hypothesis, Daubenton's bat was more active in the channelised reach than the restored reach in all months except June, and it synchronized its foraging activity with the seasonal distribution of adult aquatic insects. However, the study was undertaken just two years after restoration and the riparian vegetation had not yet established itself. Our results demonstrate the importance of aquatic insect abundance for Daubenton's bat throughout the seasons in large lowland rivers. A further decrease in aquatic insects, associated with progressive anthropogenic alteration of river environments, undoubtedly exerts a harmful influence on the conservation of this species

Aldridge, H.D.J.N. & Mackey, R.L., 1992. Variation in Habitat use and Prey Selection by Yuma Bats, *Myotis yumanensis*. *Journal of Mammalogy*, 73(3), pp.640–645.

Abstract: The purpose of our study was to assess variation in habitat use and prey selection by *Myotis yumanensis* in British Columbia. In particular we tested the hypothesis that habitat use and resulting prey choice are constant among different reproductive and age classes. We light tagged 115 individuals and observed their foraging activity for a total of 218 min on 16 nights from May to September 1989. The four reproductive and age classes pregnant, lactating, post-lactating, juvenile) all predominately foraged with in open, uncluttered habitats over land and low over water. Dietary variation suggests this species forages opportunistically on aquatic insects with changes in diet reflecting changes in availability.

Altes, R. & Titlebaum, E., 1970. Bat signals as optimally Doppler tolerant waveforms. The *Journal of the Acoustical Society of America*, 48(4), pp.1014 – 1020.

Abstract: Wide-band ambiguity function analysis is combined with techniques of variational calculus to find optimally Doppler tolerant waveforms, i.e., signals such that magnitude of correlator output is relatively unaffected by target velocity. With appropriate constraints, these signals are found to be very similar to those used by *Myotis lucifugus*.

Anderson, M. & Racey, P., 1993. Discrimination between fluttering and non-fluttering moths by brown long-eared bats, *Plecotus auritus*. *Animal Behaviour*, 46, pp.1151–1155.

Abstract: The ability of brown long-eared bats to discriminate between fluttering and non-fluttering moths in a flight cage was tested in order to determine the sensory cues used to detect prey movement. Bats chose the fluttering moth in 88 of 95 trials when all potential sensory cues were available. The fluttering moth was chosen in 91 of 106 trials when visual and ultrasonic cues were eliminated. Simultaneous video and tape recordings showed that while hovering close to potential prey, bats were more likely to remain silent than to produce echolocation pulses. The sound produced by fluttering moths contained frequencies in the 600 Hz - 23 kHz range. It is suggested that the bats are able to differentiate between motile and non-motile moths by passive listening.

Anthony, E., Stack, M. & Kunz, T., 1981. Night roosting and the nocturnal time budget of the little brown bat, *Myotis lucifugus*: effects of reproductive status, prey density, and environmental conditions. *Oecologia*, 51(2), pp.151–156.

Abstract: The insectivorous bat *Myotis lucifugus* typically apportions the night into two foraging periods separated by an interval of night roosting. During this interval, many bats occupy roosts that are used exclusively at night and are spatially separate from maternity roosts. The proportion of the night which bats spend roosting, and thus the proportion spent foraging, vary both daily and seasonally in relation to the reproductive condition of the bats, prey density, and ambient temperature. A single, continuous night roosting period is observed during pregnancy. During lactation, females return to maternity roosts between foraging bouts, and night roosts are used only briefly and sporadically. Maximum use of night roosts occurs in late summer after young become volant. Superimposed upon these seasonal trends is day-to-day variation in the bats' nightly time budget. Long night roosting periods and short foraging periods are associated with cool nights and low prey density. This behavioral response may minimize energetic losses during periods of food scarcity.

Arévalo, J. E., and Newhard, K., 2011. Traffic noise affects forest bird species in a protected tropical forest. *Revista de Biologia Tropical*, 59(June), 969–980.

Abstract: The construction of roads near protected forest areas alters ecosystem function by creating habitat fragmentation and through several direct and indirect negative effects such as increased pollution, animal mortality through collisions, disturbance caused by excessive noise and wind turbulence. Noise in particular may have strong negative effects on animal groups such as frogs and birds, that rely on sound for communication as it can negatively interfere with vocalizations used for territorial defense or courtship. Thus, birds are expected to be less abundant close to the road where noise levels are high. In this study, we examined the effects of road traffic noise levels on forest bird species in a protected tropical forest in Costa Rica. Data collection was conducted in a forest segment of the Carara National Park adjacent to the Coastal Highway. We carried out 120 ten minute bird surveys and measured road noise levels 192 times from the 19th to the 23rd of April and from the 21st to the 28th of November, 2008. To maximize bird detection for the species richness estimates we operated six 12 m standard mist nets simultaneously with the surveys. The overall mist-netting effort was 240 net/h. In addition, we estimated traffic volumes by tallying the number of vehicles passing by the edge of the park using 24 one hour counts throughout the study. We found that the relative abundance of birds and bird species richness decreased significantly with the increasing traffic noise in the dry and wet season. Noise decreased significantly and in a logarithmic way with distance from the road in both seasons. However, noise levels at any given distance were significantly higher in the dry compared to the wet season. Our results suggest that noise might be an important factor influencing road bird avoidance as measured by species richness and relative abundance. Since the protected forest in question is located in a national park subjected to tourist visitation, these results have conservation as well as management implications. A decrease in bird species richness and bird abundance due to intrusive road noise could negatively affect the use of trails by visitors. Alternatives for noise attenuation in the affected forest area include the enforcement of speed limits and the planting of live barriers.

Arita, H. & Fenton, M., 1997. Flight and echolocation in the ecology and evolution of bats. *Trends in Ecology & Evolution*, 12(2), pp.53–57.

Abstract: Flight and echolocation are key characters distinguishing most bats from other mammals. The number of ecolological niches for bats is limited by the concurrent constraints of the mammalian physiology and reproductive system and the high cost of flight and echolocation.

The recent discovery of a biomechanical coupling between echolocation and flight highlights the need to incorporate both characters as parts of a single adaptive complex in future research on the ecology and evolution of bats.

Arlettaz, È., Jones, G. & Racey, P.A., 2001. Effect of acoustic clutter on prey detection by bats. *Nature*, 414 (December), pp.742–745.

Abstract: Bats that capture animal prey from substrates often emit characteristic echolocation calls that are short-duration, frequency modulated (FM) and broadband. Such calls seem to be suited to locating prey in uncluttered habitats, including prey, but may be less effective for Finding prey among cluttered backgrounds because echoes reflecting from the substrate mask the acoustic signature of prey. Perhaps these call designs serve primarily for spatial orientation. Furthermore, it has been unclear whether the acoustic image conveyed by FM echoes enables fine texture discrimination or whether gleaning bats that forage in echo-cluttering environments must locate prey by using other cues, such as prey-generated sounds. Here we show that two species of insectivorous gleaning bats perform badly when compelled to detect silent and immobile prey in clutter, but are very efficient at capturing noisy prey items among highly cluttered backgrounds, and both dead or live prey in uncluttered habitats. These findings suggest that the short, broadband FM echolocation calls associated with gleaning bats are not adapted to detecting prey in clutter.

Armstrong, K.N., 2010. Assessing the short-term effect of minerals exploration drilling on colonies of bats of conservation significance: a case study near Marble Bar, Western Australia. *Journal of the Royal Society of Western Australia*, 93(4), pp.165–174.

Abstract: Bats are most vulnerable whilst in their roost, and activities that result in roost destruction or disturbance have the potential to cause declines in species of conservation significance. However, conservation efforts for bat colonies can be limited by a lack of understanding of the effect of certain disturbances. An evaluation drilling program conducted in close proximity to historical underground gold workings near Marble Bar provided an opportunity to examine the short-term effect of this type of activity on colonies of the bats *Macroderma gigas* and *Rhinonicteris aurantia*. A non-invasive approach to assessing the impact of the associated activity was developed, which simultaneously realised the best economy of moving a drill rig. Bats were subject to several types of potential disturbance (from noise and vibration) from earthmoving equipment, the drill rig and the booster compressor. Monitoring involved continuous acoustic and visual observations of mine entrances during drilling, direct counts of emerging bats each evening after drilling, and surveys of other mines in the local area throughout the study. *R. aurantia* was present throughout the drilling programme, but actual numbers could not be determined accurately. A marked increase in the number of *M. gigas* was observed, thought to be independent of the activities associated with the drilling programme and possibly due to concurrent human activities in other local mines or natural factors. It was concluded that short-term activities associated with drilling that are not within 25 m of a mine entrance or 85 m of the roost site within the structure, and that do not intersect workings, might not constitute a significant disturbance to these bats. However, the long term cumulative effects of this and other disturbances, and in the context of contemporaneous activities at other roosts in the district, are unknown.

Armstrong, K.N. & Kerry, L.J., 2011. Modeling the prey detection performance of *Rhinonicteris aurantia* (Chiroptera: Hipposideridae) in different atmospheric conditions discounts the notional role of relative humidity in adaptive evolution. *Journal of Theoretical Biology*, 278(1), pp.44–54.

Abstract: We examined a recent notion that differences in echolocation call frequency amongst geographic groups of constant frequency (CF)-emitting bats is the result of a trade-off between maximising prey detection range at lower frequencies and enhancing small-prey resolution at higher frequencies in different atmospheric (relative humidity; RH) environments. Isolated populations of the endemic Australian orange leaf-nosed bat *Rhinonicteris aurantia* were used as an example since geographic isolation in different environments has been a precursor to differences in their characteristic echolocation call frequencies (mean difference c. 6 kHz; means of 114.64 and 120.99 kHz). The influence of both atmospheric temperature and RH on maximum prey detection range was explored through mathematical modeling. This revealed that temperature was of similar importance to relative humidity and that under certain circumstances, each could reduce the effect of the other on ultrasound attenuation rates. The newly developed models contain significant conceptual improvements in method compared to other recent approaches, and can be applied to the situation of any other species of bat. For a given set of atmospheric conditions, the prey detection range of R. *aurantia* was reduced slightly when call frequency increased by 6 kHz, but an increase in RH, temperature or both reduced detection range significantly. A similar trend was also evident in prey detection volume ratios calculated for the same conditions. Spatial volume ratios were applied to assess the impact of changed atmospheric conditions and prey size on foraging ecology. Reductions in detection range associated with increases in RH and/or temperature also varied in relation to the size (cross sectional area) of insect prey. Modelling demonstrated that small (6 kHz) movements in call frequency could not compensate for the changes in prey detection range and spatial detection volumes that result from significant changes in atmospheric temperature or RH. The notion that differences in RH are the primary cause leading to adaptive evolution and speciation in CF-emitting bats by precipitating intraspecific differences in the mean call frequency of geographically isolated bat populations was not supported by the results of this case study.

Arnett, E.B., Baker, M., Huso, M.M.P. & Szewczak, J.M., 2010. Evaluating the effectiveness of an ultrasonic acoustic deterrent for reducing bat fatalities at wind facilities. An annual report submitted to the Bats and Wind Energy Cooperative. Bat Conservation International. Austin, Texas, USA.

No abstract

Arnett, E. B., Baker, M. Schirmacher, M. R. Hein, C. D. Huso, M. M. P., & Szewczak J. M. 2013. Evaluating the effectiveness of an ultrasonic acoustic deterrent for reducing bat fatalities at wind turbines. *PloS One*, 8(6), p.e65794.

Abstract: Large numbers of bats are killed by wind turbines worldwide and minimizing fatalities is critically important to bat conservation and acceptance of wind energy development. We implemented a 2-year study testing the effectiveness of an ultrasonic acoustic deterrent for reducing bat fatalities at a wind energy facility in Pennsylvania. We randomly selected control and treatment turbines that were searched daily in summer and fall 2009 and 2010. Estimates of fatality, corrected for field biases, were compared between treatment and control turbines. In

2009, we estimated 21-51% fewer bats were killed per treatment turbine than per control turbine. In 2010, we determined an approximate 9% inherent difference between treatment and control turbines and when factored into our analysis, variation increased and between 2% more and 64% fewer bats were killed per treatment turbine relative to control turbines. We estimated twice as many hoary bats were killed per control turbine than treatment turbine, and nearly twice as many silver-haired bats in 2009. In 2010, although we estimated nearly twice as many hoary bats and nearly 4 times as many silver-haired bats killed per control turbine than at treatment turbines during the treatment period, these only represented an approximate 20% increase in fatality relative to the pre-treatment period for these species when accounting for inherent differences between turbine sets. Our findings suggest broadband ultrasound broadcasts may reduce bat fatalities by discouraging bats from approaching sound sources. However, effectiveness of ultrasonic deterrents is limited by distance and area ultrasound can be broadcast, in part due to rapid attenuation in humid conditions. We caution that an operational deterrent device is not yet available and further modifications and experimentation are needed. Future efforts must also evaluate cost-effectiveness of deterrents in relation to curtailment strategies to allow a cost-benefit analysis for mitigating bat fatalities.

Arnold, B.D. & Wilkinson, G.S., 2011. Individual specific contact calls of pallid bats (*Antrozous pallidus*) attract conspecifics at roosting sites. *Behavioral Ecology and Sociobiology*, 65, pp.1581–1593.

Abstract: In several bird and mammal species, contact calls are utilized to maintain group cohesion and coordinate group movement. From a signal design perspective, contact calls typically exhibit acoustic features that make them easily localizable and encode information about individual or group identity. Pallid bats (*Antrozous pallidus*) are unusual among vespertilionids in that they often emit a loud, partially audible frequency-modulated social call several times in rapid succession while in flight. This call appears to function as a contact call in that it is frequently given when bats return from foraging and perform circular flights before entering a crevice roost. However, the degree to which pallid bats respond to the calls of conspecifics and what information is provided in the call is unknown. Thus, the goal of this study was to investigate pallid bat calling behavior to determine if calls attract roost mates or elicit responses from them and provide sufficient information for individual recognition. In playback studies, we found that contact calls elicit calls and approaches and that free-flying bats respond more to familiar than unfamiliar calls. In addition, analysis of frequency and temporal measurements of calls collected from multiple sites and spectral cross correlation analysis of calls recorded from the same radiotagged bats on multiple evenings revealed that the frequency pattern of contact calls is highly repeatable over time within individuals but exhibits significant differences among individuals. Thus, contact call structure appears to be unique to individuals and stable through time, which makes these calls well-suited for roost mate recognition.

Attenborough, K., 1982. Predicted ground effect for highway noise. *Journal of Sound and Vibration*, 81, pp.413–424.

Abstract: The well-established theory for propagation from a point source over an impedance boundary predicts a surface wave for low frequencies and near grazing incidence. The implications of the theoretically predicted surface wave for propagation over a locally reacting boundary are explored in terms of real and imaginary parts of surface normal impedance. Available measurements of the surface normal impedance of the ground are collected together

and reviewed. The computer predicted variation in A-weighted excess attenuation of a traffic line source with ground type is presented and discussed.

Au, W.W.L., 1997. Echolocation in dolphins with a dolphin-bat comparison. *Bioacoustics*, 8, pp.137–162.

Abstract: Dolphins possess a highly sophisticated auditory system and a keen capability for echolocation. Signals are emitted in the form of high intensity, short duration, broadband exponentially decaying pulses. The frequency spectra of echolocation signals used by many dolphins are dependent on the output intensity of the signals and not on any fine tuning by the animals. When the output intensity is low, the center frequency of the click tends to be low. As the output intensity increases, the center frequency also tends to increase. The pulses propagate from the dolphin's melon in a relatively narrow beam, and echoes are received via the lower jaw, with a slightly wider beam. Echolocating dolphins can detect targets at ranges of approximately 100 plus meters, depending on the size of the targets. Target discrimination experiments have shown that dolphins can discriminate the shape, size, material composition and internal structure of targets from the echoes. The broadband short duration properties of the signal allow the echoes to have high temporal resolution, so that within the structure of the echoes a considerable amount of information on the properties of the target can be conveyed. A brief comparison between the bat and dolphin sonar system will also be made. Bats typically emit much longer signals and a wider variety of different types of signals than dolphins. Signals used by some bats are suited to detecting Doppler shift, whereas the dolphin signal is designed to be tolerant of Doppler effects.

Aylor, D., 1972. Noise reduction by vegetation and ground. *The Journal of the Acoustical Society of America*, 51(1B), p.197.

Abstract: Transmission of random noise rough dense corn, a dense hemlock plantation, an open pine stand, dense hardwood brush and cultivated soil was measured. The relation between attenuation and frequency in these diverse cases suggested models that permit the prediction of attenuation in any configuration of vegetation and soil. The corn crop had an excess attenuation of 6 dB/100 ft for each doubling of frequency between 500 and 4000 Hz. On the other hand, the stems of the hemlock, pine, and brush all reduced noise by only 5 dB/100 at 4000 Hz. Bare ground attenuates frequencies of 200-1000 Hz, and the frequency of maximum attenuation depends on the soil permeability to air. Thus, tilling the soil reduced the frequency of peak attenuation from 700 to 350 Hz and increased maximum attenuation at 52 m from the source by nearly 80%. Furthermore, earlier conflicting reports of noise attenuation by vegetation appear reconciled if ground attenuation is taken into account. Scattering and ground attenuation are the principal factors in sound attenuation by vegetation. Both factors attenuate relatively less sound as distance from the sound source increases. Hence measurements far from the source can underestimate the effect of a narrow band of vegetation or soil.

Bailey, W. & Haythornthwaite, S., 1998. Risks of calling by the field cricket *Teleogryllus oceanicus*: potential predation by Australian long-eared bats. *Journal of Zoology*, 244, pp. 505–513.

Abstract: Male *Teleogryllus oceanicus* prefer to call from refuges and from these protected sites produce signals that contain more trill elements than produced by males calling without the

protection of refuges. We tested the vulnerability of male crickets to predation from two species of gleaning bats, *Nyctophilus major* and *N. geoffroyi*. Crickets called from the floor of darkened fly-ways where bats preyed on calling rather than silent males. Both species of bat used passive listening to locate their prey rather than echolocation. Those crickets calling from refuges avoided predation. By counting the number of passes each bat made over paired speakers emitting different digitized songs, we tested the bat's preference for different call elements or the total number of sound elements in the song per unit time. When the total number of sound elements of each signal was balanced, bats preferred trills to chirps, and when call length differed, bats preferred those signals with more total sound elements. We discuss the possibility that predation by bats is a form of counter-selection on calling in *T. oceanicus*.

Baker, M.D. & Lacki, M.J., 2006. Day-roosting habitat of female long-legged myotis in ponderosa pine forests. *Journal of Wildlife Management,* 70(1), pp.207–215.

Abstract: We studied use of day roosts by adult, female long-legged myotis (*Myotis volans*) in 4 watersheds dominated by ponderosa pine (*Pinus ponderosa*) forest east of the Cascade Crest in Washington and Oregon, USA, 2001–2003. To investigate maternity habitat in managed, xeric forests we radiotracked 87 bats to 195 snag roosts and 34 rock crevices totaling 842 roost-days. Bats changed roosts every 2.76 ± 0.1 (SE) days and averaged 3.6 6 ± 0.3 roosts per bat. Roosts were 2.0 6 0.1 km from capture sites, and bats moved 1.4 6 0.1 km between successive roosts. Six bats (6.9%) day-roosted in rock crevices exclusively, 9 bats (10.3%) used snags and rock crevices, and the remaining bats (82.8%) day- roosted in snags exclusively. Most snag roosts were thick-bark ponderosa pine (n=103; 52.8%) or thin-bark grand fir (*Abies grandis*) and white fir (*Abies concolor*)(n =74; 37.9%). Over half of all snag roosts (n =101; 52%) were used by solitary bats; 28 snag roosts (14%) housed 50 bats (large-flyout roosts). Ninety-three percent of large-flyout roosts were in ponderosa pine snags. Large-flyout roosts were larger, taller, and retained more exfoliating bark and total bark than small-flyout roosts ($P < 0.05$), and small-flyout roosts were larger, taller, and retained more exfoliating bark and total bark than random snags ($P < 0.05$). Snag roosts were closer to other snags, located in areas of greater snag density, with greater snag basal area and greater basal area of snags .25 cm diameter, and were lower in elevation than random snags ($P < 0.05$). Pregnant bats divided roost-days almost evenly between thick and thin-bark snags (52.7 vs. 47.3%), whereas lactating bats roosted in thick- bark snags more often than they did in thin-bark snags (80.3 vs. 19.7%, $P < 0.0001$). Pregnant bats roosted in both upslope and riparian zones (57.5 vs. 42.5%), but lactating bats spent more days roosting upslope than in riparian zones (73.1 vs. 26.9%, $P < 0.0001$). These findings suggest that reproductive female long-legged bats choose roosts relative to their changing physiological needs. We recommend that management of forests for sustaining habitat of female long-legged myotis in the east Cascades ensure the continued availability of both thick- and thin-bark snags in early stages of decay, in both riparian and upslope positions.

Barber, J.R., Burdett, D.L., Reed, S.R., Warner, K.A., Formichella, C., Crooks, K.R., Theobald, D.M., & Fristrup, K.M., 2011. Anthropogenic noise exposure in protected natural areas: estimating the scale of ecological consequences. *Landscape Ecology*, 26(9), pp.1281–1295.

Abstract: The extensive literature documenting the ecological effects of roads has repeatedly implicated noise as one of the causal factors. Recent studies of wildlife responses to noise have decisively identified changes in animal behaviors and spatial distributions that are caused by

noise. Collectively, this research suggests that spatial extent and intensity of potential noise impacts to wildlife can be studied by mapping noise sources and modeling the propagation of noise across landscapes. Here we present models of energy extraction, aircraft overflight and roadway noise as examples of spatially extensive sources and to present tools available for landscape scale investigations. We focus these efforts in US National Parks (Mesa Verde, Grand Teton and Glacier) to highlight that ecological noise pollution is not a threat restricted to developed areas and that many protected natural areas experience significant noise loads. As a heuristic tool for understanding past and future noise pollution we forecast community noise utilizing a spatially-explicit land-use change model that depicts the intensity of human development at sub-county resolution. For road noise, we transform effect distances from two studies into sound levels to begin a discussion of noise thresholds for wildlife. The spatial scale of noise exposure is far larger than any protected area, and no site in the continental US is free from noise. The design of observational and experimental studies of noise effects should be informed by knowledge of regional noise exposure patterns.

Barber, J.R., Crooks, K.R. & Fristrup, K.M., 2010. The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution*, 25(3), pp.180–9.

Abstract: Growth in transportation networks, resource extraction, motorized recreation and urban development is responsible for chronic noise exposure in most terrestrial areas, including remote wilderness sites. Increased noise levels reduce the distance and area over which acoustic signals can be perceived by animals. Here, we review a broad range of findings that indicate the potential severity of this threat to diverse taxa, and recent studies that document substantial changes in foraging and anti-predator behavior, reproductive success, density and community structure in response to noise. Effective management of protected areas must include noise assessment, and research is needed to further quantify the ecological consequences of chronic noise exposure in terrestrial environments.

Barber, J.R., Razak, K.A. & Fuzessery, Z.M., 2003. Can two streams of auditory information be processed simultaneously? Evidence from the gleaning bat *Antrozous pallidus*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 189, pp.843–55.

Abstract: A tenet of auditory scene analysis is that we can fully process only one stream of auditory information at a time. We tested this assumption in a gleaning bat, the pallid bat (*Antrozous pallidus*) because this bat uses echolocation for general orientation, and relies heavily on prey-generated sounds to detect and locate its prey. It may therefore encounter situations in which the echolocation and passive listening streams temporally overlap. Pallid bats were trained to a dual task in which they had to negotiate a wire array, using echolocation, and land on one of 15 speakers emitting a brief noise burst in order to obtain a food reward. They were forced to process both streams within a narrow 300 to 500 ms time window by having the noise burst triggered by the bats' initial echolocation pulses as it approached the wire array. Relative to single task controls, echolocation and passive sound localization performance was slightly, but significantly, degraded. The bats also increased echolocation interpulse intervals during the dual task, as though attempting to reduce temporal overlap between the signals. These results suggest that the bats, like humans, have difficulty in processing more than one stream of information at a time.

Barclay, R.M.R. & Brigham, M.R., 2001. Year-to-year reuse of tree-roosts by California bats (*Myotis californicus*) in southern British Columbia. *The American Midland Naturalist*, 146(1), pp.80–85.

Abstract: To document year-to-year reuse of roost trees by forest-dwelling bats we monitored trees in southern British Columbia that we first identified as maternity roosts of California bats (*Myotis californicus*) in 1995. Initially we identified roost trees by tracking radiotagged individuals. Then we revisited each tree in subsequent years up to 2000. At the start of the study the bats roosted under loose bark or in cavities in dead trees. Seven of eight trees were still standing in 2000, although all had lost bark since 1995, particularly ponderosa pines (*Pinus ponderosa*). In 1995, after radio-tagged bats had moved and the tags had fallen off, trees either were occupied by colonies of 5 to 52 *M. californicus* or they were unoccupied. In contrast, roost counts in subsequent years indicated that colonies rarely used the same trees and most observations were of one or two bats. Thus, while bats continued to use most of the trees over the 5 y period, the numbers of individuals declined and much of the use may have been by males or non-reproductive females. Although our study is preliminary, the results suggest that the suitability of roosts of tree-dwelling bats declines relatively rapidly compared to the loss of the snags themselves. More intensive studies are required given the current focus on preserving roosting habitat for forest-dwelling bats.

Barclay, R. & Cash, K., 1985. A non-commensal maternity roost of the little brown bat (*Myotis lucifugus*). *Journal of Mammalogy*, 66(4), pp.782–783.

No abstract

Bates, M.E. & Simmons, J.A., 2010. Effects of filtering of harmonics from biosonar echoes on delay acuity by big brown bats (*Eptesicus fuscus*). *The Journal of the Acoustical Society of America*, 128(2), pp.936–46.

Abstract: Big brown bats emit FM biosonar sounds containing two principal harmonics (FM1 approximately ~55-22 kHz; FM2 ~ 105-45 kHz). To examine the role of harmonics, they were selectively filtered from stimuli in electronic-echo delay discrimination experiments. Positive stimuli were delayed by 3.16 ms (55 cm simulated target range); negative stimuli were by delayed by 3.96 ms (68 cm). This large 800-µs delay difference (nearly 14 cm) was easily discriminated for echoes containing equal-strength FM1 and FM2. Performance gradually decreased as highpass filters removed progressively larger segments from FM1. For echoes with FM2 alone, performance collapsed to chance, but performance remained good for lowpass echoes containing FM1 alone. Attenuation of FM2 by 3 dB relative to FM1 also decreased performance, but shortening electronic delay of the attenuated FM2 by 48 µs counteracted amplitude-latency trading and restored performance. Bats require the auditory representations of FM1 and FM2 to be in temporal register for high delay acuity. Misalignment of neuronal responses degrades acuity, but outright removal of FM2, leaving only FM1, causes little loss of acuity. Functional asymmetry of harmonics reflects lowpass effects from beaming and atmospheric propagation, which leave FM1 intact. It may cooperate with latency shifts to aid in suppression of clutter.

Batts, S., 2006. The end of "rectrospectacle", the beginning of "of two minds" *Retrospectacle: A Neuroscience Blog*. Online: http://scienceblogs.com/retrospectacle/2006/06/14/a-17khz-pain-in-the-ear/

No abstract

Bayne, E.M., Habib, L. & Boutin, S., 2008. Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. *Conservation Biology*, 22(5), pp.1186–93.

Abstract: The effects of human activities in forests are often examined in the context of habitat conversion. Changes in habitat structure and composition are also associated with increases in the activity of people with vehicles and equipment, which results in increases in anthropogenic noise. Anthropogenic noise may reduce habitat quality for many species, particularly those that rely on acoustic signals for communication. We compared the density and occupancy rate of forest passerines close to versus far from noise-generating compressor stations and noiseless well pads in the boreal forest of Alberta, Canada. Using distance-based sampling, we found that areas near noiseless energy facilities had a total passerine density 1.5 times higher than areas near noise-producing energy sites. The White-throated Sparrow (*Zonotrichia albicollis*), Yellow-rumped Warbler (*Dendroica coronata*), and Red-eyed Vireo (*Vireo olivaceus*) were less dense in noisy areas. We used repeat sampling to estimate occupancy rate for 23 additional species. Seven had lower conditional or unconditional occupancy rates near noise-generating facilities. One-third of the species examined showed patterns that supported the hypothesis that abundance is influenced by anthropogenic noise. An additional 4 species responded negatively to edge effects. To mitigate existing noise impacts on birds would require approximately $175 million. The merits of such an effort relative to other reclamation actions are discussed. Nevertheless, given the $100 billion energy-sector investment planned for the boreal forest in the next 10 years, including noise suppression technology at the outset of construction, makes noise mitigation a cost-effective best-management practice that might help conserve high-quality habitat for boreal birds.

Becker, N.I., Encarnacado, J.A,. Tschapka, M., & Kalko, E.K.V., 2013. Energetics and life-history of bats in comparison to small mammals. *Ecological Research*, 28, pp.249–258.

Abstract: Mammals can be aligned along a slow-fast life-history continuum and a low–high metabolic rate continuum based on their traits. Small non-volant mammals occupy the fast/high end in both continua with high reproductive rates and short life spans linked with high mass-specific metabolic rates. Bats occupy the high end of the metabolic continuum, but the slow end of the life-history continuum with low reproductive rates and long life spans. Typically, both continua are linked, and similar life-history traits of species are reflected in more similar metabolic rates. We therefore hypothesized that metabolic rates are similar in species with similar life-history traits. Resting metabolic rates (RMR) were measured for three ecologically and morphologically similar sympatric bat species (*Myotis nattereri*, *M. bechsteinii*, and *Plecotus auritus*; Vespertilionidae) and compared to data from other similar-sized, temperate insectivorous mammals with other life-history strategies. The bat species share similar life-histories and RMRs, both of which differ from the remaining mammals and therefore supporting our hypothesis. To verify that bats are similar in RMR, two energetically contrasting periods were compared. RMRs in post-lactating females did not differ between bat species. It was,

however, positively correlated with parasite load in both *Myotis* species. However, RMRs differed during energy-demanding pregnancy where *M. nattereri* had the significantly lowest RMR, suggesting metabolic compensation as an energy-saving strategy. We conclude that the energy requirements of bat species with similar life-history traits resemble each other during periods of low energetic demands and are more similar to each other than to other small temperate mammals.

Bee, M.A. & Swanson, E.M., 2007. Auditory masking of anuran advertisement calls by road traffic noise. *Animal Behaviour*, 74(6), 1765–1776.

Abstract: There is growing concern that anthropogenic noise could interfere with animal behaviours by masking the perception of acoustic communication signals. To date, however, few experimental studies have tested this general hypothesis. One common source of anthropogenic noise is the sound of roadway traffic. We tested the hypothesis that road traffic noise can mask a female's perception of male signals in the grey treefrog, *Hyla chrysoscelis*, by comparing the effects of traffic noise and the background noise of a breeding chorus on female responses to advertisement calls. In this species, advertisement calls are necessary and sufficient to attract females for breeding. Using a phonotaxis assay, we presented females with an advertisement call broadcast at one of nine signal levels (37-85 dB, 6-dB steps) in one of three masking conditions: (1) no masking noise, (2) a noise simulating a moderately dense breeding chorus, or (3) a noise modelled after road traffic noise recorded in two wetlands near major roads. Females showed similar increases in response latency and decreases in orientation towards the target signal in the presence of both the chorus noise and the traffic noise maskers. Moreover, response thresholds were elevated by about 20-25 dB in the presence of both noise maskers compared to the unmasked condition. Our results suggest that realistic levels of traffic noise could place constraints on the active space of the acoustic signals of some animals.

Behrend, O. & Schuller, G., 2000. The central acoustic tract and audio-vocal coupling in the horseshoe bat, *Rhinolophus rouxi*. *European Journal of Neuroscience*, 12, pp.4268–4280.

Abstract: Doppler shift compensation (DSC) behaviour in horseshoe bats is a remarkable example of sensorimotor feedback that stabilizes the echo frequency at the bat's optimum hearing range regardless of motion-induced frequency shifts in the echoes. Searching for a related neural interface, the nucleus of the central acoustic tract (NCAT) was investigated in the echolocating horseshoe bat, *Rhinolophus rouxi*, using various neurophysiological and tracer methods. The NCAT receives bilateral auditory input from the cochlear nuclei and sends projections to regions outside the classical acoustic pathway like the pretectal area or the superior colliculus. The binaural input is excitatory from the contralateral and inhibitory from the ipsilateral ear to 53% of the units, and auditory responses were biased to frontal and contralateral directions. The best frequencies of NCAT neurons match a narrow range above the main frequency component of the bat's species-specific echolocation call (62% of the units), and the neurons exhibit extremely sharp tuning (Q_{10dB} up to 632). DSC is degraded by unilateral electrical or pharmacological microstimulation of the NCAT, and heavily impaired by unilateral lesion of the region. Altogether, the efferents of the NCAT to prevocal areas, the tuning of its neurons to the DSC-relevant echo frequency range, and the possibility to affect DSC by manipulation of the NCAT, support the assumption that the nucleus plays an important role in audio-vocal control in the horseshoe bat.

Belknap, D.B. & Suthers, R.A., 1982. Brainstem auditory evoked responses to tone bursts in the echolocating bat, *Rousettus*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 146, pp.283-289.

Summary: 1. Brainstem auditory evoked potentials (BAEPs) from subcutaneous electrodes were obtained from the megachiropteran echolocating bat, *Rousettus aegyptiacus*. 2. BAEP amplitude was measured as a function of a stimulus frequency. The lowest thresholds (defined as a 1 μV averaged response) lay between 10 and 20 kHz, and responses could be obtained from 5 to 45 kHz in most individuals (Fig. 3). Threshold increased at a rate of 30 dB/octave below 10 kHz and 40 dB/octave above 17 kHz. 3. Electrode configuration affected some components of the BAEP waveform (Fig. 1), but not the frequency response of the BAEP (Fig. 3). Pentobarbital anesthesia raised BAEP thresholds at all frequencies tested (Fig. 4), when compared with the unanesthetized state. BAEP thresholds were not affected by changes in deep rectal temperature in the range of 29–30 °C (Fig. 4). 4. Comparison of the BAEP frequency response curve with the behavioral audiogram (Fig. 6) suggests that it is an accurate predictor of the region of greatest auditory sensitivity.

Bell, G.P., 1985. The sensory basis of prey location by the California leaf-nosed bat *Macrotus californicus* (Chiroptera: Phyllostomidae). *Behavioral Ecology and Sociobiology*, 16(4), pp.343–347.

Abstract: Macrotus californicus, an insectivorous bat, captures prey on the ground, and shows great sensory flexibility in hunting for prey: it uses high frequency, low intensity, frequency modulated echolocation to locate prey in total darkness, however data from this study suggest that it uses vision preferentially, and switches off its echolocation when adequate illumination is available. When sounds of prey are available it exploits these also. It uses echolocation only 50% of the time at 4.2×10^{-2} mL, comparable to ground luminance on a brightly moonlit night, and employs vision even at 10^{-3} mL.

Bell, G.P. & Fenton, M.B., 1986. Visual acuity, sensitivity and binocularity in a gleaning insectivorous bat, *Macrotus californicus* (Chiroptera: Phyllostomidae). *Animal Behaviour*, 34, pp.409-414.

Abstract: Behavioural tests were used to examine the visual acuity and sensitivity of *Macrotus californicus,* a 12-14-g desert bat known to use vision in the location of terrestrial prey. Optomotor responses indicate single point visual acuity as fine as 3'38" of arc. For comparison, the same tests were applied to two other species of bats. *Antrozous pallidus,* a desert gleaner which locates prey by the sounds they produce, exhibited acuity of 15' of arc, and *Eptesicus fuscus,* an aerial foraging species that uses echolocation to find prey, 60' of arc. Both *M. californicus* and *A. pallidus* retained their acuity at light levels as low as 2×10^{-4} mL (approximately 2×10^{-3} lux), comparable to ground luminance on a clear, moonless night. The eyes of *M. californieus* were more anteriorly directed, and had twice the binocular overlap of the other species examined. Comparison of our data with results from other studies indicate that *M. californicus* has vision superior to other insectivorous bats, and at least equivalent to larger-eyed frugivorous and nectarivorous bats examined in previous studies.

Bender, H., 2006. Structure and function of the eastern grey kangaroo (*Macropus giganteus*) foot thump. *Journal of Zoology*, 268(4), pp.415–422.

Abstract: Most species of the family Macropodidae (kangaroos and wallabies) make a distinctive foot thump by striking the ground with their hind feet when they detect potential danger. I used the eastern grey kangaroo *Macropus giganteus* as a model to examine (1) the acoustic characteristics and structure of the thump, (2) the social context in which free-ranging kangaroos thumped when approached by a human observer on foot and (3) the intended recipient of the signal. Thumps were about two-thirds of a second in length, generally composed of two noisy pulses, and had the majority of the signal energy below 7 kHz. Only adult kangaroos, of both sexes, were observed to thump. A higher proportion of solitary kangaroos thumped than grouped kangaroos, and a higher proportion of kangaroos thumped when visibility was poor, either because of habitat type or low light levels. Given the context in which thumps were given, the foot thump appears to be a signal to a potential predator with three possible functions: to startle, signal detection or deter pursuit.

Benítez-López, A., Alkemade, R. & Verweij, P. A., 2010. The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. *Biological Conservation*, 143(6), pp.1307–1316.

Abstract: Biodiversity is being lost at an increased rate as a result of human activities. One of the major threats to biodiversity is infrastructural development. We used meta-analyses to study the effects of infrastructure proximity on mammal and bird populations. Data were gathered from 49 studies on 234 mammal and bird species. The main response by mammals and birds in the vicinity of infrastructure was either avoidance or a reduced population density. The mean species abundance, relative to non-disturbed distances (MSA), was used as the effect size measure. The impact of infrastructure distance on MSA was studied using meta-analyses. Possible sources of heterogeneity in the results of the meta-analysis were explored with meta-regression. Mammal and bird population densities declined with their proximity to infrastructure. The effect of infrastructure on bird populations extended over distances up to about 1 km, and for mammal populations up to about 5 km. Mammals and birds seemed to avoid infrastructure in open areas over larger distances compared to forested areas, which could be related to the reduced visibility of the infrastructure in forested areas. We did not find a significant effect of traffic intensity on the MSA of birds. Species varied in their response to infrastructure. Raptors were found to be more abundant in the proximity of infrastructure whereas other bird taxa tended to avoid it. Abundances were affected at variable distances from infrastructure: within a few meters for small-sized mammals and up to several hundred meters for large-sized mammals. Our findings show the importance of minimizing infrastructure development for wildlife conservation in relatively undisturbed areas. By combining actual species distributions with the effect distance functions we developed, regions sensitive to infrastructure development may be identified. Additionally, the effect distance functions can be used in models in support of decision making on infrastructure planning.

Bennett, V.J., Sparks, D.W., & Zollner, P.A., 2013. Modeling the indirect effects of road networks on the foraging activities of bats. *Landscape Ecology*, 28, 979–991.

Abstract: Negative impacts of road networks on wildlife are of global concern. While direct mortality of wildlife via roads has been well-documented, we know little about indirect effects of roads. Using a simulation model parameterized from empirical data, we explored how roads in proximity to maternity roosts influenced foraging activities of the endangered Indiana bat. First, we conducted manipulated landscape simulations to identify characteristics (such as traffic

volume, foraging habitat availability, etc.) that influenced landscape permeability. We used a classification and regression tree procedure to assess which landscape and road-related variables, alone or in combination, influenced bat movement. We determined that roads did act as filters (> 10 vehicles/5 min) or barriers (> 200 vehicles/5 min) to movement. However, it is a combination of the proportion of foraging habitat accessible without crossing a road, and roost-to-road distance that dictated whether the barrier and filter effects of roads hindered the bats' foraging abilities. We then simulated movement patterns and foraging success of Indiana bats at 32 existing maternity roosts to identify conditions under which colonies currently persist. We established a foraging success threshold, above which Indiana bats currently persist. The value represents the time virtual bats spend in foraging habitat during the simulation period. Finally, simulations from these landscapes around known maternity roosts demonstrate that the road network and landscape configuration are critical to foraging success. This modeling approach and threshold value are beneficial to road developers and represent an invaluable tool in the ecological design of transportation infrastructures.

Bennett, V.J. & Zurcher, A.A., 2013. When corridors collide: Road-related disturbance in commuting bats. *The Journal of Wildlife Management*, 77(1), pp.93–101.

Abstract: As an increasingly dominant feature in the landscape, transportation corridors are becoming a major concern for bats. Although wildlife–vehicle collisions are considered to be a major source of mortality, other negative implications of roads on bat populations are just now being realized. Recent studies have revealed that bats, like many other wildlife species, will avoid roads rather than cross them. The consequence is that roads act as barriers or filters to movement, restricting bats from accessing critical resources. Our objective was to assess specific features along the commuting route, road, or surrounding landscape (alone or in combination) that exacerbated or alleviated the likelihood of a commuting bat exhibiting an avoidance behavior in response to an approaching vehicle. At 5 frequently used commuting routes bisected by roads, we collected data on vehicles travelling along the roads (such as visibility and audibility), commuting bats (such as height), and composition of the commuting route. We revealed that commuting route structure dictated the frequency at which bats turned back along their commuting routes and avoided the road. We found that gaps (>2 m) in commuting routes, such as the road itself, caused bats to turn away just before they reached the road. Furthermore, we found that turning frequencies of bats increased with vehicle noise levels and the locations at which bats responded to vehicles corresponded with areas where noise levels were greatest, including gaps <2 m. This suggested that bats had a disturbance threshold, and only reacted to vehicles when associated noise reached a certain level. We found that threshold levels for our study species were approximately 88 dB, but this value was likely to vary among species. Thus, our findings indicate that restoring (e.g., replanting native trees and shrubs in gaps) and establishing commuting routes (such as planting tree-lines and wooded hedgerows), as well as creating road-crossing opportunities (such as interlinking canopies) will improve the permeability of a road-dominated landscape to bats. Furthermore, our study highlights the influence of the soundscape. We recommend that effective management and mitigation strategies should take into account the ecological design of the acoustic environment.

Berthinussen, A. & Altringham, J., 2012. Do bat gantries and underpasses help bats cross roads safely? *PloS One*, 7(6), p.e38775.

Abstract: Major roads can reduce bat abundance and diversity over considerable distances. To mitigate against these effects and comply with environmental law, many European countries install bridges, gantries or underpasses to make roads permeable and safer to cross. However, through lack of appropriate monitoring, there is little evidence to support their effectiveness. Three underpasses and four bat gantries were investigated in northern England. Echolocation call recordings and observations were used to determine the number of bats using underpasses in preference to crossing the road above, and the height at which bats crossed. At gantries, proximity to the gantry and height of crossing bats were measured. Data were compared to those from adjacent, severed commuting routes that had no crossing structure. At one underpass 96% of bats flew through it in preference to crossing the road. This underpass was located on a pre-construction commuting route that allowed bats to pass without changing flight height or direction. At two underpasses attempts to divert bats from their original commuting routes were unsuccessful and bats crossed the road at the height of passing vehicles. Underpasses have the potential to allow bats to cross roads safely if built on pre-construction commuting routes. Bat gantries were ineffective and used by a very small proportion of bats, even up to nine years after construction. Most bats near gantries crossed roads along severed, pre-construction commuting routes at heights that put them in the path of vehicles. Crossing height was strongly correlated with verge height, suggesting that elevated verges may have some value in mitigation, but increased flight height may be at the cost of reduced permeability. Green bridges should be explored as an alternative form of mitigation. Robust monitoring is essential to assess objectively the case for mitigation and to ensure effective mitigation.

Berthinussen, A. & Altringham, J., 2012. The effect of a major road on bat activity and diversity. *Journal of Applied Ecology*, 49(1), pp.82–89.

Abstract: 1. It is well known that roads can have a significant impact, usually negative, on species and ecosystems. However, despite their protected status in many countries, little research has been done into the effects of roads on bats. With a view to making more informed management recommendations, we address the simple question: are bat activity and diversity (as measured with ultrasonic detectors) correlated with distance from a major road? 2. Broadband acoustic surveys were conducted on 20 walked transects perpendicular to the M6, a major road in Cumbria (UK), with bat activity recorded at eight spot checks per transect at different distances from the road. Climatic and habitat variables were also recorded, and the relationships between bat activity and these variables were investigated using generalised estimated equations (GEE) and ordinal logistic regression. 3. Total bat activity, the number of species and the activity of *Pipistrellus* (the most abundant species) were all positively correlated with distance from the road. Total activity increased more than threefold between 0 and 1600 m from the road. These effects were found to be consistent over 2 years. 4. Synthesis and applications. This study is one of the first to show that roads have a major negative impact on bat foraging activity and diversity and is broadly applicable to insectivorous bat communities worldwide. Mitigation requires that roads are made more permeable to bats through the use of effective crossings, such as underpasses and overpasses, and that habitat is improved within 1 km of major roads. Because the effectiveness of current mitigation measures is unknown, well-designed monitoring of mitigation is essential.

Blake, D., Hutson, A.M., Racey, P.A., Rydell, J. & Speakman, J.R., 1994. Use of lamplit roads by foraging bats in southern England. *Journal of Zoological Society London*, 234, pp.453–462.

Abstract: Roads illuminated by white streetlamps attracted three times more foraging bats (mostly *Pipistrellus pipistrellus*) than did roads lit by orange streetlamps or unlit roads (3.2, 1.2 and 0.7 bat passes/km, respectively). More insects flew around white lamps than around orange lamps (mean 0.67 and 0.083 insects per lamp, respectively). The mean number of bat passes recorded in any 1-km section of road was positively correlated to the number of white streetlamps along the section, and also, independently, to the amount of trees and hedgerows. Bat activity was not related to the number of houses along the road, ambient temperature or cloud cover. The attractive effect of the lamps on the bats was diminished in windy weather.

Blumenfeld, D.E. & Weiss, G.H., 1975. Attenuation effects in the propagation of traffic noise. *Transportation Research*, 9(2), pp.103–106.

Abstract: The theory of traffic noise in terms of a generalized shot noise model has been developed by several authors. This paper considers the effects of nongeometric attenuation, represented as a negative exponential absorption factor on the calculation of cumulants of the noise intensity. This absorption would arise from sound propagation through tree zones or shrubbery.

Blumenrath, S. & Dabelsteen, T., 2004. Degradation of great tit (*Parus Major*) song before and after foliation: Implications for vocal communication in a deciduous forest. *Behaviour*, 141(8), pp.935–958.

Abstract: Songbirds living in temperate forests experience great seasonal changes in habitat acoustics during the part of the breeding season when singing activity is high. These changes, which are brought about by accelerated vegetation growth and leaf burst in spring, affect sound propagation and potentially render vocal communication more difficult as the total number of scattering and absorbing obstacles increases. We investigated this in a sound transmission experiment in which representative great tit (*Parus major*) songs were broadcast in a typical forest habitat before and after foliation. Speaker and microphone were placed at natural separation distances and in typical sender and receiver positions. For each song note we quantified several aspects of sound degradation and found that they all increased considerably when leaves were present. Before foliation the same amount of degradation would only be obtained by doubling the transmission distance, i.e. foliage shortens the active space of great tit song. This inevitably alters distance information, provided that distance-dependent, structural changes of received songs are used as ranging cues. Moreover, sender and receiver positions within the canopy become unfavourable compared to heights just below the canopy when the aim is to maximise song propagation distances. Altogether, the presence of foliage greatly affects the potential for vocal information transfer in great tits and requires behavioural and/or perceptual adjustment of the communicating individuals to counteract or reduce the impact of foliage on signal degradation.

Bogdanowicz, W., Fenton, M.B. & Daleszczyk, K., 1999. The relationships between echolocation calls, morphology and diet in insectivorous bats. *Journal of Zoology*, 247(3), pp.381–393.

Abstract: In this study we explored quantitatively the relationships between the size of bats, the frequencies in their echolocation calls, and the incidence of moths and beetles in their diets. We focused on the predictions of the allotonic frequency hypothesis which states that some insectivorous bats increase their access to moths that can hear echolocation calls by shifting to frequencies to which the ears of these insects are less sensitive. The hypothesis predicts that the frequencies dominating the echolocation calls of bats may be correlated with the incidence of moths in their diets. We collected data for 62 species of bats that take airborne prey, usually flying insects, 25 species of high duty cycle echolocating bats (Rhinolophidae and Hipposideridae) and 37 species that are low duty cycle echolocators (Vespertilionidae and Molossidae). For bats whose echolocation calls are dominated by frequencies < 100 kHz our regression analyses showed a parabolic dependency between moth consumption (% volume or % frequency) and echolocation call frequency (kHz), supporting the allotonic frequency hypothesis. The use of echolocation calls dominated by frequencies outside the range of best hearing by moths may indeed increase the availability of these insects to the bats. However, when the same analysis was performed with only the bat species using echolocation calls dominated by sounds > 100 kHz, the relationship was not statistically significant, suggesting that morphological characteristics rather than echolocation call frequency may limit the range of potential prey items. Our analyses also demonstrate the importance of jaw morphology as a predictor of the incidence of beetles or moths in the diets of bats, and reveal that generally bigger species (as defined by forearm length) use echolocation calls dominated by lower frequencies than smaller species. In both high duty and low duty cycle echolocating bats the relationship between body size and dominant call frequency was best described by a linear model. We also propose that perch hunting was central in the development of the high duty cycle approach to echolocation.

Bohn, K.M., Smarsh, G.C. & Smotherman, M., 2013. Social context evokes rapid changes in bat song syntax. *Animal Behaviour*, 85(6), pp.1485–1491.

Abstract: The capacity to modify vocal syntax to changes in social context is an important component of vocal plasticity and complexity in adult vertebrates, especially in human speech. The ecological significance of this behaviour has been well established in some avian species but not in mammals where complex, multisyllabic vocalizations are rare. The Brazilian free-tailed bat, *Tadarida brasiliensis*, is a mammal that sings like a bird, producing hierarchically structured songs that vary in the order and number of phrases (i.e. syntax) from one rendition to the next while simultaneously following specific organizational rules. Here, we used playback experiments to examine the function of songs and tested whether song syntax is correlated with social context. Free-tailed bats responded rapidly and robustly to echolocation calls that mimicked a bat flying past the roost but did not respond to conspecific song playbacks. We compared songs that were directed at a passing bat with songs that were produced spontaneously and found that bats produced longer songs with different phrase content and order when singing spontaneously than when singing to bats approaching their roost. Thus, free-tailed bats quickly varied song composition to meet the specific demands of different social functions. These distinct singing behaviours are similar to those of some songbirds, suggesting that bats and birds have converged upon a similar set of production modes that may reflect common neural mechanisms and ecological factors.

Boonman, A.M., Parsons, S. & Jones, G., 2003. The influence of flight speed on the ranging performance of bats using frequency modulated echolocation pulses. *The Journal of the Acoustical Society of America*, 113(1), pp.617–628.

Abstract: Many species of bat use ultrasonic frequency modulated (FM) pulses to measure the distance to objects by timing the emission and reception of each pulse. Echolocation is mainly used in flight. Since the flight speed of bats often exceeds 1% of the speed of sound, Doppler effects will lead to compression of the time between emission and reception as well as an elevation of the echo frequencies, resulting in a distortion of the perceived range. This paper describes the consequences of these Doppler effects on the ranging performance of bats using different pulse designs. The consequences of Doppler effects on ranging performance described in this paper assume bats to have a very accurate ranging resolution, which is feasible with a filterbank receiver. By modeling two receiver types, it was first established that the effects of Doppler compression are virtually independent of the receiver type. Then, used a cross-correlation model was used to investigate the effect of flight speed on Doppler tolerance and range–Doppler coupling separately. This paper further shows how pulse duration, bandwidth, function type, and harmonics influence Doppler tolerance and range–Doppler coupling. The influence of each signal parameter is illustrated using calls of several bat species. It is argued that range–Doppler coupling is a significant source of error in bat echolocation, and various strategies bats could employ to deal with this problem, including the use of range rate information are discussed.

Boonman, M., 2011. Factors determining the use of culverts underneath highways and railway tracks by bats in lowland areas. *Lutra*, 54(1), pp.3–16.

Abstract: In urbanising environments the construction of suitable underpasses for bats under highways and railway tracks is becoming increasingly important to avoid habitat fragmentation. Culverts provide valuable and low cost underpasses as they are already an intrinsic part of highway design and many bat species associated with water are likely to follow the streams or canals that flow through them. Bat detectors were employed to study the use of 54 culverts by bats in the Netherlands. The aim of the study was to define the factors that determine bats' use of culverts. Bats were observed in the vast majority of the culverts that were studied, thereby underlining the importance of culverts in habitat de-fragmentation. Species adapted to hunting in open habitats, such as the noctule (*Nyctalus noctula*) and the serotine (*Eptesicus serotinus*), were often recorded in front of the entrance but rarely inside culverts. For the three species that were regularly recorded inside culverts, Daubenton's bat (*Myotis daubentonii*), the pond bat (*Myotis dasycneme*) and the common pipistrelle (*Pipistrellus pipistrellus*), cross sectional area was the most important factor that determined their use of culverts. Height was the most important component of cross sectional area for bats. Length proved a non-significant factor, suggesting that bat underpasses are not affected by the widening of the above-lying infrastructure. Additional guidance by treelines along the banks did not increase the use of culverts by the three species. The implication of the different preferences for cross sectional area on the design of infrastructure is discussed.

Braun, M., 1994. Tuned hair cells for hearing, but tuned basilar membrane for overload protection: Evidence from dolphins, bats, and desert rodents. *Hearing Research*, 78(1), pp.98–114.

Abstract: cochlear model is presented suggesting that the organ of Corti (OC) and the basilar membrane (BM) are both tuned resonant systems, but have different functions. The OC provides frequency filtering and amplification by means of tuned outer hair cells. The BM provides resonant absorption of excessive vibrational energy as an overload protection for vulnerable elements in the OC. Evidence supporting this model is demonstrated in dolphins, bats, and desert rodents. Specialized auditory capabilities correlate with cochlear deviations, some of them dramatically changing BM compliance. In characteristic regions along the cochlea there are BM thickenings and, on both sides of the OC, hypertrophied supporting cells. Structures of striking similarity have evolved independently across orders or families, revealing multiple events of convergent evolution. In all cases, the locations of deviating structures rule out a BM function in auditory frequency selectivity but support one in resonant absorption. Cochlear microphonics and BM responses demonstrate strongest high-level absorption in the frequency bands most vital for the tested species. The assumed cause is increased internal damping in the enlarged structures during BM motion. Species with intermediate specializations supply further evidence that resonant absorption is universally the genuine function of BM mechanics in mammals, providing complementary high-level protection of low-level sensitivity.

Brinklov, S., Fenton, M.B. & Ratcliffe, J.M., 2013. Echolocation in oilbirds and swiftlets. *Frontiers in Physiology*, 41, pp.1-12.

Abstract: The discovery of ultrasonic bat echolocation prompted a wide search for other animal biosonar systems, which yielded, among few others, two avian groups. One, the South American Oilbird (*Steatornis caripensis*: Caprimulgiformes), is nocturnal and eats fruit. The other is a selection of diurnal, insect-eating swiftlets (species in the genera *Aerodramus* and *Collocalia*: Apodidae) from across the Indo-Pacific. Bird echolocation is restricted to lower frequencies audible to humans, implying a system of poorer resolution than the ultrasonic (>20 kHz) biosonar of most bats and toothed whales. As such, bird echolocation has been labeled crude or rudimentary. Yet, echolocation is found in at least 16 extant bird species and has evolved several times in avian lineages. Birds use their syringes to produce broadband click-type biosonar signals that allow them to nest in dark caves and tunnels, probably with less predation pressure. There are ongoing discrepancies about several details of bird echolocation, from signal design to the question about whether echolocation is used during foraging. It remains to be seen if bird echolocation is as sophisticated as that of tongue-clicking rousette bats. Bird echolocation performance appears to be superior to that of blind humans using signals of notable similarity. However, no apparent specializations have been found so far in the birds' auditory system (from middle ear to higher processing centers). The advent of light-weight recording equipment and custom software for examining signals and reconstructing flight paths now provides the potential to study the echolocation behavior of birds in more detail and resolve such issues.

Britzke, E.R., Gillam, E.H. & Murray, K.L., 2013. Current state of understanding of ultrasonic detectors for the study of bat ecology. *Acta Theriologica*, 58(2), pp.109–117.

Abstract: Ultrasonic detectors have become a mainstay for studying the ecology of bats throughout the world. Despite their enormous utility to address a wide variety of research and management issues, many factors that impact the applicability of collected data for answering desired questions are often ignored. Here, we review our current understanding of the utility of ultrasonic detectors for the study of bat ecology and highlight areas where additional work should be done. We gleaned information from published studies, as well as from field research

experience, and discuss areas that are in need of further research. We highlight topics such as sampling design and how it can impact results, metrics used to quantify bat activity, and identifying bats with acoustic data including how accuracy rates can be maximized. We also provide research questions that when answered will greatly improve the applicability of future studies.

Broders, H.G., Findlay, C.S. & Zheng, L., 2004. Effects of clutter on echolocation call structure of *Myotis septeptentrionalis* and *M. lucifugus*. *Journal of Mammalogy*, 85(2), pp.273–281.

Abstract: The structure of echolocation calls, and the distance over which bats perceive their environment, varies with the amount of structural clutter through which they are flying. Clutter and species had significant effects on the frequency-time characteristics of search-phase echolocation calls of northern long-eared (*Myotis septentrionalis*) and little brown bats (*M. lucifugus*). We tested an a priori derived model that predicted the pattern of differences in echolocation call variable values among clutter categories would provide insight into the relative maximum distances that bat species could perceive using echolocation. Specifically, the model predicted that species adapted to flying and foraging in cluttered habitats would have a shorter maximum perceptual distance than species adapted to flying and foraging in uncluttered habitats. The results supported this model and suggest the clutter-adapted *M. septentrionalis* had a shorter maximum perceptual distance than *M. lucifugus*, a species known to forage in a variety of habitats but mainly in uncluttered areas (i.e., over water). Using calls as the sampling unit, a neural network correctly classified .94% of the echolocation calls to species in high clutter. In medium and low clutter, .82% of the calls were correctly classified to species; however .90% correct classification was achieved by leaving, 30% of calls unclassified. Researchers should develop clutter-specific call libraries to improve species classification accuracy for echolocation calls.

Brown, C.L., Reed, S.E., Dietz, M.S. & Fristrup, K.M., 2013. Detection and classification of motor vehicle noise in a forested landscape. *Environmental Management*, 52(5), pp.1262–70.

Abstract: Noise emanating from human activity has become a common addition to natural soundscapes and has the potential to harm wildlife and erode human enjoyment of nature. In particular, motor vehicles traveling along roads and trails produce high levels of both chronic and intermittent noise, eliciting varied responses from a wide range of animal species. Anthropogenic noise is especially conspicuous in natural areas where ambient background sound levels are low. In this article, we present an acoustic method to detect and analyze motor vehicle noise. Our approach uses inexpensive consumer products to record sound, sound analysis software to automatically detect sound events within continuous recordings and measure their acoustic properties, and statistical classification methods to categorize sound events. We describe an application of this approach to detect motor vehicle noise on paved, gravel, and natural-surface roads, and off-road vehicle trails in 36 sites distributed throughout a national forest in the Sierra Nevada, CA, USA. These low-cost, unobtrusive methods can be used by scientists and managers to detect anthropogenic noise events for many potential applications, including ecological research, transportation and recreation planning, and natural resource management.

Brown, P.E., Grinnell, A.D. & Harrison, J.B., 1978. The development of hearing in the pallid bat, *Antrozous pallidus*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 126, pp.169–182.

Summary: 1. Adult pallid bats possess auditory capabilities similar to those of other echolocating Vespertilionids, albeit with unusually great sensitivity to frequencies below 15 kHz. 2. Newborn bats show no behavioral or neurophysiological responses to auditory stimuli. 3. Evoked potentials were detected first in a six day old bat in response to loud, low frequency sound. Absolute sensitivity and frequency range increase rapidly in the maturing bat. By 24 days, the evoked potential audiogram resembles that of an adult. 4. Except for the first week after birth, the infant bat emits only sounds with dominant frequencies it can hear. 5. The bat's auditory responsiveness is affected by low temperatures. In the anesthetized bat, cooling will produce a shift in the tuning curve toward lower frequencies. This is accompanied by a loss of sensitivity to higher frequencies with an increase in latency and a decrease in amplitude of the response. This occurred in both adult and juvenile bats. In bats less than two weeks old, all auditory responses disappear below 28 °C. The high degree of temporal resolution typical of adult Vespertilionids develops gradually in bats less than two weeks old. In young bats, 40 ms or longer are required for full recovery to the second of two identical stimuli, in contrast to 4 ms in the adult. By the time a bat flies at the age of one month, good temporal resolution has developed. 7. Collicular evoked potentials are relatively insensitive to angle of incidence of the signal, but single units show sharp directionality. This appears to develop mostly after about 3 weeks of age and suggests that binaural interaction matures relatively late in development.

Brumm, H. & Slabbekoorn, H., 2005. Acoustic communication in noise. *Advances in the Study of Behaviour*, 35, pp.151–209.

No abstract

Brumm, H., Voss, K., Kollmer, I. & Todt, D., 2004. Acoustic communication in noise: regulation of call characteristics in a New World monkey. *Journal of Experimental Biology*, 207, 443-448.

Abstract: This study on common marmosets *Callithrix jacchus* is the first to examine noise-dependent mechanisms of vocal plasticity in a New World monkey. Since acoustic communication can be considerably impaired by environmental noise, some animals have evolved adaptations to counteract its masking effects. The studied marmosets increased the sound level of their spontaneous calls in response to increased levels of white noise broadcast to them. Possibly, such noise-dependent adjustment of vocal amplitude serves to maintain a specific signal-to-noise ratio that is favourable for signal production. Concurrently, the adjustment of vocal amplitude can maintain a given active space for communication. In contrast to some bird species, no noise induced increase in the number of syllables per call series could be found, showing that an increased serial redundancy of vocal signals was not used to communicate under noisy conditions. Finally, we examined a possible noise-dependent prolongation of vocal signals. This approach was guided by the findings of perceptional studies, which suggest an increased detection probability of prolonged signals in noise by temporal summation. Marmosets indeed increased the duration of their call syllables along with increasing background noise levels. This is the first evidence of such mechanism of vocal plasticity in an animal communication system.

Buchalski, M.R., Fontaine, J.B., Heady III, P.A., Hayes, J.P. & Frick, W.F., 2013. Bat response to differing fire severity in mixed-conifer forest California, USA. *PloS One*, 8(3), p.e57884.

Abstract: Wildlife response to natural disturbances such as fire is of conservation concern to managers, policy makers, and scientists, yet information is scant beyond a few well-studied groups (e.g., birds, small mammals). We examined the effects of wildfire severity on bats, a tax on of high conservation concern, at both the stand (<1 ha) and landscape scale in response to the 2002 McNally fire in the Sierra Nevada region of California, USA. One year after fire, we conducted surveys of echolocation activity at 14 survey locations, stratified in riparian and upland habitat, in mixed-conifer forest habitats spanning three levels of burn severity: unburned, moderate, and high. Bat activity in burned areas was either equivalent or higher than in unburned stands for all six phonic groups measured, with four groups having significantly greater activity in at least one burn severity level. Evidence of differentiation between fire severities was observed with some *Myotis* species having higher levels of activity in stands of high-severity burn. Larger-bodied bats, typically adapted to more open habitat, showed no response to fire. We found differential use of riparian and upland habitats among the phonic groups, yet no interaction of habitat type by fire severity was found. Extent of high-severity fire damage in the landscape had no effect on activity of bats in unburned sites suggesting no landscape effect of fire on foraging site selection and emphasizing stand-scale conditions driving bat activity. Results from this fire in mixed-conifer forests of California suggest that bats are resilient to landscape-scale fire and that some species are preferentially selecting burned areas for foraging, perhaps facilitated by reduced clutter and increased post-fire availability of prey and roosts.

Bullen, R. & Fricke, F., 1982. Sound propagation through vegetation. *Journal of Sound and Vibration*, 80(1), pp.11–23.

Abstract: The propagation of sound through a large number of scatterers (i.e., trees) is treated in a similar way to a classical diffusion problem. A general differential equation governing the sound intensity is derived which is valid under certain conditions, notably that the depth of the belt of vegetation is large, and absorption small. The predictions of this theory are compared with results derived from a small scale model study, and with some field measurements. They are also compared with published field data. The implications of some of the conclusions reached for the practical achievement of effective sound attenuation are pointed out. In general, it would appear that significant noise reductions may be achieved for a predominantly high frequency source if the existing ground cover is acoustically hard, or if there is no "ground effect" attenuation between source and receiver for some other reason. In other cases, the noise reduction will be much lower and may be negative.

Bunkley, J.P. & Barber, J.R., 2015. Noise reduced foraging efficiency in pallid bats (*Antrozous pallidus*). *Ethology*, 121(11), pp.1116-1121.

Abstract: Anthropogenic noise is an emerging global pollutant. Road networks and energy extraction infrastructure are both spatially extensive and rapidly expanding sources of noise. We predict that predators reliant on acoustic cues for hunting are particularly sensitive to louder environments. Here we examined the foraging efficiency of pallid bats (*Antrozous pallidus*) when exposed to played-back traffic and gas compressor station noise in the laboratory. We show that both types of noise at each of five exposure levels (58–76 dBA, 10–640 m from

source) and low-level amplifier noise (35 dBA) increase the time required for bats to locate prey-generated sounds by twofold to threefold. The mechanism underlying these findings is unclear and, given the potential landscape-level habitat degradation indicated by our data, we recommend continued research into the effects of noise exposure on acoustically specialized predators.

Burnett, C.D. & August, P.V., 1981. Time and energy budgets for day roosting in a maternity colony of *Myotis lucifugus*. *Journal of Mammalogy*, 62(4), p.758.

Abstract: Day roosting behavior of the little brown bat (*Myotis lucifugus*) was observed in a maternity colony located in central Massachusetts. The percentages of time spent in various activities were: resting 79%, grooming 14%, active 5%, and moving 1%. Significant differences were found in the amount of time allocated to these activities by bats occupying different positions within clusters and for different times of day and year. Conspecific interactions were restricted to the period of cluster formation at dawn when late returning bats attempted to obtain central positions within groups. Using two measures of roost temperature, the energetic cost of day roosting was estimated to be 3.13-7.35 kJ, or 12-24% of the daily energy budget. Nonresting behavior, primarily grooming, accounted for more than half of the energy expended during the day roosting period.

California Department of Transportation (Caltrans) 2006. CALTRANS Standard Environmental Reference Vol 3. Biological Resources. Online: http://www.dot.ca.gov/ser/vol3/vol3.htm

No abstract

California Department of Transportation (Caltrans) 2009. Chapt 30. Highway Traffic Noise Abatement. In Project Development Procedures Manual. pp. 1–19.

Abstract: Caltrans' noise abatement policy addresses the public's sensitivity to highway generated noise and the requirements for considering construction of noise abatement facilities when they are reasonable and feasible. The abatement of highway traffic noise is a design consideration that is required by State and federal statutes and regulations and by Caltrans' policy. As part of the general environmental review process associated with all projects, project sponsors are required to evaluate if the project could result in substantially increased noise levels (termed "noise impact"); and when "reasonable" and "feasible", consider attenuating this increased noise. Using this policy and procedures, environmental studies may result in recommendations that proposed projects consider noise abatement to protect specific properties, along with preliminary designs for the abatement facilities. The Project Engineer (PE) should work with the Environmental unit in determining those preliminary designs. Later, as project details are developed, it is the responsibility of the PE to determine the feasibility and reasonableness of constructing the noise abatement facility; specifically where noise abatement facilities will be constructed, materials to be used and various other design details. Once these details have been determined, they should be reviewed by the District Environmental Unit and concurrence obtained. This Chapter provides basic guidelines to assist the PE in making the decisions they are responsible for. Specific structural and architectural design features of noise barriers, as well as other noise abatement facilities, are covered in other Caltrans manuals and the Standard Plans. The three basic types of projects involving noise abatement include: • The

construction of new highways or the reconstruction of existing highways (see Chapter 2 – Roles and Responsibilities). • The construction of noise abatement features to retrofit existing freeways through residential areas (Community Noise Abatement Program). • The construction of noise abatement features to retrofit existing freeways to reduce the level of freeway traffic noise that intrudes into public and privately owned primary and secondary schools. School noise abatement projects may be proposed as an element of the State Highway Operation and Protection Program (SHOPP).

California Department of Transportation (Caltrans) 2011. Traffic Noise Analysis Protocol for New Highway Construction, Reconstruction, and Retrofit Barrier Projects. May. California Department of Transportation Division of Environmental. Online: http://www.dot.ca.gov/hq/env/noise/pub/ca_tnap_may2011.pdf

No abstract

California Department of Transportation (Caltrans) 2013. Technical Noise Supplement to the Traffic Noise Analysis Protocol,

Abstract: This manual contains Caltrans noise analysis procedures, practices, and other useful technical background information related to the analysis and reporting of highway and construction noise impacts and abatement. It supplements and expands on concepts and procedures referred to in the Traffic Noise Analysis Protocol, which in turn is required by federal regulations in 23CFR772. The contents of this document are not official policy, standard, or regulation, and are for informational purposes—unless they are referenced in the Protocol. Except for some Caltrans-specific methods and procedures, most methods and procedures recommended in this document are in conformance with industry standards and practices. This document can be used as a stand-alone guide for highway noise training purposes or as a reference for technical concepts, methodology, and terminology needed to acquire a basic understanding of highway noise and construction noise-related issues.The TeNS consists of eight sections. Except for Section 1, each covers a specific subject of highway noise. A brief description of the subjects follows. Section 1, Introduction and Overview, summarizes the subjects covered in the TeNS. Section 2, Basics of Highway Noise, covers the physics of sound as it pertains to characteristics and propagation of highway noise, effects of noise on humans, and ways of describing noise. Section 3, Measurements and Instrumentation, provides background information on noise measurements, and discusses various noise-measuring instruments and operating procedures. Section 4, Detailed Analysis for Traffic Noise Impacts, provides guidance for conducting detailed traffic noise impact analysis studies. This section includes identifying land use, selecting receptors, determining existing noise levels, predicting future noise levels, and determining impacts. Section 5, Detailed Analysis for Noise Barrier Design Considerations, outlines the major aspects that affect the acoustical design of noise barriers, including the dimensions, location, and material; optimization of noise barriers; possible noise reflections; acoustical design of overlapping noise barriers (to provide maintenance access to areas behind barriers); and drainage openings in noise barriers. Challenges and cautions associated with noise barrier design are also discussed. Section 6, Noise Study Reports, discusses the contents of noise study reports. Section 7, Non-Routine Considerations and Issues, covers non-routine situations involving the effects of noise on distant receptors, use of sound intensity and sound power as tools in characterizing sound sources, pavement noise, noise monitoring for insulating facilities, construction noise, earthborne vibrations, California

Occupational Safety and Health Administration (OSHA) noise standards, and effects and abatement of transportation-related noise on marine and wildlife. Section 8, Glossary, provides terminology and definitions common in transportation noise. Appendix A, References Cited, provides a listing of literature directly cited or used for reference in the TeNS.

Carter, G.G., Logsdon, R., Arnold, B.D., Menchaca, A. & Medellin, R.A., 2012. Adult vampire bats produce contact calls when isolated: acoustic variation by species, population, colony, and individual. *PloS One*, 7(6), p.e38791.

Abstract: BACKGROUND: Bat pups produce individually distinct isolation calls to facilitate maternal recognition. Increasing evidence suggests that, in group-living bat species, adults often use similar calls to maintain contact. We investigated if isolated adults from all three species of the highly cooperative vampire bats (Phyllostomidae: Desmodontinae) would produce vocally distinct contact calls when physically isolated. METHODS/PRINCIPAL FINDINGS: We assessed variation in contact calls recorded from isolated captive and wild-caught adult common vampire bats (*Desmodus rotundus*), white-winged vampire bats (*Diaemus youngi*) and hairy-legged vampire bats (*Diphylla ecaudata*). We compared species-typical contact call structure, and used information theory and permuted discriminate function analyses to examine call structure variation, and to determine if the individuality of contact calls is encoded by different call features across species and populations. We found that isolated adult vampire bats produce contact calls that vary by species, population, colony, and individual. However, much variation occurred within a single context and individual. We estimated signature information for captive *Diaemus* (same colony), captive *Desmodus* (same colony), and wild *Desmodus* (different colonies) at 3.21, 3.26, and 3.88 bits, respectively. Contact calls from a captive colony of *Desmodus* were less individually distinct than calls from wild-caught *Desmodus* from different colonies. Both the degree of individuality and parameters encoding individuality differed between the bats from a single captive colony and the wild-caught individuals from different groups. This result is consistent with, but not sufficient evidence of, vocal convergence in groups. CONCLUSION: Our results show that adult vampire bats of all three species produce highly variable contact calls when isolated. Contact calls contain sufficient information for vocal discrimination, but also possess more intra-individual variation than is required for the sole purpose of identifying individuals

Carter, G.G., Skowronski, M.D., Faure, P.A. & Fenton, B., 2008. Antiphonal calling allows individual discrimination in white-winged vampire bats. *Animal Behaviour*, 76(4), pp.1343–1355.

Abstract: Mother bats use pup contact calls ("isolation calls") to find and recognize their young. In white-winged vampire bats, *Diaemus youngi*, adults produce social calls that are structurally similar to the pup isolation calls of many other bat species. In addition, *D. youngi* seem to exchange these calls in a duet-like fashion. To determine whether calls elicit precise antiphonal responses, we simultaneously recorded social calls from groups of four captive bats vocally interacting. To examine call function, we conducted isolation experiments, permuted discriminant function analyses (pDFA) of individual variation in call structure, and a habituation-discrimination playback experiment. We found that adult *D. youngi* call when isolated, and their social calls attract conspecifics and elicit antiphonal responses. Bats called within 500 ms of a conspecific more than expected based on a random calling model. These findings are the first evidence of antiphonal calling among adult bats. We found significant

individual variation in call structure, and show that bats can discriminate individual identity using social calls alone. We hypothesize that *D. youngi* use these antiphonal contact calls to mediate social interactions among individuals outside the roost.

California Department of Fish and Wildlife (CDFW), 2013. Evaluation of the petition from the Center for Biological Diversity to list Townsend's big-eared bat (*Corynorhinus townsendii*) as threatened or endangered under the California Endangered Species Act.

Abstract: The subject of this petition evaluation is the Townsend's big-eared bat (*Corynorhinus townsendii*), which was petitioned for listing as threatened or endangered under the California Endangered Species Act by the Center for Biological Diversity in a document dated October 18, 2012. The petition accurately describes the biology and ecology of Townsend's big-eared bat. Townsend's big-eared bat (Class Mammalia, Order Chiroptera) is in the Microchiropteran bat family Vespertillionidae. In California, the species is found throughout most of the state, from the inland deserts to the cool, moist coastal redwood forests, in oak woodlands of the inner Coast Ranges and Sierra Nevada foothills, and lower to mid-elevation mixed coniferous-deciduous forests. Distribution is patchy, and strongly correlated with the availability of caves and cave-like roosting habitat, with population centers occurring in areas dominated by exposed, cavity forming rock and/or historic mining districts. Townsend's big-eared bat prefers open surfaces of caves or cave-like structures, such as subsurface hard rock mines, and large undisturbed spaces in buildings, bridges, and water diversion tunnels. Specific roosts may be used only one time of year or may serve different functions throughout the year (such as for maternity roosts, hibernation, or during the breeding season). Maternity colonies may use multiple sites for different stages (pregnancy, birthing, and rearing). Males remain solitary during the maternity season. Townsend's big-eared bat appears to have fairly restrictive roost requirements with temperature appearing to be critical. Townsend's big-eared bat is highly sensitive to human disturbance, however, in some instances it can become habituated to reoccurring and predictable human activity. Foraging associations include edge habitats along streams and areas adjacent to and within a variety of wooded habitats. It is likely that Townsend's big-eared bat in California is a Lepidopteran specialist, feeding primarily on medium-sized moths. Townsend's big-eared bat is a colonial species with maternity colonies forming between March and June (based on local climate and latitude). Colony size ranges from a few dozen to several hundred. Mating generally takes place in both migratory sites and hibernacula between September or October and February. A single pup is born between May and July. Nursery colonies start to disperse in August about the time the young are weaned, and break up altogether in September and October (Pearson et al. 1952, Tipton 1983). Pearson et al. (1952) estimated annual survival at about 50% for young, and about 80% for adults. Band recoveries have yielded longevity records of 16 years, 5 months (Paradiso and Greenhall 1967) and 21 years, 2 months (Perkins 1994). Migration/Hibernation. Townsend's big-eared bat is a relatively sedentary species, for which no long-distance migrations have been reported (Barbour and Davis 1969, Humphrey and Kunz 1976, Pearson et al. 1952). The longest movement known for this species in California is 32.2 km (20 mi) (Pearson et al. 1952). There is some evidence of local migration, perhaps along an elevational gradient. Hibernation sites are generally caves or mines (Pearson et al. 1952, Barbour and Davis 1969), although animals are occasionally found in buildings (Dalquest 1947, E. Pierson pers. obs.). Deep mine shafts, known to provide significant hibernating sites in New Mexico (Altenbach and Milford 1991), may also be important in California (P. Brown pers.

comm.). Winter roosting is typically composed of mixed-sexed groups from a single individual to several hundred or several thousand, however, behavior varies with latitude. In areas with prolonged periods of non-freezing temperatures, Townsend's big-eared bat tends to form relatively small hibernating aggregations of single to several dozen individuals (Barbour and Davis 1969, Pierson et al. 1991, Pierson and Rainey 1998). Larger aggregations (75-460) are confined to areas which experience prolonged periods of freezing temperatures (Pierson and Rainey 1998). Studies in the western U.S. have shown that Townsend's big-eared bat selects winter roosts with stable, cold temperatures, and moderate air flow (Humphrey and Kunz 1976, Kunz and Martin 1982). Individuals roost on walls or ceilings, often near entrances (Humphrey and Kunz 1976, Twente 1955). If undisturbed, individuals will frequently roost less than 3 m (10 ft) off the ground (Perkins et al. 1994), and have been found in air pockets under boulders on cave floors (E. Pierson, pers. obs.). Temperature appears to be a limiting factor in roost selection. Recorded temperatures in Townsend's big-eared bat hibernacula range from -2.0°C to 13.0°C (28°F to 55°F) (Humphrey and Kunz 1976, Genter 1986, Pearson et al. 1952, Pierson et al. 1991, Twente 1955), with temperatures below 10°C (50°F) being preferred (Perkins et al. 1994, Pierson and Rainey 1998). In the Mojave Desert ecoregion in the winter, hibernating Townsend's big-eared bat have been found at temperatures of 15.5°C (60°F) as these might be the coolest temperatures available (P. Brown, pers.obs). The period of hibernation is shorter at lower elevations and latitudes.

California Department of Fish and Wildlife (CDFW), 2014. Incidental take of state listed species under the California Endangered Species Act. Online: https://www.wildlife.ca.gov/Conservation/CESA

No abstract

California Fish and Game Code (CFGC), 2013. Notice of Findings: Townsend's big-eared bat.

Abstract: NOTICE IS HEREBY GIVEN that, pursuant to the provisions of Section 2074.2 of the Fish and Game Code, the California Fish and Game Commission, at its June 26, 2013, meeting in Sacramento, California, accepted for consideration the petition submitted to list the Townsends Big-eared Bat as a threatened or endangered species. The Commission determined, based on the best available science, the extensive information contained in the petition, t he Department of Fish and Wildlife petition evaluation report, and oral testimony that designating Townsend's Big-eared Bat as an endangered or threatened species under CESA may be warranted (see Sections 2073.5 and 2074.2 of the Fish and Game Code). Pursuant to subdivision (a)(2) of Section 2074.2 of the Fish and Game Code, the aforementioned species is hereby declared a candidate species as defined by Section 2068 of the Fish and Game Code.

California Fish and Game Code (CFGC) 2014. California Game Commission Section 4150 - 4155 Nongame mammals. Online: http://www.leginfo.ca.gov/.html/fgc_table_of_contents.html

No abstract

Chaverri, G., Gillam, E.H. & Kunz, T.H., 2012. A call-and-response system facilitates group cohesion among disc-winged bats. *Behavioral Ecology*, 24(2), pp.481–487.

Abstract: Acoustic signals are important in maintaining group cohesion, particularly in highly mobile species. For these signals to facilitate group cohesion, individuals must be able to recognize, and respond to, calls emitted by group members. In this study, we document the use and recognition of complementary contact calls in Spix's disc-winged bat (*Thyroptera tricolor*), a species known to form very stable social groups despite using an extremely ephemeral roosting resource. This bat uses 2 sets of calls: "inquiry," which are emitted by flying bats that are seeking roosts or group mates, and "response," which are produced in reply to an inquiry call by individuals that have already located a roost. Here, we test if bats are capable of discriminating between the inquiry and response calls of group and nongroup mates using playback experiments. Results show that flying bats can discriminate between the inquiry and response calls emitted by group and nongroup members and can maintain contact preferentially with the former. Roosting bats, however, exhibited no preference for group over nongroup members and thus responded indiscriminately. We argue that differences in how individuals respond to calls from group and nongroup members may be partly attributed to the costs associated with flight and the potential benefits of recruiting roost mates.

Chiu, C. & Moss, C.F., 2007. The role of the external ear in vertical sound localization in the free flying bat, *Eptesicus fuscus*. *The Journal of the Acoustical Society of America*, 121(4), 2227.

Abstract: The role of the external ear in sonar target localization for prey capture was studied by deflecting the tragus of six big brown bats, *Eptesicus fuscus*. The prey capture performance of the bat dropped significantly in the tragus-deflection condition, compared with baseline, control, and recovery conditions. Target localization error occurred in the tragus-deflected bat, and mainly in elevation. The deflection of the tragus did not abolish the prey capture ability of the bat, which suggests that other cues are available used for prey localization. Adaptive vocal and motor behaviors were also investigated in this study. The bat did not show significant changes in vocal behaviors but modified its flight trajectories in response to the tragus manipulation. The tragus-deflected bat tended to attack the prey item from above and had lower tangential velocity and larger bearing from the side, compared with baseline and recovery conditions. These findings highlight the contribution of the tragus to vertical sound localization in the free-flying big brown bat and demonstrate flight adaptations the bat makes to compensate altered acoustic cues.

Chiu, C., Xian, W. & Moss, C.F., 2008. Flying in silence: Echolocating bats cease vocalizing to avoid sonar jamming. *Proceedings of the National Academy of Sciences of the United States of America*, 105(35), pp.13116–21.

Abstract: Although it has been recognized that echolocating bats may experience jamming from the signals of conspecifics, research on this problem has focused exclusively on time-frequency adjustments in the emitted signals to minimize interference. Here, we report a surprising new strategy used by bats to avoid interference, namely silence. In a quantitative study of flight and vocal behavior of the big brown bat (*Eptesicus fuscus*), we discovered that the bat spends considerable time in silence when flying with conspecifics. Silent behavior, defined here as at least one bat in a pair ceasing vocalization for more than 0.2 s (200 ms), occurred as much as 76% of the time (mean of 40% across 7 pairs) when their separation was shorter than 1 m, but only 0.08% when a single bat flew alone. Spatial separation, heading direction, and similarity in call design of paired bats were related to the prevalence of this silent behavior. Our data suggest

that the bat uses silence as a strategy to avoid interference from sonar vocalizations of its neighbor, while listening to conspecific-generated acoustic signals to guide orientation. Based on previous neurophysiological studies of the bat's auditory midbrain, we hypothesize that environmental sounds (including vocalizations produced by other bats) and active echolocation evoke neural activity in different populations of neurons. Our findings offer compelling evidence that the echolocating bat switches between active and passive sensing to cope with a complex acoustic environment, and these results hold broad implications for research on navigation and communication throughout the animal kingdom.

Chiu, C., Xian, W. & Moss, C.F., 2009. Adaptive echolocation behavior in bats for the analysis of auditory scenes. *The Journal of Experimental Biology*, 212, 1392–1404.

Echolocating bats emit sonar pulses and listen to returning echoes to probe their surroundings. Bats adapt their echolocation call design to cope with dynamic changes in the acoustic environment, including habitat change or the presence of nearby conspecifics/heterospecifics. Seven pairs of big brown bats, *Eptesicus fuscus*, were tested in this study to examine how they adjusted their echolocation calls when flying and competing with a conspecific for food. Results showed that differences in five call parameters, start/end frequencies, duration, bandwidth and sweep rate, significantly increased in the two-bat condition compared with the baseline data. In addition, the magnitude of spectral separation of calls was negatively correlated with the baseline call design differences in individual bats. Bats with small baseline call frequency differences showed larger increases in call frequency separation when paired than those with large baseline call frequency differences, suggesting that bats actively change their sonar call structure if pre-existing differences in call design are small. Call design adjustments were also influenced by physical spacing between two bats. Calls of paired bats exhibited the largest design separations when inter-bat distance was shorter than 0.5 m, and the separation decreased as the spacing increased. All individuals modified at least one baseline call parameter in response to the presence of another conspecific. We propose that dissimilarity between the time–frequency features of sonar calls produced by different bats aids each individual in segregating echoes of its own sonar vocalizations from the acoustic signals of neighboring bats.

Cho, D.S. & Mun, S., 2008. Development of a highway traffic noise prediction model that considers various road surface types. *Applied Acoustics*, 69(11), pp.1120–1128.

Abstract: A highway traffic noise prediction model has been developed for environmental assessment in South Korea. The model is based on an outdoor sound propagation method and is fully compliant with ISO 9613 and the sound power level (PWL) estimation for a road segment, as suggested in the ASJ Model-1998 that is based on PWLs. Due to that model's selection of two pavement types, such as asphalt or concrete pavement, an unacceptable traffic noise prediction is made in cases where the road surface is different from that on which the model is based. In order to address this problem, several road surface types are categorized, and the PWL of each surface type is determined and modeled by measuring the noise levels obtained from newly developed methods. An evaluation of the traffic noise prediction model using field measurements finds good agreement between predicted and measured noise levels.

Cho, D.S., Kim, J.H., Choi, T.M., Kim, B.H. & Manvell, D., 2004. Highway traffic noise prediction using method fully compliant with ISO 9613: comparison with measurements. *Applied Acoustics*, 65(9), pp.883–892.

Abstract: In this study, we introduce outdoor sound simulation that is fully compliant with ISO 9613 yet with some complementary methods that enhance its applicability; for example, calculation of sound attenuation due to undulating terrain in octave bands, geometric divergence in the near-field of the source, and short-term wind effects. Using the method, we have carried out highway traffic noise prediction and measurement for 12 sites with representative road shapes and structures. In the prediction, the sound power level for a road segment was estimated by the method suggested in ASJ Model-1998 with experimental corrections to the overall noise level and spectrum. Comparing results between predicted and measured noise levels show good correspondence at direct, diffracted and reflected sound fields within 30m from the center of the near side lane.

Christensen-Dalsgaard, J. & Carr, C.E., 2008. Evolution of a sensory novelty: tympanic ears and the associated neural processing. *Brain Research Bulletin*, 75(2-4), pp.365–70.

Abstract: Tympanic hearing is a true evolutionary novelty that appears to have developed independently in at least five major tetrapod groups-the anurans, turtles, lepidosaurs, archosaurs and mammals. The emergence of a tympanic ear would have increased the frequency range and sensitivity of hearing. Furthermore, tympana were acoustically coupled through the mouth cavity and therefore inherently directional in a certain frequency range, acting as pressure difference receivers. In some lizard species, this acoustical coupling generates a 50-fold directional difference, usually at relatively high frequencies (2-4 kHz). In ancestral atympanate tetrapods, we hypothesize that low-frequency sound may have been processed by non-tympanic mechanisms like those in extant amphibians. The subsequent emergence of tympanic hearing would have led to changes in the central auditory processing of both high-frequency sound and directional hearing. These changes should reflect the independent origin of the tympanic ears in the major tetrapod groups. The processing of low-frequency sound, however, may have been more conserved, since the acoustical coupling of the ancestral tympanate ear probably produced little sensitivity and directionality at low frequencies. Therefore, tetrapod auditory processing may originally have been organized into low- and high-frequency streams, where only the high-frequency processing was mediated by tympanic input. The closure of the middle ear cavity in mammals and some birds is a derived condition, and may have profoundly changed the operation of the ear by decoupling the tympana, improving the low-frequency response of the tympanum, and leading to a requirement for additional neural computation of directionality in the central nervous system. We propose that these specializations transformed the low- and high-frequency streams into time and intensity pathways, respectively.

Chruszcz, B.J. & Barclay, R.M.R., 2002. Thermoregulatory ecology of a solitary bat, *Myotis evotis*, roosting in rock crevices. *Functional Ecology*, 16(1), pp.18–26.

Abstract: 1. Most studies of the thermoregulatory ecology of bats have been limited to laboratory experiments or studies of individuals roosting in artificial structures. 2. We investigated the interaction between thermoregulatory behaviour and roost choice in reproductive female western long-eared bats, *Myotis evotis* (H. Allen), roosting solitarily in natural rock crevices. The study was conducted in the badlands of the South Saskatchewan River Valley, Alberta, Canada, during 1997 and 1998. 3. Individuals used torpor every day and the amount of time spent in torpor was primarily influenced by the amount of time available to do so. Minimum body temperature was influenced by ambient temperature, although the form of this relationship differed between pregnant and lactating females. Pregnant females used deep torpor more

frequently than lactating females. 4. All individuals roosted in rock crevices but pregnant and lactating females chose roosts that were different in structure and thermal characteristics. Pregnant females chose horizontal roosts that cooled at night but warmed quickly during the day, thus allowing passive rewarming from torpor. Lactating females chose vertical roosts that stayed warm at night when non-volant pups were present, thereby minimizing thermoregulatory costs to the young. 5. The behaviours observed are adaptive, but differ from those of other temperate-zone insectivorous bats that have been studied in the past. This highlights the importance of studying free-ranging animals living in natural habitat if we are to have an accurate view of thermoregulatory strategies and the importance of roost characteristics for roost-site selection.

Clare, E.L., Barber, B.R., Sweeney, B.W., Hebert, P.D.N. & Fenton, M.B., 2011. Eating local: influences of habitat on the diet of little brown bats (*Myotis lucifugus*). *Molecular Ecology*, 20(8), pp.1772–80.

Abstract: We employ molecular methods to profile the diet of the little brown bat, *Myotis lucifugus*, and describe spatial and temporal changes in diet over their maternity season. We identified 61 prey species of insects and 5 species of arachnid. The largest proportion of prey (~32%) were identified as species of the mass-emerging Ephemeroptera (mayfly) genus *Caenis*. Bats roosting in agricultural settings had lower dietary richness than those occupying a roost located on a forest fragment in a conservation area. We detected temporal fluctuations in diet over the maternity season. Dipteran (fly) species dominated the diet early in the season, replaced later by species of mayfly. Because our methodology provides species-level identification of prey, we were able to isolate environmental indicator species in the diet and draw conclusions about the location and type of their foraging habitat and the health of these aquatic systems. The species detected suggested that the bats use variable habitats; members of one agricultural roost foraged on insects originating in rivers or streams while those in another agricultural roost and the forest roost fed on insects from pond or lake environments. All source water for prey was of fair to good quality, though no species detected are intolerant of pollution thus the habitat cannot be classified as pristine. Our study outlines a model system to investigate the abiotic and biotic interactions between habitat factors through this simple food chain to the top predator.

Clark, D.R., 1979. Lead concentrations: bats vs. terrestrial small mammals collected near a major highway. *Environmental Science & Technology*, 13(3), pp.338–341.

Abstract: Meadow voles, white-footed mice, and short-tailed shrews were trapped adjacent to the Baltimore-Washington Parkway and also near Montpelier Barn, 0.61 km NW of the Parkway (Laurel, Prince Georges Co., Md.). Big brown and little brown bats were captured at their roosts in Montpelier Barn. Average lead concentrations in bats generally exceeded those in terrestrial mammals, but levels in Parkway shrews did not differ significantly from levels in bats. Concentrations in Parkway shrews and white-footed mice exceeded those published previously for these two species. Estimated dosages of lead ingested by little brown bats, Parkway shrews, and Parkway voles equaled or exceeded dosages that have caused mortality or reproductive impairment in domestic mammals. Average lead concentrations in bats and Parkway shrews equaled or exceeded those reported for small rodents that had been collected at abandoned mining sites in Wales with lead-induced renal abnormalities.

Clopton, B.M. & Spelman, F.A., 2015. Figure of inner ear cross section. Online: http://elektroarsenal.net/auditory-system.html#bookmark448.

No abstract

Coles, R.B., Guppy, A., Anderson, M.E. & Schlegel, P., 1989. Frequency sensitivity and directional hearing in the gleaning bat, *Plecotus auritus* (Linnaeus 1758). *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 165(2), pp.269–280.

Abstract: 1. The neural audiogram of the common long-eared bat, *Plecotus auritus* was recorded from the inferior colliculus (IC). The most sensitive best frequency (BF) thresholds for single neurones are below 0 dB SPL between 7-20 kHz, reaching a best value of -20 dB SPL between 12-20 kHz. The lower and upper limits of hearing occur at 3 kHz and 63 kHz, respectively, based on BF thresholds at 80 dB SPL. BF threshold sensitivities are about 10 dB SPL between 25-50 kHz, corresponding to the energy band of the sonar pulse (26-78 kHz). The tonotopic organization of the central nucleus of the IC (ICC) reveals that neurones with BFs below 20 kHz are disproportionately represented, occupying about 30% of ICC volume, occurring in the more rostral and lateral regions of the nucleus. 2. The acoustical gain of the external ear reaches a peak of about 20 dB between 8-20 kHz. The gain of the pinna increases rapidly above 4 kHz, to a peak of about 15 dB at 7-12 kHz. The pinna gain curve is similar to that of a simple, finite length acoustic horn; expected horn gain is calculated from the average dimensions of the pinna. 3. The directional properties of the external ear are based on sound diffraction by the pinna mouth, which, to a first approximation, is equivalent to an elliptical opening due to the elongated shape of the pinna. The spatial receptive field properties for IC neurones are related to the directional properties of the pinna. The position of the acoustic axis of the pinna and the best position (BP) Abbreviations: BF best frequency; BP best position; FM frequency modulation; IC inferior colliculus; ICC central nucleus of the inferior colliculus; TM tympanic membrane; SPL sound pressure level * To whom reprint requests should be sent of spatial receptive fields are both about 25 ~ from the midline between 8-30 kHz but approach the midline to 8 ~ at 45 kHz. In elevation, the acoustic axis and the BP of receptive fields move upwards by 20 ~ between 9-25 kHz, remaining stationary for frequencies up to 60 kHz. 4. The extremely high auditory sensitivity shown by the audiogram and the directionality of hearing are discussed in terms of the adaptation of the auditory system to low frequencies and the role of a large pinna in *P. auritus*. The functional significance of low frequency hearing in *P. auritus* is discussed in relation to hunting for prey by listening and is compared to other gleaning species.

Computerized Scanning and Imaging Facility (CSI)., 2015. Image: Big brown bat cochlea and ossicles 0002. Online: http://csi.whoi.edu/innerears/big-brown-bat-0002jpg. Copyright: D. Ketten WHOI CSI CT. Used with permission.

No abstract

Corcoran, A.J., Barber, J.R., Hristov, N.I. & Conner, W.E., 2011. How do tiger moths jam bat sonar? *The Journal of Experimental Biology*, 214, pp.2416–25.

Abstract: The tiger moth *Bertholdia trigona* is the only animal in nature known to defend itself by jamming the sonar of its predators - bats. In this study we analyzed the three-dimensional flight paths and echolocation behavior of big brown bats (*Eptesicus fuscus*) attacking *B. trigona* in a flight room over seven consecutive nights to determine the acoustic mechanism of the sonar-jamming defense. Three mechanisms have been proposed: (1) the phantom echo hypothesis,

which states that bats misinterpret moth clicks as echoes; (2) the ranging interference hypothesis, which states that moth clicks degrade the bats' precision in determining target distance; and (3) the masking hypothesis, which states that moth clicks mask the moth echoes entirely, making the moth temporarily invisible. On nights one and two of the experiment, the bats appeared startled by the clicks; however, on nights three through seven, the bats frequently missed their prey by a distance predicted by the ranging interference hypothesis (~15-20 cm). Three-dimensional simulations show that bats did not avoid phantom targets, and the bats' ability to track clicking prey contradicts the predictions of the masking hypothesis. The moth clicks also forced the bats to reverse their stereotyped pattern of echolocation emissions during attack, even while bats continued pursuit of the moths. This likely further hinders the bats' ability to track prey. These results have implications for the evolution of sonar jamming in tiger moths, and we suggest evolutionary pathways by which sonar jamming may have evolved from other tiger moth defense mechanisms.

Corcoran, A.J. & Conner, W.E., 2014. Bats jamming bats: Food competition through sonar interference. *Science*, 346, pp.745-747.

Communication signals are susceptible to interference ("jamming") from conspecifics and other sources. Many active sensing animals, including bats and electric fish, alter the frequency of their emissions to avoid inadvertent jamming from conspecifics. We demonstrated that echolocating bats adaptively jam conspecifics during competitions for food. Three-dimensional flight path reconstructions and audio-video field recordings of foraging bats (*Tadarida brasiliensis*) revealed extended interactions in which bats emitted sinusoidal frequency-modulated ultrasonic signals that interfered with the echolocation of conspecifics attacking insect prey. Playbacks of the jamming call, but not of control sounds, caused bats to miss insect targets. This study demonstrates intraspecific food competition through active disruption of a competitor's sensing during food acquisition.

Corcoran, A.J. & Hristov, N.I., 2014. Convergent evolution of anti-bat sounds. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*., 200(9), pp.811–21.

Abstract: Bats and their insect prey rely on acoustic sensing in predator prey encounters-echolocation in bats, tympanic hearing in moths. Some insects also emit sounds for bat defense. Here, we describe a previously unknown sound-producing organ in Geometrid moths-a prothoracic tymbal in the orange beggar moth (*Eubaphe unicolor*) that generates bursts of ultrasonic clicks in response to tactile stimulation and playback of a bat echolocation attack sequence. Using scanning electron microscopy and high-speed videography, we demonstrate that *E. unicolor* and phylogenetically distant tiger moths have evolved serially homologous thoracic tymbal organs with fundamentally similar functional morphology, a striking example of convergent evolution. We compared *E. unicolor* clicks to that of five sympatric tiger moths and found that 9 of 13 *E. unicolor* clicking parameters were within the range of sympatric tiger moths. Remaining differences may result from the small size of the *E. unicolor* tymbal. Four of the five sympatric clicking tiger moth species were unpalatable to bats (0-20 % eaten), whereas *E. unicolor* was palatable to bats (86 % eaten). Based on these results, we hypothesize that *E. unicolor* evolved tymbal organs that mimic the sounds produced by toxic tiger moths when attacked by echolocating bats.

Crampton, L.H. & Barclay, R.M.R., 2008. Selection of Roosting and Foraging Habitat by Bats in Different-Aged Aspen Mixedwood Stands. *Conservation Biology*, 12(6), pp.1347–1358.

Abstract: In aspen mixedwood forests, habitats that provide roosting and foraging sites for bats likely occur in old stands and thus may be threatened by logging. To determine if bats prefer certain ages of aspen mixedwood forest and to help predict the impacts of logging on bats, we used handheld bat detectors and mist nets to compare the relative use and foraging activity by bats in young, mature, and old stands in northern Alberta in 1993 and 1994. We assessed roost-site selection by tracking radio-tagged female little brown bats (*Myotis lucifugus*) and silver-haired bats (*Lasionycteris noctivagans*) to roost trees, which we measured and compared to a random sample of potential wildlife trees. Occurrence of all bats combined was significantly higher in old stands than in young stands in 1993. In 1994, occurrence and activity were higher in old stands than in either young or mature stands. *Myotis* spp. activity was also higher in old stands. All 27 roost trees were in old stands. Bats preferred tall (mean: 22.0 m), dying, or newly dead *Populus* spp. with heart rot and low leaf cover. Such trees were scarce in young and mature stands. Tree-roosting colonies were small (4-63 bats) and transient; most tagged bats roosted in more than one tree. Bats likely select trees large enough to house colonies and provide suitable temperatures, and these trees are most common in old stands. Roost preference may explain observed activity patterns. As more roost trees are harvested, we predict that bat abundance will decrease in remnant patches of fragmented stands. To sustain bat populations in these forests, old stands must be retained and roost sites preserved by managing the forest at the stand or landscape level.

Cryan, P.M., 2003. Sex differences in the thermoregulation and evaporative water loss of a heterothermic bat, *Lasiurus cinereus*, during its spring migration. *Journal of Experimental Biology*, 206, pp.3381–3390.

Abstract: This study quantifies sex differences in thermoregulation and water loss of a small (20–35 g) insectivorous heterothermic mammal, the hoary bat *Lasiurus cinereus*, during its spring migration. We measured body temperature, metabolic rate and evaporative water loss, and calculated wet thermal conductance, for bats exposed to air temperatures ranging from 0 to 40°C for periods of 2–5 h. Pregnant females maintained normothermic body temperatures (35.7 ± 0.7°C; mean ± S.E.M.) independent of air temperature. In contrast, males became torpid during the majority (68%) of exposures to air temperatures <25°C. The thermal neutral zone (TNZ) ranged between approximately 30°C and 34°C in both sexes and, within the TNZ, females had lower mass-specific metabolic rates (6.1 ± 0.2 mW g^{-1}) than males (9.0 ± 0.9 mW g–1). Wet thermal conductance values in torpid bats (0.7 ± 0.5 mW g^{-1} $deg.^{-1}$) were lower than those of normothermic individuals (1.1 ± 0.3 mW g^{-1} $deg.^{-1}$). Mass specific rates of evaporative water loss in males were consistently higher than in females at most air temperatures and rates of water loss in torpid bats were 63 ± 6% of normothermic values. These results suggest that male and pregnant female *L. cinereus* employ different thermoregulatory strategies during their spring migration. Females defend normothermic body temperatures, presumably to expedite embryonic growth, while males use torpor, presumably to minimize energy and water deficits. These variable thermoregulatory strategies may reflect continental differences in the summer distribution of the sexes.

Da Paz, E.C. & Zannin, P.H.T., 2010. Urban daytime traffic noise prediction models. *Environmental Monitoring and Assessment*, 163(1-4), pp.515–29.

Abstract: An evaluation was made of the acoustic environment generated by an urban highway using in situ measurements. Based on the data collected, a mathematical model was designed for the main sound levels (L_{eq}, L_{10}, L_{50}, and L_{90}) as a function of the correlation between sound levels and between the equivalent sound pressure level and traffic variables. Four valid groups of mathematical models were generated to calculate daytime sound levels, which were statistically validated. It was found that the new models can be considered as accurate as other models presented in the literature to assess and predict daytime traffic noise, and that they stand out and differ from the existing models described in the literature thanks to two characteristics, namely, their linearity and the application of class intervals.

Dalland, J.I., 1965. Hearing Sensitivity in Bats. *Science*, 150(3700), pp.1185–1186.

Abstract: Absolute hearing thresholds for two bats were determined by an operant conditioning technique. Pure tones ranging from 2.5 to 100 kilocycles per second were perceived by a single *Eptesicus fuscus*. Its maximum sensitivity was on the order of 68 decibels below 1 dyne per square centimeter and occurred at 20 kc/sec. Maximum sensitivity for a single *Myotis lucifugus* was about 64 db below 1 dyne/cm2 and occurred at 40 kc/sec. The *Myotis* clearly heard a tone of 120 kc/sec but gave no evidence of hearing below 10 kc/sec.

Daniel, S., Korine, C. & Pinshow, B., 2008. Central-place foraging in nursing, arthropod-gleaning bats. *Canadian Journal of Zoology*, 86(7), pp.623–626.

Abstract: Central-place (CP) foraging theory predicts a positive correlation between the time a breeding CP forager spends in a patch and the distance of the patch to the CP. We found that nursing female Hemprich's long-eared bats (*Otonycteris hemprichii*, Peters, 1859; Vespertilionidae) that forage around a lake in the Negev roost in only two areas: ne 0.5 - 2 km (near) and one 9 km (far) from the foraging area. If these bats are CP foragers, then the strategies of the two groups should differ. We predicted that females roosting farther away would have longer but fewer foraging bouts. Using radiotelemetry, we measured the activity of six females from the near site and three from the far site. Without exception, females from the far site made a single, prolonged foraging bout each night, while females roosting nearby made several shorter bouts. Among the females from the near site, daily foraging time, mean daily foraging bout length, and first daily foraging bout length were all significantly and positively correlated with distance between the roost and the foraging site. Our data support the prediction that female *O. hemprichii* are CP foragers. We suggest that the females trade off using a safe roost site, distant from a choice foraging area, and lower nursing frequency against using a risky roost site close to the foraging area and greater nursing frequency

Darden, S. & Pedersen, S., 2008. Sound transmission at ground level in a short-grass prairie habitat and its implications for long-range communication in the swift fox *Vulpes velox*. *The Journal of the Acoustical Society of America*, 124(2), pp.758–766.

Abstract: The acoustic environment of swift foxes *Vulpes velox* vocalizing close to the ground and the effect of propagation on individual identity information in vocalizations were quantified in a transmission experiment in prairie habitat. Sounds were propagated 0.45 m above the ground

at distances up to 400 m. Effects of transmission were measured on three sound types: synthesized sweeps with 1.3 kHz bandwidths spanning in the range of 0.3–8.0 kHz; single elements of swift fox barking sequences frequency range of 0.3–4.0 kHz and complete barking sequences. Synthesized sweeps spanning 0.3–1.6 and 1.2–2.5 kHz propagated the furthest and the latter sweeps exhibited the best transmission properties for long-range propagation. Swift fox barking sequence elements are centered toward the lower end of this frequency range. Nevertheless, measurable individual spectral characteristics of the barking sequence seem to persist to at least 400 m. Individual temporal features were very consistent to at least 400 m. The communication range of the barking sequences is likely to be farther than 400 m and it should be considered a long-ranging vocalization. However, relative to the large home ranges of swift foxes up to 16 km2 in the experimental area the barking sequence probably functions at intermediate distances.

Davies, K.T., Maryanto, I. & Rossiter, S.J., 2013. Evolutionary origins of ultrasonic hearing and laryngeal echolocation in bats inferred from morphological analyses of the inner ear. *Frontiers in Zoology*, 10(1), pp.1–15.

Abstract: INTRODUCTION: Many mammals have evolved highly adapted hearing associated with ecological specialisation. Of these, bats possess the widest frequency range of vocalisations and associated hearing sensitivities, with frequencies of above 200 kHz in some lineages that use laryngeal echolocation. High frequency hearing in bats appears to have evolved via structural modifications of the inner ear, however, studying these minute features presents considerable challenges and hitherto few such attempts have been made. To understand these adaptations more fully, as well as gain insights into the evolutionary origins of ultrasonic hearing and echolocation in bats, we undertook micro-computed tomography (μCT) scans of the cochleae of representative bat species from 16 families, encompassing their broad range of ecological diversity. To characterise cochlear gross morphology, we measured the relative basilar membrane length and number of turns, and compared these values between echolocating and non-echolocating bats, as well as other mammals. RESULTS: We found that hearing and echolocation call frequencies in bats correlated with both measures of cochlear morphology. In particular, relative basilar membrane length was typically longer in echolocating species, and also correlated positively with the number of cochlear turns. Ancestral reconstructions of these parameters suggested that the common ancestor of all extant bats was probably capable of ultrasonic hearing; however, we also found evidence of a significant decrease in the rate of morphological evolution of the basilar membrane in multiple ancestral branches within the Yangochiroptera suborder. Within the echolocating Yinpterochiroptera, there was some evidence of an increase in the rate of basilar membrane evolution in some tips of the tree, possibly associated with reported shifts in call frequency associated with recent speciation events. CONCLUSIONS: The two main groups of echolocating bat were found to display highly variable inner ear morphologies. Ancestral reconstructions and rate shift analyses of ear morphology point to a complex evolutionary history, with the former supporting ultrasonic hearing in the common bat ancestor but the latter suggesting that morphological changes associated with echolocation might have occurred later. These findings are consistent with theories that sophisticated laryngeal echolocation, as seen in modern lineages, evolved following the divergence of the two main suborders.

Dechmann, D.K.N., Heucke, S.L., Giuggioli, L., Safi, K., Voigt, C.C. & Wikelski, M., 2009. Experimental evidence for group hunting via eavesdropping in echolocating bats. *Proceedings of the Royal Society B,* 276, 2721-2728.

Abstract: Group foraging has been suggested as an important factor for the evolution of sociality. However, visual cues are predominantly used to gain information about group members' foraging success in diurnally foraging animals such as birds, where group foraging has been studies most intensively. By contrast, nocturnal animals, usch as bats, would have to rely on other cues or signals to coordinate foraging. We investigated the role of echolocation calls as inadvertently produced cues for social foraging in the insectivorous bat *Noctilio albiventris*. Females of this species live in small groups, forage over water body for swarming insects and have an extremely short daily activity period. We predicted and confirmed that (i) free-ranging bats are attracted by playbacks of echolocation calls produced during prey capture, and that (ii) bats of the same social unit forage together to benefit from passive information transfer via the change in group members' echolocation calls upon finding prey. Network analysis of high-resolution automated radio telemetry confirmed that group members flew within the predicted maximum hearind distance 94 ± 6 percent of the time. Thus, echolocation calls also serve as intraspecific communication cues. Sociality appears to allow for more effective group foraging strategies via eavesdropping on acoustical cues of group members in nocturnal mammals.

De Mey, F., Schillebeeckx, R., Vanderelst, D., Boen, A. & Peremans, H., 2010. Modelling simultaneous echo waveform reconstruction and localization in bats. *Bio Systems*, 100(2), pp.94–100.

Abstract: Echolocating bats perceive the world through sound signals reflecting from the objects around them. In these signals, information is contained about reflector location and reflector identity. Bats are able to extract and separate the cues for location from those that carry identification information. We propose a model based on Wiener deconvolution that also performs this separation for a virtual system mimicking the echolocation system of the lesser spearnosed bat, *Phyllostomus discolor*. In particular, the model simultaneously reconstructs the reflected echo signal and localizes the reflector from which the echo originates. The proposed technique is based on a model that performs a similar task based on information from the frog's lateral line system. We show that direct application of the frog model to the bat sonar system is not feasible. However, we suggest a technique that does apply to the bat biosonar and indicate its performance in the presence of noise.

DeFrance, J. & Gabillet, Y., 1999. A new analytical method for the calculation of outdoor noise propagation. *Applied Acoustics*, 57(2), pp.109–127.

Abstract: A new analytical method for the prediction of road traffic noise propagation (called MAPB in French) is presented. This method answers the need of a simple calculation tool usable in the new standard that is being elaborated in France. From the Fresnel zone concept and from simplifications of Weyl-van der Pol's theory and Geometrical Theory of Diffraction (GTD), new expressions of attenuation due to the ground as well as that due to different barrier types are developed. The complete model in a homogeneous atmosphere (MAPB-H) is obtained by combining these expressions using a classical geometric method. For the case of an atmosphere with a small constant sound speed gradient, the use of corrective length and height terms gives the complete formulation of the MAPB-F (for a positive gradient favourable to propagation) and

the MAPB-D (for a negative gradient unfavourable to propagation). Turbulence is neglected in this approach. MAPB-H is validated using a numerical Boundary Element Method (BEM). MAPB-F and MAPB-D are validated with the help of a mixed Rasmussen-Brekhovskikh numerical method, as well as with outdoor measurements. Comparisons of results obtained with the MAPB and those obtained from numerical methods and measurements show good agreement.

Denny, M., 2004. The physics of bat echolocation: Signal processing techniques. *American Journal of Physics*, 72(12), p.1465.

No abstract

Denzinger, A. & Schnitzler, H., 1994. Echo SPL influences the ranging performance of the big brown bat, *Eptesicus fuscus*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 175, pp.563–571.

Abstract: Four bats of the species *Eptesicus fuscus* were trained in a two-alternative forced-choice procedure to discriminate between two phantom targets that differed in range. The rewarded stimulus was located at a distance of 52.7 cm, while the other unrewarded stimulus was further away. Only one target was presented at a time. In the first experiment we measured the range discrimination performance at an echo SPL of-28 dB relative to the bat's sonar transmission. A 75% correct performance level was arbitrarily defined as threshold and was obtained at a delay difference of 80 µs, corresponding to a range difference of 13.8 mm. In the second experiment the delay difference was fixed at 150 µs and the echo SPL varied between -8 and -48 dB relative to sonar emissions. The performance of the bats depended on the relative echo SPL. At -28 dB the bats showed the best performance. It deteriorated at an increase of the relative echo SPL to -18 dB and -8 dB. The performance also deteriorated when the relative echo SPL was reduced to -38 dB and -48 dB. Only at low relative echo SPLs did the bats partially compensate for the reduction in echo SPL and increased the SPL of their emitted signals by a few dB. Our results support the hypothesis that neurons exhibiting paradoxical latency shift may be involved in encoding target range. This hypothesis predicts a decrease in performance at high echo SPLs as we found it in our experiments. The observed reduction in performance at very low echo SPLs may be due to a decrease in S/N ratio.

Denzinger, A. & Schnitzler, H., 1998. Echo SPL, training experience, and experimental procedure influence the ranging performance in the big brown bat, *Eptesicus fuscus*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 183, pp.213–224.

No abstract

Diamond, J.M., 2012. Distribution and roost site habitat requirements of western yellow (*Lasiurus xanthinus*) and western red (*Lasiurus blossevillii*) bats : 2011 Summary Findings. Lower Colorado River Multi-species Conservation Program. March 2012.

Abstract: The roosting ecology of western red bats (*Lasiurus blossevillii*) and western yellow bats (*Lasiurus xanthinus*) is poorly understood in the Southwestern U.S. and on the lower Colorado River (LCR) specifically. Red bats were not recorded on the lower Colorado River until after 1996 when a combination of biological contractors and a Bureau of Reclamation

biologist began observing the species on the LCR. Similar to red bats, western yellow bats are believed to be a warm season migratory species in the Southwest. Yellow bats have also begun to be detected in increasing densities on the LCR. Both the western red and western yellow bat are listed as covered species on the LCR. The purpose of this project is to implement conservation measures identified within the Lower Colorado River Multi-Species Conservation Program that calls for the conservation of habitat that works toward the recovery of threatened and endangered species as well as reduces the likelihood of additional species being listed (i.e., the covered species). This project is the first stage and is directed at identifying habitat use by these two species. We radio tracked eight western red bats and nine western yellow bats today roosting habitat on the LCR and other riparian areas to determine the characteristics associated with individual tree roosts. This first year of data collection has provided us with patterns that will be more fully explored after additional seasons of data collection. For western red bats, these patterns indicate roost selection based on a tree patch or roosting neighborhood. In contrast, yellow bats appear to select roosts for the characteristics of individual trees. It is important to note that we are in the early stages of data analysis, and these patterns must be clarified with higher level data analysis.

Dooling, R.J., 2002. Avian hearing and the avoidance of wind turbines. Technical Report NREL/TP-500-30844, National Renewable Energy Laboratory, Golden, CO. Online: http://www.nrel.gov/docs/fy02osti/30844.pdf

Summary and Recommendations: This report provides a complete summary of what is known about basic hearing capabilities in birds in relation to the characteristics of noise generated by wind turbines. It is a review of existing data on bird hearing with some preliminary estimates of environmental noise and wind turbine noise at Altamont Pass, California, in the summer of 1999. It is intended as a resource in future discussions of the role that hearing might play in bird avoidance of turbines.

The main body of this report describes hearing measurement in birds, the effects of noise on hearing, and the relationship between avian hearing and the general noise levels around wind turbines. The main body is followed by four appendices. Appendix A is a table organized by species which provides a comprehensive bibliography of the literature on hearing in the quiet (audiograms) in birds, followed by Appendix B which provides plots of the audiograms from 49 species of birds that have been tested to date. Similarly, a bibliography of the literature on how birds hear in noise is given in a table in Appendix C, with corresponding plots of masked auditory thresholds in Appendix D.

There are a number of long-standing myths about what birds can or cannot hear. One myth is that birds hear better at high frequencies than do humans or other mammals. Another myth is that birds have exceptionally acute hearing. A considerable amount of work over the past 50 years has repeatedly shown that neither of these notions is true. When hearing is defined as the softest sound that can be heard at different frequencies, birds on average hear less well than many mammals, including humans.

Birds hear best between about 1 and 5 kHz. Acoustic deterrents or “scarecrow” devices are not generally effective because birds habituate to them and eventually ignore them completely. Devices that purport to use sound frequencies outside the hearing range of humans are most certainly inaudible to birds as well because birds have a narrower range of hearing than humans do. A review of the literature on how well birds can hear in noisy (windy) conditions suggests that birds cannot hear the noise from wind turbine blades as well as humans can. In practical

terms, a human with normal hearing can probably hear a wind turbine blade twice as far away as can the average bird.
Some wind turbine blades whistle due to blade defects. Depending on the sound level of the whistle produced from a blade defect and the level of the background noise, blade whistles may help birds avoid turbine blades. Because turbine noise and wind noise are predominantly low frequency, almost all the contribution to an overall sound pressure level reading [e.g., 65 dB(A) SPL], comes from frequencies below 1 – 2 kHz. This means that adding an acoustic cue in the region of best hearing for birds (2 – 4 kHz) would add almost nothing to overall sound pressure level but might help birds hear the blades. The existence of blade defects that produce whistles suggests that minor modifications to the acoustic signature of a turbine blade, in the form of whistles, could make blades more audible to birds and at the same time make no measurable contribution to overall noise level.
It is entirely possible, however, that as birds approach a wind turbine, especially under high wind conditions, they lose the ability to see the blade (because of motion smear) before they are close enough to hear the blade. The hypothesis that louder (to birds) blade noises result in fewer fatalities is untested. Making the necessary noise measurements and comparing fatalities at turbines with noticeable whistles with those having no whistles provide one test of this hypothesis.

Dooling, R.J. & Blumenrath, S.H., 2014. Avian sound perception in noise. In: H. Brumm, ed. Animal Communication and Noise. Springer, Heidelberg, pp. 229– 250.

No abstract

Dooling, R.J., Dent, M.L., Leek, M.L. & Gleich, O., 2001. Masking by harmonic complexes in birds: behavioral thresholds and cochlear responses. *Hearing Research*, 152(1-2), pp.159–72.

Abstract: Thresholds for pure tones embedded in harmonic complexes were measured behaviorally and physiologically for three species of birds, and physiologically in gerbils. The harmonic maskers were generated using the Schroeder-phase algorithm, characterized by monotonically increasing or decreasing phase across frequency. Previous work has shown that these stimuli produce large differences in masking in humans but not budgerigars. In this study, we show that for two additional species of birds, the patterns of masking were similar to those shown for budgerigars, with masking differing only slightly for the two Schroeder-phase waveforms, and in the opposite direction from that demonstrated in humans. Amounts of masking among species corresponded qualitatively to differences in their critical ratios. Evoked potential measurements in birds and gerbils indicated responses that were consistent with the behaviorally measured thresholds in birds and humans. Results are interpreted in light of differences in frequency selectivity and cochlear temporal processing across species.

Dooling, R.J., Leek, M.R. & Popper, A.N., 2015. Effects of noise on fishes: What we can learn from humans and birds. *Integrative Zoology*, 10, pp.29-37.

Abstract: In this paper we describe the masking of pure tones in humans and birds by manmade noises and show that similar ideas can be applied when considering the potential effects of noise on fishes, as well as other aquatic vertebrates. Results from many studies on humans and birds,

both in the field and in the laboratory, show that published critical ratios can be used to predict the masked thresholds for pure tones when maskers consist of complex manmade and natural noises. We argue from these data that a single, simple measure, the species critical ratio, can be used to estimate the effect of manmade environmental noises on the perception of communication and other biologically relevant sounds. We also reason that if this principle holds for species as diverse as humans and birds, it probably also applies for all other vertebrates, including fishes.

Dooling, R. & Popper, A.N., 2007. The effects of highway noise on birds. Report prepared for the California Department of Transportation (Caltrans), Sacramento; Jones and Stokes Associates.] Online: www.dot.ca.gov/hq/env/bio/files/caltrans_birds_10-7-2007b.pdf.

No abstract

Dooling, R.J. & Popper, A.N., 2015. The Effects of Highway Noise on Birds. Version 2. Report prepared for the California Department of Transportation, Sacramento; ICF international.

(In prep)

Dooling, R.J. & Saunders, J.C., 1975. Hearing in the parakeet (*Melopsittacus undulatus*): Absolute thresholds, critical ratios, frequency difference limens, and vocalizations. *Journal of Comparative and Physiological Psychology*, 88(1), pp.1–20.

Abstract: Avoidance conditioning and the method of limits were used to measure absolute auditory thresholds, masked thresholds, and critical ratios in 4 parakeets. The same procedure was then, used to study frequency difference limena in 6 additional animals. The power spectrum and "constancy of intonation" of the parakeet call were also measured and related to the absolute and differential frequency sensitivity. The mechanism of frequency analysis in the parakeet ear was considered in relation to the present results and to the anatomical and functional differences between the avian and mammalian auditory systems.

Duchamp, J.E., Sparks, D.W. & Whitaker, Jr., J.O., 2004. Foraging-habitat selection by bats at an urban–rural interface: comparison between a successful and a less successful species. *Canadian Journal of Zoology*, 82(7), pp.1157–1164.

Abstract: We compared habitat use of two sympatric species of bat in a rural area undergoing suburban development. The two species are similar in diet and foraging-habitat use but differ in current roosting habitat, and exhibit contrasting regional population trends. Evening bat, *Nycticeius humeralis* (Rafinesque, 1818), populations are declining in central Indiana, whereas big brown bat, *Eptesicus fuscus* (Beauvois, 1796), populations are increasing. We assessed habitat selection by 22 adult female bats using radiotelemetry and compositional analysis. *Eptesicus fuscus* used several roosts across the study area; all but one roosted in human-made structures. *Nycticeius humeralis* clustered roosts within a small group of woodlots; all roosted in tree cavities. *Eptesicus fuscus* foraged for longer periods of time and nonreproductive individuals of this species had larger foraging ranges than *N. humeralis*. Both species foraged primarily in agricultural and wooded areas. During foraging, *N. humeralis* showed greater foraging-site fidelity and a stronger selection for agricultural and wooded areas than *E. fuscus*. We suggest

that *N. humeralis* in our study area is probably more sensitive to suburban development near their roosts than *E. fuscus*.

Ehret, G., 1975. Masked auditory thresholds, critical ratios, and scales of basilar membrane of the house mouse (*Mus musculus*) *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 103(3), pp.329-341.

Abstract: 1. Masked auditory thresholds were determined for the housemouse *(Mus musculus, outbred* strain NMRI) between 1 kHz and 80 kHz and for four noise spectrum levels. 2. Critical ratios (K, K_1) after Fletcher (1940), which represent bands of summated sound evaluation, were calculated. For frequencies (f) below 15 kHz critical ratios (CR-bands) remain constant (K = 35 dB; K_1 = 3162 Hz). Above 15 kHz the relation between CR-bands and f can be expressed by the following functions: $K = 13.27 \cdot 1g f - 19.87$; $K_1 = 0.456 \cdot f - 2836$. 3. From these functions the width in kHz and the number of CR-bands in the acoustic system of the mouse could be derived. The ear of *Mus musculus* is able to form maximally 10 CR-bands between 0.8 kHz and 115.4 kHz. 4. The width and number of CR-bands could be used to calculate a function for frequency distribution along the basilar membrane of the mouse, or to estimate fitting factors for Greenwood's (1961) equation respectively. The following function is proposed to be the best approximation: $f = 3350 \cdot (10^{0.21x} - 1)$, x = distance from the helicotrema. 5. Equidistant scales for the basilar membrane of *Mus musculus* are constructed. 6. The comparison of data on man, eat, and mouse shows that the CR-bands of these mammals are equal to a width of 0.67 mm on all respective basilar membranes. Thus accuracy of sound evaluation in mammals is directly proportional to the length of the respective basilar membranes.

Eillison, L.E., Everette, A.L. & Bogan, M.A., 2005. Examining patterns of bat activity in Bandelier National Monument, New Mexico, by using walking point transects. *The Southwestern Naturalist*, 50(2), pp.197–208.

Abstract: We conducted a preliminary study using small field crews, a single Anabat II detector coupled with a laptop computer, and point transects to examine patterns of bat activity at a scale of interest to local resource managers. The study was conducted during summers of 1996–1998 in Bandelier National Monument in the Jemez Mountains of northern New Mexico, a landscape with distinct vegetation zones and high species richness of bats. We developed simple models that described general patterns of acoustic activity within 4 vegetation zones based primarily on nightly variation and a qualitative index of habitat complexity. Bat acoustic activity (number of bat passes/ point) did not vary dramatically among a limited sample of transects within a vegetation zone during 1996. In 1997 and 1998, single transects within each vegetation zone were established, and bat activity did not vary annually within these zones. Acoustic activity differed among the 4 vegetation zones of interest, with the greatest activity occurring in riparian canyon bottomland, intermediate activity in coniferous forest and a 1977 burned zone, and lowest activity in pinjon-juniper woodlands. We identified 68.5% of 2,529 bat passes recorded during point-transect surveys to species using an echolocation call reference library we established for the area and qualitative characteristics of bat calls. Bat species richness and composition differed among vegetation zones. Results of these efforts were consistent with general knowledge of where different bat species typically forage and with the natural history of bats of New Mexico, suggesting such a method might have value for drawing inferences about bat activity in different vegetation zones.

Eklöf, J. & Jones, G., 2003. Use of vision in prey detection by brown long-eared bats, *Plecotus auritus*. *Animal Behaviour*, 66(5), pp.949–953.

Abstract: We investigated the ability of brown long-eared bats to make use of visual cues when searching for food. By using petri dishes containing mealworms that were subjected to different levels of illumination, we presented four bats with different sensory cues: visual, sonar and a combination of these. The bats preferred situations where both sonar cues and visual cues were available, and the visual information was more important than the sonar cues. The bats did, however, emit echolocation calls throughout the experiments.

Eng, A.S., Narins, P.M., Xu, C., Lin, W., Yu, Z., Qiu, Q., Xu, Z., & Shen, J., 2006. Ultrasonic communication in frogs. *Nature*, 400, pp.333-336

Abstract: Among vertebrates, only microchiropteran bats, cetaceans and some rodents are known to produce and detect ultrasounds (frequencies greater than 20 kHz) for the purpose of communication and/or echolocation, suggesting that this capacity might be restricted to mammals. Amphibians, reptiles and most birds generally have limited hearing capacity, with the ability to detect and produce sounds below approximately 12 kHz. Here we report evidence of ultrasonic communication in an amphibian, the concave-eared torrent frog (*Amolops tormotus*) from Huangshan Hot Springs, China. Males of *A. tormotus* produce diverse bird-like melodic calls with pronounced frequency modulations that often contain spectral energy in the ultrasonic range. To determine whether *A. tormotus* communicates using ultrasound to avoid masking by the wideband background noise of local fast-flowing streams, or whether the ultrasound is simply a by-product of the sound-production mechanism, we conducted acoustic playback experiments in the frogs' natural habitat. We found that the audible as well as the ultrasonic components of an *A. tormotus* call can evoke male vocal responses. Electrophysiological recordings from the auditory midbrain confirmed the ultrasonic hearing capacity of these frogs and that of a sympatric species facing similar environmental constraints. This extraordinary upward extension into the ultrasonic range of both the harmonic content of the advertisement calls and the frog's hearing sensitivity is likely to have co-evolved in response to the intense, predominantly low-frequency ambient noise from local streams. Because amphibians are a distinct evolutionary lineage from microchiropterans and cetaceans (which have evolved ultrasonic hearing to minimize congestion in the frequency bands used for sound communication and to increase hunting efficacy in darkness), ultrasonic perception in these animals represents a new example of independent evolution.

Engelstätter, R., Vater, M. & Neuweiler, G., 1980. Processing of noise by single units of the inferior colliculus of the bat *Rhinolophus ferrumequinum*. *Hearing Research*, 3, pp.285–300.

Abstract: For inferior colliculus units the response patterns and the thresholds for pure tones and noise of variable bandwidth were determined. In a threshold-bandwidth plot the nc.ise thresholds usually fell along two regression lines whose point of intersection established the size: of the neuronal critical bandwidth (nOB). The relevance of the small nCBs (0.2-0.4 kHz) obtained for the frequency range of the constant frequency part of the orientation Call is discussed. No fixed relation was found either between the nCBs and the neuronal critical rattles or between the size of nCB and the width of the tuning curve 3 dB above threshold of the best frequency.

Erickson, G.A. et al., 2002. Bat and Bridges Technical Bulletin (Hitchhiker Guide to Bat Roosts), California Department of Transportation, Sacramento CA 2002. Online: https://www.google.com/?gws_rd=ssl#q=Bat+and+Bridges+Technical+Bulletin+(Hitchhiker+Guide+to+Bat+Roosts

No abstract

Erickson, J. & Adams, M., 2003. A comparison of bat activity at low and high elevations in the Black Hills of western Washington. *Northwest Science*, 77(2), pp.126–130.

Abstract: We examined the differences in activity patterns and community structure of bats between low (<150 m) and high (>575 m) elevation sites in two habitats of the Capitol State Forest, Washington. Total bat activity averaged for times higher at low elevations sites than at high elevation sites. Feeding activity was almost 20 times higher at low elevation sites. However, the non-myotis group had similar activity levels at high and low elevation, where myotis group activity decreased at higher elevations. Different levels of activity between elevations could be the result of differences in insect availability, climatic conditions, and morphology of the bat species.

Esser, K. & Daucher, A., 1996. Hearing in the FM-bat *Phyllostomus discolor*: a behavioral audiogram. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 178, pp.779–785.

Abstract: Absolute auditory thresholds of six adult lesser spear-nosed bats *Phyllostomus discolor* (Chiroptera, Phyllostomidae) were determined in a two-alternative forced-choice procedure. Behavioral responses to pure tone stimuli could be elicited throughout the tested frequency range of 5-142 kHz. The shape of the average audiogram is characterized by two sensitivity peaks and a pronounced increase of thresholds around 55 kHz, and towards the limits of the tested frequency range. The spectral extent of both sensitivity peaks shows a close relation to the bandwidth of two types of species-specific vocalizations. The first low threshold area (> 10 and < 55 kHz) of the audiogram seems perfectly adapted to the directive call used for intraspecific communication, whereas the second sensitivity peak, centered around 85 kHz, covers most of the bandwidth of the species' echolocation calls.

Esser, K. & Kiefer, R., 1996. Detection of frequency modulation in the FM-bat *Phyllostomus discolor*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 178, pp.787–796.

Abstract: In a two-alternative forced-choice procedure lesser spear-nosed bats, *Phyllostomus discolor*, had to discriminate between a pure tone stimulus and a sinusoidally frequency-modulated signal generated at the same carrier frequency as the tone. Modulation depths of the SFM stimuli were reduced until the animals' performance dropped below the 75%-correct level which was used to determine difference limens for detection of frequency modulation (FMDL). The dependence of FMDLs on modulation and carrier frequency was systematically investigated. For a carrier frequency of 18.5 kHz, average FMDLs increased from 95 Hz at a modulation frequency of 10 Hz to 820 Hz at a modulation frequency of 2000 Hz which corresponds to Weber ratios (2Af/f) of 0.005 and 0.044 respectively. Further, difference limens were found to increase linearly in proportion to carrier frequency throughout a major part (9-74 kHz) of the

species' hearing range. In comparison to other mammals, *P. discolor* has a pronounced capability for frequency discrimination which might be related to the extensive use of individually distinct frequency-modulated communication calls and audio-vocal learning.

Estrada-Villegas, S., Meyer, C.F.J. & Kalko, E.K.V., 2010. Effects of tropical forest fragmentation on aerial insectivorous bats in a land-bridge island system. *Biological Conservation*, 143(3), pp.597–608.

Abstract: Habitat fragmentation causes drastic changes in the biota and it is crucial to understand these modifications to mitigate its consequences. While studies on Neotropical bats have mainly targeted phyllostomid bats, impacts of fragmentation on the equally important aerial insectivores remain largely unexplored. We studied species richness, composition, count abundance and feeding activity of aerial insectivorous bats in a system of land-bridge islands in Panama with acoustic sampling. We predicted negative effects of fragmentation on forest species while bats foraging in open space should remain essentially unaffected. Rarefaction analyses indicated higher species richness for islands than mainland sites. For forest species, multivariate analyses suggested compositional differences between sites due to effects of isolation, area and vegetation structure. Contrary to our expectations, count abundance of forest species was similar across site categories. Feeding activity, however, was curtailed on far islands compared to near islands. As expected, bats hunting in open space did not reveal negative responses to fragmentation. Interestingly, they even displayed higher abundance counts on far and small islands. On the species level, two forest bats responded negatively to size reduction or site isolation, respectively, while a forest bat and a bat hunting in open space were more abundant on islands, irrespectively of island isolation or size. Our findings suggest that small forest remnants are of considerable conservation value as many aerial insectivores intensively use them. Hence high conservation priority should be given to retain or re-establish a high degree of forest integrity and low levels of isolation.

Ethier, K. & Fahrig, L., 2011. Positive effects of forest fragmentation, independent of forest amount, on bat abundance in eastern Ontario, Canada. *Landscape Ecology*, 26(6), pp.865–876.

Abstract: While studies have found that bat abundance is positively related to the amount of forest cover in a landscape, the effects of forest fragmentation (breaking apart of forest, independent of amount) are less certain, with some indirect evidence for positive effects of fragmentation. However, in most of these studies, the variables used to quantify fragmentation are confounded with forest amount, making it difficult to interpret the results. The purpose of this study was to examine how forest amount and forest fragmentation independently affect bat abundance. We conducted acoustic bat surveys at the centers of 22 landscapes throughout eastern Ontario, Canada, where landscapes were chosen to avoid a correlation between forest amount and forest fragmentation (number of patches) at multiple spatial scales, while simultaneously controlling for other variables that could affect bat activity. We found that the effects of forest amount on bat relative abundance were mixed across species (positive for *Lasiurus borealis*, negative for *Perimyotis subflavus* and *Lasionycteris noctivagans*). When there was evidence for an effect of forest fragmentation, independent of forest amount, on bat relative abundance, the effect was positive (*Myotis septentrionalis*, *Myotis lucifugus* and *Lasiurus borealis*). We suggest that the mechanism driving the positive responses to fragmentation is higher landscape complementation in more fragmented landscapes; that is, increased access to both foraging and

roosting sites for these bat species. We conclude that fragmented landscapes that maximize complementation between roosting and foraging sites should support a higher diversity and abundance of bats.

Fahrig, L. & Rytwinski, T., 2009. Effects of Roads on Animal Abundance: an Empirical Review and Synthesis. *Ecology and Society*, 14(1), p.21.

Abstract: We attempted a complete review of the empirical literature on effects of roads and traffic on animal abundance and distribution. We found 79 studies, with results for 131 species and 30 species groups. Overall, the number of documented negative effects of roads on animal abundance outnumbered the number of positive effects by a factor of 5; 114 responses were negative, 22 were positive, and 56 showed no effect. Amphibians and reptiles tended to show negative effects. Birds showed mainly negative or no effects, with a few positive effects for some small birds and for vultures. Small mammals generally showed either positive effects or no effect, mid-sized mammals showed either negative effects or no effect, and large mammals showed predominantly negative effects. We synthesized this information, along with information on species attributes, to develop a set of predictions of the conditions that lead to negative or positive effects or no effect of roads on animal abundance. Four species types are predicted to respond negatively to roads: (i) species that are attracted to roads and are unable to avoid individual cars; (ii) species with large movement ranges, low reproductive rates, and low natural densities; and (iii and iv) small animals whose populations are not limited by road-affected predators and either (a) avoid habitat near roads due to traffic disturbance or (b) show no avoidance of roads or traffic disturbance and are unable to avoid oncoming cars. Two species types are predicted to respond positively to roads: (i) species that are attracted to roads for an important resource (e.g., food) and are able to avoid oncoming cars, and (ii) species that do not avoid traffic disturbance but do avoid roads, and whose main predators show negative population-level responses to roads. Other conditions lead to weak or non-existent effects of roads and traffic on animal abundance. We identify areas where further research is needed, but we also argue that the evidence for population level effects of roads and traffic is already strong enough to merit routine consideration of mitigation of these effects in all road construction and maintenance projects.

Falk, B., Williams, T., Aytekin, M. & Moss, C.F., 2011. Adaptive behavior for texture discrimination by the free-flying big brown bat, *Eptesicus fuscus*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 197(5), pp.491–503.

Abstract: This study examined behavioral strategies for texture discrimination by echolocation in free-flying bats. Big brown bats, *Eptesicus fuscus*, were trained to discriminate a smooth 16 mm diameter object (S+) from a size-matched textured object (S-), both of which were tethered in random locations in a flight room. The bat's three-dimensional flight path was reconstructed using stereo images from high-speed video recordings, and the bat's sonar vocalizations were recorded for each trial and analyzed off-line. A microphone array permitted reconstruction of the sonar beam pattern, allowing us to study the bat's directional gaze and inspection of the objects. Bats learned the discrimination, but performance varied with S-. In acoustic studies of the objects, the S+ and S- stimuli were ensonified with frequency-modulated sonar pulses. Mean intensity differences between S+ and S- were within 4 dB. Performance data, combined with analyses of echo recordings, suggest that the big brown bat listens to changes in sound spectra

from echo to echo to discriminate between objects. Bats adapted their sonar calls as they inspected the stimuli, and their sonar behavior resembled that of animals foraging for insects. Analysis of sonar beam-directing behavior in certain trials clearly showed that the bat sequentially inspected S+ and S-.

Faure, P. A. & Barclay, R.M.R., 1994. Substrate-gleaning versus aerial-hawking: plasticity in the foraging and echolocation behaviour of the long-eared bat, *Myotis evotis*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 174(5), pp.651–660.

Abstract: The foraging and echolocation behaviour of *Myotis evotis* was investigated during substrate-gleaning and aerial-hawking attacks. Bats gleaned moths from both the ground and a bark-covered trellis, however, they were equally adept at capturing flying moths. The calls emitted by *M. evotis* during substrate-gleaning sequences were short, broadband, and frequency-modulated (FM). Three behavioural phases were identified: search, hover, and attack. Gleaning search calls were significantly longer in duration, lower in highest frequency, and larger in bandwidth than hover/attack calls. Calls were detected in only 68% of gleaning sequences, and when they were emitted, bats ceased calling ~200 ms before attacking. Terminal feeding buzzes, the rapid increase in pulse repetition rate associated with an attempted prey capture, were never recorded during gleaning attacks. The echolocation calls uttered by *M. evotis* during aerial-hawking foraging sequences were also short duration, high frequency, FM calls. Two distinct acoustic phases were identified: approach and terminal. Approach calls were significantly different from terminal calls in all variables measured. Calls were detected in 100% of aerial-hawking attacks and terminal feeding buzzes were invariably produced. Gleaning hover/attack calls were spectrally similar to aerial approach calls, but were shorter in duration and emitted at a significantly lower (but constant) repetition rate than aerial signals. Although the foraging environment (flight cage contents) remained unchanged between tasks (substrate-gleaning vs. aerial-hawking), bats emitted significantly lower amplitude calls while gleaning. We conclude that *M. evotis* adjusts its echolocation

Faure, P.A., Fullard, J. & Barclay, R.M.R., 1990. The response of tympanate moths to the echolocation calls of a substrate gleaning bat, *Myotis evotis*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 166, pp.843–849.

Abstract: 1. Most studies examining interactions between insectivorous bats and tympanate prey use the echolocation calls of aerially-feeding bats in their analyses. We examined the auditory responses of noctuid (*Eurois astricta*) and notodontid (*Pheosia rimosa*) moth to the echolocation call characteristics of a gleaning insectivorous bat, *Myotis evotis*. 2. While gleaning, *M. evotis* used short duration (mean ± SD = 0.66 ± 0.28 ms, Table 2), high frequency, FM calls (FM sweep = 80-37 kHz) of relatively low intensity (77.3 ± 2.9, -4.2 dB SPL). Call peak frequency was 52.2 kHz with most of the energy above 50 kHz (Fig. 1). 3. Echolocation was not required for prey detection or capture as calls were emitted during only 50% of hovers and 59% of attacks. When echolocation was used, bats ceased calling 324.7 (± 200.4) ms before attacking (Fig. 2), probably using prey-generated sounds to locate fluttering moths. Mean call repetition rate during gleaning attacks was 21.7 (±15.5) calls/s and feeding buzzes were never recorded. 4. *Eurois astricta* and *P. rimosa* are typical of most tympanate moths having ears with BFs between 20 and 40 kHz (Fig. 3); apparently tuned to the echolocation calls of aerially-feeding bats. The ears of both species respond poorly to the high frequency, short duration, faint stimuli representing the

echolocation calls of gleaning *M. evotis* (Figs. 4-6). 5. Our results demonstrate that tympanate moths, and potentially other nocturnal insects, are unable to detect the echolocation calls typical of gleaning bats and thus are particularly susceptible to predation.

Fay, R.R. & Popper, A.N., 2000. Evolution of hearing in vertebrates: the inner ears and processing. *Hearing Research*, 149(1-2), pp.1–10.

Abstract: This paper considers aspects of the evolution of the vertebrate auditory system from an `ichthyocentric' perspective. It is argued that all vertebrate auditory systems are required to do certain basic tasks including acoustic feature discrimination, sound source localization, frequency analysis, and auditory scene analysis, among others. These sorts of capabilities arose very early in the evolution of the vertebrates and have been modified by selection in different species. In some cases the same structures have been involved in detection and analysis throughout the vertebrates, while in other cases the mechanism by which the same type of analysis takes place may have changed.

Fellers, G.M. & Pierson, E.D., 2002. Habitat use and foraging behavior of Townsend's big-eared bat (*Corynorhinus townsendii*) in coastal California. *Journal of Mammalogy*, 83(1), pp.167–177.

Abstract: Radiotracking studies of Townsend's big-eared bat (*Corynorhinus townsendii*) were conducted in grazed grassland and coastal forest (California bay, Douglas-fir, and redwood) at Point Reyes National Seashore in coastal central California. Radiotagged bats were used to determine the foraging patterns of both female and male bats and to locate alternate roost sites. The animals showed considerable loyalty to their primary roost sites even though the study was conducted after the nursery period had ended, when the bats would normally be dispersing for the season. Foraging patterns differed between male and female bats, with females traveling greater distances than males. Males consistently stayed close to the maternity colony both during day and night. Both sexes flew in the immediate vicinity of vegetation, both when foraging and when traveling from the roost to foraging areas. Foraging activity was concentrated primarily along the edges of riparian vegetation.

Feng, A.S., Narins, P.M., Xu, C., Lin, W., Yu, Z., Qiu, Q., Xu, Z. & Shen, J., 2006. Ultrasonic communication in frogs. *Nature*, 440(7082), pp.333–6.

Abstract: Among vertebrates, only microchiropteran bats, cetaceans and some rodents are known to produce and detect ultrasounds (frequencies greater than 20 kHz) for the purpose of communication and/or echolocation, suggesting that this capacity might be restricted to mammals. Amphibians, reptiles and most birds generally have limited hearing capacity, with the ability to detect and produce sounds below approximately 12 kHz. Here we report evidence of ultrasonic communication in an amphibian, the concave-eared torrent frog (*Amolops tormotus*) from Huangshan Hot Springs, China. Males of *A. tormotus* produce diverse bird-like melodic calls with pronounced frequency modulations that often contain spectral energy in the ultrasonic range. To determine whether A. tormotus communicates using ultrasound to avoid masking by the wideband background noise of local fast-flowing streams, or whether the ultrasound is simply a by-product of the sound-production mechanism, we conducted acoustic playback experiments in the frogs' natural habitat. We found that the audible as well as the ultrasonic components of an *A. tormotus* call can evoke male vocal responses. Electrophysiological

recordings from the auditory midbrain confirmed the ultrasonic hearing capacity of these frogs and that of a sympatric species facing similar environmental constraints. This extraordinary upward extension into the ultrasonic range of both the harmonic content of the advertisement calls and the frog's hearing sensitivity is likely to have co-evolved in response to the intense, predominantly low-frequency ambient noise from local streams. Because amphibians are a distinct evolutionary lineage from microchiropterans and cetaceans (which have evolved ultrasonic hearing to minimize congestion in the frequency bands used for sound communication and to increase hunting efficacy in darkness), ultrasonic perception in these animals represents a new example of independent evolution.

Fenton, M., 1974. The role of echolocation in the evolution of bats. American Naturalist, 108(961), pp.386–388.

No abstract

Fenton, M., 1977. Variation in the social calls of little brown bats (*Myotis lucifugus*). *Canadian Journal of Zoology*, 55, pp.1151–1157.

Abstract: The social calls of 14 *Myotis 1ucifugus* (5 adult males; 5 adult females; 2 subadult males; 2 subadult females) produced under controlled conditions were more variable than echolocation calls made by hunting individuals in the wild. The social calls contained lower frequencies and in some cases were of longer duration than the echolocation calls. Careful examination of sound spectrographs of the calls indicated tremendous variability in details of frequency and time. Although several types of calls can be recognized, a discrete classification is not feasible because of the variability. The possible significance of the variation in the calls of these bats is discussed in the context of recognition of individuals by their vocalizations.

Fenton, M.B., 1990. The foraging behaviour and ecology of animal-eating bats. *Canadian Journal of Zoology*, 68(3), pp.411–422.

Abstract: The results of recent studies of the foraging behaviour of animal-eating bats are considered in this review. The advent of small (< 1 g) radio transmitters has made it possible to collect data on individual variations in foraging behaviour for species with body mass over 15 g. These data can be combined with those from wing morphology and echolocation call design to assess the flexibility achieved by some bats. The information concerning bats can be placed in a broader perspective by considering it in the light of current ideas about foraging theory. In this review, information about bat foraging is considered in the context of structural and functional features, the former relating to bats' access to habitats of different complexity and the latter to their behavioural responses. Mechanical features involving wing morphology and perceptual features, such as the ability of echolocating bats to deal with clutter, combine to influence the behavioural flexibility of individuals. This, in turn, affects access to prey and patterns of community structure. Bats relying on airborne prey appear to be limited to small prey items, whereas those hunting nonairborne targets may take much larger prey. Variation in individual behaviour means that terms such as gleaning, perch hunting, piscivory, and camivory do not accurately define the foraging of animal-eating bats. Morphological and behavioural data suggest that sympatric animal-eating bats of similar size will show considerable overlap in prey taken and in patterns of habitat use.

Fenton, M.B., 1997. Science and the conservation of bats. *Journal of Mammalogy* ,78, pp.1-14.

Abstract: The conservation implications of some recent advances in our knowledge about the ecology and behavior of bats are presented. A central question facing bat biologists is the relative importances of roosts and food as limiting factors in the population biology of bats. There is no reason to presume that the answer is the same for all species and the available data suggest intraspecific variation. This question is important for either conservation or behavior and ecology. Eavesdropping on the species-specific echolocation calls of bats has allowed documentation of distribution and habitat use by some bats although variability of calls complicates this picture. Radiotracking and surveys have produced data on use of space by bats. Although foraging areas and roosts are vital resources for bats, the associations between species of bats and habitats are not always clear. The mobility of bats and the low cost of flight together blur the link between bats and particular habitats. Radiotracking demonstrates how mobility gives bats access to mosaics of habitats, partly reflecting their size and flight characteristics, and the scale of habitat availability. For some species, access to mosaics of habitats for foraging is critical. Activities of humans influence the habitats available to bats and can generate feeding and roosting opportunities. The use that roosting bats make of buildings is an obvious example of bats benefitting from activities of humans. Another is bats feeding in the concentrations of insects at lights. In promoting the conservation of bats, it is important to consider people's perceptions of these animals, which are colored by the impact of bats on public health. Public interest in bats has vastly outstripped scientific research about them, presenting interesting challenges and opportunities for bat biologists.

Fenton, M.B., 2003. Eavesdropping on the echolocation and social calls of bats. *Mammal Rev*. 33(3), 193–204.

Abstract: 1. Comparisons of original calls and their echoes allow echolocating microchiropteran bats to collect information about their surroundings. Echolocation calls are also a source of information for other animals. A spectacular example is the hearing-based defence of many species of insects that use echolocation calls to detect marauding bats. The role of echolocation calls remains unknown for bats that eat other bats. 2. Other eavesdroppers, biologists, regularly monitor echolocation calls to collect information about the distribution and patterns of habitat use of echolocating bats. People monitoring echolocation calls have discovered cryptic species of bats. 3. Vocal communication in bats involves social calls that serve only in communication, as well as echolocation calls that influence the behaviour of conspecifics and others. There is evidence of individual- and colony-specific social and echolocation calls. 4. The long age-spans of bats and the propensity of some species to roost in groups combine with conspicuousness of echolocation calls to set the stage for the discovery of more behavioural interactions mediated by individual-specific echolocation calls. In the echolocation of microchiropteran bats, signals can serve multiple functions, both for producers and listeners.

Fenton, M., Audet, D., Obrist, M.K., & Rydell, J. 1995. Signal strength, timing, and self-deafening: the evolution of echolocation in bats. *Paleobiology*, 21(2), pp.229–242.

Abstract: We propose that the ancestors of bats were small, nocturnal, sylvatic gliders that used echolocation for general orientation. Their echolocation calls were short, low intensity,

broadband clicks, which translated into a very short operational range. In the lineage that gave rise to bats, a switch to stronger, tonal signals permitted the use of echolocation to detect, track, and assess flying insects in subcanopy settings. We propose that these animals hunted from perches and used echo- location to detect, track, and assess flying insects, which they attacked while gliding. In this way, the perfection of echolocation for hunting preceded the appearance of flapping flight, which marked the emergence of bats. Flapping flight had appeared by the Eocene when at least eight families are known from the fossil record. Stronger signals and adaptations to minimize self-deafening were central to the perfection of echolocation for locating flying prey. Echolocation constituted a key innovation that permitted the evolution and radiation of bats. At the same time, however, its short effective range imposed a major constraint on the size of bats. This constraint is associated with flight speed and the very small time intervals from detection of, and contact with a flying target. Gleaning and high duty cycle echolocation are two derived approaches to hunting prey in cluttered situations, places where echoes from background and other objects arrive before or at the same time as echoes from prey. Both had appeared by the Eocene.

Fenton, M. & Bell, G., 1979. Echolocation and feeding behaviour in four species of *Myotis* (Chiroptera). *Canadian Journal of Zoology*, 57, pp.1271–1277.

Abstract: We have compared the echolocation and feeding behaviours of *Myotis lucifugus*, *M. californicus*, *M. volans*, and *M. auriculus* based on observations and recordings of bats in the field. *Myotis lucifugus* and *M. californicus* appeared to detect prey at close range (<1 m) and regularly made several attempts to capture insects over short distances; both used similar frequency modulated echolocation calls. *Myotis volans* detected prey at greater distances (5-10 m), made only one attempt to capture insects per pass through a feeding area, and used an echolocation call with a distinct constant-frequency component. *Myotis auriculus* fed mainly on resting insects, mostly moths. The echolocation calls of this species were of shorter duration, lower intensity, broader frequency range with a higher frequency of maximum energy, and showed an initial upward sweep in frequency relative to the calls of the other *Myotis* we studied. *Myotis auriculus* did not increase their pulse repetition rate as they closed with stationary prey, and they appeared to fix on resting insects from about 2 m. This species rarely made more than one attempt to capture an insect per pass through a feeding area.

Fenton, M.B., Faure, P.A. & Ratcliffe, J.M., 2012. Evolution of high duty cycle echolocation in bats. The Journal of Experimental Biology, 215, pp.2935–44.

Abstract: Duty cycle describes the relative “on time” of a periodic signal. In bats, we argue that high duty cycle (HDC) echolocation was selected for and evolved from low duty cycle (LDC) echolocation because increasing call duty cycle enhanced the ability of echolocating bats to detect, lock onto and track fluttering insects. Most echolocators (most bats and all birds and odontocete cetaceans) use LDC echolocation, separating pulse and echo in time to avoid forward masking. They emit short duration, broadband, downward frequency modulated (FM) signals separated by relatively long periods of silence. In contrast, bats using HDC echolocation emit long duration, narrowband calls dominated by a single constant frequency (CF) separated by relatively short periods of silence. HDC bats separate pulse and echo in frequency by exploiting information contained in Doppler-shifted echoes arising from their movements relative to background objects and their prey. HDC echolocators are particularly sensitive to amplitude and frequency glints generated by the wings of fluttering insects. We hypothesize that

narrowband/CF calls produced at high duty cycle, and combined with neurobiological specializations for processing Doppler-shifted echoes, were essential to the evolution of HDC echolocation because they allowed bats to detect, lock onto and track fluttering targets. This advantage was especially important in habitats with dense vegetation that produce overlapping, time-smeared echoes (i.e. background acoustic clutter). We make four specific, testable predictions arising from this hypothesis.

Fenton, M.B. & Griffin, D.R., 1997. High-altitude pursuit of insects by echolocating bats. *Journal of Mammalogy*, 78(1), p.247.

Abstract: Bat detectors on helium-filled kite balloons revealed echolocating bats active at altitudes - 600 m above the ground over Brachystegia woodland in the Sengwa Wildlife Research Area, Zimbabwe. Feeding buzzes indicated that bats were actively foraging to 600 m. At least seven species of bats were detected, including six molossids and one emballonurid.

Fenton, M.B., Merriam, H.G. & Holroyd, G.L., 1983. Bats of Kootenay, Glacier, and Mount Revelstoke national parks in Canada: identification by echolocation calls, distribution, and biology. *Canadian Journal of Zoology*, 61(11), pp.2503–2508.

Abstract: We studied the behaviour, echolocation calls, and distribution of bats in Kootenay, Glacier, and Mount Revelstoke national parks in British Columbia, Canada. Presented here are keys for identification of nine species of bats by their echolocation calls as rendered by two different bat-detecting systems. The species involved include *Myotis lucifugus*, *M. evotis*, *M. volans*, *M. septentrionalis*, *M. californicus*, *Lasionycteris noctivagans*, *Eptesicus fuscus*, *Lasiurus cinereus*, and *L. borealis*. The distribution of these species within the three parks was assessed by capturing bats in traps and mist nets and by monitoring of their echolocation calls. Most of the species exploited concentrations of insects around spotlights, providing convenient foci of activity for assessing distribution. Although most species of *Myotis* were commonly encountered away from the lights, *Lasiurus cinereus* in Kootenay National Park was only regularly encountered feeding on insects at lights. This species was not detected in Glacier National Park, and although we regularly encountered it in the town of Revelstoke, it was rarely encountered in Mount Revelstoke National Park. Another focus of bat activity was small pools in cedar forest in Mount Revelstoke National Park. This involved high levels of *Myotis* spp. activity at dusk as the bats came to the pools to drink.

Fenton, M.B. & Morris, G.K., 1976. Opportunistic feeding by desert bats (*Myotis spp*.). *Canadian Journal of Zoology*, 54, pp.526–530.

Abstract: By using a “black light” and playback of sounds made by foraging insectivorous bats, we examined opportunistic feeding behavior of bats near Camp Verde, Arizona, between I and 10 June 1975. Bats were significantly most active during 15-min periods when the light was on and insects were aggregated over it. Bats feeding over the light selectively pursued and captured larger insects, apparently ignoring the smaller ones. Bats did not respond to sounds simulating feeding buzzes of bats, but showed a slight response to the foraging sounds of other bats. Opportunistic feeding by insectivorous bats allows effective exploitation of patchily distributed food resources and can lead to selective feeding when “hatches” of insects are involved. Opportunistic feeding is not incompatible with selective feeding, and may eventually be established as a strategy common to most insectivorous bats.

Fenton, M. & Portfors, C., 1998. Compromises: sound frequencies used in echolocation by aerial-feeding bats. *Journal of Zoology*, 76, pp.1174–1182.

Abstract: Hunting aerial-feeding bats, species that take airborne prey (usually flying insects), use echolocation to detect, track, and assess targets. The echolocation calls of aerial-feeding bats at sites in Canada (British Columbia and Ontario), Mexico, Brazil, and Zimbabwe were significantly dominated by frequencies between 20 and 60 kHz, although at the more tropical locations some aerial-feeding bats used echolocation calls with most energy <20 or >60 kHz. The impact of frequency-specific attenuation, perhaps combined with frequency-specific, hearing-based defenses of some insects, suggests that by using echolocation calls <20 kHz, bats could both extend the effective range of echolocation and make their calls less conspicuous to insect ears. Bats using calls >60 kHz would be less conspicuous to the insects. We found two patterns of echolocation-call behaviour. Most adjacent echolocation calls, and all that were dominated by sounds >20 kHz, showed large (80%) overlap in bandwidth. The other pattern involved much less overlap in bandwidth (0–30%) between adjacent calls and was evident in the calls of the molossid *Tadarida midas*, which used echolocation calls dominated by sounds <20 kHz. This behaviour would allow the echolocating bat to extend its effective range of perception by separating in frequency the echoes returning from adjacent calls.

Fenton, M. B., Skowronski, M., McGuire. L. P., and Faure, P.A.,2011). Variation in the use of harmonics in the calls of laryngeally echolocating bats. *Acta Chriopterologica*, 13(1), pp.169-178.

Abstract: The echolocation calls of bats may contain a single acoustic element (the fundamental frequency or a harmonic) or multiple acoustic elements that may (or may not) include the fundamental element. We hypothesize that the detection of harmonics is affected by three factors: 1) species, 2) situation, and 3) recording quality. To test our hypotheses, we recorded and analyzed approximately 2,300 calls from 17 species and 1 subspecies in 6 families of bats using a 1-channel and 4-channel microphone array. The percentage of calls with multiple acoustic elements varied from 0 to 83% across species. Furthermore, recordings from a 4-channel microphone array (1 m tetrahedron arrangement) revealed that the percent of calls with multiple acoustic elements varied across channels by up to 50%, indicating the effect of bat position relative to the microphone. In some species, presence of multiple acoustic elements was predicted by call energy: calls with sufficient energy (threshold varied by species) had multiple acoustic elements above the noise floor of the recording system. In the remaining species that produced calls with multiple acoustic elements, we found two clusters of calls. In one cluster, the presence of multiple acoustic elements was predicted by received call energy. In the 2nd cluster, call energy was lower, and almost all calls included multiple acoustic elements. The detection of harmonics independent of recorded energy suggests the intriguing possibility that harmonics are used differently in these species. Finally, to test the effect of situation, we recorded the echolocation calls of big brown bats (*Eptesicus fuscus*) flying in three settings: an anechoic flight room, during roost emergence, and foraging in an open area. Call energy shifted to lower frequencies and fewer acoustic elements as the recording distance and the volume of the flight environment increased (i.e., as clutter decreased). Comparing flight room with foraging calls revealed that the second harmonic of open air foraging signals decreased by about 30 dB (relative to the fundamental). Overall, our results show that detection of echolocation signals with harmonics varied significantly across species. We also demonstrate that relative harmonic

intensity varies according to the flight situation within a species, and when combined with the effects of call directionality and relative position of bat and microphone, these factors influence harmonic detection in echolocation recordings.

Fenzl, T. & Schuller, G., 2007. Dissimilarities in the vocal control over communication and echolocation calls in bats. *Behavioural Brain Research*, 182(2), pp.173–9.

Abstract: Bats, like other mammals, use communication calls for social interaction, but rely at the same time on sophisticated echolocation systems for orientation and prey capture. Both call types are of laryngeal origin, but can be distinguished on the basis of their spectral and temporal features and apparently their functional involvement as well. Although they share a common final motor pathway, there is evidence that separate vocally active brainstem areas are involved in the functional control of communication and echolocation calls. This review summarizes findings that support the above assumption, and focus on the functional involvement of the periaqueductal gray, the paralemniscal area, and the nucleus of the brachium of the inferior colliculus, in differentiated vocal control.

Ferrara, F.J. & Leberg, P.L., 2005. Influence of investigator disturbance and temporal variation on surveys of bats roosting under bridges. *Wildlife Society Bulletin*, 33(3), pp.1113–1122.

Abstract: Given the importance of roost sites to bats, monitoring roost use is an important tool for assessing the local status of some species. We surveyed bridges for day-roosting bats in the Kisatchie National Forest of Louisiana to assess how temporal patterns of bridge use and disturbance from surveyors might affect survey results. We found no support for the hypothesis that surveys of day-roosts affected bat use of bridges. The 3 most common species roosting under bridges, Rafinesque's big-eared bats (*Corynorhinus rafinesquii*), eastern pipistrelles (*Pipistrellus subflavus*), and big brown bats (*Eptesicus fuscus*), exhibited strikingly different patterns of seasonal use. Because of seasonal variation in bridge use, a monitoring program would need to involve a minimum of a summer and a winter survey to document all common species that use bridges. Surveys during the day detected many more bats than surveys conducted at night. Although individuals tended to return to the same roosts over long periods of time, tagged bats often were absent during intervening surveys. Because individuals used multiple roosts, at least 3 surveys within a season will be necessary if an objective is to determine which specific bridges are used as roosts by locally abundant species.

Firzlaff, U. & Schuller, G., 2004. Directionality of hearing in two CF/FM bats, *Pteronotus parnellii* and *Rhinolophus rouxi*. *Hearing Research*, 197(1-2), pp.74–86.

Abstract: The head-related transfer function (HRTF) has been measured in two CF/FM bats, *Pteronotus parnellii* and *Rhinolophus rouxi* from 575 positions in the frontal hemisphere. *P. parnellii* showed an increase of the elevation angle of the axis of highest pinna gain with increasing frequency followed by a specific decrease at 75 kHz. Such a drop of elevation angle of the acoustic axis was not seen in *R. rouxi*. The HRTF further showed a spectral notch dependent on elevation and frequency in *P. parnellii*, but not in *R. rouxi*. The functional implications of this difference between both bat species are discussed. Frequencies at maximum pinna gain values did not clearly match the frequencies of the harmonics of the echolocation calls whereas spatial resolution of interaural intensity differences was best in a frequency range

that included the higher harmonics of the echolocation calls in both bat species. However, specializations of HRTF patterns matching the exact frequencies of the harmonics of the echolocation calls could not be observed in both bat species.

Fontaine, B. & Peremans, H., 2009. Bat echolocation processing using first-spike latency coding. *Neural Networks,* 22(10), pp.1372–82.

Abstract: To perform echolocation, so-called FM-bats emit short pulses i.e., with a duration of a few milliseconds, and analyse the echoes coming from their environment. One individual echo, due to its short duration, will cause neurons in the early auditory system to generate between 1 and 3 spikes only. Hence, we argue that it is advantageous for FM-bats to use spike-time rather that firing rate information. We present a simple spike-time model of the monaural and binaural pathways up to the midbrain, to show that spike-time information can indeed be processed by the known neural architecture. In particular, we show that a First Spike Latency (FSL) code, as provided by the auditory nerves, can represent both the monaural and binaural intensity cues induced by the head-related transfer function in the peripheral system. We also show that ascending centres enhance the cues conveyed by such an FSL code. Finally, we present experimental results, comparing the FSL code based model proposed here with a more classic firing rate code, and we show that first-spike latency is a more biologically plausible alternative.

Fontaine, B. & Peremans, H., 2011. Compressive sensing: a strategy for fluttering target discrimination employed by bats emitting broadband calls. *The Journal of the Acoustical Society of America,* 129(2), pp.1100–10.

Abstract: When foraging, so-called FM-bats emit sequences of frequency modulated (FM) calls in order to detect, identify, and localize edible prey. Once a potential target has been detected, various call and call sequence parameters, such as frequency sweep, pulse duration, and inter pulse interval (IPI) vary. In this paper, the possible functions of the variation of the IPI are studied. In particular, it is conjectured that the IPI patterns are an adaptive behavior that optimizes the signal design parameters in order to improve information retrieval. Such an irregular sampling strategy would be useful whenever bats need to characterize signal modulation (e.g., the wing beat of an insect) using a call emission rate lower than the signal modulation of interest. This problem can be recast as extracting features, in this case the joint acoustic and modulation frequency representation, from signals sampled at frequencies well below the Nyquist cut-off frequency. To study the possibility of such target classification using a sub-Nyquist sampling scheme, results derived in the context of compressive sensing are used. Processing echoes collected from both rotating computer fans and fluttering locusts, it is shown that such a strategy would allow FM-bats to discriminate between targets based on their different fluttering rates.

Forman, R.T.T. & Alexander, L.E., 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics,* 29(1), pp.207–231.

Abstract: A huge road network with vehicles ramifies across the land, representing a surprising frontier of ecology. Species-rich roadsides are conduits for few species. Roadkills are a premier mortality source, yet except for local spots, rates rarely limit population size. Road avoidance, especially due to traffic noise, has a greater ecological impact. The still-more-important barrier effect subdivides populations, with demographic and probably genetic consequences. Road

networks crossing landscapes cause local hydrologic and erosion effects, whereas stream networks and distant valleys receive major peak-flow and sediment impacts. Chemical effects mainly occur near roads. Road networks interrupt horizontal ecological flows, alter landscape spatial pattern, and therefore inhibit important interior species. Thus, road density and network structure are informative landscape ecology assays. Australia has huge road-reserve networks of native vegetation, whereas the Dutch have tunnels and overpasses perforating road barriers to enhance ecological flows. Based on road-effect zones, an estimated 15–20% of the United States is ecologically impacted by roads.

Francis, C. D., 2014. Road noise and signal divergence via developmental plasticity in an arthropod. *Functional Ecology*, 28, 547–548.

No abstract

Francis, C.D. & Barber, J.R., 2013. A framework for understanding noise impacts on wildlife: an urgent conservation priority. *Frontiers in Ecology and the Environment*, 11(6), pp.305–313.

Abstract: Anthropogenic noise is an important environmental stressor that is rapidly gaining attention among biologists, resource managers, and policy makers. Here we review a substantial literature detailing the impacts of noise on wildlife and provide a conceptual framework to guide future research. We discuss how several likely impacts of noise exposure have yet to be rigorously studied and outline how behavioral responses to noise are linked to the nature of the noise stimulus. Chronic and frequent noise interferes with animals' abilities to detect important sounds, whereas intermittent and unpredictable noise is often perceived as a threat. Importantly, these effects can lead to fitness costs, either directly or indirectly. Future research should consider the range of behavioral and physiological responses to this burgeoning pollutant and pair measured responses with metrics that appropriately characterize noise stimuli. This will provide a greater understanding of the mechanisms that govern wildlife responses to noise and help in identifying practical noise limits to inform policy and regulation.

Francis, C.D., Ortega, C.P. & Cruz, A., 2009. Noise pollution changes avian communities and species interactions. *Current biology*, 19(16), pp.1415–9.

Abstract: Humans have drastically changed much of the world's acoustic background with anthropogenic sounds that are markedly different in pitch and amplitude than sounds in most natural habitats. This novel acoustic background may be detrimental for many species, particularly birds. We evaluated conservation concerns that noise limits bird distributions and reduces nesting success via a natural experiment to isolate the effects of noise from confounding stimuli and to control for the effect of noise on observer detection biases. We show that noise alone reduces nesting species richness and leads to different avian communities. Contrary to expectations, noise indirectly facilitates reproductive success of individuals nesting in noisy areas as a result of the disruption of predator-prey interactions. The higher reproductive success for birds within noisy habitats may be a previously unrecognized factor contributing to the success of urban-adapted species and the loss of birds less tolerant of noise. Additionally, our findings suggest that noise can have cascading consequences for communities through altered species interactions. Given that noise pollution is becoming ubiquitous throughout much of the

world, knowledge of species-specific responses to noise and the cumulative effects of these novel acoustics may be crucial to understanding and managing human-altered landscapes.

Francis, C.D., Paritis, J., Ortega, C.P. & Cruz, A., 2011. Landscape patterns of avian habitat use and nest success are affected by chronic gas well compressor noise. *Landscape Ecology*, 26(9), pp.1269–1280.

Abstract: Anthropogenic noise is becoming a dominant component of soundscapes across the world and these altered acoustic conditions may have severe consequences for natural communities. We modeled noise amplitudes from gas well compressors across a 16 km2 study area to estimate the influence of noise on avian habitat use and nest success. Using species with noise responses representative of other avian community members, across the study area we estimated gray flycatcher (*Empidonax wrightii*) and western scrub-jay (*Aphelocoma californica*) occupancy, and gray flycatcher nest success, which is highly dependent on predation by western scrub-jays. We also explore how alternative noise management and mitigation scenarios may reduce area impacted by noise. Compressor noise affected 84.5% of our study area and occupancy of each species was approximately 5% lower than would be expected without compressor noise. In contrast, flycatcher nest success was 7% higher, reflecting a decreased rate of predation in noisy areas. Not all alternative management and mitigation scenarios reduced the proportion of area affected by noise; however, use of sound barrier walls around compressors could reduce the area affected by noise by 70% and maintain occupancy and nest success rates at levels close to those expected in a landscape without compressor noise. These results suggest that noise from compressors could be effectively managed and, because habitat use and nest success are only two of many ecological processes that may change with noise exposure, minimizing the anthropogenic component of soundscapes should be a conservation priority.

Frenckell, B. Von & Barclay, R.M.R., 1987. Bat activity over calm and turbulent water. *Canadian Journal of Zoology*, 65(2), pp.219–222.

Abstract: A comparison of the activity of the little brown bat (*Myotis lucifugus*) over calm pools and fast-flowing riffles was performed in southwestern Alberta. Bat activity was assessed by monitoring echolocation calls using ultrasonic detectors. Activity was higher over pools than riffles. This could be due to differences in prey abundance or accessibility in the two habitats. Alternatively, water noise at turbulent sites may interfere with the bats' echolocation abilities. Sticky traps were used to assess prey abundance, and water noise was recorded for intensity-frequency analysis. Insect abundance at the height where the bats flew (< 1 m above the water) did not differ between sites, but insects close to or at water level at calm pools may be more accessible than at fast-flowing riffles. Further, water noise at riffles may decrease the efficiency with which bats detect targets.

Fukui, D., Murakami, M., Nakano, S. & Aoi, T., 2006. Effect of emergent aquatic insects on bat foraging in a riparian forest. *The Journal of Animal Ecology*, 75(6), pp.1252–1258.

Abstract: 1. Riparian zones serve several ecological functions for bats. They provide a source of prey and likely provide favourable structural habitats and shelter from predators. Many studies have shown that bats use the space above streams, ponds or riparian vegetation as feeding habitat. These studies, however, have never distinguished between the effects of habitat structure and prey availability on the foraging activities of bats. Such effects can only be distinguished by

an experimental approach. We predicted that bat activity along a stream is influenced by the number of emerged aquatic insects. 2. We evaluated the response of terrestrial consumers, insectivorous bats, to changes in the abundance of emergent aquatic insects by conducting a manipulative field experiment. In a deciduous riparian forest in Japan, aquatic insect flux from the stream to the riparian zone was controlled with an insect-proof cover over a 1.2 km stream reach. 3. We estimated the abundance of emergent aquatic and flying terrestrial arthropods near the treatment and control reaches using Malaise traps. The foraging activity of bats was evaluated in both treatment and control reaches using ultrasonic detectors. 4. The insect-proof cover effectively reduced the flux of emergent aquatic insects to the riparian zone adjacent to the treatment reach. Adjacent to the control reach, adult aquatic insect biomass was highest in spring, and then decreased gradually. Terrestrial insect biomass increased gradually during the summer at both treatment and control reaches. 5. Foraging activity of bats was correlated with insect abundance. In spring, foraging activity of bats at the control reach was significantly greater than at the treatment reach, and increased at both sites with increasing terrestrial insect abundance. 6. Our result suggests that the flux of aquatic insects emerging from streams is one of the most important factors affecting the distribution of riparian-foraging bats. As is the case with other riparian consumers, resource subsidies from streams can directly enhance the performance or population density of riparian-dependent bats. To conserve and manage bat populations, it is important to protect not only forest ecosystems, but also adjacent aquatic systems such as streams.

Fullard, J., 1979. Jamming bat echolocation: the clicks of arctiid moths. *Canadian Journal of Zoology,* 57, pp.647–649.

Abstract: power spectra and frequency-time structures) arc remarkably similar to those LIT frequency modulated echolocation calls produced by many bath as they close with their prey. We suspect that the clicks are initially processed as echoes by the auditory systems of the bats and function by interfering with information processing by the bat.

Fullard, J.H., Ratcliffe, J.M. & Jacobs, D.S., 2008. Ignoring the irrelevant: auditory tolerance of audible but innocuous sounds in the bat-detecting ears of moths. *Die Naturwissenschaften,* 95(3), pp.241–5.

Abstract: Noctuid moths listen for the echolocation calls of hunting bats and respond to these predator cues with evasive flight. The African bollworm moth, *Helicoverpa armigera*, feeds at flowers near intensely singing cicadas, *Platypleura capensis*, yet does not avoid them. We determined that the moth can hear the cicada by observing that both of its auditory receptors (A1 and A2 cells) respond to the cicada's song. The firing response of the A1 cell rapidly adapts to the song and develops spike periods in less than a second that are in excess of those reported to elicit avoidance flight to bats in earlier studies. The possibility also exists that for at least part of the day, sensory input in the form of olfaction or vision overrides the moth's auditory responses. While auditory tolerance appears to allow *H. armigera* to exploit a food resource in close proximity to acoustic interference, it may render their hearing defence ineffective and make them vulnerable to predation by bats during the evening when cicadas continue to sing. Our study describes the first field observation of an eared insect ignoring audible but innocuous sounds.

Fuller, R. A., Warren, P. H. & Gaston, K. J. 2007. Daytime noise predicts nocturnal singing in urban robins. *Biol. Lett*. 3, 368–370.

Abstract: Ambient noise interferes with the propagation of acoustic signals through the environment from sender to receiver. Over the past few centuries, urbanization and the development of busy transport networks have led to dramatic increases in the levels of ambient noise with which animal acoustic communications must compete. Here we show that urban European robins *Erithacus rubecula*, highly territorial birds reliant on vocal communication, reduce acoustic interference by singing during the night in areas that are noisy during the day. The effect of ambient light pollution, to which nocturnal singing in urban birds is frequently attributed, is much weaker than that of daytime noise

Furmankiewicz, J., Ruczynski, I., Urban, R.U. & Jones, G., 2011. Social calls provide tree-dwelling bats with information about the location of conspecifics at roosts. *Ethology*, 117(6), pp.480–489.

Abstract: Animals can use signals emitted by other animals as sources of information. Auditory signals are important in communication networks, as they can potentially convey information about the location and state of conspecifics and other species over long distances. Signalling is important in fission–fusion societies, in which animals from the same social group temporarily split into subgroups and frequently change roost sites. We used playbacks of social calls of the noctule *Nyctalus noctula* produced in roosts, to show how bats might maintain group cohesion and to test the hypothesis that noctules can locate conspecifics when returning from foraging trips by eavesdropping on or communicating with roosting individuals. Noctules responded strongly to broadcasted social calls. Their reactions included inspections and landing on a loudspeaker broadcasting social calls and occasional social vocalisation. Responses by other bat species to the noctule social calls were negligible. The high amplitude, low-frequency vocalisations emitted by noctules in roosts can propagate over long distances and allow group members to announce their position. Bats can extract information about the location of roosts containing conspecifics by eavesdropping or by communication. Social calls may thus be sufficient to locate conspecifics in roosts and maintain spatial associations of groups in mammals.

Fuzessery, Z., 1994. Response selectivity for multiple dimensions of frequency sweeps in the pallid bat inferior colliculus. *Journal of Neurophysiology*, 72(3), pp.1061–1079.

Abstract: 1. While hunting, the pallid bat uses passive sound localization at low frequencies to find terrestrial prey, and echolocation for general orientation. It must therefore process two different types of acoustic input at the same time. The pallid bat's echolocation pulse is a downward frequency-modulated (FM) sweep from 60 to 30 kHz. This study examined the response selectivity of single neurons in the pallid bat's central nucleus of the inferior colliculus (ICC) for FM sweeps, comparing the response properties of the high-frequency population, tuned to the biosonar pulse, with the low-frequency population, tuned below the pulse. The working hypothesis was that the high-frequency population would exhibit a response selectivity for downward FM sweeps that was not present in the low-frequency population. 2. Neurons were tested for their selectivity for FM sweep direction, duration, frequency range and bandwidth, and rate of frequency change. The extent to which they responded exclusively to tones, noise, and FM sweeps was also examined. Significant differences in the response properties of neurons in the two populations were found. In the low-frequency population, all neurons responded to tones, but only 50% responded to FM sweeps. Only 23% were selective for sweep direction. In the high-frequency population, all neurons responded to FM sweeps, but 31% did not respond to

tones. Over one-half of this population was selective for sweep direction, and of those that were selective, all preferred the downward sweep direction of the biosonar pulse. A large percentage (31%) responded exclusively to downward sweeps, and not to tones or upward sweeps. None of the cells in either population responded to noise, or did so only at very high relative thresholds. 3. Both populations contained neurons that were selective for short stimulus durations that approximated the duration of the biosonar pulse, although the percentage was greater in the high frequency population (58% vs. 20%). In the high-frequency population, 31% of the neurons tested for duration responded exclusively to both the sweep direction and duration of the biosonar pulse. 4. Downward FM-selective neurons, with one exception, were generally insensitive to the rate of frequency change of the FM sweep, as well as the frequency range and bandwidth of the sweep. They responded similarly to both the full 60- to 30-kHz sweep and to 5-kHz bandwidth portions of the full sweep. 5. The percentage of neurons in the entire population that responded exclusively to downward FM sweeps approximating the biosonar pulse is an order of magnitude greater than has been reported in the IC of most other bats studied. This suggests that such selectivity is not needed simply for the selective detection of biosonar echoes. Instead, this extreme functional specialization in the pallid bat auditory midbrain may serve the demands of having to process active and passive acoustic information at the same time. The response selectivity observed may function to
maintain the separation between two parallel channels for echolocation and passive listening.

Fuzessery, Z., 1996. Monaural and binaural spectral cues created by the external ears of the pallid bat. *Hearing Research*, 95, pp.1–17.

Abstract: The acoustic properties of external ears transform the spectra of incident sound in a location-dependent manner, and provide monaural and binaural spectral information used in 2-dimensional localization. Human studies suggest that binaural spectral differences, and spectral peaks and notches in monaural transfer functions, may all provide spatial information. This study examined the acoustic properties of the pallid bat ear to determine directionality, interaural intensity differences, spectral peaks and notches in transfer functions, as well as acoustic gain. The pallid bat is a gleaning bat that uses passive sound localization to find prey, and echolocation for general orientation. It is capable of very accurate passive sound localization, and the primary focus of this study was to determine the spectral cues that might support this localization acuity. Results show that the external ears of this bat create spectral maxima and minima that vary systematically with azimuth and elevation. The monaural spectral cues resemble those reported in humans and cats, and suggest that similar spectral cues are used across taxa. The ears also create robust interaural spectral differences that vary systematically with both sound azimuth and elevation. These monaural and binaural spectral cues may provide the basis for the 1° angular resolution apparent in it this bat's passive sound localization performance.

Fuzessery, Z.M., Buttenhoff, P., Andrews, B. & Kennedy, J.M., 1993. Passive sound localization of prey by the pallid bat (*Antrozous p. pallidus*). *J. Comp. Physiol. A*, 171, pp.767-777.

Summary: The pallid bat (*Antrozous p. pallidus*) uses passive sound localization to capture terrestrial prey. This study of captive pallid bats examined the roles of echolocation and passive sound localization in prey capture, and focused on their spectral requirements for accurate

passive sound localization. Crickets were used as prey throughout these studies. All tests were conducted in dim, red light in an effort to preclude the use of vision. Hunting performance did not differ significantly in red light and total darkness, nor did it differ when visual contrast between the terrestrial prey and the substrate was varied, demonstrating that the bats did not use vision to locate prey. Our bats apparently used echolocation for general orientation, but not to locate prey. They did not increase their pulse emission rate prior to prey capture, suggesting that they were not actively scanning prey. Instead, they required prey-generated sounds for localization. The bats attended to the sound of walking crickets for localization, and also attacked small, inanimate objects dragged across the floor. Stationary and/or anesthetized crickets were ignored, as were crickets walking on substrates that greatly attenuated walking sounds. Cricket communication sounds were not used in prey localization; the bats never captured stationary, calling crickets. The accuracy of their passive sound localization was tested with an open-loop passive sound localization task that required them to land upon an anesthetized cricket tossed on the floor. The impact of a cricket produced a single 10–20 ms duration sound, yet with this information, the bats were able to land within 7.6 cm of the cricket from a maximum distance of 4.9 m. This performance suggests a sound localization accuracy of approximately ±1° in the horizontal and vertical dimensions of auditory space. The lower frequency limit for accurate sound localization was between 3–8 kHz. A physiological survey of frequency representation in the pallid bat inferior colliculus suggests that this lower frequency limit is around 5 kHz.

Fuzessery, Z.. & Hall, J., 1999. Sound duration selectivity in the pallid bat inferior colliculus. *Hearing Research*, 137(1-2), pp.137–154.

Abstract: Neurons selective for sound duration have been reported in the auditory midbrain and cortex of several specialized vertebrate species that process behaviorally relevant signals of stereotypic duration. This study examines duration selectivity in the inferior colliculus (IC) of the pallid bat to determine if this selectivity is limited to regions that serve echolocation, or if it extends to low frequency regions that serve passive listening. It also focuses on the temporal response properties of duration-selective neurons to elucidate mechanisms that may underlie the creation of this selectivity. Of 140 neurons tested, 36% were selective for short durations of 97 ms, and acted as short-pass or bandpass duration filters. Sixteen percent, termed long duration neurons, differed in that they required minimum sound durations of 5-50 ms before responding, and all acted as long-pass duration filters. Short duration neurons were equally common in the high-frequency region serving echolocation and the lateral low-frequency region that serves passive listening, indicating that selectivity for short duration sounds was not associated only with the specialized function of echolocation. Long duration neurons were most common in the medial low-frequency region IC. Selectivity for short and long duration sounds was therefore not uniformly distributed across the IC. Analyses of the temporal response properties of short duration neurons, and the application of bicuculline to block Q-aminobutyric acid-A receptors, were used to infer the synaptic interactions that underlie the creation of duration selectivity, the role of inhibition in its creation, and whether a coincidence mechanism proposed by Casseday et al. (Science 264 (1994): 847-850) is consistent with the behavior of the duration-selective neurons recorded in the pallid bat IC. Present results suggest that while some neurons do behave in a manner that is consistent with the coincidence mechanism, the behaviors of others suggest that more than one mechanism may create a selectivity for short duration sounds.

Fyhri, A. & Klaeboe, R., 2009. Road traffic noise, sensitivity, annoyance and self-reported health: a structural equation model exercise. *Environment international*, 35(1), pp.91–7.

Abstract: The proposed effect of road traffic noise on hypertension and ischemic heart disease finds mixed empirical support. One problem with many studies is that the directions of the causal relationships are not identified. This is often the case when cross-sectional data and multivariate regression models are utilised. The aim of the study was to explore the relationship between road traffic noise and health. More specifically the relationships between noise complaints, noise sensitivity and subjectively reported hypertension and heart problems were investigated. 1842 respondents in Oslo, Norway were interviewed about their experience of the local environment and their subjective health complaints. The interviews were conducted as part of two surveys. Individual measures of air pollution (NO(2)) and noise (L_{den}) were calculated. The data were analysed using Structural Equation Models. Only sensitivity to noise is related to hypertension and chest pain. No relationships between noise exposure and health complaints were identified. Rather than noise being the causal agent leading to health problems, the results suggest that the noise-health relationships in these studies may be spurious. It is conceivable that individual vulnerability is reflected both in ill health and in being sensitive to noise. The benefit of including more contextual variables in a model of noise-health relationships is supported.

Gadziola, M.A., Grimsley, J.M.S., Faure, P.A. & Wenstrup, J.J., 2012. Social vocalizations of big brown bats vary with behavioral context. *PloS One*, 7(9), p.e44550.

Abstract: Bats are among the most gregarious and vocal mammals, with some species demonstrating a diverse repertoire of syllables under a variety of behavioral contexts. Despite extensive characterization of big brown bat (*Eptesicus fuscus*) biosonar signals, there have been no detailed studies of adult social vocalizations. We recorded and analyzed social vocalizations and associated behaviors of captive big brown bats under four behavioral contexts: low aggression, medium aggression, high aggression, and appeasement. Even limited to these contexts, big brown bats possess a rich repertoire of social vocalizations, with 18 distinct syllable types automatically classified using a spectrogram cross-correlation procedure. For each behavioral context, we describe vocalizations in terms of syllable acoustics, temporal emission patterns, and typical syllable sequences. Emotion-related acoustic cues are evident within the call structure by context-specific syllable types or variations in the temporal emission pattern. We designed a paradigm that could evoke aggressive vocalizations while monitoring heart rate as an objective measure of internal physiological state. Changes in the magnitude and duration of elevated heart rate scaled to the level of evoked aggression, confirming the behavioral state classifications assessed by vocalizations and behavioral displays. These results reveal a complex acoustic communication system among big brown bats in which acoustic cues and call structure signal the emotional state of a caller.

Gaisler, J., Rehák, Z. & Bartonicka, T., 2009. Bat casualties by road traffic (Brno-Vienna). *Acta Theriologica*, 54(2), pp.147–155.

Abstract: We studied the impact of road E461, Brno-Vienna, on bat mortality, with the goal to predict this impact after the road has been reconstructed and turned into highway, R52. In the Czech territory, two proposed road sections of E461 were selected, 3.5 and 4.5 km long, and divided into segments 100 m in length. Bat carcasses were picked up from emergency stopping lanes, and bat activity was recorded by ultrasound detectors along the road and 100 m away on

both sides from the central strip. From May to October 2007, 25 checks of bat mortality performed at weekly intervals revealed 119 bat carcasses representing 11 or 12 species. *Pipistrellus nathusii*, *P. pygmaeus* and *Myotis daubentonii* were the most frequent traffic casualties. The greatest mortality was documented from early July to mid-October, with a peak in September. Monitoring bat activity by ultrasound detectors (one night per month in May, June and September) yielded 12 bat species and 3 species couples (*Myotis mystacinus/brandtii*, *M. emarginatus/alcathoe*, *Plecotus auritus/austriacus*), mostly the same taxa as found dead on the road. Significantly greater bat numbers were revealed in the section where the road was situated between two artificial lakes, as compared to a road section without any lakes directly adjacent to the road. In the former section, significant correlation was found between the number of carcasses found and the activity detected, according to road segments.

Gao, L., Balakrishnan, S., He, W., Yan, Z. & Muller, R., 2011. Ear deformations give bats a physical mechanism for fast adaptation of ultrasonic beam patterns. *Physical Review Letters*, 107(21), p.214301.

Abstract: A large number of mammals, including humans, have intricate outer ear shapes that diffract incoming sound in a direction- and frequency-specific manner. Through this physical process, the outer ear shapes encode sound-source information into the sensory signals from each ear. Our results show that horseshoe bats could dynamically control these diffraction processes through fast nonrigid ear deformations. The bats' ear shapes can alter between extreme configurations in about 100 ms and thereby change their acoustic properties in ways that would suit different acoustic sensing tasks.

Gardiner, J.D., Codd, J.R. & Nudds, R.L., 2011. An association between ear and tail morphologies of bats and their foraging style. *Canadian Journal of Zoology*, 89(2), pp.90–99.

Abstract: Most studies relating bat morphology to flight ecology have concentrated on the wing membrane. Here, canonical variance analysis showed that the ear and tail morphologies of bats also strongly relate to foraging strategy, which in turn is correlated with flight style. Variations in tail membrane morphology are likely to be a trade-off between increases in the mechanical cost of flight and improvements in foraging and flight performance. Flying with large ears is also potentially energetically expensive, particularly at high flight speeds. Large ears, therefore, are only likely to be affordable for slow foraging gleaning bat species. Bats with faster foraging flight styles tend to have smaller ears, possibly to cut the overall drag produced and reduce the power required for flight. Variations in the size of ears and tail membranes appear to be driven primarily by foraging strategy and not by body size, because the scaling relationships found are either weak or not significant. Ear size in bats may be a result of a trade-off between acoustic and aerodynamic performance.

Geipel, I., Jung, K. & Kalko, E., 2013. Perception of silent and motionless prey on vegetation by echolocation in the gleaning bat *Micronycteris microtis*. *Proceedings of the Royal Society B*, 280, pp.1-7.

Abstract: Gleaning insectivorous bats that forage by using echolocation within dense forest vegetation face the sensorial challenge of acoustic masking effects. Active perception of silent and motionless prey in acoustically cluttered environments by echolocation alone has thus been

regarded impossible. The gleaning insectivorous bat *Micronycteris microtis* however, forages in dense understory vegetation and preys on insects, including dragonflies, which rest silent and motionless on vegetation. From behavioural experiments, we show that *M. microtis* uses echolocation as the sole sensorial modality for successful prey perception within a complex acoustic environment. All individuals performed a stereotypical three-dimensional hovering flight in front of prey items, while continuously emitting short, multiharmonic, broadband echolocation calls. We observed a high precision in target localization which suggests that *M. microtis* perceives a detailed acoustic image of the prey based on shape, surface structure and material. Our experiments provide, to our knowledge, the first evidence that a gleaning bat uses echolocation alone for successful detection, classification and precise localization of silent and motionless prey in acoustic clutter. Overall, we conclude that the three-dimensional hovering flight of *M. microtis* in combination with a frequent emission of short, high-frequency echolocation calls is the key for active prey perception in acoustically highly cluttered environments.

Ghose, K. & Moss, C.F., 2006. Steering by hearing: a bat's acoustic gaze is linked to its flight motor output by a delayed, adaptive linear law. *The Journal of Neuroscience*, 26(6), pp.1704–10.

Abstract: Adaptive behaviors require sensorimotor computations that convert information represented initially in sensory coordinates to commands for action in motor coordinates. Fundamental to these computations is the relationship between the region of the environment sensed by the animal (gaze) and the animal's locomotor plan. Studies of visually guided animals have revealed an anticipatory relationship between gaze direction and the locomotor plan during target-directed locomotion. Here, we study an acoustically guided animal, an echolocating bat, and relate acoustic gaze (direction of the sonar beam) to flight planning as the bat searches for and intercepts insect prey. We show differences in the relationship between gaze and locomotion as the bat progresses through different phases of insect pursuit. We define acoustic gaze angle, theta(gaze), to be the angle between the sonar beam axis and the bat's flight path. We show that there is a strong linear linkage between acoustic gaze angle at time t [theta(gaze)(t)] and flight turn rate at time t + tau into the future [theta(flight) (t + tau)], which can be expressed by the formula theta(flight) (t + tau) = ktheta(gaze)(t). The gain, k, of this linkage depends on the bat's behavioral state, which is indexed by its sonar pulse rate. For high pulse rates, associated with insect attacking behavior, k is twice as high compared with low pulse rates, associated with searching behavior. We suggest that this adjustable linkage between acoustic gaze and motor output in a flying echolocating bat simplifies the transformation of auditory information to flight motor commands.

Ghose, K., Moss, C.F. & Horiuchi, T.K., 2007. Flying big brown bats emit a beam with two lobes in the vertical plane. *The Journal of the Acoustical Society of America*, 122(6), pp.3717–24.

Abstract: The sonar beam of an echolocating bat forms a spatial window restricting the echo information returned from the environment. Investigating the shape and orientation of the sonar beam produced by a bat as it flies and performs various behavioral tasks may yield insight into the operation of its sonar system. This paper presents recordings of vertical and horizontal cross sections of the sonar beam produced by *Eptesicus fuscus* (big brown bats) as they fly and pursue prey in a laboratory flight room. In the horizontal plane the sonar beam consists of one large lobe

and in the vertical plane the beam consists of two lobes of comparable size oriented frontally and ventrally. In level flight, the bat directs its beam such that the ventral lobe is pointed forward and down toward the ground ahead of its flight path. The bat may utilize the downward directed lobe to measure altitude without the need for vertical head movements.

Gillam, E.H., 2007. Eavesdropping by bats on the feeding buzzes of conspecifics. *Canadian Journal of Zoology*, 85(7), 795–801.

Abstract: Echolocation calls of most bats are emitted at high intensities and subject to eavesdropping by nearby conspecifics. Bats may be especially attentive to "feeding buzz" calls, which are emitted immediately before attack on airborne insects and indicate the potential presence of prey in the nearby area. Although previous work has shown that some species are attracted to feeding buzzes, these studies did not provide a well-controlled test of eavesdropping, as comparisons were made between responses to natural and altered signals (e.g., forward versus backward broadcasts of calls). In this study, I assessed the importance of feeding buzzes by conducting playbacks of controlled echolocation stimuli. I presented free-flying Brazilian free-tailed bats, *Tadarida brasiliensis* (I. Geoffroy, 1824), with echolocation call sequences in which feeding buzz calls were either present or absent, as well as a silence control. I determined levels of bat activity by counting the number of echolocation calls and bat passes recorded in the presence of each stimulus, and found significantly greater bat activity in response to broadcasts that contained feeding buzzes than to broadcasts without feeding buzzes or to the silence control. These results indicate that bats are especially attentive to conspecific feeding buzz calls and that eavesdropping may allow a bat to more readily locate rich patches of insect prey.

Gillam, E.H. & Chaverri, G., 2012. Strong individual signatures and weaker group signatures in contact calls of Spix's disc-winged bat, *Thyroptera tricolor*. *Animal Behaviour*, 83(1), pp.269–276.

Abstract: Spix's disc-winged bats, *Thyroptera tricolor*, form small, long-term social groups in which members are loyal to a patch of forest but move on a daily basis between highly ephemeral roosting sites (partly unfurled Heliconia leaves). This species has been shown to exchange social calls that facilitate contact with nearby bats and recruitment to roost sites. During flight, *T. tricolor* emits "inquiry" calls that frequently elicit a response from individuals that have already entered a furled leaf. These "response" calls are then followed by the flying bat entering the occupied leaf roost. In this study, we examined variation in the structure of inquiry and response calls, and assessed whether calls encode information about individual or group identity that would allow for acoustic discrimination to occur. We found that both inquiry and response calls were sufficiently consistent within individuals, and divergent between individuals, to permit separation of individual bats based on call structure. We also found some evidence for group-specific signatures, although these were less defined than differences observed between individuals. While this does not confirm that Spix's disc-winged bats can discriminate between individuals and groups based on call information, our results indicate that both call types have a broad enough parameter space for this to occur.

Gillam, E.H., Chaveri, G., Montero K. & Sagot, M., 2013. Social calls produced within and near the roost in two species of tent-making bats, *Dermanura watsoni* and *Ectophylla alba*. *PloS One*, 8(4), p.e61731.

Abstract: Social animals regularly face the problem of relocating conspecifics when separated. Communication is one of the most important mechanisms facilitating group formation and cohesion. Known as contact calls, signals exchanged between conspecifics that permit group maintenance are widespread across many taxa. Foliage-roosting bats are an excellent model system for studying the evolution of contact calling, as there are opportunities to compare closely related species that exhibit major differences in ecology and behavior. Further, foliage-roosting bats rely on relatively ephemeral roosts which leads to major challenges in maintaining group cohesion. Here, we report findings on the communication signals produced by two tent-making bats, *Dermanura watsoni* and *Ectophylla alba*. We found that both species produced calls in the early morning near the roost that were associated with roostmate recruitment. Calling often ended once other bats arrived at the tent, suggesting that calls may be involved in roostmate recruitment and group formation. The structure and function of these calls are described and future research directions are discussed.

Gillam, E.H. & McCracken, G.F., 2007. Variability in the echolocation of *Tadarida brasiliensis*: effects of geography and local acoustic environment. *Animal Behaviour*, 74(2), pp. 277–286.

Abstract: We examined variation in the echolocation calls of Brazilian free-tailed bats, *Tadarida brasiliensis*, on a broad geographical scale and in response to local environmental variables. Significant differences in call structure were observed among populations throughout the species range in the United States, but this variation was not associated with geographical distance or local weather conditions. Observed variability between sites was primarily due to differences between bats, and the flexibility in call structure that can be achieved by individuals. During this study, we observed that bats recorded in the presence of high frequency sounds from chorusing insects used higher call frequencies than bats recorded in silence. This led us to test the hypothesis that bats adjust echolocation call structure in response to local ambient noise. We broadcast experimentally manipulated ultrasonic insect sounds to free-flying Brazilian free-tailed bats and found a positive correlation between the frequency of the insect sound stimulus and the call frequencies used by bats. These results document that bats adjust echolocation call structure to avoid acoustic interference from ambient noise in their local environment.

Gillam, E.H., Ulanovsky, N. & McCracken, G.F., 2007. Rapid jamming avoidance in biosonar. *Proceedings of the Royal Society of London*, Series B, 274, pp.651-660.

No abstract

Goerlitz, H.R., Greif, S. & Siemers, B.M., 2008. Cues for acoustic detection of prey: insect rustling sounds and the influence of walking substrate. *The Journal of Experimental Biology*, 211(Pt 17), pp.2799–806.

Abstract: When insects walk, they generally produce sounds. These can reveal the walkers' presence and location to potential predators such as owls, bats and nocturnal primates. Additionally, predators might extract information on taxon, palatability, size or profitability from the rustling sounds. In contrast to ear morphology, hearing physiology and psychoacoustics of acoustically oriented predators, little attention has hitherto been paid to the acoustic structure and information content of prey sounds. An important element in the ecology of acoustic prey detection remained virtually unexplored: the influence of the substrate type on rustling sounds. In

this study, we analysed amplitude and frequency parameters from insects walking on various natural substrates, in both Germany (Carabus beetles) and Madagascar (various beetles and cockroaches). The data show that rustling sound amplitude and frequency content depend on substrate type. On moist substrates arthropods produced less intense and less broadband rustling sounds than on dry substrates. Sound pressure level was reduced by about 6 dB, halving the detection range for the predator. For a given insect, rustling sound amplitude increased with walking speed. Finally, we found that the previously established correlation of arthropod size and rustling amplitude holds across multiple substrates. Based on these data, we provide for the first time estimates of realistic detection distances in the field. These distances range from below 1 m to over 13 m, depending on the substrate, insect mass, walking speed and background noise level. These estimates are crucial for an understanding of the foraging ecology, foraging efficiency and sensory ecology of acoustic predators.

Goerlitz, H.R., ter Hofstede, H.M., Zeale, M.R.K., Jones, G. & Holderid, M,W., 2010. An aerial-hawking bat uses stealth echolocation to counter moth hearing. *Current Biology*, 20(17), pp.1568–72.

Abstract: Ears evolved in many nocturnal insects, including some moths, to detect bat echolocation calls and evade capture. Although there is evidence that some bats emit echolocation calls that are inconspicuous to eared moths, it is difficult to determine whether this was an adaptation to moth hearing or originally evolved for a different purpose. Aerial-hawking bats generally emit high-amplitude echolocation calls to maximize detection range. Here we present the first example of an echolocation counterstrategy to overcome prey hearing at the cost of reduced detection distance. We combined comparative bat flight-path tracking and moth neurophysiology with fecal DNA analysis to show that the barbastelle, *Barbastella barbastellus*, emits calls that are 10 to 100 times lower in amplitude than those of other aerial-hawking bats, remains undetected by moths until close, and captures mainly eared moths. Model calculations demonstrate that only bats emitting such low-amplitude calls hear moth echoes before their calls are conspicuous to moths. This stealth echolocation allows the barbastelle to exploit food resources that are difficult to catch for other aerial-hawking bats emitting calls of greater amplitude.

Goerlitz, H.R., Hübner, M. & Wiegrebe, L., 2008. Comparing passive and active hearing: spectral analysis of transient sounds in bats. *The Journal of Experimental Biology*, 211(Pt 12), pp.1850–8.

Abstract: In vision, colour constancy allows the evaluation of the colour of objects independent of the spectral composition of a light source. In the auditory system, comparable mechanisms have been described that allows the evaluation of the spectral shape of sounds independent of the spectral composition of ambient background sounds. For echolocating bats, the evaluation of spectral shape is vitally important both for the analysis of external sounds and the analysis of the echoes of self-generated sonar emissions. Here, we investigated how the echolocating bat *Phyllostomus discolor* evaluates the spectral shape of transient sounds both in passive hearing and in echolocation as a specialized mode of active hearing. Bats were trained to classify transients of different spectral shape as low- or highpass. We then assessed how the spectral shape of an ambient background noise influenced the spontaneous classification of the transients. In the passive-hearing condition, the bats spontaneously changed their classification boundary depending on the spectral shape of the background. In the echo-acoustic condition, the

classification boundary did not change although the background- and spectral-shape manipulations were identical in the two conditions. These data show that auditory processing differs between passive and active hearing: echolocation represents an independent mode of active hearing with its own rules of auditory spectral analysis.

Gołebiewski, R., 2008. The influence of turbulence on noise propagation from a point source above a flat ground surface. *Applied Acoustics*, 69, pp.358–366.

Abstract: The presence of turbulence in the atmosphere affects the interaction between anacoustic wave and the ground surface. The noise attenuation by the ground in the presence of atmospheric turbulence is smaller than in non-turbulent atmosphere. A simple engineering model of noise propagation above a flat ground surface, for stationary and moving point sources, has been proposed. The model takes into account the air absorption and ground effect in the presence of turbulence. As well as parameters for type of ground and air absorption, the model introduces two adjustable parameters which must be deduced from in situ measurements at two ranges or two heights. The model's free parameters have been obtained as a function of the resultant sound speed gradient on the basis of the field measurements performed for a stationary noise source. Also, using field data for a vehicle moving at steady speeds up to 100 km/h, the model has been verified for a moving point source.

Gołebiewski, R., & Makarewicz, R., 2002. Engineering formulas for ground effects on broad-band noise. *Applied Acoustics*, 63, pp.993–1001.

Abstract: A simple approximation of ground effect is analyzed for two cases: (1) stationary point source and (2) moving line source (train). The approximation contains three adjustable parameters that are estimated from the exact theory (case 1) and from field measurements (case 2). Finally, the results of computation are used for noise prediction.

Greenwood, D., 1961. Auditory masking and the critical band. *The Journal of the Acoustical Society of America*, 33, pp.484–502.

Abstract: Masked audiograms were studied as a function of the bandwidth, level, and frequency of a masking noise. In a reverse procedure audiograms were determined when a movable narrow, and approximately rectangular band of noise was used as signal in the presence of one or more masking tones. In both cases changes in the masked audiograms as a function of bandwidth made it possible to measure critical bandwidth. When masked audiograms were studies as a function of level, discontinuous changes in their height and shape occurred when the masking stimulus reached a certain "transition" level. If masking noises of subcritical or critical width were used, the growth of masking with level contained a discontinuity at a level of the masking stimulus equal to about 50 db SL. An abrupt change in the shape of the masked audiograms occurred at the same level. The change of shape when a *pure tone* was the masking stimulus consisted in the appearance of a "notch" one critical bandwidth above the frequency of the masking tone. Findings associated with the bandwidth parameter suggest interpretations of the critical band and of masking. The changes occurring at the transition level may indicate the threshold of the inner hair cells.

Griffin, D.R., 1958. Listening in the dark. New Haven, Conn. Yale University Press.

No abstract

Griffin, D., Dunning, D., Cahlander, D.A. & Webster, F.A., 1962. Correlated orientation sounds and ear movements of horseshoe bats. *Nature*, 196, pp.1185–1186.

No abstract

Griffin, D.R. & Grinnell, A.D., 1958. Ability of bats to discriminate echoes from louder noise. *Science*, 128, pp.145-147.

No abstract

Griffin, D. & Hartridge, H., 1946. Supersonic cries of bats. *Nature*, 158, pp.46–48.

No abstract

Griffin, D.R., McCue, J.J.G. & Grinnell, A.D., 1963. The resistance of bats to jamming. *Journal of Experimental Zoology*, 152(3), pp.229–250.

No abstract

Griffin, D., Webster, F. & Michael, C., 1960. The echolocation of flying insects by bats. *Animal Behaviour*, 8, pp.141–154.

Abstract: 1. Bats of the genus *Myotis* (*M. lucifugus*, *M. subulatus leibii* and *M. keenii septentrionalis*) have been studied while pursuing and capturing small insects under laboratory conditions. It is apparently important to provide fairly large numbers of such insects in order to elicit insect catching behaviour indoors. 2. Insect catches are individually directed pursuit manoeuvres; each insect is detected, located, and intercepted in flight within about half a second. 3. Certain individual bats caught mosquitos (*Culex quinquefaciatus*) and fruit flies (*Drosophila robusta* and *D. melanogaster*) at remarkably high rates which could be measured conservatively by the gain in weight of the bat. Sometimes a bat would average as many as 10 mosquitos or 14 fruit flies per minute during a period of several minutes. In four cases motion pictures showed two separate *Drosophila* catches within half a second. 4. The orientation sounds of the hunting bat are adjusted in a manner that seems appropriate for the echolocation of single insects one at a time. There is a *search phase* before the occurrence of any apparent reaction to the insect. In this phase the frequency drops from about 100 to 50 kilocycles during each pulse of sound, and the pulses are emitted by *M. lucifugus* at intervals of 50 to 100 milliseconds. 5. When an insect is detected the search phase gives way to an *approach phase* characterized by a progressive shortening of the pulse-to-pulse interval and, if necessary, a sharp turn towards the insect. In this phase the pulse duration may shorten somewhat, but the frequencies remain approximately the same as in the search phase or drop slightly. 6. When the bat is within a few centimetres of the insect there is a *terminal phase* in which the pulse duration and interval between pulses shorten to about 0·5 millisecond and 5 or 6 milliseconds respectively. Contrary to a conclusion reached earlier on the basis of much less adequate data (Griffin, 1953), the frequency *drops* in the terminal phase, sometimes to 25 or 30 kilocycles. This is the buzz, which also occurs in many cases when the bat is dodging wires or landing. 7. The distance from the insect at which detection occurs can be judged by the shift from search to approach patterns. This distance of detection is commonly about 50 cm. for *Drosophila*, and it occasionally may be as much as a metre with fruit flies or mosquitos. 8. Two *M. lucifugus* which had become adept at catching *Drosophila* in the laboratory were exposed to broad band thermal noise either at low frequencies

(0·1–15 kilocycles) or high (20–100 kilocycles). The low frequency noise had an approximately uniform spectrum level of about 50 decibels per cycle band width (re 0·0002 dyne/cm^2) from 0·1 to 8 kilocycles. It was thus very loud compared to the flight sounds of *Drosophila* which have a fundamental frequency of a few hundred cycles/second and a maximum sound pressure level of 20–25 decibels at the distances of detection by these bats. The high frequency noise was of low and varying intensity, but it discouraged or prevented insect catching. The low frequency noise, on the other hand, had no effect on insect catching; the bats gained weight in this noise (and in the dark) just as rapidly as in the quiet. Although bats sometimes detect insect prey by passive listening to sounds emanating from the insects themselves, these experiments appear to us to establish conclusively that small and relatively silent insects are often detected by echolocation.

Griffiths, S.R., 2013. Echolocating bats emit terminal phase buzz calls while drinking on the wing. *Behavioural Processes*, 98, pp.58–60.

Abstract: Echolocating bats are known to produce terminal buzz calls during pursuit and capture of airborne prey, however the use of buzz calls while drinking on the wing has not been previously investigated. In this study I recorded the first empirical evidence that bats produce terminal phase buzz calls while drinking on the wing. Every drinking pass recorded during this study was characterised by a terminal buzz which bats emitted immediately prior to touching the water surface with their mouth. The characteristic frequency (the frequency at the end or flattest portion of the pulse) of echolocation call sequences containing drinking buzzes varied from 25 kHz to 50 kHz, suggesting multiple bat species present at the study site emit buzzes while drinking on the wing. As feeding buzz calls appear to be ubiquitous among echolocating bat taxa, the prevalence of drinking buzzes clearly warrants further investigation. Drinking buzzes could potentially be used to document rates of drinking by bats in the same way that feeding buzzes are used to infer foraging activity.

Grinnell, A., 1963. The neurophysiology of audition in bats: intensity and frequency parameters. *The Journal of Physiology*, 167, pp.38–66.

No abstract

Grothe, B. & Park, T., 1998. Sensitivity to interaural time differences in the medial superior olive of a small mammal, the Mexican free-tailed bat. *The Journal of Neuroscience*, 18(16), pp.6608–6622.

Abstract: Neurons in the medial superior olive (MSO) are thought to encode interaural time differences (ITDs), the main binaural cues used for localizing low-frequency sounds in the horizontal plane. The underlying mechanism is supposed to rely on a coincidence of excitatory inputs from the two ears that are phase-locked to either the stimulus frequency or the stimulus envelope. Extracellular recordings from MSO neurons in several mammals conform with this theory. However, there are two aspects that remain puzzling. The first concerns the role of the MSO in small mammals that have relatively poor low-frequency hearing and whose heads generate only very small ITDs. The second puzzling aspect of the scenario concerns the role of the prominent binaural inhibitory inputs to MSO neurons. We examined these two unresolved issues by recording from MSO cells in the Mexican free-tailed bat. Using sinusoidally amplitude-modulated tones, we found that the ITD sensitivities of many MSO cells in the bat were remarkably similar to those reported for larger mammals. Our data also indicate an

important role for inhibition in sharpening ITD sensitivity and increasing the dynamic range of ITD functions. A simple model of ITD coding based on the timing of multiple inputs is proposed. Additionally, our data suggest that ITD coding is a by-product of a neuronal circuit that processes the temporal structure of sounds. Because of the free-tailed bat's small head size, ITD coding is most likely not the major function of the MSO in this small mammal and probably other small mammals.

Gruver, J. C. & Keinath, D.. 2006. Townsend's Big-eared Bat (*Corynorhinus townsendii*): A technical conservation assessment. USDA Forest Service, Rocky Mountain Region. Online: http://www.fs.fed.us/r2/projects/scp/assessments/townsendsbigearedbat.pd.

No abstract

Guarato, F., Windmill, J. & Gachagan, A., 2013. A beam based method for target localization: inspiration from bats' directivity and binaural reception for ultrasonic sonar. *The Journal of the Acoustical Society of America*, 133(6), pp.4077–86.

Abstract: The process of echolocation is accomplished by bats partly using the beam profiles associated with their ear shapes that allow for discrimination between different echo directions. Indeed, knowledge of the emitted signal characteristic and measurement of the echo travel time from a target make it possible to compensate for attenuation due to distance, and to focus on filtering through the receivers' beam profiles by comparing received echoes to the original signal at all frequencies in the spectrum of interest. From this basis, a beam profile method to localize a target in three-dimensional space for an ultrasonic sensor system equipped with an emitter and two receivers is presented. Simulations were conducted with different noise levels, and only the contribution of the receivers' beam profiles was considered to estimate the orientation of the target with respect to the receivers. The beam pattern of the *Phyllostomus discolor's* ear was adopted as that of a receiver. Analyses of beam resolution and frequency ranges were conducted to enhance the accuracy of orientation estimates. The choice of appropriate resolution and frequency ranges guarantee that error mean values for most of the orientations are within [0.5°, 1.5°], even in noisy situations: Signal-to-noise ratio values considered in this work are 35 and 50 dB.

Guppy, A. & Coles, R., 1988. Acoustical and neural aspects of hearing in the Australian gleaning bats, *Macroderma gigas* and *Nyctophilus gouldi*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 162, pp.653–668.

Abstract: 1. The maximum acoustic gain of the external ear in *Macroderma gigas* was found to be 25-30 dB between 5-8 kHz and in *Nyctophilus gouldi* it reached 15-23 dB between 7-22 kHz. Pinna gain reached a peak of 16 dB near 4.5-6 kHz in *M. gigas* and 12-17 dB between 7-12 kHz in *N. gouldi*, with average gain of 6-10 dB up to 100 kHz. Pinna gain curves resemble that of a finite conical horn, including resonance. 2. The directional properties of the external ear in both species result from sound diffraction at the pinna face, as it approximates a circular aperture. The frequency dependent movement of the acoustic axis in azimuth and elevation is attributed to the asymmetrical structure of the pinnae. 3. Evoked potentials and neuronal responses were studied in the inferior colliculus. In *M. gigas*, the neural audiogram has sensitivity peaks at 10-20 kHz and 35-43 kHz, with extremely low thresholds (-18 dB SPL) in the low frequency region. In *N. gouldi*, the neural audiogram has sensitivity peaks at 8-14 kHz (lowest threshold 5 dB SPL) and

22-45 kHz. Removal of the contralateral pinna causes a frequency dependent loss in neural threshold sensitivity of up to 10-15 dB in both species. 4. The high frequency peak in the audiogram coincides with the sonar energy band in both species, whereas the low frequency region is used for social communication. Highly sensitive low frequency hearing is discussed in relation to hunting in bats by passive listening.

Habault, D. & Filippi, P.J.T., 1981. Ground effect analysis: Surface wave and layer potential representations. *Journal of Sound and Vibration*, 79(4), pp.529–550.

Abstract: This paper presents two kinds of analytical exact expressions of the sound field reflected by a plane boundary, as obtained by using either surface wave or layer potentials representations. Both solutions are first expressed as a sum of integrals which have a form suitable for numerical computation. Then these integrals are expanded into convergent series which provide analytical approximations of the solution. Numerical techniques are proposed for computing (a) the surface wave representation and (b) the approximation deduced from the layer potentials representation. This approximation and the classical one (sum of the surface wave and the first two terms of the asymptotic series) are compared with the exact solution. Several examples show that the approximate formulas established here are valid on a range much wider than the validity domain of the classical ones.

Hage, S.R. Jiang, T., Berquist, S.W., Feng, J., &Metzner, W. 2014. Ambient noise causes independent changes in distinct spectro-temporal features of echolocation calls in horseshoe bats. *The Journal of Experimental Biology*, 217, pp.2440–4.

Abstract: One of the most efficient mechanisms to optimize signal-to-noise ratios is the Lombard effect - an involuntary rise in call amplitude due to ambient noise. It is often accompanied by changes in the spectro-temporal composition of calls. We examined the effects of broadband-filtered noise on the spectro-temporal composition of horseshoe bat echolocation calls, which consist of a constant-frequency component and initial and terminal frequency-modulated components. We found that the frequency-modulated components became larger for almost all noise conditions, whereas the bandwidth of the constant-frequency component increased only when broadband-filtered noise was centered on or above the calls' dominant or fundamental frequency. This indicates that ambient noise independently modifies the associated acoustic parameters of the Lombard effect, such as spectro-temporal features, and could significantly affect the bat's ability to detect and locate targets. Our findings may be of significance in evaluating the impact of environmental noise on echolocation behavior in bats.

Hagen, E.. 2009. "Bats." Arizona State University (ASU) - Ask a Biologist. 4 November 2009. Online: http://askabiologist.asu.edu/echolocation.

No abstract

Hague, D., Buck, J. & Bilik, I., 2011. A deterministic filterbank compressive sensing model for bat biosonar. *The Journal of the Acoustical Society of America*, 132(6), pp.4041–4052.

Abstract: The big brown bat (*Eptesicus fuscus*) uses frequency modulated (FM) echolocation calls to accurately estimate range and resolve closely spaced objects in clutter and noise. They resolve glints spaced down to 2 µs in time delay which surpasses what traditional signal processing techniques can achieve using the same echolocation call. The Matched Filter (MF)

attains 10–12 μs resolution while the Inverse Filter (IF) achieves higher resolution at the cost of significantly degraded detection performance. Recent work by Fontaine and Peremans [J. Acoustic. Soc. Am. 125, 3052–3059 (2009)] demonstrated that a sparse representation of bat echolocation calls coupled with a decimating sensing method facilitates distinguishing closely spaced objects over realistic SNRs. Their work raises the intriguing question of whether sensing approaches structured more like a mammalian auditory system contains the necessary information for the hyper-resolution observed in behavioral tests. This research estimates sparse echo signatures using a gammatone filterbank decimation sensing method which loosely models the processing of the bat's auditory system. The decimated filterbank outputs are processed with '1 minimization. Simulations demonstrate that this model maintains higher resolution than the MF and significantly better detection performance than the IF for SNRs of 5–45dB while undersampling the return signal by a factor of six.

Halcrow Group Limited, 2006. Good practice in enhancement of highway design for bats. Workshop report. February 2006. Available Online: http://webarchive.nationalarchives.gov.uk/20120810121037/http:/www.highways.gov.uk/knowledge_compendium/assets/documents/Portfolio/Best%20Practice%20in%20Enhancement%20of%20Highway%20Design%20for%20Bats%20-%20775.pdf

No abstract

Halfwerk, W., Bot, S., Buikx, J., van der Velde, M. Kondeur, J., Ten Cate, C. Slabbekoorn, H. 2011. Low-frequency songs lose their potency in noisy urban conditions. *Proceedings of the National Academy of Sciences of the United States of America*, 108(35), pp.14549–54.

Abstract: Many animal species communicate with their mates through acoustic signals, but this communication seems to become a struggle in urbanized areas because of increasing anthropogenic noise levels. Several bird species have been reported to increase song frequency by which they reduce the masking impact of spectrally overlapping noise. However, it remains unclear whether such behavioral flexibility provides a sufficient solution to noisy urban conditions or whether there are hidden costs. Species may rely on low frequencies to attract and impress females, and the use of high frequencies may, therefore, come at the cost of reduced attractiveness. We studied the potential tradeoff between signal strength and signal detection in a successful urban bird species, the great tit (*Parus major*). We show that the use of low-frequency songs by males is related to female fertility as well as sexual fidelity. We experimentally show that urban noise conditions impair male-female communication and that signal efficiency depends on song frequency in the presence of noise. Our data reveal a response advantage for high-frequency songs during sexual signaling in noisy conditions, whereas low-frequency songs are likely to be preferred. These data are critical for our understanding of the impact of anthropogenic noise on wild-ranging birds, because they provide evidence for low-frequency songs being linked to reproductive success and to be affected by noise-dependent signal efficiency.

Halfwerk, W., Holleman, L.J.M., Lessells, C., & Slabbekoorn, H. 2011. Negative impact of traffic noise on avian reproductive success. *Journal of Applied Ecology*, 48(1), pp.210–219.

Abstract: 1. Traffic affects large areas of natural habitat worldwide. As a result, the acoustic signals used by birds and other animals are increasingly masked by traffic noise. Masking of

signals important to territory defence and mate attraction may have a negative impact on reproductive success. Depending on the overlap in space, time and frequency between noise and vocalizations, such impact may ultimately exclude species from suitable breeding habitat. However a direct impact of traffic noise on reproductive success has not previously been reported. 2. We monitored traffic noise and avian vocal activity during the breeding season alongside a busy Dutch motorway. We measured variation in space, time and spectrum of noise and tested for negative effects on avian reproductive success using long-term breeding data on great tits *Parus major*. 3. Noise levels decreased with distance from the motorway, but we also found substantial spatial variation independent of distance. Noise also varied temporally with March being noisier than April, and the daytime being noisier than night-time. Furthermore, weekdays were clearly noisier than weekends. Importantly, traffic noise overlapped in time as well as acoustic frequency with avian vocalization behaviour over a large area. 4. Traffic noise had a negative effect on reproductive success with females laying smaller clutches in noisier areas. Variation in traffic noise in the frequency band that overlaps most with the lower frequency part of great tit song best explained the observed variation. 5. Additionally, noise levels recorded in April had a negative effect on the number of fledglings, independent of clutch size, and explained the observed variation better than noise levels recorded in March. 6. Synthesis and applications. We found that breeding under noisy conditions can carry a cost, even for species common in urban areas. Such costs should be taken into account when protecting threatened species, and we argue that knowledge of the spatial, temporal and spectral overlap between noise and species-specific acoustic behaviour will be important for effective noise management. We provide some cost-effective mitigation measures such as traffic speed reduction or closing of roads during the breeding season.

Halfwerk, W, Jones, P.L., Taylor, R.C., Ryan, M.J., & Page, R.A. 2014. Risky ripples allow bats and frogs to eavesdrop on a multisensory sexual display. *Science*, 343, pp.413–6.

Abstract: Animal displays are often perceived by intended and unintended receivers in more than one sensory system. In addition, cues that are an incidental consequence of signal production can also be perceived by different receivers, even when the receivers use different sensory systems to perceive them. Here we show that the vocal responses of male túngara frogs (*Physalaemus pustulosus*) increase twofold when call-induced water ripples are added to the acoustic component of a rival's call. Hunting bats (*Trachops cirrhosus*) can echolocate this signal by-product and prefer to attack model frogs when ripples are added to the acoustic component of the call. This study illustrates how the perception of a signal by-product by intended and unintended receivers through different sensory systems generates both costs and benefits for the signaler.

Hallberg, B., Larsson, C. & Iraelsson, S., 1989. Outdoor sound level variations due to fluctuating meteorological parameters. *Applied Acoustics*, 26, pp.235–240.

Abstract: Simultaneous measurements of meteorological parameters and octave-band sound levels from a point source, over finite impedance ground, have been carried out. A ray-tracing model was used to predict sound levels. A 5 min measurement period was divided into l0-s intervals, and the effect of the meteorological fluctuations on the measured and predicted sound levels was studied. The meterological fluctuations were rather large due to the lapse conditions. The results with the ray-tracing model were more sensitive to meteorological variations than was indicated by the measurements. Averages of the predicted sound levels, based on the l0 s

intervals, were compared with those predicted from average meteorological conditions, as well as with average measured sound levels. The first of these ray-tracing results was in better agreement with the measurements. It seems that during periods with large meteorological fluctuations, the predicted sound level based on averages can be quite in error. It was also concluded that meteorological fluctuations on a longer tine-scale can give similar results to the small-scale turbulence effect, causing decoherence of sound rays.

Hanson, C.E., Towers, D.A. & Meister, L.D., 2006. Transit Noise and Vibration Impact Assessment. U. S. Federal Transit Administration (FTA). Office of Planning and Environment. Online: http://www.fta.dot.gov/documents/FTA_Noise_and_Vibration_Manual.pdf

Abstract: This report is the second edition of a guidance manual originally issued in 1995 which presents procedures for predicting and assessing noise and vibration impacts of proposed mass transit projects. All types of bus and rail projects are covered. Procedures for assessing noise and vibration impacts are provided for different stages of project development, from early planning before mode and alignment have been selected through preliminary engineering and final design. Both for noise and vibration, there are three levels of analysis described. The framework acts as a screening process, reserving detailed analysis for projects with the greatest potential for impacts while allowing a simpler process for projects with little or no effects. This updated guidance contains noise and vibration impact criteria that are used to assess the magnitude of predicted impacts. A range of mitigation measures are described for dealing with adverse noise and vibration impacts. There is a discussion of noise and vibration during the construction stage and also discussion of how the technical information should be presented in the Federal Transit Administration's environmental documents. This guidance will be of interest not only to technical specialists who conduct the analyses but also to transit agency staff, federal agency reviewers, and members of the general public who may be affected by the projects.

Harris, M.M., 1979. Handbook of Noise Control. McGraw-Hill, Inc. New York, NY.

No abstract

Hartley, D. & Suthers, R., 1987. The sound emission pattern and the acoustical role of the noseleaf in the echolocating bat, *Carollia perspicillata*. *The Journal of the Acoustical Society of America*, 82(6), pp.1892–1900.

Abstract: *Carollia perspicillata* (Phyllostomidae) is a frugivorous bat that emits low-intensity, boradband, frequency-modulated echolocation pulses through nostrils surrounded by a noseleaf. The emission pattern of this bat is of interest because the ration between the nostril spacing and the emitted wavelength varies during the pulse, causing complex interference patterns in the horizontal dimension. Sound pressures around the bat were measured using a movable microphone and were referenced to those at a stationary microphone positioned directly in front of the animal. Interference between the nostrils was confirmed by blocking one nostril, which eliminated sidelobes and minima in the emission patterns, and by comparison of real emission patterns with simple computer models, The positions of minima in the patterns indicate effective nostril spacing of over a half-wavelength. Displacement of the dorsal lancet of the noseleaf demonstrated that this structure directs sound in the vertical dimension.

Hartley, D. & Suthers, R., 1989. The sound emission pattern of the echolocating bat, *Eptesicus fuscus*. *The Journal of the Acoustical Society of America*, 85(3), pp.1348–1351.

Abstract: The emission pattern of *Eptesicus fuscus* was found to be consistent with those of the other frequency-modulating (FM) bats studied in similar detail in that there is a mainlobe aimed forward of the animal together with a prominent - 6 dB ventral lobe. This ventral lobe cannot be explained as the first sidelobe of a piston source mounted in an infinite baffle and must be formed by some other acoustic means. Nevertheless, a piston source with a radius comparable to that of the open mouth can nicely explain the changes in the width of the mainlobe with wavelengths greater than the mouth dimensions, however, some additional sound "focusing" may occur, presumably due to diffraction by the head.

Heffner H. E, Heffner R. S. 2007. Hearing ranges of laboratory animals. J. *Am. Assoc. Lab Animal Science*, 46, pp.20–22.

Abstract: Any attempt to assess the effects of sounds on animals must consider species differences in hearing abilities. Although the hearing ranges of most species overlap to a large degree, considerable variation occurs in high- and low-frequency hearing as well as in absolute sensitivity. As a result, a sound that is easily audible to one species may be less audible, or even inaudible, to another. The purpose of this review is to describe the variation in the hearing ranges of common laboratory animals.

Heffner, R.S., Koay, G. & Heffner, H.E., 2003. Hearing in American leaf-nosed bats. III: *Artibeus jamaicensis*. *Hearing Research*, 184(1-2), pp.113–122.

Abstract: We determined the audiogram of the Jamaican fruit-eating bat (Phyllostomidae: *Artibeus jamaicensis*), a relatively large (40-50 g) species that, like other phyllostomids, uses low-intensity echolocation calls. A conditioned suppression/avoidance procedure with a fruit juice reward was used for testing. At 60 dB SPL the hearing range of *A. jamaicensis* extends from 2.8 to 131 kHz, with an average best sensitivity of 8.5 dB SPL at 16 kHz. Although their echolocation calls are low-intensity, the absolute sensitivity of *A. jamaicensis* and other "whispering" bats does not differ from that of other mammals, including other bats. The high-frequency hearing of *A. jamaicensis* and other Microchiroptera is slightly higher than expected on the basis of selective pressure for passive sound localization. Analysis suggests that the evolution of echolocation may have been accompanied by the extension of their high-frequency hearing by an average of one-half octave. With respect to low-frequency hearing, all bats tested so far belong to the group of mammals with poor low-frequency hearing, i.e., those unable to hear below 500 Hz.

Heffner, R.S., Koay, G. & Heffner, H.E., 2006. Hearing in large (*Eidolon helvum*) and small (*Cynopterus brachyotis*) non-echolocating fruit bats. *Hearing Research*, 221(1-2), pp.17–25.

Abstract: Comparing the hearing abilities of echolocating and non-echolocating bats can provide insight into the effect of echolocation on more basic hearing abilities. Toward this end, we determined the audiograms of two species of non-echolocating bats, the straw-colored fruit bat (*Eidolon helvum*), a large (230-350 g) African fruit bat, and the dog-faced fruit bat (*Cynopterus brachyotis*), a small (30-45 g) bat native to India and Southeast Asia. A conditioned suppression/avoidance procedure with a fruit juice reward was used for testing. At 60 dB SPL,

the hearing range of *E. helvum* extends from 1.38 to 41 kHz with best sensitivity at 8k Hz; the hearing range of *C. brachyotis* extends from 2.63 to 70 kHz with best sensitivity at 10 kHz. As with all other bats tested so far, neither species was able to hear below 500 Hz, suggesting that they may not use a time code for perceiving pitch. Comparison of the high-frequency hearing abilities of echolocating and non-echolocating bats suggests that the use of laryngeal echolocation has resulted in additional selective pressure to hear high frequencies. However, the typical high-frequency sensitivity of small non-echolocating mammals would have been sufficient to support initial echolocation in the early evolution of bats, a finding that supports the possibility of multiple origins of echolocation.

Heffner, R.S., Koay, G. & Heffner, H.E., 2013. Hearing in American leaf-nosed bats. IV: the Common vampire bat, *Desmodus rotundus*. *Hearing Research*, 296, pp.42–50.

Abstract: We behaviorally determined the audiograms of three Common vampire bats (Phyllostomidae, *Desmodus rotundus*), a species specialized to exist exclusively on blood. The bats were trained to respond to pure tones in a conditioned suppression/avoidance procedure for a blood reward and a mild punisher for failures to detect the tones. Common vampire bats have a hearing range from 716 Hz to 113 kHz at a level of 60 dB. Their best hearing is at 20 kHz where they are slightly more sensitive than other bats, and they have a second peak of good sensitivity at 71 kHz. They have unusually good sensitivity to low frequencies compared to other bats, but are less sensitive to low frequencies than most mammals. Selective pressures affecting high-frequency hearing in bats and mammals in general are discussed.

Hellstrom, P.A., 1995. The relationship between sound transfer functions and hearing levels. *Hearing Research*, 88, pp.54–60.

Abstract: The effects of individual differences in sound transfer function (STF) from free sound field to the tympanic membrane on hearing levels was studied in the right and left ears of 55 young male and 45 young female subjects. Furthermore, canal volumes and lengths have been recorded. STFs were measured in 1/3-octave bands using a miniature microphone and an attached probe. STF measurements were performed in the 0.5-16 kHz frequency range. Audiograms were registered with linear frequency sweep from 0.25 to 8 kHz. Transfer function spectra and magnitudes as well as ear canal dimensions were compared to hearing levels. There was a significant relationship between the dimensions of the ear canal and hearing levels. Large, compared to small, ear canal volumes resulted in a shift of STFs towards lower frequencies. STF spectra and magnitudes had a significant effect on hearing levels. Subject with low-frequency-dominated STFs have higher hearing thresholds than subjects with lower magnitude STFs.

Hendriks, R., 1998. General guidelines for studying the effects of noise. California Technical Advisory TAN-98-01-R9701. Online: http://www.dot.ca.gov/hq/env/noise/pub/General%20Guidelines%20For%20Studying%20the%20Effects%20of%20Noisse%20Barriers%20on%20Distance%20Receivers.pdf.

No abstract

Hendriks, R., 2002. Distance Limits for Traffic Noise Prediction Models TAN-02-02, California Department of Transportation (Caltrans), Division of Environmental Analysis, Office of Noise, Air, and Hazardous Waste Management Sacramento,. Online:

http://www.dot.ca.gov/hq/env/noise/pub/Distance%20Limits%20for%20Traffic%20Noise%20Prediction%20Models.pdf.

No abstract

Henson, O.W., Jr., 1965. The activity and function of the middle ear muscles in echolocating bats. J. *Physiol.* (Lond.) 180, 871-887.

No abstract

Henson, O., Koplas, P. & Keating, A., 1990. Cochlear resonance in the mustached bat: behavioral adaptations. *Hearing Research*, 50, pp.259–274.

Abstract: Mustached bats. *Pteronotus p. parnefiii*, use complex, multiharmonic biosonar signals with prominent approx. 60 kHz (CF) components. The sense of hearing is especially acute to sounds near 60 kHz and the cochlea shows a number of specializations m the 60 kHz region. Foremost is a remarkable degree of cochlear resonance. In this study it is shown that: 1) any sounds near the resonance frequency elicit a pronounced resonance that continues after the stimulus terminates; 2) Doppler-shifted echoes of the bat's own cries may cause resonance; 3) continuous resonance can be produced by stimulating the ear with broadband noise but such resonance does not interfere with the bat's ability to Doppler-shift compensate during simulated flight; 4) significant changes in the resonance frequency of the cochlea occur during and after flight; 5) the changes in resonance can be dependent or independent of body temperature changes; and 6) mustached bats continuously adjust the CF component of their pulses to keep the second harmonic echoes in a constant frequency band near the resonance frequency. Thus. mustached bats not only compensate for Doppler-shifts imposed by their movements relative to that of a target. but they cochlear resonance compensate to deal with small changes in the micromechanical properties of the cochlea.

Herrera-Montes, M.I. & Aide, T.M., 2011. Impacts of traffic noise on anuran and bird communities. *Urban Ecosystems*, 14(3), pp.415–427.

Abstract: Anurans and birds rely on sound for a number of social behaviors. Species that use roadside habitats are exposed to traffic noise that can mask important social signals and directly affect the community diversity and composition. We evaluate the impact of traffic noise on anuran and bird species richness, species occurrence, and composition in Puerto Rico, where there is a high density of highways and cars that generate high levels of noise pollution. We compared paired forest sites near (100 m, n=20, dB>60) and far (>300 m, n=20, dB<60) from highways, with similar vegetation structure, but different levels of noise. We found that the anuran community was not affected by traffic noise. In contrast, bird species richness and occurrence were significantly lower in sites near the highway, and bird species composition also varied significantly. Bird species with low-frequency songs were only detected in sites far from highways. The differences in the ecology and communication behavior between anurans and birds could explain these results. Anurans mainly call at night, when traffic activity was low. In contrast, bird singing activity occurs during the day and overlaps with the high levels of traffic noise. In addition, in natural habitats, Puerto Rican anurans occur at high densities and form noisy choruses (>80 dB), which may allow them to tolerate high levels of anthropogenic noise.

Hickey, M.B.C., Acharya, L., Pennington, S., 1996. Resource partitioning by two species of vespertilionid bats (*Lasiurus cinereus* and *Lasiurus borealis*). *Journal of Mammalogy* 77(2), pp.325–334.

Abstract: Partitioning of resources between *Lasiurus cinereus* and *L. borealis* was studied at a site where these species feed on insects (mostly moths) that fly around street lights. No consistent evidence of temporal resource partitioning was found in 4 years of observation. For 3 years of analysis of diets, the food-niche breadth of *L. cinereus* (25-35 g) was consistently larger than that of *L. borealis* (7-13 g). Niche overlap varied among years and was highest in a year when availability of insects was unusually low.

Hickey, M.B.C. & Fenton, M.B., 1996. Behavioural and thermoregulatory responses of female hoary bats. *Ecoscience*, 3(4), pp.414–422.

Abstract: Responses of lactating hoary bats, *Lasiurus cinereus* (Palisot de Beauvois), to variation in prey availability were studied in 1989 and 1990. We used temperature-sensitive radiotransmitters to monitor the bats' thermoregulatory patterns and a combination of radio-tracking and direct observations of bats with unique combinations of colour bands to document foraging behaviour. Typically, bats foraged in concentrations of moths attracted to street lights and tagged bats returned to the same site each night. Nightly prey availability varied and bats responded to the changes in food availability by changing their use of space and entering torpor. Bats spent significantly mole time out of range of our radio-tracking station (and away from their usual foraging sites) when prey availability was low, presumably searching for alternate foraging sites. Bats also used heterothermy, entering torpor when temperature and prey availability were low. *Lasiurus cinereus* always used torpor for part of the night when minimum ambient temperatures were < 13 degrees C. When minimum ambient temperatures were between 13 and 21 degrees C there was individual variation in the thermoregulatory strategy adopted by different bats on the same night. The same individual sometimes adopted a different thermoregulatory strategy on different nights with the same minimum ambient temperature.

Hoffmann, F.F., Hejduk, J., Caspers, B., Siemers, B. M. & Voigt, C.C., 2007. In the mating system of the bat *Saccopteryx bilineata*, bioacoustic constraints impede male eavesdropping on female echolocation calls for their surveillance. *Canadian Journal of Zoology*, 85(8), 863–872.

Abstract: At night, bats utter loud echolocation calls at high repetition rates that may reveal the location and current behaviour of callers to eavesdropping bats. Given the strong attenuation of echolocation calls, we predicted that territorial males of a harem-polygynous species ought to forage at close distance to females to survey their movements by social eavesdropping. We estimated a maximum detection distance of 38 m for echolocation calls of Saccopteryx bilineata (Temminck, 1838) (Chiroptera; Emballonuridae) broadcasted within the forest under the sound transmission conditions of our study site and for an assumed signal detection threshold of 20 dB SPL (50 m for a threshold of 0 dB SPL). We then simultaneously radio-tracked the nocturnal movements of eight male–female pairs that each rested in the same harem territory during the day and measured the distances at which dyads foraged. Male–female pairs foraged at a median distance of 139 m. In the case of 90% of simultaneous bearings, males foraged at distances that prevented eavesdropping on 44 kHz echolocation calls (>38 m; 87% of radio fixes >50 m).

Males and females of the same daytime territory roosted, on average, 226 ± 194 m apart from each other at night. Thus, males were most likely unaware of where females foraged as a result of the strong attenuation of female echolocation calls. In general, such acoustic constraints on social eavesdropping may promote extra-harem group paternities, female choice, and sperm competition in bats, and may therefore present an important selective force in the evolution of bat mating systems.

Hoffmann, S., Baier, L., Borina, R., & Schuller, G., 2008. Psychophysical and neurophysiological hearing thresholds in the bat *Phyllostomus discolor*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 194(1), pp.39–47.

Abstract: Absolute hearing thresholds in the spear-nosed bat *Phyllostomus discolor* have been determined both with psychophysical and neurophysiological methods. Neurophysiological data have been obtained from two different structures of the ascending auditory pathway, the inferior colliculus and the auditory cortex. Minimum auditory thresholds of neurons are very similar in both structures. Lowest absolute thresholds of 0 dB SPL are reached at frequencies from about 35 to 55 kHz in both cases. Overall behavioural sensitivity is roughly 20 dB better than neural sensitivity. The behavioural audiogram shows a first threshold dip around 23 kHz but threshold was lowest at 80 kHz (-10 dB SPL). This high sensitivity at 80 kHz is not reflected in the neural data. The data suggest that *P. discolor* has considerably better absolute auditory thresholds than estimated previously. The psychophysical and neurophysiological data are compared to other phyllostomid bats and differences are discussed.

Holderegger, R. & Di Giulio, M., 2010. The genetic effects of roads: A review of empirical evidence. *Basic and Applied Ecology*, 11(6), pp.522–531.

Abstract: Roads exert various effects of conservation concern. They cause road mortality of wildlife, change the behaviour of animals and lead to habitat fragmentation. Roads also have genetic effects, as they restrict animal movement and increase the functional isolation of populations. We first formulate theoretical expectations on the genetic effects of roads with respect to a decrease in genetic diversity and an increase in genetic differentiation or distance of populations or individuals. We then review the empirical evidence on the genetic effects of roads based on the available literature. We found that roads often, but not always, decrease the genetic diversity of affected populations due to reduced population size and genetic drift. Whether the reduction in genetic diversity influences the long-term fitness of affected populations is, however, not yet clear. Roads, especially fenced highways, also act as barriers to movement, migration and gene flow. Roads therefore often decrease functional connectivity and increase the genetic differentiation of populations or the genetic distance among individuals. Nevertheless, roads and highways rarely act as complete barriers as shown by genetic studies assessing contemporary migration across roads (by using assignment tests). Some studies also showed that road verges act as dispersal corridors for native and exotic plants and animals. Genetic methods are well suited to retrospectively trace such migration pathways. Most roads and highways have only recently been built. Although only few generations might thus have passed since road construction, our literature survey showed that many studies found negative effects of roads on genetic diversity and genetic differentiation in animal species, especially for larger mammals and amphibians. Roads may thus rapidly cause genetic effects. This result stresses the importance of defragmentation measures such as over- and underpasses or wildlife bridges across roads.

Holderied, M.W., Baker, C., Vespe, M., Jones, G., 2008. Understanding signal design during the pursuit of aerial insects by echolocating bats: tools and applications. *Integrative and Comparative Biology*, 48(1), pp.74–84.

Abstract: Bats are among the few predators that can exploit the large quantities of aerial insects active at night. They do this by using echolocation to detect, localize, and classify targets in the dark. Echolocation calls are shaped by natural selection to match ecological challenges. For example, bats flying in open habitats typically emit calls of long duration, with long pulse intervals, shallow frequency modulation, and containing low frequencies-all these are adaptations for long-range detection. As obstacles or prey are approached, call structure changes in predictable ways for several reasons: calls become shorter, thereby reducing overlap between pulse and echo, and calls change in shape in ways that minimize localization errors. At the same time, such changes are believed to support recognition of objects. Echolocation and flight are closely synchronized: we have monitored both features simultaneously by using stereo photogrammetry and videogrammetry, and by acoustic tracking of flight paths. These methods have allowed us to quantify the intensity of signals used by free-living bats, and illustrate systematic changes in signal design in relation to obstacle proximity. We show how signals emitted by aerial feeding bats can be among the most intense airborne sounds in nature. Wideband ambiguity functions developed in the processing of signals produce two-dimensional functions showing trade-offs between resolution of time and velocity, and illustrate costs and benefits associated with Doppler sensitivity and range resolution in echolocation. Remarkably, bats that emit broadband calls can adjust signal design so that Doppler-related overestimation of range compensates for underestimation of range caused by the bat's movement in flight. We show the potential of our methods for understanding interactions between echolocating bats and those prey that have evolved ears that detect bat calls.

Holderied, M.W. & von Helversen, O., 2003. Echolocation range and wingbeat period match in aerial-hawking bats. *Proceedings. Biological Sciences / The Royal Society*, 270(1530), 2293–2299.

Abstrract: Aerial-hawking bats searching the sky for prey face the problem that flight and echolocation exert independent and possibly conflictingi nfluences on call intervals.T hese bats can only exploit their full echolocation range unambiguously if they emit their next call when all echoes from the preceding call would have arrived. H owever, not every call interval is equally available. The need to reduce the high energetic costs of echolocation forces aerial-hawking bats to couple call emission to their wingbeat. We compared the wingbeat periods of 11 aerial-hawking bat species with the delays of the last-expected echoes. Acoustic flight-path tracking was employed to measure the source levels (SLs) of echolocation calls in the field. SLs were very high, extending the known range to 133 dB peak equivalent sound pressure level. We calculated the maximum detection distances for insects, larger flying objects and background targets. Wingbeat periods were derived from call intervals. Small and medium-sized bats in fact matched their maximum detection range for insects and larger flying targetst o their wingbeat period. The tendency to skip calls correlated with the species' detection range for background targets. We argue that a species' call frequency is at such a pitch that the resulting detection range matches their wingbeat period.

Holderied, M.W., Jones, G. & von Helversen, O., 2006. Flight and echolocation behaviour of whiskered bats commuting along a hedgerow: range-dependent sonar signal design,

Doppler tolerance and evidence for "acoustic focussing". *The Journal of Experimental Biology*, 209, pp.1816–26.

Abstract: Echolocating bats obtain three-dimensional images of their surroundings in complete darkness by emitting sonar signals and evaluating returning echoes. When flying close to objects, bats risk collision and therefore depend on the accuracy of images--particularly in the perceived distance of obstacles, which is coded by the time delay between call and echo. Yet, during flight, such accuracy is perturbed first because bats call and receive echoes at different positions and second because echoes are modified by Doppler shifts. Certain call designs avoid both sources of ranging error, but only for a limited range of distances [the "distance of focus" (DOF)]. Here, we show that whiskered bats (*Myotis mystacinus*) using broadband echolocation calls adjust call design in a range-dependent manner so that nearby obstacles are localised accurately. Such behaviour is adaptive because it reduces collision risk. The bats also reduced call duration to some extent as they approached obstacles so that most returning echoes arrived after they finished calling. This reduction in call duration during the approach to obstacles was neither the only nor the main factor that influenced DOF. Indeed, both duration and bandwidth of calls influenced DOF independently, with lower bandwidths and longer durations giving greater DOF. Our findings give a new perspective on the adaptive significance of echolocation call design in nature and have implications for sonar engineering.

Holderied, M., Korine, C. & Moritz, T., 2011. Hemprich's long-eared bat (*Otonycteris hemprichii*) as a predator of scorpions: whispering echolocation, passive gleaning and prey selection. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology,*197(5), pp.425–33.

Abstract: Over 70% of the droppings of the gleaning bat *Otonycteris hemprichii* can contain scorpion fragments. Yet, some scorpions found in its desert habitat possess venom of the highest known toxicity, rendering them a very dangerous prey. In this study, we describe how *O. hemprichii* catches and handles scorpions, quantify its flight and echolocation behaviour in the field, investigate what sensory modality it uses to detect scorpions, and test whether it selects scorpions according to their size or toxicity. We confirmed that *O. hemprichi* is a whispering bat (approx. 80 dB peSPL) with short, multi-harmonic calls. In a flight room we also confirmed that *O. hemprichii* detects scorpions by their walking noises. Amplitudes of such noises were measured and they reach the flying bat at or below the level of echoes of the loess substrate. Bats dropped straight onto moving scorpions and were stung frequently even straight in their face. Stings did not change the bats' behaviour and caused no signs of poisoning. Scorpions were eaten including poison gland and stinger. Bats showed no preference neither for any of the scorpion species nor their size suggesting they are generalist predators with regard to scorpions.

Hole, L.R. & Hauge, G., 2003. Simulation of a morning air temperature inversion break-up in complex terrain and the influence on sound propagation on a local scale. *Applied Acoustics*, 64(4), pp.401–414.

Abstract: A mesoscale atmospheric model is used to model the break up of a morning air-temperature inversion during a clear weather situation with low wind speeds at ground. Modified slope-radiation parameterization in the model results in more realistic predicted air temperature profiles when compared to profiles measured with a tethered balloon. A wave number integration

code is used to demonstrate how the modelled atmospheric profiles can be used to predict the reduction of sound level along ground during inversion break-up.

Hom, K., Linnenschmidt, M., Simmons, A., and Simmons, J. 2015. Echolocation behavior of flying big brown bats in not affected by noise exposure. North American Society for Bat Research 45th Annual Symposium. October 28-31, 2015, Monterey California.

Abstract: Echolocation is a highly developed perceptual modality based on acute hearing of faint echoes reflected from objects the environment. Big brown bats (*Eptesicus fuscus*) are entirely dependent on their echolocation for guidance to fly, forage, and catch prey. Echolocation performance is likely to be highly sensitive to disruption if hearing sensitivity is impaired. It is generally known that exposure to intense noise (90 - 120 dB SPL) causes temporary or even permanent loss of hearing sensitivity in terrestrial mammals. Our experiments test the hypothesis that big brown bats are less susceptible to noise-induced hearing loss than non-echolocating terrestrial mammals. Four bats were exposed to ultrasonic noise spanning their audiometric range (20 - 100 kHz, 116 dB SPL for 1 hour). Their echolocation performance while flying through an acoustically-complex maze was compared before and after exposure. For the same maze configuration, the bats did not alter either the number or the temporal pattern (strobe groups) of their sonar calls prior to noise exposure compared to 20 min, 24 hours or 48 hours after exposure. One of the four bats showed more errors (collisions) 20 min post-exposure than pre-exposure while the other bats showed no difference in performance. Thus, it appears that noise exposure has little or no influence on echolocation behavior.

Horn, J.W., Arnett, E.B., & Kunz, T.H., 2008. Behavioral Responses of Bats to Operating Wind Turbines. *Journal of Wildlife Management*, 72(1), pp.123–132.

Abstract: Wind power is one of the fastest growing sectors of the energy industry. Recent studies have reported large numbers of migratory tree-roosting bats being killed at utility-scale wind power facilities, especially in the eastern United States. We used thermal infrared (TIR) cameras to assess the flight behavior of bats at wind turbines because this technology makes it possible to observe the nocturnal behavior of bats and birds independently of supplemental light sources. We conducted this study at the Mountaineer Wind Energy Center in Tucker County, West Virginia, USA, where hundreds of migratory tree bats have been found injured or dead beneath wind turbines. We recorded nightly 9-hour sessions of TIR video of operating turbines from which we assessed altitude, direction, and types of flight maneuvers of bats, birds, and insects. We observed bats actively foraging near operating turbines, rather than simply passing through turbine sites. Our results indicate that bats 1) approached both rotating and nonrotating blades, 2) followed or were trapped in blade-tip vortices, 3) investigated the various parts of the turbine with repeated fly-bys, and 4) were struck directly by rotating blades. Blade rotational speed was a significant negative predictor of collisions with turbine blades, suggesting that bats may be at higher risk of fatality on nights with low wind speeds.

Hotchkin, C. & Parks, S., 2013. The Lombard effect and other noise-induced vocal modifications: insight from mammalian communication systems. *Biological Reviews of the Cambridge Philosophical Society*, 88(4), pp.809–24.

Abstract: Humans and non-human mammals exhibit fundamentally similar vocal responses to increased noise, including increases in vocalization amplitude (the Lombard effect) and changes

to spectral and temporal properties of vocalizations. Different research focuses have resulted in significant discrepancies in study methodologies and hypotheses among fields, leading to particular knowledge gaps and techniques specific to each field. This review compares and contrasts noise-induced vocal modifications observed from human and non-human mammals with reference to experimental design and the history of each field. Topics include the effects of communication motivation and subject-specific characteristics on the acoustic parameters of vocalizations, examination of evidence for a proposed biomechanical linkage between the Lombard effect and other spectral and temporal modifications, and effects of noise on self-communication signals (echolocation). Standardized terminology, cross-taxa tests of hypotheses, and open areas for future research in each field are recommended. Findings indicate that more research is needed to evaluate linkages among vocal modifications, context dependencies, and the finer details of the Lombard effect during natural communication. Studies of non-human mammals could benefit from applying the tightly controlled experimental designs developed in human research, while studies of human speech in noise should be expanded to include natural communicative contexts. The effects of experimental design and behavioural context on vocalizations should not be neglected as they may impact the magnitude and type of noise-induced vocal modifications.

Huang, X., Xu, C. & Bai, L., 2012. Is the cochlea coiled to provide sound localization? *EPL (Europhysics Letters)*, 98(5), p.58002.

Abstract: The potential physical effect of the cochlear shape on sound localization is studied from the perspective of signal processing. The sensory hair cells are taken to form a sensor array, and a numerical model is used to simulate the external sound pressure perceived by the sensory hair cells directly, that is, via bone conduction. The cognitive process is thus approximated as a signal processing array. The sound localization capabilities of a straight cochlea and a spiral cochlea are compared by examining the simulated acoustic images. The results demonstrate that the spiral shape can achieve better vertical sound localization. The analysis therefore indicates that the cochlear spiral shape might not only have evolved for space conservation reasons but also for possible perceptual benefits.

Hubner, M. & Wiegrebe, L., 2003. The effect of temporal structure on rustling-sound detection in the gleaning bat, *Megaderma lyra*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 189, pp.337–346.

Abstract: For a gleaning bat hunting prey from the ground, rustling sounds generated by prey movements are essential to invoke a hunting behaviour. The detection of prey-generated rustling sounds may depend heavily on the time structure of the prey-generated and the masking sounds due to their spectral similarity. Here, we systematically investigate the effect of the temporal structure on psychophysical rustling-sound detection in the gleaning bat, *Megaderma lyra*. A recorded rustling sound serves as the signal; the maskers are either Gaussian noise or broadband noise with various degrees of envelope fluctuations. Exploratory experiments indicate that the selective manipulation of the temporal structure of the rustling sound does not influence its detection in a Gaussian-noise masker. The results of the main experiment show, however, that the temporal structure of the masker has a strong and systematic effect on rustling-sound detection: When the width of irregularly spaced gaps in the masker exceeded about 0.3 ms, rustling-sound detection improved monotonically with increasing gap duration. Computer

simulations of this experiment reveal that a combined detection strategy of spectral and temporal analysis underlies rustling-sound detection with fluctuating masking sounds.

Huebschman, B.D., 2010. The use of frequency resolution in echolocation for modeling three dimensional environments. *The Journal of the Acoustical Society of America*, 128(6), pp.EL384–9.

Abstract: Bats use echolocation to navigate three dimensional obstacles while locating, identifying, and engaging targets. A theory is offered of image processing during the search and navigation phase of echolocation that uses Doppler frequency shifts. The information in frequency changes across the angle of elevation can be used to generate a three dimensional model of the environment when combined with the timing and the relative amplitude of the returned signals. The mathematics of frequency shifts for an emitter traveling at a large fraction of the velocity of propagation (c) is presented. Reported behavior that can be explained by this phenomenon is discussed.

Huihua, Z., Shuyi, Z., Mingxue, Z., & Jiang, Z., 2003. Correlations between call frequency and ear length in bats belonging to the families Rhinolophidae and Hipposideridae. *Journal of Zoology*, 259(2), pp.189–195.

Abstract: Echolocation calls of 10 species of rhinolophid and four species of hipposiderid bats were recorded in China. Close negative relationships were found within Rhinolophidae and Hipposideridae between call frequency and ear length. Multiple regression and residual analysis were used to evaluate the influences of forearm length and ear length on call frequency and ear size. Ear length proved to be a more important morphological parameter influencing the call frequency in rhinolophids but not in hipposiderids. Ears are largely shaped by echolocation calls in both families. The influence of body size on ear size was significant in rhinolophids but not in hipposiderids, and the enlarged ears of rhinolophids correlated with the lower frequencies that rhinolophids used relative to larger body size.

Humboldt State University Bat Lab. 2011. Echolocation call characteristics of western US bats. March 2011. Online: http://www.sonobat.com/download/WesternUS_Acoustic_Table_Mar2011.pdf

No abstract

Humphries, M.M., Thomas, D.W. & Speakman, J.R., 2002. Climate-mediated energetic constraints on the distribution of hibernating mammals. *Nature*, 418, pp.313–316.

No abstract

Humphrey, S. R. & Kunz, T.H., 1976. Ecology of a Pleistocene relict, the western big-eared bat (*Plecotus townsendii*) in the southern Great Plains. *Journal of Mammalogy*, 57, pp.470-494.

Abstract: In karst regions of western Oklahoma and Kansas, *Plecotus townsendii* is locally ubiquitous but low in density. Natality is low but reproductive effort and preweaning survival of young are comparatively high. Movement data show no consistent pattern of dispersal that would account for a low density. P. townsendii uses nursery roosts that are marginal or uninhabitable

for locally sympatric cave-dwelling species. Reproductive success depends on the ability of individuals in small nursery colonies to maintain a high degree of thermal exchange during pregnancy and lactation. This is facilitated by the formation of dense clusters in which metabolic heat is shared directly by body contact. In our judgment, the selection of intrinsically warm nursery sites is essential for reproductive success. In early and late winter most P. townsendii are absent from caves; presumably they occupy alternate roosts and forage on warm evenings. These bats seem to require relatively cold temperatures to hibernate. In autumn and early winter some individuals hibernate singly near cave entrances where ambient temperatures are variable but cool cave rock stabilizes body temperatures. By midwinter, these sites reach subfreezing temperatures and many bats move deep into caves, where they may form clusters. Both sexes lose over half their body weight before spring. Owing to this large weight loss, susceptibility to predation in midwinter, and probable late winter foraging efforts, we suspect substantial winter mortality as the prevailing limiting factor. The relictual nature of populations in the southern plains is made comprehensible by the species' reproductive, dispersal, and hibernating performance. From this ecological performance we infer that *P. townsendii* occurred across the southern United States during the Wisconsin glaciation, when numerous trees grew on the southern plains and the climate was moist with short, cool summers and long, mild winters. The present isolated taxa use caves as refugia from intolerable post-Pleistocene winters. The small size of *P. townsendii* populations, rather severe ecological limitations, and high sensitivity to disturbance lead us to conclude that visitation of nurseries by humans could threaten the species' survival in the Great Plains.

ICF Jones & Stokes. 2009. Technical Noise Supplement. November (ICF J&S 00183.08) Sacramento, CA. Prepared for California Department of Transportation (Caltrans), Sacramento, CA.

Abstract: The TeNS consists of nine sections. Except for Section 1, each covers a specific subject of highway noise. A brief description of the subjects follows. Section 1, “Introduction and Overview,” summarizes the subjects covered in the TeNS. Section 2, “Basics of Highway Noise,” covers the physics of sound as it pertains to characteristics and propagation of highway noise, effects of noise on humans, and ways of describing noise. Section 3, “Measurements and Instrumentation,” provides background information on noise measurements, and discusses various noise-measuring instruments and operating procedures. Section 4, “Traffic Noise Impact Screening Procedure,” was developed to assist in determining whether a highway project has the potential to cause a traffic noise impact. If the project does not pass the screening procedure, a detailed noise analysis should be performed. If the project passes the screening procedure, prudent engineering judgment should still be exercised to determine whether a detailed analysis is warranted. Section 5, “Detailed Analysis for Traffic Noise Impacts,” provides guidance for studying those projects failing the screening procedure, projects that are controversial or sensitive, or projects where the net effects of topography and shielding are complex or ambiguous. This section includes identifying land use, selecting receivers, determining existing noise levels, predicting future noise levels, and determining impacts. Section 6, “Detailed Analysis for Noise Barrier Design Considerations,” outlines the major aspects that affect the acoustical design of noise barriers, including the dimensions, location, and material; optimization of noise barriers; possible noise reflections; acoustical design of overlapping noise barriers (to provide maintenance access to areas behind barriers); and drainage openings in noise barriers. It also points out some difficulties and cautions. Section 7, “Noise

Study Reports," discusses the contents of noise study reports. Section 8, "Non-Routine Considerations and Issues," covers non-routine and sometimes controversial issues involving the effects of noise on distant receivers, use of sound intensity and sound power as tools in characterizing sound sources, pavement noise, noise monitoring for insulating homes, construction noise, earthborne vibrations, California Occupational Safety and Health Administration (OSHA) noise standards, and effects and abatement of transportation-related noise on marine and wildlife. Section 9, "Glossary," provides terminology and definitions common in transportation noise. Appendix A, "References Cited," provide a listing of literature directly cited or used for reference in the TeNS.

ICF, 2014. California Environmental Quality Act 2014. CEQA Statute and guidelines. Online: http://resources.ca.gov/ceqa/docs/2014_CEQA_Statutes_and_Guidelines.pdf

No abstract

Iglesias, C., Mata, C. & Malo, J.E., 2012. The influence of traffic noise on vertebrate road crossing through underpasses. *Ambio*, 41(2), pp.193–201.

Abstract: Noise produces multiple effects on ecosystems and it influences habitat use by vertebrates near roads. Thus, it may reduce the effectiveness of mitigation measures installed on roads to alleviate population fragmentation. This study analyses the effects of noise on the use by vertebrates of 19 underpasses at a motorway. It employs generalised linear models to test the effect of three noise indicators at the underpasses and in their vicinity on the crossing frequency of eight animal species. The results show that the road crossings are subjected to high and variable noise levels. Nevertheless, there is no consistent response to noise by vertebrates. This suggests that wildlife use of underpasses is determined more by habitat characteristics than by the levels of noise tolerated. The conclusion is that noise abatement measures on roads in areas of faunal sensitivity should focus on general noise reduction rather than on making individual crossing places quieter.

Jackson, M.E., Asi, N.S. & Fullard, J.H., 2010. Auditory sensitivity and ecological relevance: the functional audiogram as modelled by the bat detecting moth ear. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology,*196(7), pp.453–62.

Abstract: Auditory sensitivity has often been measured by identifying neural threshold in real-time (online) which can introduce bias in the audiograms that are produced. We tested this by recording auditory nerve activity of the notodontid moth *Nadata gibbosa* elicited by bat-like ultrasound and analysing the response offline. We compared this audiogram with a published online audiogram showing that the bias introduced can result in a difference in the audiogram shape. In the second part of our study we compared offline audiograms using spike number as threshold with others that used spike period and stimulus/spike latency, variables that have been suggested as providing behaviourally functional criteria. These comparisons reveal that functional audiograms are more flatly tuned than simple spike audiograms. The shapes of behavioural audiograms are discussed in the context of the selection pressure that maintains their shape, bat predation. Finally, we make predictions on the distance from bats at which notodontid moths use negative phonotaxis or the acoustic startle response.

Jacobs, D.S., Barclay, R.M.R. & Walker, M.H., 2007. The allometry of echolocation call frequencies of insectivorous bats: why do some species deviate from the pattern? *Oecologia*, 152(3), pp.583–94.

Abstract: The peak echolocation frequency of insectivorous bats generally declines as body size increases. However, there are notable exceptions to this rule, with some species, such as *Rhinolophus clivosus*, having a higher than expected peak frequency for their body size. Such deviations from allometry may be associated with partitioning of foraging habitat (the foraging habitat hypothesis) or insect prey (the prey detection hypothesis). Alternatively, the deviations may be associated with the partitioning of sonar frequency bands to allow effective communication in a social context (the acoustic communication hypothesis). We tested the predictions of these hypotheses through comparisons at the family, clade and species level, using species of rhinolophids in general and *R. clivosus*, a species with a wide distribution, as a specific test case. We compared the wing parameters, echolocation frequency and ecology of *R. clivosus* to those of the sympatric *R. capensis*. *Rhinolophus clivosus* has a much higher echolocation frequency than predicted from its wing loading or body mass. Furthermore, contrary to the predictions of the foraging habitat hypothesis, we found no difference in foraging habitat between *R. clivosus* and *R. capensis*. The size range of insect prey taken by the two species also overlapped almost completely, contrary to the prey detection hypothesis. On the other hand, the variation of echolocation frequencies around the allometric relationship for rhinolophids was smaller than that for *Myotis* spp., supporting the prediction of the acoustic communication hypothesis. We thus propose that the relatively high peak frequency of *R. clivosus* is the result of partitioning of sonar frequency bands to minimize the ambiguity of echolocation calls during social interactions.

Jahelková, H., Horáček, I. & Bartonička, T., 2008. The advertisement song of *Pipistrellus nathusii* (Chiroptera, Vespertilionidae): a complex message containing acoustic signatures of individuals. *Acta Chiropterologica*, 10(1), pp.103–126.

Abstract: Males of Nathusius' pipistrelle (*Pipistrellus nathusii*) are well known for their complex acoustic advertisement behaviour performed either as songflight (SF) or sedentary display (SD). We analysed phonologic, syntactic and semantic characteristics of these calls based on 2,924 acoustic records obtained from individual males repeatedly occupying 33 roosts in southern Bohemia from 1999 to 2006. Both SF and SD calls are composed of three main phonologically contrasting motifs (A, B, C) and under specific contexts often supplemented with two accessory motifs (D, E). Besides the major syntagmatic string ABC we recorded further 15 syntagms containing the main motif A and 10 syntagms without this motif. At the peak of the mating season and with the SD, the complexity of the vocalisation increases (increased variation in syntagmatic structure and syllabic composition of particular motifs, as well as in length of syntagmatic strings). The motif A corresponds to advertisement calls of congeneric species and is related to agonistic vocalisation, and B, C, D are specific for *P. nathusii*. B and C exhibit the largest between-individual but low within-individual variation, and their combination provides an acoustic signature of an individual and uniquely identified each particular male. Motif D corresponds to calls of mother-young communication and shows the largest syllabic variation. Motif E is a series of steep FM signals evocative of the act of landing. The message of a complete advertisement call (ABCED) could be thus: "(A): Pay attention, here is a *P. nathusii*, (B, C): I am male X, (E): land here, (D): we share a common social identity and common

communication pool". The individual characteristics of the performance of B, C, and D motifs were found to be invariant both within a season and over a series of successive years.

Jakobsen, L., Kalko, E.K. V. & Surlykke, A., 2012. Echolocation beam shape in emballonurid bats, *Saccopteryx bilineata* and *Cormura brevirostris*. *Behavioral Ecology and Sociobiology*, 66(11), pp.1493–1502.

Abstract: The shape of the sonar beam plays a crucial role in how echolocating bats perceive their surroundings. Signal design may thus be adapted to optimize beam shape to a given context. Studies suggest that this is indeed true for vespertilionid bats, but little is known from the remaining 16 families of echolocating bats. We investigated the echolocation beam shape of two species of emballonurid bats, *Cormura brevirostris* and *Saccopteryx bilineata*, while they navigated a large outdoor flight cage on Barro Colorado Island, Panama. *C. brevirostris* emitted more directional signals than did *S. bilineata*. The difference in directionality was due to a markedly different energy distribution in the calls. *C. brevirostris* emitted two call types, a multiharmonic shallowly frequency-modulated call and a multiharmonic sweep, both with most energy in the fifth harmonic around 68 kHz. *S. bilineata* emitted only one call type, multiharmonic shallowly frequency-modulated calls with most energy in the second harmonic (~46 kHz). When comparing same harmonic number, the directionality of the calls of the two bat species was nearly identical. However, the difference in energy distribution in the calls made the signals emitted by *C. brevirostris* more directional overall than those emitted by *S. bilineata*. We hypothesize that the upward shift in frequency exhibited by *C. brevirostris* serves to increase directionality, in order to generate a less cluttered auditory scene. The study indicates that emballonurid bats are forced to adjust their relative harmonic energy instead of adjusting the fundamental frequency, as the vespertilionids do, presumably due to a less flexible sound production.

Jakobsen, L., Ratcliffe, J.M. & Surlykke, A., 2013. Convergent acoustic field of view in echolocating bats. *Nature*, 493(7430), pp.93–6.

Abstract: Most echolocating bats exhibit a strong correlation between body size and the frequency of maximum energy in their echolocation calls (peak frequency), with smaller species using signals of higher frequency than larger ones. Size-signal allometry or acoustic detection constraints imposed on wavelength by preferred prey size have been used to explain this relationship. Here we propose the hypothesis that smaller bats emit higher frequencies to achieve directional sonar beams, and that variable beam width is critical for bats. Shorter wavelengths relative to the size of the emitter translate into more directional sound beams. Therefore, bats that emit their calls through their mouths should show a relationship between mouth size and wavelength, driving smaller bats to signals of higher frequency. We found that in a flight room mimicking a closed habitat, six aerial hawking vespertilionid species (ranging in size from 4 to 21 g, ref. 5) produced sonar beams of extraordinarily similar shape and volume. Each species had a directivity index of 11 ± 1 dB (a half-amplitude angle of approximately 37°) and an on-axis sound level of 108 ± 4 dB sound pressure level referenced to 20 μPa root mean square at 10 cm. Thus all bats adapted their calls to achieve similar acoustic fields of view. We propose that the necessity for high directionality has been a key constraint on the evolution of echolocation, which explains the relationship between bat size and echolocation call frequency. Our results suggest that echolocation is a dynamic system that allows different species, regardless of their body size, to converge on optimal fields of view in response to habitat and task.

Jameson, J.W. & Hare, J.F., 2009. Group-specific signatures in the echolocation calls of female little brown bats (*Myotis lucifugus*) are not an artifact of clutter at the roost entrance. *Acta Chiropterologica*, 11(1), pp.163–172.

Abstract: In species where conspecifics form discrete social groups, the production of signals advertising group membership may promote cohesion among group members. Female little brown bats (*Myotis lucifugus*) show high fidelity to maternity roost sites where they aggregate in large numbers every spring to rear young. While the presence of group-specific signatures has been demonstrated in the echolocation calls of this species, differential clutter at recording sites may account for the observed differences. Bats optimize their ability to maneuver and detect prey within a given environment by tailoring their echolocation calls to physical attributes of that environment. Therefore, if clutter is responsible for the apparent group specificity in the calls of little brown bats, groups of bats experiencing similar levels of clutter at roost entrances should emit similar calls. We examined the effect of differential clutter on the emergence calls of *M. lucifugus* by comparing recorded echolocation calls of bats emerging from three maternity roosts in Georgian Bay, Ontario. The roosts varied in distance from each other and in their proximity to surrounding clutter. The more distant group emerged in an environment with clutter deemed intermediate to the two more proximate roost entrances and yet was the most acoustically distinct. The finding that similarity among emergence calls correlated better with spatial proximity than with the level of clutter around roost entrances is consistent with the development of true group-specific signatures in the emergence calls of *M. lucifugus*.

Jantzen, M.K. & Fenton, M.B., 2013. The depth of edge influence among insectivorous bats at forest–field interfaces. *Canadian Journal of Zoology*, 91(5), pp.287–292.

Abstract: Species-specific variations in wing morphology and echolocation call characteristics often define which of three structural habitat types (open, cluttered, and edge) different bat species most frequently and efficiently use for foraging. Although edges are recognized as important habitats for commuting and foraging bats, no study to date has examined the depth of edge influence (DEI), the extent of quantitative changes in activity with distance from an edge, for any bat species. We focused our study on five species: northern long-eared bat, *Myotis septentrionalis* (Trouessart, 1897); hoary bat, *Lasiurus cinereus* (Beauvois, 1796); little brown bat, *Myotis lucifugus* (LeConte, 1831); silver-haired bat, *Lasionycteris noctivagans* (LeConte, 1831); big brown bat, *Eptesicus fuscus* (Beauvois, 1796). We predicted DEI would vary with species-specific differences in wing morphology and echolocation call characteristics. From June to August in 2010 and 2011, we passively recorded echolocation calls three to four times per month at eight sites in eastern Ontario, Canada. We found that species' activity was highest at the edge, regardless of wing morphology and echolocation call characteristics. The DEI for all species was approximately 40 m into both forests and fields. Understanding the effects of DEI on bats will enable more effective acoustic monitoring in future studies and may provide crucial information for management decisions.

Jarvis, J., Bohn, K.M., Tressler, J., & Smoherman, M. 2010. A mechanism for antiphonal echolocation by Free-tailed bats. *Animal Behaviour*, 79(4), pp.787–796.

Abstract: Bats are highly social and spend much of their lives echolocating in the presence of other bats. To reduce the effects of acoustic interferences from other bats' echolocation calls, we hypothesized that bats might shift the timing of their pulse emissions to minimize temporal

overlap with another bat's echolocation pulses. To test this hypothesis we investigated whether free-tailed bats (*Tadarida brasiliensis*) echolocating in the lab would shift the timing of their own pulse emissions in response to regularly repeating artificial acoustic stimuli. A robust phase-locked temporal pattern in pulse emissions was displayed by every bat tested which included an initial suppressive phase lasting more than 60 ms after stimulus onset, during which the probability of emitting pulses was reduced by more than fifty percent, followed by a compensatory rebound phase, the timing and amplitude of which were dependent on the temporal pattern of the stimulus. The responses were non-adapting and were largely insensitive to broad changes in the acoustic properties of the stimulus. Randomly occurring noise-bursts also suppressed calling for up to 60 ms, but the time-course of the compensatory rebound phase was more rapid than when the bats were responding to regularly repeating patterns of noise bursts. These findings provide the first quantitative description of how external stimuli may cause echolocating bats to alter the timing of subsequent pulse emissions.

Jen, P.H. & Chen, D., 1988. Directionality of sound pressure transformation at the pinna of echolocating bats. *Hearing Research*, 34(2), pp.101–117.

Abstract: The directionality of sound pressure transformation at the pinna of three species of bats was studied by measuring the sound pressure level of a tone (25, 45, 65 and 85 kHz) at the tympanic membrane as a function of azimuth and elevation of the sound source under free-field conditions. The tympanic sound pressure level varied with location of the sound source. The directionality of sound pressure transformation pattern of the pinna of each bat was studied by plotting isopressure contours. The area within each isopressure contour decreased with increasing tonal frequency. For each tonal frequency, the point of maximal sound pressure was always located in the frontal ipsilateral sound field. This point shifted medially with increasing tonal frequency along the horizontal plane in all species tested, but it shifted in a species-specific manner along the vertical plane. Removal or distortion of the pirma and tragus resulted in either uncircumscribed or irregular isopressure contours for all tonal frequencies tested. Acoustic pressure gain of the external ear reached 16-23 dB for frequencies at 15 - 18 kHz. The importance of the external ear to the directionality of the bat's echolocation system is discussed.

Jen, P.H. & Sun, X., 1984. Pinna orientation determines the maximal directional sensitivity of bat auditory neurons. Brain Research, 301(1), pp.157–161.

Abstract: The auditory response areas of 192 inferior collicular neurons (IC) of *Eptesicus fuscus* were studied under free field acoustic stimulation. The boundary of the auditory response area of a neuron expands with stimulus intensity (Fig. 1). However, there is a response center within each neuron's response area at which the neuron has the maximal sensitivity. All response centers of the 192 neurons are located within a limited space of the bat's contralateral auditory space. The position of the response center of a neuron changes with different pinna orientations (Figs. 2 and 3) providing a bat with versatility in maximizing the sensitivity of its echolocation system.

Jen, P.H., Sun, X. & Kamada, T., 1982. Responses of cerebellar neurons of the CF-FM bat, *Pteronotus parnellii* to acoustic stimuli. *Brain Research*, 252(1), pp.167–171.

Abstract: Single units (125) which faithfully discharged action potentials to acoustic stimuli (35 ms in duration with 0.5 ms rise and decay times) were recorded in the cerebellar vermis and

hemispheres of the CF-FM bat, *Pteronotus parnellii*. These units had response latencies between 1.5 and 27 ms and minimum thresholds between 2 and 83.5 dB SPL. Best frequencies (BFs) of these units ranged from 30.32 to 79.28 kHz, but more than half (64 units, 51.2~) were between 59.73 and 63.32 kHz. While most tuning curves of these units were either broad or irregular, those curves with BFs tuned at around 61 kHz which is the frequency of the predominant CF component of the bat's echolocation signals were extremely narrow with Q_{10}-dB values as high as 153. Those units (29) with BFs tuned near the 61 kHz also showed off-responses. These data indicate that auditory specialization for processing of species specific orientation signals also exists in the cerebellum of this bat.

Jennings, N., Parsons, S., & Pocock, M.J.O., 2008. Human vs. machine: identification of bat species from their echolocation calls by humans and by artificial neural networks. *Canadian Journal of Zoology*, 86(5), pp.371–377.

Abstract: The shape of the sonar beam plays a crucial role in how echolocating bats perceive their surroundings. Signal design may thus be adapted to optimize beam shape to a given context. Studies suggest that this is indeed true for vespertilionid bats, but little is known from the remaining 16 families of echolocating bats. We investigated the echolocation beam shape of two species of emballonurid bats, *Cormura brevirostris* and *Saccopteryx bilineata*, while they navigated a large outdoor flight cage on Barro Colorado Island, Panama. *C. brevirostris* emitted more directional signals than did *S. bilineata*. The difference in directionality was due to a markedly different energy distribution in the calls. *C. brevirostris* emitted two call types, a multiharmonic shallowly frequency-modulated call and a multiharmonic sweep, both with most energy in the fifth harmonic around 68 kHz. *S. bilineata* emitted only one call type, multiharmonic shallowly frequency-modulated calls with most energy in the second harmonic (~46 kHz). When comparing same harmonic number, the directionality of the calls of the two bat species was nearly identical. However, the difference in energy distribution in the calls made the signals emitted by *C. brevirostris* more directional overall than those emitted by S. bilineata. We hypothesize that the upward shift in frequency exhibited by *C. brevirostris* serves to increase directionality, in order to generate a less cluttered auditory scene. The study indicates that emballonurid bats are forced to adjust their relative harmonic energy instead of adjusting the fundamental frequency, as the vespertilionids do, presumably due to a less flexible sound production.

Jensen, M.E. & Miller, L.A., 1999. Echolocation signals of the bat *Eptesicus serotinus* recorded using a vertical microphone array: effect of flight altitude on searching signals. *Behavioral Ecology and Sociobiology*, 47(1-2), pp.60–69.

Abstract: The acoustic behaviour of *Eptesicus serotinus* was investigated in the field using a 13.5-m vertical, linear microphone array that allowed for simultaneous recordings at three different heights and for the calculation of flight altitude and distance from the array. Recordings were made at two locations that differed in bat species diversity. *E. serotinus* hunted on average at an altitude of 10.7 m (±2.7) at one location and 6.8 m (±3.6) at the other location. Search signals were 5-17 ms long depending on flight altitude, and consisted of two to three frequency-modulated harmonics. For bats flying below 8-10 m altitude, signal duration decreased with decreasing flight altitude, whereas signal interval, terminal frequency, peak frequency and frequency range of the first harmonic increased. Above 8-10 m flight altitude, the signal parameters were fairly constant. The -10 dB bandwidth and duty cycle did not change with flight

altitude. Source levels were calculated to between 121 and 125 dB peSPL re 20, uPa at 10 cm. For bats flying higher than 9 m, the microphone placed 1.5 m above the ground recorded significantly reduced signal durations and frequency ranges of the first harmonic compared to the same signals recorded with the microphones at heights of 7 or 15 m. We caution the use of ground recordings to fully describe the echolocation signals of high-flying bats. We demonstrate that flight altitude significantly influences the structure of sonar signals from *E. serotinus*.

Jensen, M.E., Moss, C.F. & Surlykke, A., 2005. Echolocating bats can use acoustic landmarks for spatial orientation. *The Journal of Experimental Biology*, 208, pp.4399–410.

Abstract: We investigated the echolocating bat's use of an acoustic landmark for orientation in a complex environment with no visual information. Three bats of the species *Eptesicus fuscus* were trained to fly through a hole in a mist net to receive a food reward on the other side. In all experiments, the vocal behavior of the bats was recorded simultaneously using a high-speed video recording system, allowing for a 3D reconstruction of the flight path. We ran three types of experiments, with different spatial relations between the landmark and net hole. In the first experiment, the bat's behavior was studied in test trials with the landmark placed 10 cm to the left of the net opening; between test trials, the positions of the net opening and landmark were moved, but the spatial relationship between the two remained fixed. With the landmark adjacent to the net opening, the bats quickly found the hole. In the second experiment, bats were tested in control trials in which the landmark was moved independently of the hole, breaking the established spatial relationship between the two. In control trials the bats repeatedly crashed into the net next to the landmark, and inspected the area around it. In the final experiment, the landmark was removed altogether from the set-up. Here the bats spent more time per trial searching for the net opening with an increased number of inspections as well as crashes into the net. However, over the course of a test day without the landmark, bats reduced the time spent per trial and focused inspections and crashes around the hole. The behavioral data show for the first time that the echolocating bat can learn to rely on an acoustic landmark to guide spatial orientation.

Johnson, A.J., Brack Jr., V. & Rolley, R.E., 1998. Overwinter weight loss of Indiana bats (*Myotis sodalis*) from hibernacula subject to human visitation. *American Midland Naturalist*, 139, pp.255-261.

Abstract: Overwinter weight loss of Indiana bats (*Myotis sodalis*) was assessed during the 1989–1990 and 1990–1991 winters at three hibernacula (high, low, and no human visitation) in southern Indiana. We weighed 4264 *M. sodalis* captured during the autumn swarming and spring emergence periods. Mean spring weights were less than mean autumn weights for males and females in both years. Overwinter weight loss, expressed as a percentage of mean autumn weight, ranged from 15% to 33% and was least at the cave that received no human visitation in three of four sex-year combinations. The magnitude of overwinter weight loss differed among caves in three of four tests, but the effect of cave on weight loss was inconsistent between sexes in both years and between years within sex. Percent weight loss was less at the hibernaculum with low visitation ($\bar{x}$ = 5.5 visits/winter) than at the hibernaculum with high visitation ($\bar{x}$ = 378 visits/winter) in two of four sex-year combinations. Increases of populations in both disturbed hibernacula suggest *M. sodalis* is affected by limiting factors other than, or in addition to, human visitation in winter.

Johnson, J.S. & Lacki, M.J., 2013. Summer heterothermy in Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) roosting in tree cavities in bottomland hardwood forests. *Journal of Comparative Physiology B*, 183(5), pp.709–21.

Abstract: Many small mammals are heterothermic endotherms capable of maintaining an elevated core body temperature or reducing their thermoregulatory set point to enter a state of torpor. Torpor can confer substantial energy savings, but also incurs ecological costs, such as hindering allocation of energy towards reproduction. We placed temperature-sensitive radio transmitters on 44 adult Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) and deployed microclimate data loggers inside 34 day roosts to compare the use of torpor by different sex and reproductive classes of bats during the summer. We collected 324 bat-days of skin-temperature data from 36 females and 4 males. Reproductive females employed fewer torpor bouts per day than non-reproductive females and males ($P < 0.0001$), and pregnant and lactating females had higher average ($P < 0.0001$) and minimum ($P < 0.0001$) skin temperatures than non-reproductive females. Pregnant females spent less time torpid ($P < 0.0001$) than non-reproductive females, but lactating females used relatively deep, long torpor bouts. Microclimates varied inside tree species with different configurations of entrances to the roost cavity ($P < 0.0001$). Bats spent more time torpid when roosting in water tupelo (*Nyssa aquatica*) trees possessing only a basal entrance to the cavity ($P = 0.001$). Of the tree species used as roosts, water tupelo cavities exhibited the least variable daytime and nighttime temperatures. These data demonstrate that use of summer torpor is not uniform among sex and reproductive classes in Rafinesque's big-eared bat, and variation in microclimate among tree roosts due to species and structural characteristics facilitates the use of different thermoregulatory strategies in these bats.

Johnston, D., Tatarian, D. G. & Pierson, E., 2004. California bat mitigation techniques, solutions and effectiveness. H. T. Harvey and Associates. Prepared for California Department of Transportation (Caltrans) Office of Biological Studies and Technical Assistance, Sacramento, California 127 pp.

No abstract

Jones, G., 1999. Scaling of echolocation call parameters in bats. *The Journal of Experimental Biology*, 202(Pt 23), pp.3359–67.

Abstract: I investigated the scaling of echolocation call parameters (frequency, duration and repetition rate) in bats in a functional context. Low-duty-cycle bats operate with search phase cycles of usually less than 20 %. They process echoes in the time domain and are therefore intolerant of pulse-echo overlap. High-duty-cycle (>30 %) species use Doppler shift compensation, and they separate pulse and echo in the frequency domain. Call frequency scales negatively with body mass in at least five bat families. Pulse duration scales positively with mass in low-duty-cycle quasi-constant-frequency (QCF) species because the large aerial-hawking species that emit these signals fly fast in open habitats. They therefore detect distant targets and experience pulse-echo overlap later than do smaller bats. Pulse duration also scales positively with mass in the Hipposideridae, which show at least partial Doppler shift compensation. Pulse repetition rate corresponds closely with wingbeat frequency in QCF bat species that fly relatively slowly. Larger, fast-flying species often skip pulses when detecting distant targets. There is probably a trade-off between call intensity and repetition rate because "whispering" bats (and hipposiderids) produce several calls per predicted wingbeat and because batches of calls are

emitted per wingbeat during terminal buzzes. Severe atmospheric attenuation at high frequencies limits the range of high-frequency calls. Low-duty-cycle bats that call at high frequencies must therefore use short pulses to avoid pulse-echo overlap. Rhinolophids escape this constraint by Doppler shift compensation and, importantly, can exploit advantages associated with the emission of both high-frequency and long-duration calls. Low frequencies are unsuited for the detection of small prey, and low repetition rates may limit prey detection rates. Echolocation parameters may therefore constrain maximum body size in aerial-hawking bats.

Jones, G., 2003. Mysterious Mystacina: how the New Zealand short-tailed bat (*Mystacina tuberculata*) locates insect prey. *Journal of Experimental Biology*, 206(23), pp.4209–4216.

Abstract: New Zealand short-tailed bat *Mystacina tuberculata* evolved in the absence of terrestrial mammals and initially with few potential predators. Unusual among bats, it is well adapted for the capture of prey on the ground. Bats from Fiordland, New Zealand had relatively low wing loadings and aspect ratios adapted for flight in cluttered habitats. We predicted that *M. tuberculata* would locate prey in air (uncluttered space) by echolocation. Echolocation call sequences associated with prey capture (terminal buzzes) were heard in the field, and bats detected and localized prey suspended on fishing line by echolocation in a flight cage. The bats emitted brief, multiharmonic echolocation calls at low duty cycle during search phase, and 64% of calls contained most energy in the fundamental harmonic. Approach- and terminal phase calls were also broadband and multiharmonic. We predicted that bats would not use echolocation to locate prey hidden on the ground in leaf litter (cluttered space). Bats seemed unable to locate hidden prey precisely from the air and instead hunted for such prey while crawling. Echolocation calls were emitted at a low repetition rate on the ground, suggesting that here echolocation was used for orientation and not for prey detection. We experimentally removed cues available to the bats and showed that bats located mealworms in leaf litter by listening for prey generated noises and possibly by olfaction.

Jones, G., 2008. Sensory ecology: echolocation calls are used for communication. *Current Biology*, 18(1), pp.R34–5.

Abstract: Noctule bats locate tree roosts faster by eavesdropping on the echolocation calls of conspecifics. Increasing evidence suggests that echolocation is important not only for orientation and finding prey, but also for communication.

Jones, G., 2008. Sensory ecology: noise annoys foraging bats. *Current biology*, 18(23), pp.R1098–100.

Abstract: Traffic noise reduces foraging time and effort in greater mouse-eared bats, presumably by masking rustling sounds made by moving arthropods. Anthropogenic noise is becoming a major concern in conservation biology.

Jones, G., 2010. Molecular evolution: gene convergence in echolocating mammals. *Current Biology*, 20(2), pp.R62–4.

Abstract: The motor protein prestin confers sensitive and selective hearing in mammals. Remarkably, prestin amino-acid sequences of echolocating dolphins have converged to resemble those of distantly related echolocating bats.

Jones, G. & Siemers, B.M., 2011. The communicative potential of bat echolocation pulses. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology,*197(5), pp.447–57.

Abstract: Ecological constraints often shape the echolocation pulses emitted by bat species. Consequently some (but not all) bats emit species-specific echolocation pulses. Because echolocation pulses are often intense and emitted at high rates, they are potential targets for eavesdropping by other bats. Echolocation pulses can also vary within species according to sex, body size, age, social group and geographic location. Whether these features can be recognised by other bats can only be determined reliably by playback experiments, which have shown that echolocation pulses do provide sufficient information for the identification of sex and individual in one species. Playbacks also show that bats can locate conspecifics and heterospecifics at foraging and roost sites by eavesdropping on echolocation pulses. Guilds of echolocating bat species often partition their use of pulse frequencies. Ecology, allometric scaling and phylogeny play roles here, but are not sufficient to explain this partitioning. Evidence is accumulating to support the hypothesis that frequency partitioning evolved to facilitate intraspecific communication. Acoustic character displacement occurs in at least one instance. Future research can relate genetic population structure to regional variation in echolocation pulse features and elucidate those acoustic features that most contribute to discrimination of individuals.

Jones, G. & Teeling, E.C., 2006. The evolution of echolocation in bats. *Trends in Ecology & Evolution,* 21(3), pp.149–56.

Abstract: Recent molecular phylogenies have changed our perspective on the evolution of echolocation in bats. These phylogenies suggest that certain bats with sophisticated echolocation (e.g. horseshoe bats) share a common ancestry with non-echolocating bats (e.g. Old World fruit bats). One interpretation of these trees presumes that laryngeal echolocation (calls produced in the larynx) probably evolved in the ancestor of all extant bats. Echolocation might have subsequently been lost in Old World fruit bats, only to evolve secondarily (by tongue clicking) in this family. Remarkable acoustic features such as Doppler shift compensation, whispering echolocation and nasal emission of sound each show multiple convergent origins in bats. The extensive adaptive radiation in echolocation call design is shaped largely by ecology, showing how perceptual challenges imposed by the environment can often override phylogenetic constraints.

Jones, H., D. Stredulinsky and P. Vermeulen, P. 1980. An experimental and theoretical study of the modelling of road traffic noise and its transmission in the urban environment. *Applied Acoustics,* 13(4), pp.251–265.

Abstract: This paper describes experiments conducted on the modelling of traffic noise using a 1/80th scale model of a subdivision of a city. The emphasis in this study was on the correct evaluation of ground absorption effects. There were essentially four phases to the study. First, the applicability of various scaling law regimes was examined. It was shown that 1/80th scaling using air as a transmission medium was at least a practical choice. The second phase concerned itself with the choice of materials for the model, particularly that which was to simulate the ground. An impedance measuring apparatus was developed and used to test materials. The third part of the work concerned itself with the development of an anechoic enclosure and a sound source to simulate traffic noise; modulated Hartmann whistles were used for this purpose.

Finally, a model of part of a residential area of Calgary was built and sound transmission measurements obtained. These results were compared with field measurements. It was shown that good agreement existed between the field and model measurements.

Jones, P.L., Page, R.A., Harbauer, M. & Siemers, B.M., 2011. Behavioral evidence for eavesdropping on prey song in two Palearctic sibling bat species. *Behavioral Ecology and Sociobiology*, 65, pp.333–340.

Abstract: Eavesdropping on prey communication signals has never before been reported for a Palearctic bat species. In this study, we investigated whether lesser and greater mouse-eared bats, *Myotis blythii oxygnathus* and *Myotis myotis*, find tettigoniid bushcrickets (Tettigoniidae) by eavesdropping on their mate-attraction song. Tettigoniids are known to be the most important prey item for *M. blythii oxygnathus*, while carabid beetles and other epigaeic arthropods are the most important prey for its sibling species, *M. myotis*, in many places in Europe. *M. myotis* locates walking beetles by listening for their rustling sounds. We compared these two species' response to four acoustic prey cues: calling song of two tettigoniid species, the rustling sound made by walking carabid beetles, and a control tone. Individuals of both bat species attacked the speaker playing tettigoniid song, which clearly indicates that both species eavesdrop on prey-generated advertisement signals. There were, however, species differences in response. *M. blythii oxygnathus* exhibited stronger predatory responses to the calling song of two species of tettigoniid than to the beetle rustling sound or the control. *M. myotis*, in contrast, exhibited stronger predatory responses to the beetle rustling and to one tettigoniid species but not the other tettigoniid or the control. Our study (1) for the first time demonstrates eavesdropping on prey communication signals for Palearctic bats and (2) gives preliminary evidence for sensory niche partitioning between these two sympatric sibling bat species.

Jung, K. & Kalko, E.K. V., 2011. Adaptability and vulnerability of high flying Neotropical aerial insectivorous bats to urbanization. *Diversity and Distributions*, 17(2), pp.262–274.

Abstract: Urbanization is a dominant demographic trend throughout the world that involves massive habitat alterations. Understanding how urbanization affects biota is a crucial prerequisite for development and application of effective species conservation programmes. Our study focuses on Neotropical high flying aerial insectivorous bats, an ecologically important, but so far seriously understudied group of vertebrates. Location Panama. Methods Using acoustic monitoring, we assessed and compared species occurrence, composition and activity of aerial insectivorous bats at three site categories located on the isthmus in Panama: forest, urban areas and a forest– town interface. Results In 2 years of field work, we recorded 44,744 bat passes over the microphone and identified a total of 25 aerial insectivorous bat species. Species richness was highest in the forest, decreased towards the forest–town interface and was lowest at the urban sites, while dominance (Berger-Parker-Index) increased from the forest to the urban sites. Overall, general bat activity (passes min)1) was highest at the forest–town interface and lowest at the urban sites. Multivariate analysis suggests compositional differences in species occurrence and activity among site categories with mainly molossid species occurring in urban areas. Main conclusions Our results clearly demonstrate species-specific differences between high flying aerial insectivorous bats concerning their adaptability and vulnerability to urban areas. Our results suggest that a suite of morphological traits including species mobility determine persistence of aerial insectivorous species in cities. Our results underline the necessity for detailed assessments of species-specific habitat requirements and dynamics of species occurrence

and activity over time to develop meaningful conservation tools targeted at aerial insectivorous bats.

Jung, K., Kalko, E.K. V. & von Helversen, O., 2007. Echolocation calls in Central American emballonurid bats: signal design and call frequency alternation. *Journal of Zoology*, 272(2), pp.125–137.

Abstract: In southern Central America, 10 species of emballonurid bats occur, which are all aerial insectivores: some hunt flying insects preferably away from vegetation in open space, others hunt in edge space near vegetation and one species forages mainly over water. We present a search call design of each species and link signal structure to foraging habitat. All emballonurid bats use a similar type of echolocation call that consists of a central, narrowband component and one or two short, frequency-modulated sweeps. All calls are multi-harmonic, generally with most energy concentrated in the second harmonic. The design of search calls is closely related to habitat type, in particular to distance of clutter. Emballonurid bats foraging in edge space near vegetation and over water used higher frequencies, shorter call durations and shorter pulse intervals compared with species mostly hunting in open, uncluttered habitats. Peak frequency correlated negatively with body size. Regular frequency alternation between subsequent calls was typical in the search sequences of four out of 10 species. We discuss several hypotheses regarding the possible role of this frequency alternation, including species identification and partitioning of acoustic channels. Furthermore, we propose a model of how frequency alternation could increase the maximum detection distance of obstacles by marking search calls with different frequencies.

Jung, K., Molinari, J. & Kalko, E.K. V, 2014. Driving factors for the evolution of species-specific echolocation call design in new world free-tailed bats (Molossidae). *PloS One*, 9(1), p.e85279.

Abstract: Phylogeny, ecology, and sensorial constraints are thought to be the most important factors influencing echolocation call design in bats. The Molossidae is a diverse bat family with a majority of species restricted to tropical and subtropical regions. Most molossids are specialized to forage for insects in open space, and thus share similar navigational challenges. We use an unprecedented dataset on the echolocation calls of 8 genera and 18 species of New World molossids to explore how habitat, phylogenetic relatedness, body mass, and prey perception contribute to echolocation call design. Our results confirm that, with the exception of the genus *Molossops*, echolocation calls of these bats show a typical design for open space foraging. Two lines of evidence point to echolocation call structure of molossids reflecting phylogenetic relatedness. First, such structure is significantly more similar within than among genera. Second, except for allometric scaling, such structure is nearly the same in congeneric species. Despite contrasting body masses, 12 of 18 species call within a relatively narrow frequency range of 20 to 35 kHz, a finding that we explain by using a modeling approach whose results suggest this frequency range to be an adaptation optimizing prey perception in open space. To conclude, we argue that the high variability in echolocation call design of molossids is an advanced evolutionary trait allowing the flexible adjustment of echolocation systems to various sensorial challenges, while conserving sender identity for social communication. Unraveling evolutionary drivers for echolocation call design in bats has so far been hampered by the lack of adequate model organisms sharing a phylogenetic origin and facing similar sensorial challenges. We thus believe that knowledge of the echolocation call diversity of New World

molossid bats may prove to be landmark to understand the evolution and functionality of species-specific signal design in bats.

Kalko, E., 1995. Insect pursuit, prey capture and echolocation in pipestirelle bats (Microchiroptera). *Animal Behaviour*, 50, pp.861–880.

Abstract: The foraging and echolocation behaviour of three European pipistrelles (*Pipistrellus pipistrellus*, *P. nathusii* and *P. kuhlii*) was studied under natural conditions. The pipistrelles were photographed with two 35 mm cameras under stroboscopic illumination, and their echolocation signals were recorded simultaneously. This permits a three-dimensional reconstruction of the flight paths of bat and prey, and allows the details of echolocation behaviour to be studied in the context of natural foraging behaviour. The general relationships between foraging and echolocation behaviour were consistent among the three species. Foraging behaviour consisted of four stages: search flight (before detection of prey), approach flight (pursuit after detection of prey), capture and retrieval of prey. These stages correlated with phases in echolocation behaviour: search, approach, and terminal phase followed by a pause. Detection of prey occurred at distances of 1.14-2.20 m. The search cone extending from the bat's mouth was up to 150" wide. The pipistrelles caught prey in mid-air, either with the tail membrane alone or by funnelling it with a wing onto the tail membrane. Except for some intra- and interspecific differences in sound duration, pulse interval, bandwidth and terminal frequency in search phase, the structure and pattern of the echolocation signals were similar in the three pipistrelles. In the approach and terminal phases, pulse duration and pulse interval decreased with the approach to the target, while bandwidth and sweep rate increased. While pursuing insects, the pipistrelles precisely avoided an overlap between outgoing signal and the echo returning from the prey. Furthermore, the bats stopped emitting signals several centimetres before they reached the insect.

Kalko, E. & Schnitzler, H., 1989. Two-wave-front interference patterns in frequency-modulated echolocation signals of bats flying low over water. *The Journal of the Acoustical Society of America*, 85(2), pp.961–962.

No abstract

Kalko, E.K. V., Schnitzler, H., Kaipf, I. & Grinnell, A.D., 1998. Echolocation and foraging behavior of the lesser bulldog bat, *Noctilio albiventris* : preadaptations for piscivory? *Behavioral Ecology and Sociobiology*, 42(5), pp.305–319.

Abstract: We studied variability in foraging behavior of *Noctilio albiventris* (Chiroptera:Noctilionidae) n Costa Rica and Panama and related it to properties of its echolocation behavior. *N. albiventris* searches for prey in high (> 20 cm) or low (< 20 cm) search flight, mostly over water. It captures insects in mid-air (aerial captures) and from the water surface (pointed dip). We once observed an individual dragging its feet through the water (directed random rake). In search flight, *N. albiventris* emits groups of echolocation signals (duration 10-1 I ms) containing mixed signals with constant-frequency (CF) and frequency-modulated (FM) components, or pure CF signals. Sometimes, mostly over land, it produces long FM signals (duration 15-21 ms). When *N. albiventris* approaches prey in a pointed dip or in aerial captures, pulse duration and pulse interval are reduced, the CF component is eliminated, and a terminal phase with short FM signals (duration 2 ms) at high repetition rates (150-170 Hz) is emitted. Except for the last pulses in the terminal phase *N. albiventris* avoids overlap between

emitted signals and echoes returning from prey. During rakes, echolocation behavior is similar to that in high search flight. We compare *N. albiventris* with its larger congener, *N. leporinus*, and discuss behavioral and morphological specializations that can be interpreted as preadaptations favoring the evolution of piscivory as seen in *N. leporinus*. Prominent among these specializations are the CF components of the echolocation signals which allow detection and evaluation of fluttering prey amidst clutter-echoes high variability in foraging strategy and the associated echolocation behavior, as well as morphological specializations such as enlarged feet for capturing prey from the water surface.

Kamata, E., Inoue, S., Zheng, M., Kasimori, Y. & Kambara, T., 2004. A neural mechanism for detecting the distance of a selected target by modulating the FM sweep rate of biosonar in echolocation of bat. *Bio Systems*, 76(1-3), pp.55–64.

Abstract: Most species of bats making echolocation use frequency modulated (FM) ultrasonic pulses to measure the distance to targets. These bats detect with a high accuracy the arrival time differences between emitted pulses and their echoes generated by targets. In order to clarify the neural mechanism for echolocation, we present neural model of inferior colliculus (IC), medial geniculate body (MGB) and auditory cortex (AC) along which information of echo delay times is processed. The bats increase the downward frequency sweep rate of emitted FM pulse as they approach the target. The functional role of this modulation of sweep rate is not yet clear. In order to investigate the role, we calculated the response properties of our models of IC, MGB, and AC changing the target distance and the sweep rate. We found based on the simulations that the distance of a target in various ranges may be encoded the most clearly into the activity pattern of delay time map network in AC, when the sweep rate of FM pulse used is coincided with the observed value which the bats adopt for each range of target distance.

Kanwal, J. & Matsumura, S., 1994. Analysis of acoustic elements and syntax in communication sounds emitted by mustached bats. *The Journal of the Acoustical Society of America*, 96, pp.1229–1254.

Abstract: Mustached bats, *Pteronotus parnellii parnellii* spend most of their lives in the dark and use their auditory system for acoustic communication as well as echolocation. The sound spectrograms of their communication sounds or "calls" revealed that this species produces a rich variety of calls. These calls consist of one or more of the 33 different types of discrete sounds or "syllables" that are emitted singly and/or in combination. These syllables can be furthered classified as 19 simple syllables, 14 composites, and three subsyllables. Simple syllables consist of characteristic geometric patterns of CF (constant frequency), FM (frequency modulation), and NB (noise burst) sounds that are defined quantitatively using statistical criteria. Composites consist of simple syllables or sub syllables conjoined without any silent interval. Most syllable types exhibit a large intrinsic variation in their physical structure compared to the stereotypic echolocation pulses. Syllable domains are defined on the basis of multiple parameters, although these can be collapsed into three dimensions that capture 99% of the measured variation among different types of syllables. Temporal analysis of multisyllabic constructs reveals several syntactical rules for syllable transitions.

Kaseloo, P., 2005. Synthesis of noise effects on wildlife populations. *Road Ecology Center*, (September), pp.1–75.

Abstract: This report contains a summary of ongoing work on the effects of noise on wildlife populations to date. Because the numbers and/or diversity of species have been used as indicators of the effects of noise, a number of studies that have indicated one or both of these factors for species alongside roads are included, although noise is not specifically mentioned in some of these reports. There is a paucity of information on the response of invertebrates to noise, particularly the levels likely to be encountered along roads. Significant populations of some species are found along rights-of-way, although others such as aquatic forms may be adversely affected; whether by the road itself or by noise is unclear. Existing information (although incomplete) would suggest that fish are unlikely to be adversely affected by noise levels from road. Reptiles and amphibians show some barrier effect due to roads, but there is no clear evidence of a noise effect alone. Recent work has suggested that behavior in burrowing toads may be affected by noise and this will require further study. Birds have received the most study and, in some cases, are strongly adversely affected both in numbers and in breeding by the proximity to roads. In other cases the effect is the opposite and there are reports of many species using roadside habitat in some areas. Large mammals may be repelled by noise, although in most cases the effect appears to be slight to moderate. Small mammals do not appear to be adversely affected by road noise occurring in significant numbers in rights-of-way. There appears to be a physical barrier effect of roads. This report also includes recommendations for future work based on the state of knowledge on the subject. This report will be of most interest to those responsible for environmental impact assessments, road ecologists and those concerned with incorporating environmental concerns into highway planning.

Kastein, H.B., Winter, R., Kumar, A.K.V., Kandula, S. & Schmidt, S., 2013. Perception of individuality in bat vocal communication: discrimination between, or recognition of, interaction partners? *Animal Cognition*, 16(6), pp.945–59.

Abstract: Different cognitive processes underlying voice identity perception in humans may have precursors in mammals. A perception of vocal signatures may govern individualised interactions in bats, which comprise species living in complex social structures and are nocturnal, fast-moving mammals. This paper investigates to what extent bats recognise, and discriminate between, individual voices and discusses acoustic features relevant for accomplishing these tasks. In spontaneous presentation and habituation-dishabituation experiments, we investigated how *Megaderma lyra* perceives and evaluates stimuli consisting of contact call series with individual-specific signatures from either social partners or unknown individuals. Spontaneous presentations of contact call stimuli from social partners or unknown individuals elicited strong, but comparable reactions. In the habituation-dishabituation experiments, bats dishabituated significantly to any new stimulus. However, reactions were less pronounced to a novel stimulus from the bat used for habituation than to stimuli from other bats, irrespective of familiarity, which provides evidence for identity discrimination. A model separately assessing the dissimilarity of stimuli in syllable frequencies, syllable durations and inter-call intervals relative to learned memory templates accounted for the behaviour of the bats. With respect to identity recognition, the spontaneous presentation experiments were not conclusive. However, the habituation-dishabituation experiments suggested that the bats recognised voices of social partners as the reaction to a re-habituation stimulus differed after a dishabituation stimulus from a social partner and an unknown bat.

Kay, L., 1962. A plausible explanation of the bat's echolocation acuity. *Animal Behaviour*, 10, pp.34–41.

No abstract

Kazial, K.A., Kenny, T.L. & Burnett, S.C., 2008. Little brown bats (*Myotis lucifugus*) recognize individual identity of conspecifics using sonar calls. *Ethology*, 114, 469e478.

Abstract: Bats use sonar calls to locate prey and orient in their environment but they may also be used by conspecifics to obtain information about a caller. Statistical analysis of sonar calls provides evidence that variation carries social information about a caller, including individual identity. We hypothesized that little brown bats (*Myotis lucifugus*) would be able to recognize individuals given the potential fitness benefits of doing so. We performed playback trials using a habituation-discrimination design to determine whether little brown bats are able to recognize the individual identity of a caller based on variation in their sonar calls. Each subject bat was played the calls of bat A until they habituated (defined as a 50% decrease from the beginning call rate), then the calls of bat B or a new call sequence of bat A (a control, referred to as bat A') were played. Each subject received a unique pair of playback recordings (bat A and B) from adult female bats from the same colony (but a different colony from the subject) and the order of trials was randomized. The response measures were habituation time (s) and call rate (calls/s). Within a trial, subjects habituated to calls of bat A and transferred this habituation to the bat A' sequence. In addition, they increased their call rates when played calls of bat B. Comparing between trials, subjects increased their call rate to the calls of bat B to a greater relative extent than to the calls of bat A'. These results provide the first evidence that bats recognize individual identity of conspecifics (as opposed to discrimination of groups), which has implications for the social interactions of bats.

Kazial, K.A., & Masters, W.M., 2004. Female big brown bats, *Eptesicus fuscus*, recognize sex from a caller's echolocation signals. *Animal Behaviour*, 67(5), pp.855–863.

Abstract: The echolocation calls of bats function in prey capture and navigation but are not commonly regarded as communicative signals. However, because bats' echolocation calls show patterns of variability, they may transmit information about a bat, such as its age, individual identity or sex. For echolocation calls to function in this manner, variation in calls must be reliably linked to the characteristics of the bat, as has been shown in a number of studies. However, few studies have asked whether bats respond to this variation. We tested whether female big brown bats can identify the sex of an unfamiliar bat from playbacks of its echolocation calls. Playback consisted of a 30-s preplayback period, a 60-s playback period of either male or female echolocation calls, and a 30-s postplayback period. In the playback and postplayback periods the vocalization rates of female bats changed significantly relative to the preplayback period depending on the sex of the playback stimulus, indicating that they could determine sex from the echolocation calls. These findings support the possibility that echolocation calls play a role in communication in big brown bats.

Keeley, A.T.H., & Keeley, B.W., 2004. The Mating System of *Tadarida brasiliensis* (Chiroptera: Molossidae) in a Large Highway Bridge Colony. Journal of Mammalogy, 85(1), pp.113–119.

Abstract: We observed mating by Brazilian free-tailed bats (*Tadarida brasiliensis*) in central Texas between 21 March and 5 April 1998. We documented copulations in large and small day roosts and in temporary night roosts. Focal animal sampling at a highway bridge revealed an aggressive and a passive male copulation strategy that may function as adaptations to different roost conditions. During aggressive copulation, the male separates a female from a roost cluster and restricts her movements during mating while he emits characteristic calls. During passive copulation, the male moves very slowly onto a female that roosts in a dense cluster. Passive copulations occur without resistance from the female and without male vocalizations. Both males and females mate with multiple partners, suggesting that mating is promiscuous. The mating system in a large highway bridge colony is characterized as mating aggregations or swarming because mating occurs in large, temporally unstable multimale and multifemale mating groups, with no apparent male territories or defense of females.

Keeley, B. & Tuttle, M., 1999. Bats in American bridges. Bat conservation Inernational, Austin, TX, 78716. Resource Publication, pp.1–6.

Abstract: Bridges and culverts were evaluated as bat roosting habitat in 25 U.S. states at elevations from sea level to 10,000 feet. Field surveys were conducted at 2,421 highway structures. Scientific literature was reviewed, and local biologists and engineers were interviewed, leading to the discovery of approximately 4,250,000 bats of 24 species living in 211 highway structures. Only one percent of existing structures had ideal conditions for day roosting, but at little or no extra cost a much larger percentage could provide habitat for bats in the future. Most species chose concrete crevices that were sealed at the top, at least 6-12 inches deep, 0.5-1.25 inches wide, and 10 feet or more above ground, typically not located over busy roadways. Retrofitting existing bridges and culverts proved highly successful in attracting bats, especially where bats were already using them at night. Providing bat habitat in bridges or culverts, either during initial construction or through subsequent retrofitting, is an exceptionally feasible and popular means of mitigation that is highly cost-effective in demonstrating a pro-active commitment to the environment. Advice for incorporating bat roosts, both before and after construction, is provided. Environmental and economic benefits, impacts on structural integrity and public safety, and management of occupied structures are discussed.

Kerth, G., 2008. Causes and Consequences of Sociality in Bats. *BioScience*, 58(8), pp.737–746.

Abstract: Bats are among the most diverse and most gregarious of all mammals. This makes them highly interesting for research on the causes and consequences of sociality in animals. Detailed studies on bat sociality are rare, however, when compared with the information available for other social mammals, such as primates, carnivores, ungulates, and rodents. Modern field technologies and new molecular methods are now providing opportunities to study aspects of bat biology that were previously inaccessible. Consequently, bat social systems are emerging as far more complex than had been imagined. Variable dispersal patterns, complex olfactory and acoustic communication, flexible context-related interactions, striking cooperative behaviors, and cryptic colony structures in the form of fission-fusion systems have been documented. Bat research can contribute to the understanding of animal sociality, and specifically to important topics in behavioral ecology and evolutionary biology, such as dispersal, fission-fusion behavior, group decision making, and cooperation.

Kerth, G. & Melber, M., 2009. Species-specific barrier effects of a motorway on the habitat use of two threatened forest-living bat species. *Biological Conservation*, 142(2), pp.270–279.

Abstract: It is generally recognized that roads can adversely affect local animal populations but little is known how roads affect bats. In particular, no study compared the response of bats that differ in foraging ecology to motorways that cut through the breeding habitat. As bats are key species in conservation, such data are urgently needed for designing management plans. Using radio-telemetry, mist netting, and mark-recapture data we investigated the effects of a motorway with heavy traffic on the habitat use of two threatened forest-living bats. We compared barbastelle bats (*Barbastella barbastellus*), which forage in open space, to Bechstein's bats (*Myotis bechsteinii*), which glean prey from the vegetation. Five of six radiotracked barbastelle bats crossed the motorway during foraging and roost switching, flying through underpasses and directly over the motorway. In contrast, only three of 34 radiotracked Bechstein's bats crossed the motorway during foraging, all three using an underpass. Bechstein's bats, unlike barbastelle bats, never crossed the motorway during roost switching. Moreover, only in Bechstein's bats individuals foraging close to the motorway had smaller foraging areas than individuals foraging further away, whereas other forest edges had no such effect. Our data show that motorways can restrict habitat accessibility for bats but the effect seems to depend on the species' foraging ecology and wing morphology. We suggest that motorways have stronger barrier effects on bats that forage close to surfaces than on bats that forage in open space, and discuss the implications of our findings for bat conservation during road construction.

Kilgour, R.J., Faure, P.A. & Brigham, R.M., 2013. Evidence of social preferences in big brown bats (*Eptesicus fuscus*). *Canadian Journal of Zoology*, 91, pp.756–760.

Abstract: Among social species, iterative interactions may lead to social preferences among group-mates and often are associated with increased mating opportunities or improved indirect fitness benefits. Although preferential associations have been documented in multiple species, this phenomenon has never been empirically studied in bats—the second largest order of mammals, where many of the 1200+ species live in groups of tens to hundreds of individuals. Given the current understanding of the social behaviour exhibited in this species, we explored the possibility that adult female big brown bats (*Eptesicus fuscus* (Beauvois, 1796)) show preferential association between group-mates using a pairwise choice design with individuals from a captive colony. Focal individuals were placed in a Y-maze and were given free choice of two familiar conspecifics. We measured the time focal individuals spent in close proximity to each conspecific. Our results indicate that some bats exhibit preferential association between group-mates, as multiple individuals spent significantly more time in close proximity to one conspecific versus another, despite randomizing the position of stimulus bats between trials. Given the frequent and long-term associations between group members of this species, social preferences could play a significant role in the outcomes of their long-term fitness.

Kimball, J., 2011. Figure of inner ear with Organ of Corti. Online: http://users.rcn.com/jkimball.ma.ultranet/BiologyPages/H/Hearing.

No abstract

Kitzes, J. & Merenlender, A., 2014. Large roads reduce bat activity across multiple species. *PloS One*, 9(5), p.e96341.

Abstract: Although the negative impacts of roads on many terrestrial vertebrate and bird populations are well documented, there have been few studies of the road ecology of bats. To examine the effects of large roads on bat populations, we used acoustic recorders to survey bat activity along ten 300 m transects bordering three large highways in northern California, applying a newly developed statistical classifier to identify recorded calls to the species level. Nightly counts of bat passes were analyzed with generalized linear mixed models to determine the relationship between bat activity and distance from a road. Total bat activity recorded at points adjacent to roads was found to be approximately one-half the level observed at 300 m. Statistically significant road effects were also found for the Brazilian free-tailed bat (*Tadarida brasiliensis*), big brown bat (*Eptesicus fuscus*), hoary bat (*Lasiurus cinereus*), and silver-haired bat (*Lasionycteris noctivagans*). The road effect was found to be temperature dependent, with hot days both increasing total activity at night and reducing the difference between activity levels near and far from roads. These results suggest that the environmental impacts of road construction may include degradation of bat habitat and that mitigation activities for this habitat loss may be necessary to protect bat populations

Knight, C. R. & Swaddle, J., 2011. How and why environmental noise impacts animals: An integrative, mechanistic review. *Ecology Letters*, 14, 1052–1061.

Abstract: The scope and magnitude of anthropogenic noise pollution are often much greater than those of natural noise and are predicted to have an array of deleterious effects on wildlife. Recent work on this topic has focused mainly on behavioural responses of animals exposed to noise. Here, by outlining the effects of acoustic stimuli on animal physiology, development, neural function and genetic effects, we advocate the use of a more mechanistic approach in anthropogenic environments. Specifically, we summarise evidence and hypotheses from research on laboratory, domestic and free-living animals exposed to biotic and abiotic stimuli, studied both observationally and experimentally. We hope that this molecular- and cellular-focused literature, which examines the effects of noise on the neuroendocrine system, reproduction and development, metabolism, cardiovascular health, cognition and sleep, audition, the immune system, and DNA integrity and gene expression, will help researchers better understand results of previous work, as well as identify new avenues of future research in anthropogenic environments. Furthermore, given the interconnectedness of these physiological, cellular and genetic processes, and their effects on behaviour and fitness, we suggest that much can be learned from a more integrative framework of how and why animals are affected by environmental noise.

Knörnschild, M., Feifel, M. & Kalko, E.K.V., 2013. Mother–offspring recognition in the bat Carollia perspicillata. *Animal Behaviour*, 86(5), pp.941–948.

Abstract: Parental care is crucial for offspring survival in many taxa but its burden and costs are often not equally distributed between the sexes. In bats, the majority of parental care is provided by females, making examples of paternal support towards pups exceedingly rare. One exception to this general pattern seemed to be the polygynous Seba's short-tailed fruit bat *Carollia perspicillata*; two earlier studies suggested that paternal care occurs, i.e. that harem males prompt females to retrieve vocalizing pups. To corroborate this suggestion, we investigated the occurrence of maternal and paternal care in reaction to pup isolation calls in *C. perspicillata*. Acoustic measurements of 905 isolation calls from 17 pups revealed sufficient inter-individual

variation to encode an individual vocal signature. Correspondingly, mothers were capable of using this individual signature to discriminate between their own pups and age-matched pups from other females belonging to their colony. Maternal experience was positively correlated with the strength of response behaviour during playbacks. Thus, our results indicate that pup isolation calls were used to elicit maternal care and that mothers recognize their pups based on an individual signature in isolation calls. However, in contrast to the previous studies mentioned above, we found no evidence that harem males reacted to pup isolation calls by prompting the respective mothers to retrieve their vocalizing pups. Instead, our results demonstrate that harem males engaged in courtship activities that were unaffected by pup isolation calls.

Knörnschild, M., Glöckner, V. & Helversen, O. Von, 2010. The Vocal Repertoire of Two Sympatric Species of Nectar-Feeding Bats (*Glossophaga soricina* and *G. commissarisi*). *Acta Chiropterologica*, 12(1), pp.205–215.

Abstract: We recorded social vocalizations from two sympatric species of glossophagine bats, *Glossophaga soricina* and *G. commissarisi*, using habituated captive groups that were housed in separate flight cages. Whenever possible, the species-specific vocalization types were described in the light of the social context in which they were produced. Several vocalization types within each species' repertoire had remarkable similarities to vocalization types in the other species' repertoire. Out of these, four vocalization types with interspecific acoustic similarities (approach pulses, distress calls, aggressive trills, and alert calls) were used in similar behavioral contexts in both species. Approach pulses were produced whenever a bat was flying towards an already occupied roost. Distress calls were uttered whenever a bat was attacked by conspecifics or restrained by the observer, whereas aggressive trills were produced during aggressive encounters prior to physical contact. Alert calls were uttered when bats were disturbed or when several individuals were circling the same location. The interspecific similarity of both the social context and the acoustic structure of vocalization types suggest that the potential for interspecific communication is high in *G. soricina* and *G. commissarisi*.

Knörnschild, M. & von Helversen, O., 2008. Nonmutual vocal mother–pup recognition in the greater sac-winged bat. *Animal Behaviour*, 76(3), pp.1001–1009.

Abstract: We investigated the acoustical component of the recognition process leading to successful mother- pup reunions in the greater sac-winged bat, *Saccopteryx bilineata*, using both a statistical approach and playback experiments. Statistical evidence for individual distinctiveness was found in the isolation calls uttered by pups and, to a weaker degree, in the echolocation pulse trains emitted by mothers. In contrast to other bat species, isolation calls of S. bilineata pups were complex and multisyllabic, with most of the vocal signature information encoded in the composite syllables at the end of calls. Playback experiments with free-living bats revealed that mothers were able to discriminate between their own pup and an alien young on the basis of isolation calls alone, which confirms the results of the acoustical analysis on vocal signatures in isolation calls. Pups, on the other hand, indiscriminately vocalized in response to echolocation pulse trains from their own and alien mothers, rendering the mother-pup recognition process unidirectional. The one-sidedness of the vocal recognition process in S. bilineata as well as in other bat species might be explained by a lack of selection pressures that shape mutual vocal parent-offspring recognition in other species of mammals and birds. To our knowledge, this study is the first in which playbacks were used to elicit antiphonal calling behaviour between bat mothers and pups experimentally. We argue that vocal responses to

playback stimuli are a more feasible and reliable response measure for conducting mother-pup recognition playbacks in bats than the phonotaxis behaviour used in the past.

Knörnschild, M., Jung, K., Nagy, M., Metz, M. & Kalko, E., 2012. Bat echolocation calls facilitate social communication. *Proceedings. Biological sciences / The Royal Society*, 279, pp.4827–35.

Abstract: Bat echolocation is primarily used for orientation and foraging but also holds great potential for social communication. The communicative function of echolocation calls is still largely unstudied, especially in the wild. Eavesdropping on vocal signatures encoding social information in echolocation calls has not, to our knowledge, been studied in free-living bats so far. We analysed echolocation calls of the polygynous bat *Saccopteryx bilineata* and found pronounced vocal signatures encoding sex and individual identity. We showed experimentally that free-living males discriminate approaching male and female conspecifics solely based on their echolocation calls. Males always produced aggressive vocalizations when hearing male echolocation calls and courtship vocalizations when hearing female echolocation calls; hence, they responded with complex social vocalizations in the appropriate social context. Our study demonstrates that social information encoded in bat echolocation calls plays a crucial and hitherto underestimated role for eavesdropping conspecifics and thus facilitates social communication in a highly mobile nocturnal mammal.

Koay, G., Bitter, K.S., Heffner, H.E. & Heffner, R.S., 2002. Hearing in American leaf-nosed bats. I: *Phyllostomus hastatus*. *Hearing Research*, 171(1-2), pp.96–102.

Abstract: We determined the audiogram of *Phyllostomus hastatus* (the greater spear-nosed bat), a large, omnivorous American leaf-nosed bat native to Central and South America. A conditioned suppression/avoidance procedure with a fruit juice reward was used for testing. At an intensity of 60 dB sound pressure level (SPL re 20 WN/m2), the hearing range of *P. hastatus* extends from 1.8 to 105 kHz, with a best sensitivity of 1 dB SPL at 20 kHz. Both its high-frequency and low-frequency hearing are not unusual for a small mammal. Despite its use of low-intensity echolocation calls there was no evidence for unusual sensitivity to either the frequencies used for echolocation or to the main frequencies of its communication calls, suggesting no selective "tuning" of the audiogram. Its behavioral pure-tone thresholds are lower than the multi-unit thresholds in the inferior colliculus.

Koay, G., Heffner, H.E. & Heffner, R.S., 1997. Audiogram of the big brown bat (*Eptesicus fuscus*). *Hearing Research*, 105(1-2), pp.202–210.

Abstract: The audio grams of three big brown bats (*Eptesicus fuscus*) were determined using a conditioned avoidance procedure. The average audiogram ranged from 0.850 kHz at 106 dB to 120 kHz at 83 dB SPL, with a best threshold of 7 dB at 20 kHz and a distinct decrease in sensitivity at 45 kHz. The results confirm those of a previous study by Dalland (1965a) that the big brown bat has good high-frequency hearing coupled with poor low-frequency hearing. Comparative analysis suggests that the bat's good high-frequency hearing initially evolved for passive sound localization and that it was later co-opted for use in echolocation. In addition, the restricted low-frequency hearing of the big brown bat is typical of mammals with good high-frequency hearing.

Koay, G., Kearns, D., Heffner, H.E. & Heffner, R.S., 1998. Passive sound-localization ability of the big brown bat (*Eptesicus fuscus*). *Hearing Research*, 119, pp.37–48.

Abstract: The passive sound-localization ability (i.e. minimum audible angle) of the big brown bat, *Eptesicus fuscus*, was determined using a conditioned avoidance procedure in which the animals were trained to discriminate left sounds from right sounds. The mean threshold of three bats for a 100-ms broadband noise burst was 143, a value that is about average for mammals. A similar threshold of 153 was obtained for one animal when it was retested with one of its own recorded echolocation calls as the stimulus. The two bats tested on pure-tone localization were able to localize high-frequency, but not low-frequency tones, even when a low-frequency tone was amplitude modulated, a result indicating that these bats are not able to use binaural time-difference cues for localization. Finally, given the width of the bat's field of best vision, as determined by a count of its ganglion-cell density, its sound-localization acuity is consistent with the hypothesis that the role of passive sound localization is to direct the eyes to the source of a sound.

Kobayasi, K. & Hiryu, S., 2012. Vocalization of echolocation-like pulses for interindividual interaction in horseshoe bats (*Rhinolophus ferrumequinum*). *The Journal of the Acoustical Society of America*, 132, pp.417–422.

Abstract: Although much is known about the echolocation of horseshoe bats (*Rhinolophus* spp.), little is known about the characteristics and function of their communication calls. This study focused on a stereotyped behavior of a bat approaching a companion animal in the colony, and examined their interaction and vocalization during this behavior. The bats emit echolocation-like vocalizations when approaching each other and these vocalizations contain a "buildup" pulse sequence, in which the frequency of the pulse increases gradually to normal echolocation pulse frequencies. The results suggest that the echolocation-like pulses serve an important role in communication within the colony.

Kobler, J.B., Wilson, B.S., Henson, Jr., O.W. & Bishop, A.L., 1985. Echo intensity compensation by echolocating bats. *Hearing Research*, 20(2), pp.99–108.

Abstract: When mounted on a swinging pendulum, mustache bats. Pteronotus p. parnellii, emit ultrasonic pulses as they move toward and away from fixed targets. During forward swings they systematically decrease the intensity of their emitted pulses and during backward swings they increase the intensity. In this way, echo strength is continuously adjusted and apparently optimized for signal analysis. We have called this behavior echo intensity compensation. Pteronotus simultaneously Doppler and echo intensity compensate during forward swings of the pendulum but during backward swings they only echo intensity compensate. *Pteronotus* can regulate the intensity of both the constant frequency and frequency modulated components of their pulses; this regulation is independent of vestibular cues, pulse repetition rates, pulse durations and pulse-echo intervals.

Konishi, M., and Knudsen, E. I. 1979. The oilbird: hearing and echolocation. *Science*, 204(4391), pp.425-427.

Abstract: Oilbirds can navigate in total darkness by echolocation. The sound energy in their sonar cries is unevenly distributed over the range from about 1 to 15 kilohertz, with a dominant

frequency range of 1.5 to 2.5 kilohertz. This corresponds to the most sensitive range of their hearing as determined by neurophysiological methods. Behavioral tests in their home cave indicate that the smalles t object avoided by them is a disk 20 centimeters in diameter.

Köppl, C., 2011. Birds--same thing, but different? Convergent evolution in the avian and mammalian auditory systems provides informative comparative models. *Hearing Research*, 273(1-2), pp.65–71.

Abstract: Birds have been and continue to be enlightening, comparative models in auditory research. This review highlights their particular appeal as a vertebrate group that evolved independently a similar division of labour to that seen in the mammalian cochlea, between classic sensory hair cells and hair cells specialising in amplification. Through studying both the similarities and differences between the avian and mammalian inner ear, profound insights into the principles of operation of such a divided system may be gained. For example, the prevailing model of the relationship between basilar-membrane displacement and afferent rate-level functions in mammals is reinforced by characteristic differences observed in birds, which correlate with known differences in basilar-papilla mechanics. Furthermore, birds arguably represent the most extreme case of hair cells using bundle motility for mechanical amplification at high frequencies, up to about 10 kHz. They should thus be informative for elucidating the operation and possibly the limitations of this ancestral amplifying mechanism at high frequencies.

Kössl, M., 1994. Evidence for a mechanical filter in the cochlea of the "constant frequency" bats, *Rhinolophus rouxi* and *Pteronotus parnellii*. *Hearing Research*, 72, pp.73–80.

Abstract: To investigate the function of basilar membrane (BM) thickenings in the cochlea of bats which use constant frequency (CF) echolocation calls, acoustic distortion products were measured while placing the primary stimuli f_1 and f_2 at frequencies which are represented in the thickened BM regions. In *Rhinolophus*, for primary stimuli between about 80-100 kHz, pronounced maxima of the level of distortion products ($2f_1$-f_2, $3f_1$-$2f_2$, 4f1-$3f_2$) can be measured if the frequency separation between the two primary tones is chosen so that the resulting distortion frequency matches the dominant CF frequency (resting frequency, RF). The distortion maxima extend from the individual RF down to frequencies which are 2-4 kHz lower. The data indicate that the thickened BM region in the basal half turn of the cochlea strongly oscillates at the bats' RF and slightly below. The hearing threshold, however, is at a maximum at the RF (see Kössl 1993). Therefore, the RF oscillations are thought to be involved in absorbing the respective frequency such that the more apically located frequency place of the RF is insensitive and a mechanical notch filter is established. In *Pteronotus*, there are maxima of the level of $2f_1$-f_2 at distortion frequencies around the RF of about 61.5 kHz up to the frequency of a strong stimulus-frequency otoacoustic emission (SFOAE) which is a few hundred Hz higher. Pronounced distortions in the RF range can only be elicited when the stimulus frequencies are between about 62 to 72 kHz. Similar to the situation in *Rhinolophus*, this frequency band is represented on a stretch of thickened BM.

Kössl, M. & Vater, M., 1985. Evoked acoustic emissions and cochlear microphonics in the mustache bat, *Pteronotus parnellii*. *Hearing Research*, 19, pp.157–170.

Abstract: In the echolocating bat. *Pteronotus parnellii*. otoacoustic responses at a frequency of 62 kHz are measureable in the external ear canal during continuous and after transient acoustic stimulation. These responses are interpreted to represent emissions from the cochlea. They can reach an amplitude as large as 70 dB SPL and occur in the frequency range most important for echolocation, namely on the average about 700 Hz above the constant frequency component of the orientation call. A sharp maximum of the amplitude of cochlear microphonic potentials at about 62 kHz could be correlated with the emission frequency. In one bat an evoked otoacoustic response changed to a spontaneous otoacoustic emission. The frequency and amplitude of the evoked otoacoustic responses reversibly decreased after exposure for 1 min to continuous sound of more than 85 dB SPL with frequencies of about 2.5-7.5 kHz above the emission frequency. Similar effects occurred during anaesthesia or cooling. A possible relation between the existence of otoacoustic emissions and morphological specializations of the cochlea is disussed.

Kuc, R., 2009. Model predicts bat pinna ridges focus high frequencies to form narrow sensitivity beams. *The Journal of the Acoustical Society of America*, 125, 3454–3459.

Abstract: The pinnae of bats contain ridges whose function was previously thought to be structural. This paper suggests that ridges form a reflecting Fresnel lens that focuses high-frequency acoustic signals into the ear canal to form a narrow elevation sensitivity beam. *E. fuscus* ridges are modeled as a series of four paraboloidal strips and the tragus is considered to act as a secondary reflecting element analogous to a Cassegrain system. A diffraction grading having the equivalent spacing suggests frequencies above 150 kHz. Using an example 170 kHz, a random search for ridge dimensions that minimize side-lobes in the frequency magnitude response yields the tapered ridge structure observed in *E. fuscus* and produces an 18° (full width half energy) beam width. We speculate that the possible high-frequency sources are ecologically (prey) generated and/or the third harmonic of the call. The attenuation at such high frequencies requires that the source be close by. Passive prey localization in the postbuzz stage, when echoes overlap call transmissions and the prey is within 8cm, could improve prey capture efficiency. An experiment using 40 kHz ultrasound with human observers verifies that frequencies beyond the audiometric range, when sufficiently intense, can still be perceived.

Kuc, R., 2010. Morphology suggests nose-leaf and pinnae cooperate to enhance bat echolocation. *The Journal of the Acoustical Society of America*, 128, 3190–3199.

Abstract: A protruding noseleaf and concave pinna structures suggest that some bats may use these to enhance their echolocation capabilities. This paper considers two possible mechanisms that each exploit the combination of direct and delayed acoustic paths to achieve more complex emission or sensitivity echolocation patterns. The first is an emission mechanism, in which the protruding noseleaf vibrates to emit sound in both the forward and backward directions, and pinna structures reflect the backward emission to enhance the forward beam. The second is a reception mechanism, which has a direct echo path to the ear canal and a delayed path involving pinna structures reflecting onto the noseleaf and then into the ear canal. A model using Davis' Round-eared bat illustrates that such direct and delayed acoustic paths provide target elevation cues. The model demonstrates the delayed pinna component can increase the on-axis emission strength, narrow the beam width, and sculpt frequency-dependent beam patterns useful for echolocation.

Kujawa, S.G. & Liberman, M.C., 2009. Adding insult to injury: cochlear nerve degeneration after "temporary" noise-induced hearing loss. *J. Neuroscience* 29, 14077-14085.

Abstract: Overexposure to intense sound can cause temporary or permanent hearing loss. Postexposure recovery of threshold sensitivity has been assumed to indicate reversal of damage to delicate mechano-sensory and neural structures of the inner ear and no persistent or delayed consequences for auditory function. Here, we show, using cochlear functional assays and confocal imaging of the inner ear in mouse, that acoustic overexposures causing moderate, but completely reversible, threshold elevation leave cochlear sensory cells intact, but cause acute loss of afferent nerve terminals and delayed degeneration of the cochlear nerve. Results suggest that noise-induced damage to the ear has progressive consequences that are considerably more widespread than are revealed by conventional threshold testing. This primary neurodegeneration should add to difficulties hearing in noisy environments, and could contribute to tinnitus, hyperacusis, and other perceptual anomalies commonly associated with inner ear damage.

Kunz, T. H., and Martin, R. A. 1982. *Plecotus townsendii*. *Mammalian Species*, 175, pp.1-6.

No abstract

Kurta, A., Bell, G.P., Nagy, K.A. & Kunz, T.H., 1989. Energetics of pregnancy and lactation in free ranging little brown bats (*Myotis lucifugus*). *Physiological Zoology*, 62(3), pp.804–818.

Abstract: We combined field measurements of metabolic rate, made with doubly labeled water, with data from ourprevious studies to examine reproductive energetics in 24 female little brown bats (*Myotis lucifugus*). Including estimates of tissue or milk production, *M. lucifugus* required an average of3 3. 7 kJd^{-1} of assimilated energy in pregnancy compared to 41.3 kJ d^{-1} during lactation. Predicted insect consumption was 5.5 g d^{-1} for a 9-g pregnant female and 6.7g d^{-l} for a 7.9-g lactating female. About 2% of total energy assimilated during pregnancy was stored as new tissue, whereas lactating females exported 32% as milk. Estimated assimilated energy demand on the first day oflactation was 33.8 kJ d^{-1} and increased to 60.3 kJ d^{-1} at peak lactation. By subtracting laboratory measurements of roosting costs from observed metabolized energy expenditure, we calculated that foraging flight by 9-gpregnant *M. lucifugus* required 4.46 kJ h^{-1}; this was 13% less than allometric predictions. Foraging fight accounted for the largest proportion of the daily metabolized energy budget during pregnancy (61%) and lactation (66%). The large amount of energy devoted to foraging by this aerial-feeding bat may partially explain the low proportion of energy it allocates to tissue production and milk export.

Kurze, U.J., 1971. Noise from complex road traffic. *Journal of Sound and Vibration*, 19(2), pp.167–177.

Abstract: The noise from freely flowing tragic is calculated considering traffic mixes, numerous roads, barriers, and other influences that can be approximated by the superposition of contributions from statistically independent elements. The basic statistical parameters derived are the cumulants of the intensity distribution. Subsequently, approximations are given for the standard deviation of the sound pressure level and probability distributions of the sound pressure level are shown for typical traffic mixes.

Kurze, U.J., 1974. Frequency curves of road traffic noise. *Journal of Sound and Vibration*, 33(2), pp.171–185.

Abstract: Based on statistical properties of the noise from freely flowing traffic on a long road, an approximate formula is derived for the distribution of sound pressure levels. Distribution functions calculated from this formula check well with examples of skew distributions evaluated from field measurements.

Kusch, J. & Schmitz, A., 2013. Environmental factors affecting the differential use of foraging habitat by three sympatric species of *Pipistrellus*. *Acta Chiropterologica*, 15(1), pp.57–67.

Abstract: We identified several ecological parameters that may promote the foraging habitat differentiation by sympatric bat species. The exploitation of discrete habitats was shown to facilitate the coexistence of morphologically similar species. Bats represent a model species group, where many morphologically similar species exploit similar resources, e.g. insects as prey organisms. We studied three closely related species of bats in a Central European region of sympatric occurrence – the common pipistrelle (*Pipistrellus pipistrellus*), Nathusius' pipistrelle (*P. nathusii*), and the soprano pipistrelle (*P. pygmaeus*). We employed point locality data and niche-based species distribution modelling (maximum entropy modelling, "MaxEnt") to model the habitat use by these species. A restricted distribution of *P. pygmaeus* and *P. nathusii* compared to *P. pipistrellus* was observed that may indicate a stronger habitat specialization of these two species compared to *P. pipistrellus*. Land cover, as well as several climatic variables influenced the habitat use of all three species (e.g., the precipitation in spring, and the temperature minimum in late summer). Despite an overlap in foraging habitat parameters, differences among species concerning their preferred habitat were noted. Responses to isothermality, mean diurnal range of temperature, temperature seasonality, and land cover differed among species. The data identify microclimatic factors, besides vegetation and other land cover types, as important effectors for habitat partitioning in these three *Pipistrellus* species.

Lacki, M.J., Hayes, J.P., and Kurta A., 2007. Bats in Forests: Conservation and Management. The John Hopkins University Press, Baltimore. 329 pp.

No abstract

Laiolo, P., 2010. The emerging significance of bioacoustics in animal species conservation. *Biological Conservation*, 143(7), pp.1635–1645.

Abstract: This review reports on the effects of human activities on animal acoustic signals published in the literature from 1970 to 2009. Almost 5% of the studies on variation in animal communication tested or hypothesised on human impacts, and showed that habitat fragmentation, direct human disturbance, introduced diseases, urbanization, hunting, chemical and noise pollution may challenge animal acoustic behaviour. Although acoustic adaptations to anthropogenic habitats have been documented, human impacts have most often generated neutral variation or potential maladaptive responses. Negative impacts have been postulated in the sexual signals of fishes, amphibians, birds, and mammals; these are concerning as any maladaptive alteration of sexual behaviour may have direct bearings on breeding success and ultimately population growth rate. Acoustic communication also facilitates other vital behaviours

influenced by human-driven perturbations. Bat and cetacean echolocation, for instance, is disrupted by noise pollution, whereas bird and mammal alarming is also affected by introduced diseases and hunting. Mammal social signals are sensitive to noise pollution and hunting, and birds selecting habitats by means of acoustic cues are especially vulnerable to habitat loss. Anthropogenic intervention in these cases may have a negative impact on individual survival, recruitment and group cohesion, limiting rescue-effects and triggering Allee effects. Published evidence shows that acoustic variation may be used as an early-warning indicator of perturbations even when not directly affecting individual fitness. Acoustic signalling can be studied in a broad range of ecosystems, can be recorded, analyzed, synthesised and played back with relative ease and limited economic budget, and is sensitive to many types of impacts, thus can have great conservation significance.

Lancaster, W., Henson Jr., O.W., Keating, W.A., 1995. Respiratory muscle activity in relation to vocalization in flying bats. *Journal of Experimental Biology*, 198, pp.175–191.

Abstract: The structure of the thoracic and abdominal walls of *Pteronotus parnellii* (Microchiroptera: Mormoopidae) was described with respect to their function in respiration and vocalization. We monitored electromyographic activity of respiratory and flight muscles in relation to echolocative vocalization. In flight, signals were telemetered with a small FM transmitter modified to summate the low-frequency myopotentials with biosonar signals from a ceramic-crystal microphone. Recordings were also made from the same bats confined to a small cage. Vocalizations were used as the parameter by which all muscle activities were correlated. A discrete burst of activity in the lateral abdominal wall muscles accompanied each vocalization. Diaphragmatic myopotentials occurred between groups of calls and did not coincide with activity of the abdominal wall or with vocalizations. Flight muscles were not active in resting bats. During flight, vocalizations and the abdominal muscle activity that accompanied them coincided with myopotentials of the pectoralis and serratus ventralis muscles. We propose that contractions of the lateral abdominal wall provide the primary power for the production of intense biosonar vocalization in flying and in stationary bats. In flight, synchronization of vocalization with activity of the pectoralis and serratus ventralis jointly contribute to the pressurization of the thoraco-abdominal cavity. This utilization of pressure that is normally generated in flight facilitates respiration and allows for the production of intense vocalizations with little additional energetic expenditure.

Larsson, C., Hallberg, B. & Israelsson, S., 1988. A method to estimate meteorological effects on sound propagation near the ground. *Applied Acoustics*, 25(1), pp.17–31.

Abstract: A method for calculation of the conditions for sound propagation in the atmospheric surface layer is presented. The wind and temperature gradients cause refraction of the sound rays, and hence influence the sound level. The curvature of a nearly horizontal sound ray can be calculated by using measurements of wind and temperature. Meteorological measurements of wind and temperature carried out over a long period of time can be used for computing the distribution of the curvature for a given localisation of source and receiver. An example of the use of this method is presented. Meteorological measurements, taken over a period of one year at a site in southern Sweden, were used to calculate the cumulative distribution of the curvature for different orientations of the source and the receiver. Modifications on the material were made in order to simulate weather conditions for other sites.

Larsson, C. & Israelsson, S., 1991. Effects of meteorological conditions and source height on sound propagation near the ground. *Applied Acoustics*, 33(2), pp.109–121.

Abstract: Simultaneous measurements of sound propagation from a loudspeaker and meteorological variables were carried out for various ground covers and meteorological conditions. The wind and temperature gradients cause refraction of the sound rays, and hence influence the sound level. The curvature of a nearly horizontal sound ray can be calculated by using measurements of wind and temperature. The curvature is found to be closely connected to the sound level, when distinctions between octave band, ground, distance, source and receiver heights are made. A new variable, the sound propagation parameter, W, including refraction, distance, source and receiver heights, is introduced. The parameter is used to examine if a specific set-up of source-receiver can be sensitive to meteorological effects. The sound level for different octave bands and ground cover is given for negative and positive values of W, outside an interval close to W= O, where large scattering of the sound level is found.

Lausen, C.L. & Barclay, R.M.R., 2006. Benefits of living in a building:big brown bats (*Eptesicus fuscus*) in rocks versus buildings. *Journal of Mammalogy*, 87(2), pp.362–370.

Abstract: Individuals of some species of bats roost in human-made structures despite the apparent availability of natural roosts. We compared patterns of thermoregulation in relation to microclimate and compared reproductive timing for maternity colonies of big brown bats (*Eptesicus fuscus*) roosting in natural and building roosts in the prairies of southeastern Alberta. During pregnancy, bats roosting in buildings used torpor less frequently than did rockroosting bats, but achieved lower body temperatures when torpid. Less-frequent use of torpor leaves more active days for fetal development, and bats in building roosts gave birth earlier than those in rock roosts. We observed predators and predation in rock roosts, but not in building roosts, and suggest that bats roosting in rocks use shallower torpor to remain vigilant. Patterns of torpor use suggest that bats in buildings save more energy than rock-roosting individuals by roosting in the warmer microenvironments of buildings and by achieving lower body temperatures when ambient conditions are cold and foraging is not productive. The warmer building roosts are also conducive to juvenile growth, and young building-roosting bats fledged 1–2 weeks before rock bats. We propose that advantages for bats roosting in buildings (lower predation risk, earlier births, faster juvenile growth rates, and increased energy savings) lead to greater long-term reproductive success for building-roosting bats and make buildings preferred roosts.

Lawrence, B. & Simmons, J., 1982. Echolocation in bats: the external ear and perception of the vertical positions of targets. *Science*, 218(4571), pp.481–483.

Abstract: Echolocating bats (*Eptesicus fuscus*) can perceive changes of as little as 3° of arc in the vertical angles separating pairs of horizontal rods. This acuity depends upon modification of sounds entering the external ear canal by the structures of the external ear. Deflection of the tragus degrades the acuity of vertical-angle perception from 3° to about 12° to 14°. The pinna-tragus structure produces a strong secondary echo of sounds entering the external ear canal, and the delay of this echo after the time when the sound directly enters the ear canal apparently encodes the vertical direction of a sound source.

Lawrence, B. & Simmons, J., 1982. Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *The Journal of the Acoustical Society of America* 71(2), pp.585–590.

Abstract: The absorption of sound propagating through the atmosphere under laboratory conditions of 25°C and 50% relative humidity was measured at frequencies from 30 to 200 kHz. The attenuating effect on the passage of utrasonic sounds through air ranged from 0.7 dB/m at 30 kHz to 8 dB/m at 200kHz. These measurements confirm theoretical expectations and earlier observations that atmospheric attenuation is progressively more severe at higher frequencies and that the atmosphere acts as a low-pass filter for conducting sounds in the frequency range used for echolocation by bats. Different species of bas use different portions of this range of frequencies, and bats emitting sonar signals predominantly above 100 kHz encounter especially sever attenuation of over 3 dB/m. With the greatly restricted operating distances for echolocation at such high frequencies, bats using these higher frequencies must be under compelling ecological pressures of a higher priority than long-range detection of targets.

Lawton, B.W., 2001. Damage to human hearing by airborne sound of very high frequency or ultrasonic frequency. Prepared by the Institute of Sound and Vibration Research for the Health and Safety Executive. Contract research report 343/3001. Online: http://www.hse.gov.uk/research/crr_pdf/2001/crr01343.pdf.

Abstract: A number of Damage Risk Criteria and Maximum Permissible Levels were first recommended by individual researchers in the 1960s. These tentative recommendations, supported by limited experimental and survey data, were then taken up by national and international bodies. For the very high frequencies, 10-20 kHz, the limits were given as one-third-octave band Sound Pressure Levels in the range 75-85 dB, to avoid unpleasant subjective effects in exposed persons; higher noise levels were found to cause annoyance, tinnitus, headaches, fatigue and even nausea. For ultrasonic components above 20 kHz, the limits were set to avoid hearing damage in the audible (lower) frequencies. One-third-octave band levels of 105-115 dB were observed to produce no temporary hearing loss, and were therefore judged non-hazardous in respect of permanent hearing damage. Since the introduction of these recommended limits, there have been no reports showing systematic hearing loss trends associated with occupational exposure to very high frequency noise. Review of the scant literature shows few workers represented, and none with more than about five years daily contact with potentially harmful noise. Workday exposure conditions are not described sufficiently to judge if any recognised limit had been exceeded. The reported hearing deficits were unconnected to exposure duration (in years), and were more dominated by age than by noise. Moreover, conventional wideband noise, of such a level and duration as to be recognised as an “ordinary” occupational hazard, can cause hearing loss in the very high frequency range. In addition to the noise-sensitive frequencies 3, 4 and/or 6 kHz., there may be a second region of susceptible frequencies over the range 12-16 kHz. To aid identification of possible noise-induced hearing damage in the 12-16 kHz region, preliminary data are presented showing the expected threshold shift due to natural ageing. None of the recommended limits have a fully-developed Exposure Level, combining noise level and duration on a daily basis. Where duration is considered at all, there is an equal-energy trading relationship: halving of noise duration allows a 3 dB increase in level. However, the recommended limits have two stated aims: to avoid subjective effects and to avoid hearing damage. In sensitive individuals, adverse subjective effects might be expected to appear shortly

after the start of a very high frequency noise exposure. An increase of permitted band level, in line with any duration correction, would hasten the onset of subjective effects in sensitive individuals, and probably involve a larger proportion of the exposed population. Both of these outcomes are undesirable: a relaxation of maximum acceptable level, to account for reduced daily duration, works to thwart one stated aim of any recommended limit. After consideration of the relevant literature on subjective and auditory effects, there seems to have been no significant progress since Damage Risk Criteria and Maximum Permissible Levels were first proposed in the 1960s. As a first step forward, a structured survey of subjective effects, linked to measured band levels, would confirm (or otherwise) the long-established limits for unprotected ears, and establish the prevalence of adverse subjective effects. A dose response relation might follow. It is too early to think of a dose-response relation for hearing injury. A census is needed to determine how many ultrasonic tools are in use throughout UK industry, and how many workers are exposed to potentially harmful acoustic output from these devices? Once the population at risk has been quantified, paths for future research may be opened.

Lazure, L. & Fenton, M.B., 2011. High duty cycle echolocation and prey detection by bats. *The Journal of Experimental Biology*, 214(Pt 7), pp.1131–7.

Abstract: There are two very different approaches to laryngeal echolocation in bats. Although most bats separate pulse and echo in time by signalling at low duty cycles (LDCs), almost 20% of species produce calls at high duty cycles (HDCs) and separate pulse and echo in frequency. HDC echolocators are sensitive to Doppler shifts. HDC echolocation is well suited to detecting fluttering targets such as flying insects against a cluttered background. We used two complementary experiments to evaluate the relative effectiveness of LDC and HDC echolocation for detecting fluttering prey. We measured echoes from fluttering targets by broadcasting artificial bat calls, and found that echo amplitude was greatest for sounds similar to those used in HDC echolocation. We also collected field recordings of syntopic LDC and HDC bats approaching an insect-like fluttering target and found that HDC bats approached the target more often (18.6% of passes) than LDC bats (1.2% of passes). Our results suggest that some echolocation call characteristics, particularly duty cycle and pulse duration, translate into improved ability to detect fluttering targets in clutter, and that HDC echolocation confers a superior ability to detect fluttering prey in the forest understory compared with LDC echolocation. The prevalence of moths in the diets of HDC bats, which is often used as support for the allotonic frequency hypothesis, can therefore be partly explained by the better flutter detection ability of HDC bats.

Lee, P.L. & Wang, J.H., 2009. The simulation of binaural hearing caused by a moving sound source. *Computers & Structures*, 87(17-18), pp.1102–1110.

Abstract: Auditory perception of the sound with respect to a moving sound source passing by the observer was investigated in this work. The sound pressure at the entrance of the external ear canal was calculated by the solution of the Ffowcs Williams–Hawkings equation. Furthermore, the Hilbert Huang transformation is used to find the instantaneous frequencies of acoustic signal. Results show that the Interaural Level Difference and the frequencies shifting are eventful cues to perceive the direction and the speed of the moving sound source. In addition, the perceived loudness level will be larger in the motional case than that found in the stationary cases.

Lee, Y. & Mccracken, G.F., 2004. Flight Activity and Food Habits of Three Species of *Myotis* bats (Chiroptera:Vespertilionidae) in Sympatry. *Zoological Studies* 43(3), pp.589–597.

Abstract: Spatiotemporal distributions in nocturnal flight activities and variations in food resource use among the little brown (*Myotis lucifugus*), northern long-eared (*M. septentrionalis*), and Indiana myotis (*M. sodalis*) were studied in central and northern Indiana where the 3 species occur in sympatry. We netted pairs of these 3 species on the same nights at 4.3% to 8.5% of the total netting sites, while all 3 species were netted on the same night at only 1 site (~1.1%). When each species was captured alone, the mean capture time of the little brown myotis was earlier than those of the Indiana and northern long-eared myotis; but the 3 species did not differ in heights of capture. At sites where paired species were caught, the mean capture time of the Indiana myotis shifted from being no different from, to being earlier than, that of the northern long-eared myotis; and the mean capture height of the Indiana myotis shifted from being no different from, to being higher than, that of the little brown myotis. Based on analyses of feces, the little brown myotis has a more-diverse diet, feeds on more beetles of a smaller size range, and consumes more aquatic insects than do the Indiana and northern long-eared myotis. While the northern long-eared myotis fed primarily on beetles, moths, and dipterans, and took greater quantities of large-sized (4~6 mm and > 6 mm) beetles, moths were the major prey of the Indiana myotis. Variations in diets among these 3 species are consistent with their foraging behavior, are correlated to their temporal activities, and support predictions based on previously reported differences in their mean lengths of the maxillary tooth-row.

Lengagne, T., 2008. Traffic noise affects communication behaviour in a breeding anuran, *Hyla arborea*. *Biological Conservation*, 141(8), pp.2023–2031.

Abstract: Modern human societies generate new patterns of noise that may affect acoustic communication in many animal species. Whilst animals have evolved several mechanisms to cope with natural background noise, the rapid increase of anthropogenic alteration of acoustic environment could challenge the potential for adjustments of communicative systems. Because acoustic communication is involved in crucial behaviours, noise pollution can be particularly detrimental in affecting breeding success or survival. I investigated the impact of traffic noise on acoustic communication in a tree frog by way of an experimental approach using noise playback. Traffic noise triggered a decrease of the males' calling activity, with males being more affected when noise amplitude increased. Additionally, the males' social situation (calling in chorus versus alone) exerted a strong influence on sensitiveness to noise. Males were only weakly affected by noise pollution when calling in a chorus situation, probably because they were more stimulated and because traffic noise emergence was lower. Moreover results showed that in response to noise playback, males are not able to adjust their temporal or frequency call structures to increase efficiency of the information transfer. Understanding species' ability to adapt their communicative systems to cope with human-made noise constitutes an important contribution to wildlife conservation.

Le Prell, C.G., Henderson D., Fay R.R. & Popper A.N., eds. 2012. Noise-induced hearing loss: Scientific advances. Springer Science+Business Medica LLC, New York.

No Abstract

Leonard, M. & Fenton, M., 1984. Echolocation calls of *Euderma maculatum* (Vespertilionidae): use in orientation and communication. *Journal of Mammalogy*, 65(1), pp.122–126.

No abstract

Leonard, M.L. & Horn, A.G., 2005. Ambient noise and the design of begging signals. *Proceedings. Biological sciences / The Royal Society*, 272(1563), pp.651–6.

Abstract: The apparent extravagance of begging displays is usually attributed to selection for features, such as loud calls, that make the signal costly and hence reliable. An alternative explanation, however, is that these design features are needed for effective signal transmission and reception. Here, we test the latter hypothesis by examining how the begging calls of tree swallow (*Tachycineta bicolor*) nestlings and the response to these calls by parents are affected by ambient noise. In a field study, we found that call length, amplitude and frequency range all increased with increasing noise levels at nests. In the laboratory, however, only call amplitude increased in response to the playback of noise to nestlings. In field playbacks to parents, similar levels of noise abolished parental preferences for higher call rates, but the preference was restored when call amplitude was increased to the level that nestlings had used in the laboratory study. Our results show that nestling birds, like other acoustic signallers, consistently increase call amplitude in response to ambient noise and this response appears to enhance discrimination by receivers. Thus, selection for signal efficacy may explain some of the seemingly extravagant features of begging displays.

Lesiński, G., Sikora, A. & Olszewski, A., 2010. Bat casualties on a road crossing a mosaic landscape. *European Journal of Wildlife Research*, 57(2), pp.217–223.

Abstract: A year-round study was conducted on a 16.6-km road section crossing Kampinos National Park near Warsaw (central Poland). We found 61 road-killed bats belonging to seven species. The most abundant were: *Nyctalus noctula*, *Plecotus auritus*, and *Barbastella barbastellus*. Bats were found between the middle of April and the end of October with peaks in July/August and October. The density of bat casualties differed slightly in various habitats surrounding the road—lower values than expected were found only for windbreaks and bushes. The prediction that low-flying species are killed more frequently was not confirmed—the most abundant *N. noctula* usually flies at heights over 10 m above the ground. *N. noctula*, *Myotis nattereri*, and *Pipistrellus nathusii* were killed more frequently while *Eptesicus serotinus* less frequently than could be expected from the frequency with which they were captured in mist-nets on forest lanes.

Li, Y. & Song, Y.D., 2007. Neurophysiological study on sensorimotor control mechanism in superior colliculus of echolocating bat. *ISA Transactions*, 46(2), pp.157–65.

Abstract: This paper investigates the neural processes associated with bat sonar vocal production and their relationship with spatial orientation. The bat's heavy reliance on sound processing is reflected in specializations of auditory and motor neural structures. These specializations were utilized by investigating the mammalian superior colliculus (SC); a midbrain sensory motor nucleus mediating orientating behaviours in mammals, including vocal motor orientating. Behavioural and neurophysiological experiments were conducted in the insectivorous

echolocating bat, *Eptesicus fuscus*. Chronic neural recording techniques were specifically developed to study neuronal activity. Potential application of the results on control systems is also addressed.

Li, Y., Want, J., Metzner, W., Luo, B., Jiang, T., Yang, S., Shi, L., Huang, X., Yue, W. & Feng, J. 2014. Behavioral responses to echolocation calls from sympatric heterospecific bats: implications for interspecific competition. *Behavioral Ecology and Sociobiology*, 68(4), pp.657–667.

Abstract: Mutual recognition is the product of species coexistence, and has direct effects on survival and reproduction of animals. Bats are able to discriminate between sympatric different heterospecifics based on their echolocation calls, which has been shown both in free-flying and captive bats. To date, however, the factors that may determine the behavioral responses of bats to echolocation calls from sympatric heterospecifics have rarely been tested, especially under well controlled conditions in captive bats. Hence, we aimed at tackling this question by performing playback experiments (habituation–dishabituation) with three horseshoe bat species within the constant-frequency bat guild, which included big-eared horseshoe bats (*Rhinolophus macrotis*), Blyth's horseshoe bats (*Rhinolophus lepidus*), and Chinese horseshoe bats (*Rhinolophus sinicus*).We studied the behavioral responses of these three species to echolocation calls of conspecifics, to other two species, and to another heterospecifics bat, Stoliczka's trident bat (*Asellisus stoliczkanus*), which also belongs to this guild. We found that the three rhinolophid species displayed a series of distinct behaviors to heterospecific echolocation but few to conspecific calls after habituation, suggesting that they may have been able to discriminate sympatric heterospecific echolocation calls from those of conspecifics. Interestingly, the behavioral responses to heterospecific calls were positively correlated with the interspecific overlap index in trophic niche, whereas call design had only a minor effect. This implies that the behavioral responses of these bats to heterospecific echolocation calls may be related to the degree of interspecific food competition.

Liberman, M.C. & Dodds, L.W., 1984. Single-neuron labeling and chronic cochlear pathology II: Stereocilia damage and alterations of spontaneous discharge rates. *Hearing Research*. 16, 43–53.

Abstract: The spontaneous discharge rates (SRs) sampted from auditory-nerve fihcrs in cases of chronic cochlear pathology arc often abnormally low. The application of intraceilular labeling techniques to noise-exposed ears makes it possible to accurately correlate fiber populations showing SR abnormalities with the cochlear locations from which these responses originate. The correlations reveal that a decrease in the mean rates of spontaneous discharge is typicallv associated with selective loss of the tallest row of stcrcoctlia from the inner hair cells. In cochlcar regions where virtually all of the tall stereocilia arc missing from the inner hair cells. the maximum rates of spontaneous discharge are less than l/3 normal values. We suggest that the loss of tall stercocilia causes the dccrcase in SR because much of the resting current in the inner hair cell normally flows through the stereocilia membrane**.** Thus, the loss of that membrane leads to a hyperpolarization of the inner hair cell which, in turn. decreases the spontaneous rclcase of vesicles at the synapse. An interpretation is also suggested for the "compression" of the SR distribution commonly seen among high-frequency neurons in normal animals.

Lindner, L. & Marks, L., 2006. Use of vocal signatures for the inventory of free-flying neotropical bats. *Biotropica,* 31(3), pp.507–516.

Abstract: An ongoing study is being conducted to test the efficacy of the Anabat II detector and analysis system in obtaining reliable vocal signatures for the identification of non-phyllostomid species of bats. We sampled a wide range of elevations and associated habitat types throughout Belize. Anabat provides an instantaneous output of echolocation call structure with a laptop computer. Select sequences can be saved directly to the hard drive, avoiding extraneous noise and sound distortion commonly associated with tape recorders. To date, 18 of the 37 species known or expected to occur in the study region were identified by recognizable differences in the time-frequency characteristics of echolocation calls. In general, each family is recognizable by call structure patterns and species readily separated by frequency range parameters. Species that commute or forage at high altitudes are not susceptible to capture but are conspicuous by acoustic sampling. Further work is needed to determine limitations of the equipment, establish better sampling procedures, and develop a comprehensive library of vocal signatures incorporating the range of variation inherent in each species. As this work progresses, we predict the addition of hitherto unknown species occurring within the study region.

Liu, Y., Metzner, W. & Feng, J., 2013. Vocalization during copulation behavior in greater horseshoe bats, *Rhinolophus ferrumequinum*. *Chinese Science Bulletin*, 58(18), pp.2179–2184.

Abstract: Vocal communication plays an important role for individual recognition and male-female interaction during mating in greater horseshoe bats, especially in respect to mate fidelity, which ensures that the bats can maintain a stable social organization. Few studies, however, have addressed the calling behavior during copulating in bats. Here, we initially report the copulation vocalizations and behaviors of both male and female greater horseshoe bats. During copulation, the male assumed a dorsal position and arched his back, arming around the female using his feet and thumbs. The male repeatedly produced very short constant frequency (SCF) syllables with high intensity and repetition rate (male 1: 16.48±4.8 ms, male 2: 17.79±4.03 ms) when he tried to insert the penis into the female, and then long syllables (male 1: 42.08±12.67 ms, male 2: 43.02±11.44 ms) after penile insertion. The female bats sometime refused the male bats in the early phase of copulations as emitting noise bursts and broad-band vocalizations, but kept silence during actual copulation. We also found that the SCF copulation calls of one male remained stable peak frequencies on different copulation days although its echolocation call frequency varied each day. Moreover, different male individuals maintained their own “private frequency” in the SCF copulation calls. Therefore, we predicted that the SCF copulation calls may serve as an indicator for female greater horseshoe bats to recognize the mating males in order to maintain mate fidelity because horseshoe bats exhibit sexual segregation before mating. Our results stipulate further studies on mating system and copulation strategies in polygynous bats. Such work may also aid in promoting the preservation of greater horseshoe bats.

Long, C. V, Flint, J.A. & Lepper, P.A., 2010. Wind turbines and bat mortality: Doppler shift profiles and ultrasonic bat-like pulse reflection from moving turbine blades. *The Journal of the Acoustical Society of America,* 128(4), pp.2238–45.

Abstract: Bat mortality resulting from actual or near-collision with operational wind turbine rotors is a phenomenon that is widespread but not well understood. Because bats rely on

information contained in high-frequency echoes to determine the nature and movement of a target, it is important to consider how ultrasonic pulses similar to those used by bats for echolocation may be interacting with operational turbine rotor blades. By assessing the characteristics of reflected ultrasonic echoes, moving turbine blades operating under low wind speed conditions (<6 m s^{-1}) were found to produce distinct Doppler shift profiles at different angles to the rotor. Frequency shifts of up to ±700-800 Hz were produced, which may not be perceptible by some bat species. Monte Carlo simulation of bat-like sampling by echolocation revealed that over 50 rotor echoes could be required by species such as *Pipistrellus pipistrellus* for accurate interpretation of blade movement, which may not be achieved in the bat's approach time-window. In summary, it was found that echoes returned from moving blades had features which could render them attractive to bats or which might make it difficult for the bat to accurately detect and locate blades in sufficient time to avoid a collision.

Long, G., 1977. Masked auditory thresholds from the bat, *Rhinolophus ferrumequinum*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 116, pp.247–255.

Abstract: Thresholds for pure tones masked by broad band white noise were measured in the bat, *Rhinolophus ferrumequinum*, using a classically conditioned response to shock. The critical ratios obtained from the masked thresholds differ from those obtained from other mammals in that some of the fine structure of the behavioural hearing curve is reflected in the critical ratio curve. This difference is discussed in relation to specializations of the auditory system of this bat.

Lopez, P. T., Narins, P. M., Lewis, E. R. & Moore, S. W. 1988. Acoustically induced call modification in the white-lipped frog, *Leptodactylus albilabris*. *Animal Behaviour*, 36, 1295-1308.

Abstract: The vocalization behaviour of *Leptodactylus albilabris* was investigated using field playback experiments. To assess the response of males to pre-recorded natural 'chirp' (advertisement call) and natural 'chuckle" (aggressive call) stimuli of gradually increasing broadcast intensity, three parameters (intensity, dominant frequency and repetition rate) of the chirp call were analysed. Of the males tested, 69% showed a significant increase in chirp intensity with increased levels of both stimulus types. In response to playback of the chirp stimulus, males actively modified the dominant frequency of their chirp calls over a mean range of 91·42 Hz, and in one case as much as 400 Hz. Moreover, 12 of 17 males shifted the frequency of their call towards the dominant frequency of the chirp stimulus (2175 Hz) by either increasing or decreasing the dominant frequency of their chirp calls. In response to the natural chuckle stimulus, 83% of the males showed either a decrease or no significant change in the dominant frequency of their chirps. All eight males for which both the chirp frequency and intensity were analysed and that showed an increase in chirp intensity also showed a concomitant increase in chirp dominant frequency. These results are the first to document quantitatively the plasticity of advertisement call intensity and dominant frequency in an anuran. The possible effects of advertisement call modification on male mating success in *L. albilabris* is discussed.

Lu, Y. & Jen, P.H.-S., 2003. Binaural interaction in the inferior colliculus of the big brown bat, *Eptesicus fuscus*. *Hearing Research*, 177(1-2), pp.100–110.

Abstract: Binaural interaction plays an important role in shaping response properties of central auditory neurons. Using single unit recording and iontophoresis, we examined frequency tuning curves (FTCs), interaural intensity difference (IID) curves, and rate-intensity functions of inferior collicular (IC) neurons of the big brown bat, *Eptesicus fuscus*, under closed system or free field stimulation conditions. We isolated 46 EI (excitation-inhibition), 24 EO (monaural excitation) and 6 EE (excitation-excitation) neurons. Inhibitory FTCs of EI neurons plotted under ipsilateral sound stimulation fell within (n =10, 22%), partly overlapped (n =26, 56%), or almost entirely encompassed (n =10, 22%) excitatory FTCs plotted by contralateral sound stimulation. The discharge rate of EI neurons was a sigmoid function of IID. The peak discharge rate occurred at IIDs at which contralateral sound stimulation was stronger than ipsilateral sound stimulation. Application of bicuculline, an antagonist for Q-aminobutyric acid A receptors, raised the IID curves and broadened the excitatory FTCs but partly or completely abolished the ipsilateral inhibitory FTCs. For EE neurons, excitatory FTCs and rate-intensity functions plotted by contralateral sound stimulation were always broader and higher than those plotted by ipsilateral sound stimulation. The sharpness of FTCs of EI neurons was significantly greater at ipsilateral 30° than at 30° contralateral. This direction-dependent frequency tuning was effectively abolished by occlusion of the ipsilateral ear. Possible mechanisms underlying these observations are discussed.

Lundberg, J. & McFarlane, D. a., 2009. Bats and bell holes: The microclimatic impact of bat roosting, using a case study from Runaway Bay Caves, Jamaica. *Geomorphology*, 106, pp.78–85.

Abstract: The microclimatic effect of bats roosting in bell holes (blind vertical cylindrical cavities in cave roofs) in Runaway Bay Caves, Jamaica, was measured and the potential impact of their metabolism on dissolution modelled. Rock temperature measurements showed that bell holes with bats get significantly hotter than those without bats during bat roosting periods (by an average of 1.1 °C). The relationship is clearest for bell holes with more than about 300 g aggregate bat body mass and for bell holes that are moderately wide and deep, of W:D ratio between 0.8 and 1.6. Measurement of temperature decay after abandonment showed that rock temperature returns to normal each day during bat foraging periods. Metabolic activity from a typical population of 400 g bat (10 individuals) yields 41 g of CO_2, 417.6 kJ of heat, and 35.6 g of H2O in each 18 hour roost period, and could produce a water film of ~0.44 mm, that is saturated with CO_2 at ~5%. The resultant rock dissolution is estimated at ~0.005 cm3 $CaCO_3$ per day. The metabolic heat ensures that the focus of dissolution remains vertical regardless of geological controls. A typical bell hole 1 m deep may be formed in some 50,000 years by this mechanism alone. Addition of other erosional mechanisms, such as direct bacterial bio-erosion, or the formation of exfoliative organo-rock complexes, would accelerate the rate of formation. The hypothesis is developed that bell holes are initiated and formed by bat-mediated condensation corrosion and are governed by geographic distribution of clustering bats and their roosting behaviour.

Luo, B., Jiang, T., Liu, L., Wang, J., Lin, A., Wei, X. & Feng, J. 2013. Brevity is prevalent in bat short-range communication. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*,199(4), pp.325–33.

Abstract: Animal communication follows many coding schemes. Less is known about the coding strategy for signal length and rates of use in animal vocal communication. A generalized

brevity (negative relation between signal length and frequency of use) is innovatively explored but remains controversial in animal vocal communication. We tested brevity for short-range social and distress sounds from four echolocating bats: adult black-bearded tomb bat *Taphozous melanopogon*, Mexican free-tailed bat *Tadarida brasiliensis*, adult greater horseshoe bat *Rhinolophus ferrumequinum*, and adult least horseshoe bat *Rhinolophus pusillus*. There was a negative association between duration and number of social but not distress calls emitted. The most frequently emitted social calls were brief, while most distress calls were long. Brevity or lengthiness was consistently selected in vocal communications for each species. Echolocating bats seem to have convergent coding strategy for communication calls. The results provide the evidence of efficient coding in bat social vocalizations, and lay the basis of future researches on the convergence for neural control on bats' communication calls.

Luo, J., Clarin, B.M., Borissov, I.M. & Siemers, B.M., 2014. Are torpid bats immune to anthropogenic noise? *The Journal of Experimental Biology*, 217(Pt 7), 1072–8.

Abstract: Anthropogenic noise has a negative impact on a variety of animals. However, many bat species roost in places with high levels of anthropogenic noise. Here, we tested the hypothesis that torpid bats are insensitive to anthropogenic noise. In a laboratory experiment, we recorded skin temperature (T_{sk}) of bats roosting individually that were subjected to playbacks of different types of noise. We found that torpid bats with T_{sk} ~10°C lower than their active T_{sk} responded to all types of noise by elevating T_{sk}. Bats responded most strongly to colony and vegetation noise, and most weakly to traffic noise. The time of day when torpid bats were exposed to noise had a pronounced effect on responses. Torpid bats showed increasing responses from morning towards evening, i.e. towards the onset of the active phase. Skin temperature at the onset of noise exposure ($T_{sk,start}$, 17–29°C) was not related to the response. Moreover, we found evidence that torpid bats rapidly habituated to repeated and prolonged noise exposure.

Luo, J., Koselj, K., Zsebok, S., Siemers, S.M. & Goerliz, H.R. 2013. Global warming alters sound transmission: differential impact on the prey detection ability of echolocating bats. *Journal of the Royal Society, Interface*, 11, pp.1–10.

Abstract: Climate change impacts the biogeography and phenology of plants and animals, yet the underlying mechanisms are little known. Here, we present a functional link between rising temperature and the prey detection ability of echolocating bats. The maximum distance for echo-based prey detection is physically determined by sound attenuation. Attenuation is more pronounced for high-frequency sound, such as echolocation, and is a nonlinear function of both call frequency and ambient temperature. Hence, the prey detection ability, and thus possibly the foraging efficiency, of echolocating bats and susceptible to rising temperatures through climate change. Using present-day climate data and projected temperature rises, we modelled this effect for the entire range of bat call frequencies and climate zones around the globe. We show that depending on call frequency, the prey detection volume of bats will either decrease or increase: species calling above a crossover frequency will lose and species emitting lower frequencies will gain prey detection volume, with crossover frequency and magnitude depending on the local climatic conditions. Within local species assemblages, this may cause a change in community composition. Global warming can thus directly affect the prey detection ability of individual bats and indirectly their interspecific interactions with competitors and prey.

Lou, J., Siemers, I. M., and Kosel, K. 2015. How anthropgenic noise affects foraging. *Global Change Biology,* 21, pp.3278-3289.

Abstract: The influence of human activity on the biosphere is increasing. While direct damage (e.g. habitat destruction) is relatively well understood, many activities affect wildlife in less apparent ways. Here, we investigate how anthropogenic noise impairs foraging, which has direct consequences for animal survival and reproductive success. Noise can disturb foraging via several mechanisms that may operate simultaneously, and thus, their effects could not be disentangled hitherto. We developed a diagnostic framework that can be applied to identify the potential mechanisms of disturbance in any species capable of detecting the noise. We tested this framework using Daubenton's bats, which find prey by echolocation. We found that traffic noise reduced foraging efficiency in most bats. Unexpectedly, this effect was present even if the playback noise did not overlap in frequency with the prey echoes. Neither overlapping noise nor nonoverlapping noise influenced the search effort required for a successful prey capture. Hence, noise did not mask prey echoes or reduce the attention of bats. Instead, noise acted as an aversive stimulus that caused avoidance response, thereby reducing foraging efficiency. We conclude that conservation policies may seriously underestimate numbers of species affected and the multilevel effects on animal fitness, if the mechanisms of disturbance are not considered.

Luther, D. & Gentry, K., 2013. Sources of background noise and their influence on vertebrate acoustic communication. *Behaviour,* 150, pp.1–24.

Abstract: Many animals rely on long-range communication for species recognition, mate selection and territorial defense, but background noise from the environment can constrain their communication. Background noise from both biotic and abiotic sources is ubiquitous. In general, acoustic noise from abiotic sources, including anthropogenic noise, has energy mostly below 1 kHz. Arthropods tend to produce sounds in the 4–10 kHz range, while birds, amphibians and mammals generally have vocalizations with frequencies between 1 and 5 kHz. There are several ways that signalers could improve the efficiency of their acoustic signals to counteract the constraints of background noise. Signalers could make long-term and short-term signal adjustments to increase the detectability and discriminability of their signals. As predicted by signal detection theory adjustments can include increases in contrast between signals and noise, such as the intensity of the signal, the structure of the signal and an increase in signal redundancy. Our study reviews the sources of acoustic background noise, adjustments made by signalers to increase signal efficacy, and the influence of acoustic background noise on the evolution of acoustic communication in terrestrial vertebrate species.

Lynch, E., Joyce, D. & Fristrup, K., 2011. An assessment of noise audibility and sound levels in U.S. National Parks. *Landscape Ecology,* 26(9), pp.1297–1309.

Abstract: Throughout the United States, opportunities to experience noise-free intervals are disappearing. Rapidly increasing energy development, infrastructure expansion, and urbanization continue to fragment the acoustical landscape. Within this context, the National Park Service endeavors to protect acoustical resources because they are essential to park ecology and central to the visitor experience. The Park Service monitors acoustical resources in order to determine current conditions, and forecast the effects of potential management decisions. By community noise standards, background sound levels in parks are relatively low. By wilderness criteria,

levels of noise audibility are remarkably high. A large percentage of the noise sources measured in national parks (such as highways or commercial jet traffic) originates outside park boundaries and beyond the management jurisdiction of NPS. Many parks have adopted noise mitigation plans, but the regional and national scales of most noise sources call for conservation and management efforts on similar scales.

Macías, S., Mora, E.C., Kossl, M., Abel, C. & Foeller, E., 2009. The auditory cortex of the bat *Molossus molossus*: disproportionate search call frequency representation. *Hearing Research*, 250(1-2), pp.19–26.

Abstract: The extent of the auditory cortex in the bat *Molossus molossus* was electrophysiologically investigated. Best frequencies and minimum thresholds of neural tuning curves were analyzed to define the topography of the auditory cortex. The auditory cortex encompasses an average cortical surface area of $5mm^2$. Characteristic frequencies are tonotopically organized with low frequencies being represented caudally and high frequencies rostrally. However, a large interindividual variability in the tonotopic organization was found. In most animals, the caudal 50% was tonotopically organized. More anterior, a variable area was found. A distinct field with reversed topography was not consistently found. Within the demarcated auditory cortex, frequencies of 30-40 kHz, which correspond to the frequency range of search calls emitted during hunting, are overrepresented, occupying 49% of the auditory cortex surface. High minimum thresholds >50 dB SPL were found in a narrow dorsal narrow area. Neurons with multipeaked tuning curves (20%) preferentially were located in the dorsal part of the auditory cortex. In accordance with studies in other bat species, the auditory cortex of *M. molossus* is highly sensitive to the dominant frequencies of biosonar search calls.

Mackey, R.L. & Barclay, M.R., 1989. The influence of physical clutter and noise on the activity of bats over water. *Canadian Journal of Zoology*, 67, pp.1167–1170.

Abstract: To determine why some bats concentrate their activity over calm water rather than turbulent water, we studied the effects of surface clutter and running-water noise on the foraging activity of *Myotis lucifugus* (little brown bats), which commonly fly within 0.5 m of the water surface, and *Eptesicus fuscus* (big brown bats), which forage at greater heights, in southwestern Alberta, Canada. In paired experiments over calm water, artificial clutter reduced the activity of *M. lucifugus*, but not that of *E. fuscus*, compared with natural conditions. Playbacks of the sound of turbulent water reduced the activity of both *M. lucifugus* and *E. fuscus* in paired experiments over calm water. Clutter is an obstacle to flight and produces extraneous background echoes that must be discriminated from prey echoes. Water noise may also interfere with prey detection. The result may be reduced foraging efficiency by bats and a preference for calm bodies of water over turbulent ones.

Makarewicz, R., 1998. Attenuation of outdoor noise due to air absorption and ground effect. *Applied Acoustics*, 53(1-3), pp.133–151.

Abstract: Industrial noise (stationary sources) is assessed by the sound level, L_A, and road traffic noise and railroad noise (moving sources) are described in terms of the time-average sound level, L_{AT}, which depends upon the sound exposure level, L_{AE}. To predict their values in an open space with minimum computer time, simple models of air absorption and ground effect have been developed: the air absorption with the fully determined equivalent absorption coefficient, (Y, the

ground effect with the A-weighted power level, L_{WA}, and the ground coefficient, y. The estimates of both parameters, L_{WA} and y, are based on L_A and L_{AG} measurements. The theory yields L_A and L_{AT} as functions of the distance to the receiver and its height above the ground surface.

Maltby, A., Jones, K.E. & Jones, G., 2010. Understanding the evolutionary origin and diversification of bat echolocation calls. In Handbook of Mammalian Vocalization - An Integrative Neuroscience Approach. Handbook of Behavioral Neuroscience. Elsevier, pp. 37–47.

Abstract: The production of sound and the interpretation of the resulting echoes (echolocation) is used by some birds, dolphins and many bats. However, the complexity, sophistication and diversity of the design of echolocation calls are unparalleled within bats. Most bats echolocate by emitting frequencies between 20 and 60 kHz (ranging from 9 to 212 kHz) and the specific frequencies they use are a compromise between the costs associated with the likelihood of target detection and call attenuation. Bats have evolved a variety of designs, from simple broadband clicks to constant frequency calls. Interpretation of how different call designs have evolved has been hampered by the lack of a robust phylogenetic framework. However, recent improvements in our understanding of bat evolutionary relationships suggest that laryngeal echolocation either evolved once and was subsequently lost in non-echolocating bats, or evolved independently twice in different bat lineages. Reconstructing ancestral call designs is challenging, but it is suggested that early echolocating bats used calls that were tonal, short, broadband and multiharmonic. There is some suggestion that flight evolved before echolocation, and that coevolution with insects and plants has shaped the evolution of call designs in bats. The key to understanding call evolution may be in understanding the genetic basis of echolocation, and this seems an active and important area for future research.

Mann, S.L., Steidl. R. J., and Dalton, Y. M. 2002. Effects of cave tours on breeding Myotis velifer. *Journal of Wildlife Management,* 66, pp.618-624.

Abstract: Human activity in caves can affect bats adversely, especially bats that assemble in maternity colonies where appropriate roosts are restricted to areas with a narrow range of microclimates necessary to raise young. We assessed behavioral responses of a maternity colony of about 1,000 cave myotis (*Myotis velifer*) to experimental cave tours by manipulation 3 factors: size of tour groups, whether tour groups talked, and a combination of light intensity and color used to illuminate trails. We also considered the effects of distances between bat roosts and the tour group as well as season. We measured 4 behavioral responses of bats: number of takeoffs, number of landings, activity level, and vocalization intensity. Light intensity affected bat behavior most; all bat responses were highest in trials with high-intensity white light and lowest in trials with no light. When tour groups talks, takeoffs, landings, and activity level increased. Size of tour groups and treatment interactions did not affect bat behaviors. When bats roosted near the tour route, takeoffs and activity level increased. In addition, all behavioral responses increased as the maternity season progressed. Designing cave tours to minimize short-term effects on bats will require careful consideration of cave lighting and tour frequency, route location, and noise levels.

Marten, K. & Marler, P., 1977. Sound transmission and its significance for animal vocalization. *Behavioral Ecology and Sociobiology*, 290, pp.271–290.

Abstract: 1. Sound transmission was measured in open fields, mixed deciduous forest with and without leaves and coniferous forest in Dutchess County, New York. Attenuation of white noise and pure tones was measured between one microphone close to a loudspeaker and another microphone 100 m away, at the same height. Graphs of excess attenuation (E.A. in dB/100 m) against frequency were obtained at 0.15, 1, 2, 5, and 10 m above the ground. An analysis of variance was conducted to estimate effects of height, frequency and habitat. 2. Height and frequency affect sound transmission more than habitat. With a sound source close to the ground (15 cm and 1 m) all frequencies were more attenuated than at greater heights. The patterns of E.A. as a function of sound frequency were basically similar in all habitats. At all source heights the lower the frequency the better the sound carried, with the exception that close to the ground, sounds below 2 kHz were excessively attenuated. Comparing open field and forest, trees improved transmission of frequencies below 3 kHz, especially close to the ground. 3. Some general trends can be predicted for maximization of transmission distances of animal sounds in these habitats. For an animal vocalizing higher than 1 m above the ground, the lower the frequency the further the sound travels. Close to the ground, low frequencies are again preferred for maximization of transmission distances, but the frequencies must be pitched above a range of attenuated, low-pitched sounds, the limits of which vary to some extent with habitat, creating the "sound window" of Morton. This "window" of least-attenuated frequencies, only occurring close to the ground, tends to be pitched somewhat lower in forest than in open habitats. However, for an animal producing sounds in the habitats tested, perch height and sound frequency are more important than the habitat in determining how far the sound will carry.

Masters, W., 1991. The structure of echolocation sounds used by the big brown bat *Eptesicus fuscus*: some consequences for echo processing. *The Journal of the Acoustical Society of America* 89(3), pp.1402–1413.

Abstract: Analysis of the sonar emissions produced by five big brown bats (*Eptesicus fuscus*) during detection and range-discrimination tests shows that each bat has a distinctive, "personal" emission. This may help bats distinguish their own emissions from those of others and thereby prevent jamming. Emissions usually contain three harmonics and are strongly frequency swept. Modeling of the sweep shape showed it to be more nearly linear in log time than hyperbolic (linear period modulation), which is optimal for Doppler tolerance. However, logarithmic time and linear period modulation are similar in their Doppler properties, and so bats may suffer little penalty for using a slightly nonoptimal sweep shape. We suggest that bats use logarithmic time modulation rather than linear period modulation in order to simplify signal processing during approach to prey, as this type of modulation stabilizes the filtering of echoes resulting from the bat's automatic gain control. Likewise, the use of several harmonics in the emission may simplify signal processing of Doppler-shifted echoes by reducing the number of matched filters needed for reception.

Masters, W. & Raver, K., 1996. The degradation of distance discrimination in big brown bats (*Eptesicus fuscus*) caused by different interference signals. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology,*179, pp.703–713.

Abstract: The ability of two big brown bats (*Eptesicus fuscus*) to discriminate the distance to an electronically synthesized "phantom" target by echolocation was tested in the presence of interfering signals presented slightly before the target echo. Interfering signals were chosen to have differing degrees of similarity to the typical echolocation emission used by the bat in this

task (which was the signal used to create the phantom target), and we predicted that the degree of disruption of ranging would be proportional to the similarity of the interference to the target echo. This prediction was not confirmed; rather, all interference signals not identical to the target echo increased the threshold to about twice that found with no interference. When the interference was identical to the target echo, the threshold increased to about 4 times that with no interference. When each bat was presented with phantom target "echoes" appropriate for the other bat, its range discrimination threshold increased about tenfold, and in this case the degree of interference of different signals was related to their similarity to the target echo, not to their similarity to the bat's "normal" signal. We suggest that *Eptesicus* may suppress interference by a more sophisticated strategy than simple linear matched filtering.

Masters, W. & Raver, K., 2000. Range discrimination by big brown bats (*Eptesicus fuscus*) using altered model echoes: implications for signal processing. *The Journal of the Acoustical Society of America* 107(1), pp.625–637.

Abstract: The sonar emissions of two big brown bats (*Eptesicus fuscus*) were modeled to create a "'normal'" echolocation signal for each bat which was then used as an artificial echo to synthesize a phantom target. The bat's task was to indicate which of two phantom targets ~presented singly! was the "'near'" target and which the "'far'" target. Threshold range discrimination at a nominal target distance of 80 cm was about 0.6 cm for both bats. The normal signal was then modified to change the relative energy in each harmonic, the signal duration, the curvature of the frequency sweep, the absolute frequency, the phase of the second and third harmonics relative to the first, or the Doppler shift of the signal. To determine which modifications affected ranging performance, the altered models were used in tests of range discrimination that were interleaved on a day-to-day basis with tests using the normal model. Of the 12 modifications tested, only those changing the curvature of the frequency sweep affected performance. This result appears not to be predicted by current models of echo processing in FM bats. *Eptesicus* may be able to compensate for certain types of distortions of a returning echo, an ability possibly related to Doppler tolerance or to the characteristics of the natural variation in a bat's emissions.

Masters, W., Raver, K. & Kazial, K., 1995. Sonar signals of big brown bats, *Eptesicus fuscus*, contain information about individual identity, age and family affiliation. *Animal Behaviour*, 50, pp.1243–1260.

Abstract: We examined the possibility that the echolocation (sonar) signals used by big brown bats convey information beyond species identity (e.g. individual identity, family membership, age class, sex). The echolocation signals of six adult females, their 12 offspring, and eight additional offspring were recorded as bats performed a standardized laboratory target-detection task. Sonar signals were analysed for consistency within individuals, and for similarity within families, within age classes (adult versus juvenile), and within sex for juveniles. Evidence was found for individual distinctiveness of emissions, for resemblance of the sonar emissions used by different individuals within a family, and for differences between the emissions of adults and juveniles. No evidence was found for differences between the echolocation calls of juvenile males and females. Individual differences in sonar signals may allow a bat to identify other bats by their sonar calls and may also prevent jamming of the bat's sonar receiver. Similarity within families suggests a heritable component to call variation, although learning cannot be ruled out and is indeed suggested by the findings that the sonar signals of family members (a mother and

her offspring) are more evenly distributed in cross-correlation space than expected by chance, and that heritability estimates are higher based on mother-offspring comparisons than on sibling-sibling comparisons. The finding that the emissions of juveniles differ from those of adults and that the repeatability of sonar signals improves with the age of the juvenile suggests that acquisition of a stable, adult-like signal requires several months, well beyond the time young start flying, at about 1 month. The ability to recognize other individuals or classify them by age and family on the basis of their echolocation calls could be important to bats in a number of social interactions, including mother-offspring recognition, territoriality and altruism.

Matheson, A.L., Campbell, K.L. & Willis, C.K.R., 2010. Feasting, fasting and freezing: energetic effects of meal size and temperature on torpor expression by little brown bats *Myotis lucifugus*. *The Journal of Experimental Biology*, 213, pp.2165–73.

Abstract: Torpor is an adaptation for energy conservation employed by many species of small-bodied endotherms. However, surprisingly little is known regarding proximate factors influencing day-to-day variation in torpor expression in the wild. We used open-flow respirometry to quantify torpor expression in nine little brown bats (*Myotis lucifugus*, LeConte 1831) at two ambient temperatures (7 degrees C and 17 degrees C) following either sham feeding or consumption of a high-protein meal (50% or 100% of the mass required to reach satiation for each individual). Food consumption significantly increased the time spent normothermic before torpor entry but did not affect either the rate of body cooling or torpid metabolic rate. Bats did not fully exploit potential energy savings by maximising their use of torpor. Instead they varied torpor expression such that total energy expenditure over the course of each 22-h trial was balanced against gross energy intake immediately before the trial, independent of ambient temperature. This was accomplished by adjusting the timing of entry into torpor (thus altering the time spent torpid), rather than by modulating torpid metabolic rate. However, pre-trial body mass was also a significant predictor of torpor expression, which suggests that energy reserves combine with recent foraging success to influence individuals' decisions about depth and duration of their torpor bouts. We also present evidence that little brown bats use the heat generated through digestion (i.e. the heat increment of feeding) to substitute for active thermogenesis at sub-thermoneutral temperatures, thereby reducing the energetic costs of thermoregulation prior to torpor entry.

Matsuo, I., 2011. Evaluation of the echolocation model for range estimation of multiple closely spaced objects. *The Journal of the Acoustical Society of America*, 130(2), pp.1030–7.

Abstract: Experimental evidence indicates that bats can use frequency-modulated echolocation to identify objects with an accuracy of less than 1 μs. However, when modeling this process, it is difficult to estimate the delay times of multiple closely spaced objects by analyzing the echo spectrum, because the sequence of delay separations cannot be determined without information on the temporal changes in the interference patterns of the echoes. To extract the temporal changes, Gaussian chirplets with a carrier frequency compatible with bat emission sweep rates are introduced. The delay time for object 1 (T(1)) is estimated from the echo spectrum around the onset time. The T(2) is obtained by adding the T(1) to the delay separation between objects 1 and 2. Further objects are located in sequence by this procedure. Here echoes were measured from single and multiple objects at a low signal-to-noise ratio. It was confirmed that the delay time for a single object could be estimated with an accuracy of about 1.3 μs. The range accuracy was less than 6 μs when the frequency bandwidth was less than 10 kHz. The delay time for

multiple closely spaced objects could be estimated with a high range resolution by extracting the interference pattern.

McAlpine, D. & Grothe, B., 2003. Sound localization and delay lines: do mammals fit the model? *Trends in Neurosciences*, 26(7), pp.347–50.

Abstract: The current dominant model of binaural sound localization proposes that the lateral position of a sound source is determined by the position of maximal activation within an array of binaural coincidence-detector neurons that are tuned to different interaural time differences (ITDs). The tuning of a neuron for an ITD is determined by the difference in axonal conduction delay from each ear--the so-called "delay line" hypothesis. Although studies in birds appear to support this model, recent evidence from mammals suggests that the model does not provide accurate descriptions of how ITDs are encoded in the mammalian auditory brainstem or of how ITD-sensitive neurons contribute to mammalian sound localization.

McClure, C.J.W., Ware, H.E., Carlisle, J., Kaltenecker, G. & Barber, J.R., 2013. An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. *Proceedings. Biological sciences / The Royal Society*, 280(1773), p.20132290.

Abstract: Many authors have suggested that the negative effects of roads on animals are largely owing to traffic noise. Although suggestive, most past studies of the effects of road noise on wildlife were conducted in the presence of the other confounding effects of roads, such as visual disturbance, collisions and chemical pollution among others. We present, to our knowledge, the first study to experimentally apply traffic noise to a roadless area at a landscape scale-thus avoiding the other confounding aspects of roads present in past studies. We replicated the sound of a roadway at intervals-alternating 4 days of noise on with 4 days off-during the autumn migratory period using a 0.5 km array of speakers within an established stopover site in southern Idaho. We conducted daily bird surveys along our "Phantom Road" and in a nearby control site. We document over a one-quarter decline in bird abundance and almost complete avoidance by some species between noise-on and noise-off periods along the phantom road and no such effects at control sites-suggesting that traffic noise is a major driver of effects of roads on populations of animals.

McGregor, P.K. & Krebs, J.R., 1984. Sound degradation as a distance cue in great tit (*Parus major*) song. *Behavioral Ecology and Sociobiology*, 16(1), pp.49–56.

Abstract: We report an experiment designed to test the ideas that: 1. male songbirds can use cues from the distortion of song by environmental factors (degradation) to estimate the distance of another singing male; 2. song degradation is assessed by reference to an internal standard. Great tits respond more strongly to undegraded than to degraded songs when both are played at the same amplitude and from the same position in the territory. This difference in response is shown only if the playback song is "familiar" to the test bird; familiar songs being those sung either by the test bird or neighbours of the test bird. We interpret these results as evidence that cues from song degradation can be used to estimate the distance of a singing conspecific and that degradation assessment is only possible if the bird has an internal representation of the song (because either it and/or a neighbour sings the song). We discuss the implications of these results for Morton's (1982) ranging hypothesis, and for the distinction between learning and

performance in bird song. Our results partially support the ranging hypothesis, but question the nature of "unrangeable" songs sensu Morton. The finding that birds can assess the degree of degradation of songs that they do not sing, supports the idea that birds learn more songs than they sing.

Mcgregor, P.K., Krebs, J.R. & Ratcliffe, L.M., 1983. The reaction of great tits (*Parus major*) to playback of degraded and undegraded songs: the effect of familiarity with the stimulus song type. *The Auk*, 100, pp.898–906.

Abstract: We played degraded and undegraded song types to territorial Great Tits. Each bird was tested with degraded and undegraded renditions of a song type in its repertoire and of a song not in its repertoire. The birds responded less strongly to degraded than to undegraded songs, and the difference was significant only if the test song was of the same type as, or similar to, on in the bird's repertoire. These results are consistent with Richards' (1981) hypothesis that degradation cues are used to judge distance and Morton's (1982) idea that degradation may be judged by comparison with a standard consisting of the bird's own rendition of the song. We also found that birds are better able to discriminate between undegraded and degraded song types if their neighbors sing the song. The results are discussed in relation to hypotheses concerning song matching and neighbor-stranger discrimination.

McGregor, P.K. & Peake, T.M., 2000. Communication networks: social environments for receiving and signalling behaviour. *Acta Ethologica*, 2(2), pp.71–81.

Abstract: Communication and social behaviour are inextricably linked, with communication mediating important social behaviours such as resource defence and mate attraction. However, the social environment in which communication occurs is often ignored in discussions of communication behaviour. We argue that networks of several individuals are the common social environment for communication behaviour. The consequences for receivers and signallers of communicating in a network environment are the main subjects of this review. Eavesdropping is a receiving behaviour that is only possible in the environment of a network and therefore we concentrate on this behaviour. The main effect of communication networks on signallers is to create competition with other signallers for receiver attention. We discuss the consequences of such competition. To conclude, we explore the role of signals and signalling interactions as sources of information that animals exploit to direct their behaviour.

McGuire, L.P. & Fenton, M.B., 2010. Hitting the wall: Light affects the obstacle avoidance ability of free-flying little brown bats (*Myotis lucifugus*). *Acta Chiropterologica*, 12(1), pp.247–250.

No abstract

McGuire, L.P., Fenton, M.B. & Guglielmo, C.G., 2009. Effect of age on energy storage during prehibernation swarming in little brown bats (*Myotis lucifugus*). *Canadian Journal of Zoology*, 87(6), pp.515–519.

Abstract: At temperate latitudes insectivorous bats face substantial nutritional demands prior to hibernation. As temperature decreases and availability of insect prey declines, bats must deposit nutrient stores for hibernation. The use of torpor allows bats to limit energy expenditures resulting in a net energy gain despite decreased energy intake. However, subadult bats have

lower initial fat stores than adults and may have greater difficulty depositing sufficient nutrient stores to survive the winter. We used plasma metabolite analysis to determine the fueling performance of little brown bats (*Myotis lucifugus* (LeConte, 1831)) during swarming to see if subadults compensated for the increased challenges by increased feeding throughout the swarming period. During the period of our study (August and September), adult bats gained mass, while subadults lost mass. There was, however, no difference in nutrient intake of the age groups as indicated by plasma metabolite concentrations. The number of bats using torpor while roosting in the hibernaculum by day increased exponentially coincident with the onset of mating and a decrease in nutrient intake. The results are consistent with wild bats using torpor to minimize energy expenditure and compensate for lower nutrient intake. The difference in mass change in adults and subadults despite the same nutrient intake indicates that subadults incur greater energetic costs.

Mehr, M., Brandl, R., KNeib, T., & Muller, J., 2012. The effect of bark beetle infestation and salvage logging on bat activity in a national park. *Biodiversity and Conservation*, 21(11), pp.2775–2786.

Abstract: Salvage logging—the removal of dead trees in disturbed forest stands—has been controversially discussed. We investigated the impact of bark beetle attacks and subsequent salvage logging on insectivorous bats in a temperate mountain forest. We quantified bat activity (25,373 min counts; 32 plots) using batcorders during 221 all-night surveys in stands killed by bark beetles, with dead trees removed or not, and in vital, single- or multi-layered mature forest stands. We analysed the differences in activity of all bats in general and of bats of foraging guilds (open habitat, forest edge, closed habitat) in these habitats using a generalized linear Poisson mixed model, with plot and observation as random factors, and temperature and habitat as fixed factors. Only open-habitat foragers were slightly more active in salvage-logged stands than in bark-beetle-affected stands; they generally benefited from an open forest canopy, whereas closed-habitat foragers did not. Our results indicated that: (1) bats are less affected by salvage logging after a disturbance of a magnitude typical for European forests, probably because enough roosts are present in surrounding areas, (2) habitats for open foragers are improved by bark beetle infestation and (3) bats are poor bioindicators of negative impacts of salvage logging after natural disturbance in forests with a composition typical for Central Europe.

Melcón, M.L., Yovel, Y., Denzinger, A., and Schnitzler, H.U., 2011. How greater mouse-eared bats deal with ambiguous echoic scenes. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology,*197(5), pp.505–14.

Abstract: Echolocating bats have to assign the received echoes to the correct call that generated them. Failing to do so will result in the perception of virtual targets that are positioned where there is no actual target. The assignment of echoes to the emitted calls can be ambiguous especially if the pulse intervals between calls are short and kept constant. Here, we present first evidence that greater mouse-eared bats deal with ambiguity by changing the pulse interval more often, in particular by reducing the number of calls in the terminal group before landing. This strategy separates virtual targets from real ones according to their change in position. Real targets will always remain in a constant position, and virtual targets will jitter back and forth according to the change in the time interval.

Melendez, K. V., Jones, D.L. & Feng, A.S., 2006. Classification of communication signals of the little brown bat. *The Journal of the Acoustical Society of America*, 120(2), pp.1095–1102.

Abstract: Little brown bats, *Myotis lucifugus*, are known for their ability to echolocate and utilize their echolocation system to navigate, and locate and identify prey. Their echolocation signals have been characterized in detail but their communication signals are less well understood despite their widespread use during social interactions. The goal of this study was to develop an automatic classification algorithm for characterizing the communication signals of little brown bats. Sound recordings were made overnight on five individual male bats housed separately from a large group of captive bats for 7 nights, using a bat detector and a digital recorder. The spectral and temporal characteristics of recorded sounds were first analyzed and classified by visual observation of a call's temporal pattern and spectral composition. Sounds were later classified using an automatic classification scheme based on multivariate statistical parameters in MATLAB. Human- and machine-based analysis revealed five discrete classes of bat's communication signals: downward frequency-modulated calls, steep frequency-modulated calls, constant frequency calls, broadband noise bursts, and broadband click trains.

Metzner, W., 1996. Anatomical basis for audio-vocal integration in echolocating horseshoe bats. *The Journal of Comparative Neurology*, 368(2), pp.252–269.

Abstract: Neurophysiological recordings suggest that audio-vocal neurons located in the paralemniscal tegmentum of the midbrain in horseshoe bats provide an interface between the pathways for auditory sensory processing and those for the motor control of vocalization. To verify these physiological results anatomically, the projection pattern of the audio-vocally active area in the paralemniscal tegmentum was investigated by using extracellular tracer injections of wheat germ agglutinin conjugated to horseradish peroxidase. Several nuclei of the lemniscal auditory pathway (dorsal nucleus of the lateral lemniscus, central nucleus of the inferior colliculus, lateral superior olive) as well as the nucleus of the central acoustic tract appear to project to the paralemniscal tegmentum. Other possible sources of afferent projections are a small but distinctly labeled structure within the lateral hypothalamic area, the substantia nigra pars compacta, the deep mesencephalic nucleus, the rostral portion of the inferior colliculus, the deep and intermediate layers of the superior colliculus, and several small areas in the rhombencephalic reticular formation. No direct efferent projection from the audio-vocally active area of the paralemniscal tegmentum to primarily auditory structures was found. Instead, the main targets were structures that are involved in the control of different motor patterns. These targets include the deep and intermediate layers of the superior colliculus and the dorsomedial portion of the facial nucleus, both of which most probably control pinna movements in cats, and the reticular formation medial and caudal to the facial nucleus and rostral to the nucleus ambiguus, which represents an area involved in the control of vocalization. Hence, the anatomical projection pattern suggests that the paralemniscal tegmentum in horseshoe bats serves as a link between the processing of auditory information and the control of vocalization and related motor patterns.

Metzner, W., 2002. Doppler-shift compensation behavior in horseshoe bats revisited: auditory feedback controls both a decrease and an increase in call frequency. *Journal of Experimental Biology* 1616, pp.1607–1616.

Abstract: Among mammals, echolocation in bats illustrates the vital role of proper audio-vocal feedback control particularly well. Bats adjust the temporal, spectral and intensity parameters of their echolocation calls depending on the characteristics of the returning echo signal. The mechanism of audio-vocal integration in both mammals and birds is, however, still largely unknown. Here, we present behavioral evidence suggesting a novel audiovocal control mechanism in echolocating horseshoe bats (*Rhinolophus ferrumequinum*). These bats compensate for even subtle frequency shifts in the echo caused by flight induced Doppler effects by adjusting the frequency of their echolocation calls. Under natural conditions, when approaching background targets, the bats usually encounter only positive Doppler shifts. Hence, we commonly believed that, during this Doppler-shift compensation behavior, horseshoe bats use auditory feedback to compensate only for these increases in echo frequency (=positive shifts) by actively lowering their call frequency below the resting frequency (the call frequency emitted when not flying and not experiencing Doppler shifts). Re-investigation of the Doppler-shift compensation behavior, however, shows that decreasing echo frequencies (=negative shifts) are involved as well: auditory feedback from frequencies below the resting frequency, when presented at similar suprathreshold intensity levels as higher echo frequencies, cause the bat's call frequency to increase above the resting frequency. However, compensation for negative shifts is less complete than for positive shifts (22% versus 95 %), probably because of biomechanical restrictions in the larynx of bats. Therefore, Doppler-shift compensation behavior involves a quite different neural substrate and audio-vocal control mechanism from those previously assumed. The behavioral results are no longer consistent with solely inhibitory feedback originating from frequencies above the resting frequency. Instead, we propose that auditory feedback follows an antagonistic push/pull principle, with inhibitory feedback lowering and excitatory feedback increasing call frequencies. While the behavioral significance of an active compensation for echo frequencies below RF remains unclear, these behavioral results are crucial for determining the neural implementation of audio-vocal feedback control in horseshoe bats and possibly in mammals in general.

Metzner, W. & Schuller, G., 2010. Vocal Control in echolocating bats. In Handbook of Mammalian Vocalization - An Integrative Neuroscience Approach. Handbook of Behavioral Neuroscience. Elsevier, pp. 403–415.

Abstract: Call production in the bat larynx follows the general mammalian pattern. However, several adaptations in the design of the larynx and vocal tract enable bats to produce precisely timed, high-intensity ultrasonic echolocation calls. Whereas the laryngeal innervation by the vocal motor nucleus, the nucleus ambiguus, also follows the common mammalian scheme, certain brainstem areas feeding into the nucleus ambiguus play a peculiar role in bats and operate in parallel to the descending connections from the periaqueductal gray to the final common vocal motor pathway commonly described in other mammals. Some brainstem areas exclusively control echolocation pulses, but not social calls. A similar separated involvement in either echolocation or communication may also occur at higher levels of vocal control, such as in the anterior cingulate cortex, and involve differential gene expression. Most brainstem areas involved in vocal control also receive auditory inputs, providing the audio – vocal feedback quintessential for bat echolocation.

Misawa, H. & Suga, N., 2001. Multiple combination-sensitive neurons in the auditory cortex of the mustached bat. *Hearing Research*, 151(1-2), pp.15–29.

Abstract: The mustached bat, *Pteronotus parnellii*, emits biosonar pulses consisting of four constant-frequency (CF_{1-4}) and four frequency modulated (FM_{1-4}) components. The FM-FM area of its auditory cortex consists of three subdivisions, containing either FM_1- FM_2, FM_1-FM_3 or FM_1-FM_4 combination-sensitive neurons. The FM-FM area also contains `multiple combination-sensitive' neurons: FM_1-$FM_{2,3}$, FM_1-$FM_{3,4}$, FM_1-$FM_{2,4}$, and FM_1-$FM_{2,3,4}$ neurons. All FM-FM neurons are tuned to a time delay (echo delay) of FM_n (n= 2-4) from FM_1. In the present study, we made the following four major findings. (1) Multiple combinationsensitive neurons show the strongest response to a combination of more than two signal elements. (2) Multiple combination-sensitive neurons are located in about 100 Wm wide bands at the boundaries between two adjacent subdivisions of the FM-FM area. (3) Isobest- delay contour lines across the three single combination-sensitive subdivisions are not interrupted by multiple combination sensitive bands. (4) Each subdivision of the FM-FM area has frequency-vs.-frequency coordinates in terms of best FM_1 and best FM_n frequencies for facilitation, although such coordinates were not obtained with single tone bursts.

Møhl, B. & Surlykke, A., 1989. Detection of sonar signals in the presence of pulses of masking noise by the echolocating bat, *Eptesicus fuscus*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*,165, pp.119–124.

Abstract: Two big brown bats (*Eptesicus fuscus*) were trained to report the presence or absence of a virtual sonar target. The bats' sensitivity to transient masking was investigated by adding 5 ms pulses of white noise delayed from 0 to 16 ms relative to the target echo. When signal and masker occurred simultaneously, the bats required a signal energy to noise spectrum level ratio of 35 dB for 50% probability of detection. When the masker was delayed by 2 ms or more there was no significant masking and echo energy could be reduced by 30 dB for the same probability of detection. The average duration of the most energetic sonar signal of each trial was measured to be 1.7 ms and 2.4 ms for the two bats, but a simple relation between detection performance and pulse duration was not found. In a different experiment the masking noise pulses coincided with the echo, and the duration of the masker was varied from 2 to 37.5 ms. The duration of the masker had little or no effect on the probability of detection. The findings are consistent with an aural integration time constant of about 2 ms, which is comparable to the duration of the cries. This is an order of magnitude less than found in backward masking experiments with humans and may be an adaptation to the special constraints of echolocation. The short time of sensitivity to masking may indicate that the broad band clicks of arctiid moths produced as a countermeasure to bat predation are unlikely to function by masking the echo of the moth.

Monazzam, M.R. & Fard, S.M.B., 2011. Impacts of Different Median Barrier Shapes on a Roadside Environmental Noise Screen. *Environmental Engineering Science*, 28(6), pp.435–441.

Abstract: The aim of this article was to investigate the environmental noise effects of different median barrier shapes in the presence of a plain roadside noise barrier. A two-dimensional boundary element method was used to calculate the insertion loss of different profiled barriers over a frequency range of 50–4,000 Hz. Erecting a 1-m plain median barrier in the middle of a 40-m-wide highway has shown a considerable reduction in efficiency of a 3-m plain roadside barrier. From this point, different profiled median barriers were designed to reduce the negative effects of median barriers. It was found that sloped barriers with 108 compared with other profiled barriers have better efficiency. Comparing the overall results of tested models, the best

performance improvement related to the reference barrier was seen in the barrier model "'KAI'" by 1.41 dB (A).

Monroy, J.A., Carter, M.E., Miller, K.E. & Covey. E., 2011. Development of echolocation and communication vocalizations in the big brown bat, *Eptesicus fuscus*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology,*197(5), pp.459–67.

Abstract: Big brown bats form large maternity colonies of up to 200 mothers and their pups. If pups are separated from their mothers, they can locate each other using vocalizations. The goal of this study was to systematically characterize the development of echolocation and communication calls from birth through adulthood to determine whether they develop from a common precursor at the same or different rates, or whether both types are present initially. Three females and their six pups were isolated from our captive breeding colony. We recorded vocal activity from postnatal day 1 to 35, both when the pups were isolated and when they were reunited with their mothers. At birth, pups exclusively emitted isolation calls, with a fundamental frequency range <20 kHz, and duration >30 ms. By the middle of week 1, different types of vocalizations began to emerge. Starting in week 2, pups in the presence of their mothers emitted sounds that resembled adult communication vocalizations, with a lower frequency range and longer durations than isolation calls or echolocation signals. During weeks 2 and 3, these vocalizations were extremely heterogeneous, suggesting that the pups went through a babbling stage before establishing a repertoire of stereotyped adult vocalizations around week 4. By week 4, vocalizations emitted when pups were alone were identical to adult echolocation signals. Echolocation and communication signals both appear to develop from the isolation call, diverging during week 2 and continuing to develop at different rates for several weeks until the adult vocal repertoire is established.

Morris, A.D., Miller, D.A. & Kalcounis-Rueppell, M.C., 2010b. Use of forest edges by bats in a managed pine forest landscape. *Journal of Wildlife Management*, 74(1), pp.26–34.

Abstract: Forest edges often have increased species richness and abundance (edge effect) and affect spatial behaviors of species and dynamics of species interactions. Landscapes of intensively managed pine (*Pinus* spp.) stands are characterized by a mosaic of patches and linear forest edges. Managed pine forests are a primary landscape feature of the southeastern United States, but the effects of intensive management on bat communities are poorly understood. Insectivorous bats are important top predators in nocturnal forest food webs. We examined bat foraging behavior along forest edges and in 4 structurally distinct stand types (open-canopy pine, prethinned pine, thinned pine, and unmanaged forest) within a managed pine forest in the coastal plain of North Carolina, USA. During May–August, 2006 and 2007, we recorded echolocation calls using Pettersson D240X bat detectors linked to digital recorders at 156 sites. We also sampled nocturnal flying insects at each site using Malaise insect traps. We used negative binomial count regression models to describe bat foraging behavior relative to forest edges, stand types, and prey availability. Although some species showed affinities for certain stand types and prey items, bat activity patterns were most strongly related to forest edges. Edges were used extensively by 6 aerial-hunting bat species, but avoided by *Myotis* species. Forest edges function similarly to natural forest gaps, by providing foraging opportunities for aerial-hunting bat species. Therefore, the maintenance of forest edges in managed pine landscapes may enhance foraging habitat for aerial-hunting bat species.

Moss, C.F, Bohn, K., Gilkenson, H. & Surlykke, A., 2006. Active listening for spatial orientation in a complex auditory scene. *PLoS Biology*, 4(4), p.e79.

Abstract: To successfully negotiate a complex environment, an animal must control the timing of motor behaviors in coordination with dynamic sensory information. Here, we report on adaptive temporal control of vocal-motor behavior in an echolocating bat, *Eptesicus fuscus*, as it captured tethered insects close to background vegetation. Recordings of the bat's sonar vocalizations were synchronized with high-speed video images that were used to reconstruct the bat's three-dimensional flight path and the positions of target and vegetation. When the bat encountered the difficult task of taking insects as close as 10-20 cm from the vegetation, its behavior changed significantly from that under open room conditions. Its success rate decreased by about 50%, its time to initiate interception increased by a factor of ten, and its high repetition rate "terminal buzz" decreased in duration by a factor of three. Under all conditions, the bat produced prominent sonar "strobe groups," clusters of echolocation pulses with stable intervals. In the final stages of insect capture, the bat produced strobe groups at a higher incidence when the insect was positioned near clutter. Strobe groups occurred at all phases of the wingbeat (and inferred respiration) cycle, challenging the hypothesis of strict synchronization between respiration and sound production in echolocating bats. The results of this study provide a clear demonstration of temporal vocal-motor control that directly impacts the signals used for perception.

Moss, C.F., Chiu, C. & Surlykke, A., 2011. Adaptive vocal behavior drives perception by echolocation in bats. *Current Opinion in Neurobiology*, 21, pp.645–52.

Abstract: Echolocation operates through adaptive sensorimotor systems that collectively enable the bat to localize and track sonar objects as it flies. The features of sonar signals used by a bat to probe its surroundings determine the information available to its acoustic imaging system. In turn, the bat's perception of a complex scene guides its active adjustments in the features of subsequent sonar vocalizations. Here, we propose that the bat's active vocal-motor behaviors play directly into its representation of a dynamic auditory scene.

Moss, C.F. & Sinha, S.R., 2003. Neurobiology of echolocation in bats. *Current Opinion in Neurobiology*, 13(6), pp.751–758.

Abstract: Echolocating bats (sub-order: Microchiroptera) form a highly successful group of animals, comprising approximately 700 species and an estimated 25% of living mammals. Many echolocating bats are nocturnal predators that have evolved a biological sonar system to orient and forage in three-dimensional space. Acoustic signal processing and vocal-motor control are tightly coupled, and successful echolocation depends on the coordination between auditory and motor systems. Indeed, echolocation involves adaptive changes in vocal production patterns, which, in turn, constrain the acoustic information arriving at the bat's ears and the time-scales over which neural computations take place.

Moss, C. F. & Surlykke, A., 2010. Probing the natural scene by echolocation in bats. Frontiers in Behavioral Neuroscience, 4(August), 1–16.

Abstract: Bats echolocating in the natural environment face the formidable task of sorting signals from multiple auditory objects, echoes from obstacles, prey, and the calls of conspecifics. Successful orientation in a complex environment depends on auditory information processing,

along with adaptive vocal-motor behaviors and flight path control, which draw upon 3-D spatial perception, attention, and memory. This article reviews field and laboratory studies that document adaptive sonar behaviors of echolocating bats, and point to the fundamental signal parameters they use to track and sort auditory objects in a dynamic environment. We suggest that adaptive sonar behavior provides a window to bats' perception of complex auditory scenes.

Moss, C. & Zagaeski, M., 1994. Acoustic information available to bats using frequency-modulated sounds for the perception of insect prey. *The Journal of the Acoustical Society of America*, 95, pp.2745–2756.

Abstract: Through the present study, the acoustic information available to an echolocating bat that uses brief frequency-modulated (F M) sonar sounds for the pursuit and capture of insect prey has been characterized. Computer-generated sonar pulses were broadcast at tethered insects, and the returning echoes were recorded on analog tape at high speed for off-line analyses. Echoes from stationary and fluttering insects were displayed using time waveform, spectrogram, power spectrum, and cross-correlation representations. The results show echo signatures for the different insect species studied, which change with the angle of incident sound. Sequences of echoes from fluttering insects show irregular changes in sound amplitude and time-frequency structure, reflecting a random temporal relation between the changing wing position and the arrival of incident sound. A set of recordings that controlled the temporal relation between incident sound and insect wing position suggests that information about the spatial profile of a flying insect could be enhanced if the bat were to produce a sequence of sounds that synchronized briefly with the moving target's wing-beat cycle. From this study, it has been proposed that the FM bat receives stroboscopic-like glimpses of fluttering prey whose spatial representation depends on the operation of the bat's sonar receiver.

Müller, R., Pannala, M., Reddy, O.P.K. & Meymand, S.A., 2012. Design of a dynamic sensor inspired by bat ears. *Smart Materials and Structures*, 21(9), p.094025.

Abstract: In bats, the outer ear shapes act as beamforming baffles that create a spatial sensitivity pattern for the reception of the biosonar signals. Whereas technical receivers for wave-based signals usually have rigid geometries, the outer ears of some bat species, such as horseshoe bats, can undergo non-rigid deformations as a result of muscular actuation. It is hypothesized that these deformations provide the animals with a mechanism to adapt their spatial hearing sensitivity on short, sub-second time scales. This biological approach could be of interest to engineering as an inspiration for the design of beamforming devices that combine flexibility with parsimonious implementation. To explore this possibility, a biomimetic dynamic baffle was designed based on a simple shape overall geometry based on an average bat ear. This shape was augmented with three different biomimetic local shape features, a ridge on its exposed surface as well as a flap and an incision along its rim. Dynamic non-rigid deformations of the shape were accomplished through a simple actuation mechanism based on linear actuation inserted at a single point. Despite its simplicity, the prototype device was able to reproduce the dynamic functional characteristics that have been predicted for its biological paragon in a qualitative fashion.

Müller, R. & Schnitzler, H., 1999. Acoustic flow perception in cf-bats: Properties of the available cues. The *Journal of the Acoustical Society of America*, 105(5), pp.2958–2966.

Abstract: Signal design in cf-bats is hypothesized to be commensurate with the evaluation of time-variant echo parameters, imposed by changes in the sound channel occurring as the bat flies by a target. Two such parameters, the proportional changes in Doppler frequency and sound pressure amplitude, are surveyed, employing a simplified acoustic model in order to assess their fitness for target localization given a translational movement within a plane. This is accomplished by considering the properties of the scalar fields given by the value of these putative sensory variables as a function of position in a plane. The considered criteria are: existence and extent of ambiguity areas (i.e., multiple solutions for target position), magnitude of the variables (relevant with regard to perceptual thresholds), as well as magnitude and orthogonality of the gradients (relevant to localization accuracy). It is concluded that these properties render the considered variables compatible with gross judgements of target position. This may be sufficient for behavioral contexts like obstacle avoidance, where adoption of suitable safety margins could compensate for the variance and bias associated with estimates of target location.

Mun, S. & Cho, D.-S., 2009. Noise measuring technique and field evaluation based on the effects of vehicles and pavement types. *Canadian Journal of Civil Engineering*, 36(11), pp.1816–1824.

Abstract: A measuring technique for tire–pavement interaction noise (coast-by noise) that uses a proposed close proximity (CPX) method equipped with surface microphones has been employed to perform pavement noise evaluations on nine different pavement sections as well as two on-site highways. Through field tests, the appropriate noise measuring procedures have been developed and validated for evaluating light and heavy vehicles and various pavement surfaces at varying vehicle speeds. The results show that tire–pavement noise levels vary widely according to the various surface types, vehicle types, and vehicle speeds. In addition, it was found that power-by noise (power-train plus tire–pavement interaction noise) measurements, based on the proposed CPX method, were able to determine the sound power levels used for outdoor sound propagation models.

Musicant, A.D. & Butler, R. a., 1984. The psychophysical basis of monaural localization. *Hearing Research*, 14(2), pp.185–190.

Abstract: Listeners were required to locate, monaurally, noise bursts emanating from the horizontal plane ipsilateral to the functioning ear. Loudspeakers were positioned from 0 through 180” azimuth, separated by 15”. Stimulus bandwidth was 1.0 kHz, and centered at 4.0-14.0 kHz in steps of 0.5 kHz. The location judgments were governed by the frequency composition of the stimuli. not by their place of origin. With a miniature microphone positioned at the entrance of the external ear canal. the relative amplification provided by the pinna was obtained for the stimuli employed in the localization tests. For each differently centered noise burst, that loudspeaker position re other positions which was associated with the greatest amplification of the stimulus was the one most likely to have been chosen as the source of that stimulus during the localization tests.

Naguib, M., 1996. Ranging By Song in Carolina Wrens *Thryothorus Ludovicianus*: Effects of Environmental Acoustics and Strength of Song Degradation. *Behaviour*, 133(7), pp.541–559.

Abstract: Territorial male song birds most frequently hear conspecific song that has been degraded (distorted) by transmission through the environment. Their ability to use this accumulated degradation in conspecific song to assess the distance of its singer requires a receiver to discriminate between different degrees of degradation by taking into account the acoustical properties of the habitat. Ranging accurately when acoustical properties change seasonally then requires a receiver to reassess previous associations of degradation with distance. Here I tested the possibility that Carolina wrens (*Thryothorus ludovicianus*) discriminate between different levels of song degradation and change their association of degradation with distance when the acoustical properties of their territories change. In response to playback of a single song, either undegraded or degraded (at two different levels), most subjects flew to the far side of the loudspeaker only in response to degraded songs. In addition, behavioral responses beyond the loudspeaker were consistently stronger to playback of degraded songs than to playback of undegraded songs. Responses indicate that wrens discriminated between different levels of degradation and suggest that they adjusted their association of degradation with distance as habitat conditions changed. Such adjustment of associating a given level of degradation with distance is an important requirement for accurate ranging, in particular under changing acoustical conditions of the environment. In addition, rapid ranging on the basis of only one song might facilitate processing of additional information such as 1) Present a singers identity and motivation. Resulting selective attention to the closest rival might increase the reliability or speed of decoding such additional information.

Naguib, M., 1998. Perception of degradation in acoustic signals and its implications for ranging. *Behavioral Ecology and Sociobiology*, 42, pp.139–142.

No abstract

Naguib, M., 2003. Reverberation of rapid and slow trills: Implications for signal adaptations to long-range communication. *The Journal of the Acoustical Society of America*, 113(3), p.1749.

Abstract: Many acoustic signals in animals include trills, i.e., rapid repetitions of similar elements. Elements within these trills usually are frequency modulated and are degraded by reverberation during long-range transmission. Reverberation primarily affects consecutive elements with the same frequency characteristics and thus imposes a major constraint in the evolution of design and perception of long-range signals containing trills. Here transmission of frequency-unmodulated trills with different element repetition rates was studied. Trills were generated at different frequencies to assess frequency dependence of reverberation and then broadcast under three acoustic conditions— an open field and to assess seasonal changes in transmission properties, a deciduous forest before and after foliage had emerged. Reverberation was quantified at different positions within trills. The results show strong effects of vegetation density (season), transmission distance, frequency, element repetition rate, and element position within the trill on effects of reverberation. The experiments indicate that fast trills transmit less well than slow trills and thus are less effective in long-range communication. They show in particular that selection on trills should not act only on element repetition rate within trills but also on the trill duration as effects of reverberation increased with trill duration.

Naguib, M., 2013. Living in a noisy world: indirect effects of noise on animal communication. *Behaviour*, 150, pp.1–16.

Abstract: Noise is a ubiquitous feature in natural as well as in urban habitats. The presence of noise can have multiple direct and indirect effects on communication. Noise can directly mask signals leading to reduced detection and recognition. Noise also affects internal physiological processes which can influence attention and decision rules and, thus, indirectly affect communication. Also community effects of noise leading to lower densities or different community composition with respect to copying style or personality will affect communication through different communication distances and different daily behavioural routines. All these direct and indirect effects of noise on communication have been well documented but often are treated separately. This review focusses on some of the indirect effects of noise on animal communication, considering spatial responses, attentional effects and differential effects of noise depending on an animal's characteristics, its personality. It evaluates how noise can indirectly influence communication and, thus, social network structure and processes of sexual and natural selection.

Naguib, M. & Wiley, R.H., 2001. Estimating the distance to a source of sound: mechanisms and adaptations for long-range communication. *Animal Behaviour*, 62(5), pp.825–837.

Abstract: Acoustic signals are used for long-range communication in many animals from insects to birds and mammals. Long-range signals are used primarily by males to advertise and defend their home ranges or territories or to attract mates. During transmission over long distances, the structure of signals becomes progressively degraded. At the position at which a receiver makes a decision to respond, the characteristics of signals can differ markedly from those at the source. This degradation impairs extraction of information coded in the signal but also allows receivers to assess the distance (range) of the signaller. Auditory distance assessment (called "ranging") is particularly important in territorial species as the optimal initial response often depends on the distance of the signaller. Perception of distance is comparatively well studied in animals but this work is not well integrated with information from related fields such as sound perception in humans or other animals. Here we review recent advances in studies of distance estimation and relate these to fundamental issues in sound transmission and sound perception. We consider the different components of signal degradation and how they can be measured in a perceptually meaningful way. We discuss limitations on the perception of degradation and the possibility that signallers might send deceptive information about their actual distance from a receiver. By integrating studies of auditory distance perception and studies of sound perception in animals and humans, we provide a framework for understanding the evolutionary implications of sound degradation in communication.

Necknig, V. & Zahn, A., 2011. Between-species jamming avoidance in pipistrelles? *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology,*197(5), pp.469–73.

Abstract: Past studies have reported that bats modify the spectral-temporal features of their vocalizations to avoid interference from the vocalizations of conspecifics (jamming avoidance). We tested for within, and between-species jamming avoidance in two sympatrically occurring species of vespertilionid bats, *Pipistrellus pipistrellus* and *Pipistrellus nathusii*. In both species the peak frequencies of the narrowband frequency component from samples of bats flying with conspecifics varied more than those from samples of bats flying alone, indicating intraspecific jamming avoidance. If individuals of the two species were recorded together, we found no reaction of *P. nathusii*. *P. pipistrellus*, however, used significantly higher frequencies than when

recorded alone. As the narrowband frequency of this species normally overlaps with the frequency modulated (FM) part of *P. nathusii* calls, this can be interpreted as an interspecific jamming avoidance response.

Nelson, B., 2000. Avian dependence on sound pressure level as an auditory distance cue. *Animal Behaviour*, 59(1), pp.57–67.

Abstract: Sound pressure level (SPL) has received little attention as a distance cue or signal for communication because of the methodological difficulty of determining source SPL from free-ranging signallers and because SPL is presumed to be unreliable as a distance cue. Eastern towhees, *Pipilo erythrophthalmus* (Emberizidae, Passeriformes), in south-central Florida give a simple call during territorial interactions. I obtained measurements of call-source SPL with a calibrated microphone positioned 100+/-10 cm from caged male eastern towhees. Measurements of source SPL were highly variable, but much of this variation can be predicted from measurements of call duration or call frequency variables (spectrotemporal variables). Male towhees accurately perceived the distance of a speaker after it played synthetic calls that matched the amplitude and structure of natural 84-dB and 78-dB call types. Subjects flew further in response to an attenuated (-6 or -12 dB) version of an otherwise identical 84-dB call and flew shorter in response to an amplified (+6 dB) version of this same call. Towhees misjudged speaker distance in approximately half of the trials that included a discrepancy (-6, -12 or +6 dB SPL) between playback source SPL and predicted spectrotemporal variables. These distance errors suggest that towhees assess auditory distance partly from the difference between perceived SPL and source SPL, determined from spectrotemporal variables.

Nelson, B.S. & Suthers, R.A., 2004. Sound localization in a small passerine bird: discrimination of azimuth as a function of head orientation and sound frequency. *Journal of Experimental Biology*, 207, pp.4121–4133.

Abstract: Sound localization is critical to communication when signalers are distributed widely in space and when reverberations that accumulate over distance might otherwise degrade temporal patterns in vocalizations. We readdress the accuracy with which a small passerine bird, the eastern towhee, *Pipilo erythrophthalmus* L., is able to resolve azimuth in the field. We then report results from two-alternative forced-choice (2AFC) experiments in which three of four subjects were able to discriminate an estimated speaker separation angle of approximately 7°. Subjects oriented laterally when discriminating azimuth in the 2AFC task and each subject preferred a different head orientation. Side biases occurred as a function of head orientation and, as a consequence, we conducted a second 2AFC experiment in which subjects were required to discriminate between two closely spaced lights. Subjects oriented similarly in this visual task, however, side biases did not occur as a function of head orientation. Despite side biases in the auditory task, performance generally declined when subjects were played tones with frequencies near ~3 kHz.

Nemeth, E. & Brumm, H., 2010. Birds and anthropogenic noise: are urban songs adaptive? *The American Naturalist*, 176(4), pp.465–75.

Abstract: In cities with intense low-frequency traffic noise, birds have been observed to sing louder and at a higher pitch. Several studies argue that higher song pitch is an adaptation to reduce masking from noise, and it has even been suggested that the song divergence between

urban and nonurban songs might lead to reproductive isolation. Here we present models of signal transmission to compare the benefits of raised song amplitude and song pitch in terms of sound transmission. We chose two bird species that sing with higher pitch in urban areas, the great tit (*Parus major*) and the blackbird (*Turdus merula*). For both species, we calculated communication distances in response to different levels of urban noise and in their natural forest habitats. We found that an increase in vocal pitch increased communication distance only marginally. In contrast, vocal amplitude adjustments had a strong and significantly larger effect. Our results indicate that frequency changes of urban songs are not very effective in mitigating masking from traffic noise. Increased song pitch might not be an adaptation to reduce signal masking but a physiological side effect of singing at high amplitudes or an epiphenomenon of urbanization that is not related to signal transmission.

Nemeth, E. & Brumm, H., 2010. Blackbirds sing higher-pitched songs in cities: adaptation to habitat acoustics or side-effect of urbanization? *Animal Behaviour*, 78, 637-641.

Abstract: When animals colonize cities they often have to adapt their physiology, life history and behaviour to the novel environment. Songbirds rely on acoustic communication for reproduction, and recent studies indicate that songs vary between urban and nonurban habitats. In cities, birds sing louder or use higher frequencies compared to their conspecifics in forests. These habitat-specific differences in song have been interpreted as an adaptation of the city birds to mitigate acoustic masking by low-frequency traffic noise. We compared the songs of blackbirds, *Turdus merula*, from the city centre of Vienna and the Vienna Woods and found that forest birds sang at lower frequencies and with longer intervals between songs. This difference in song pitch might reflect an adaptation to urban ambient noise. However, the song divergence could also be the result of more intense vocal interaction in the more densely populated city areas or a side-effect of physiological adaptation to urban habitats. We emphasize the need for experimental studies in blackbirds, but also in other species,

Nemeth, E., Pieretti, N., Zollinger, S. A., Geberzahn, N., Partecke, J., Brumm, H., and Miranda, A.C. 2013. Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. *Proceedings of the Royal Society B*: Biological Sciences, 280, p.20122798.

Abstract: When animals live in cities, they have to adjust their behaviour and life histories to novel environments. Noise pollution puts a severe constraint on vocal communication by interfering with the detection of acoustic signals. Recent studies show that city birds sing higher-frequency songs than their conspecifics in non-urban habitats. This has been interpreted as an adaptation to counteract masking by traffic noise. However, this notion is debated, for the observed frequency shifts seem to be less efficient at mitigating noise than singing louder, and it has been suggested that city birds might use particularly high-frequency song elements because they can be produced at higher amplitudes. Here, we present the first phonetogram for a songbird, which shows that frequency and amplitude are strongly positively correlated in the common blackbird (*Turdus merula*), a successful urban colonizer. Moreover, city blackbirds preferentially sang higher-frequency elements that can be produced at higher intensities and, at the same time, happen to be less masked in low-frequency traffic noise.

Neubaum, D.J., O'Shea, T.J. & Wilson, K.R., 2006. Autumn migration and selection of rock crevices as hibernacula by big brown bats in Colorado. *Journal of Mammalogy*, 87(3), pp.470–479.

Abstract: Movements, distribution, and roosting requirements of most species of temperate-zone bats in autumn are poorly understood. We conducted the 1st radiotelemetry study of autumn migrations and prehibernation roost selection of bats in western North America. Big brown bats (*Eptesicus fuscus*, n = 55) in the Poudre River watershed, Colorado, moved from low-elevation summer ranges to high-elevation locations in autumn, where they roosted in rock crevices during the period leading up to winter hibernation. We characterized rock crevices used as roosts in autumn at these higher elevations at microhabitat and landscape scales. We used logistic regression combined with an information theoretic approach to determine which variables were most important in roost selection. At the microhabitat scale, autumn roosts were higher to the ground above and below the exit point and were in deeper crevices that had more constant temperatures than randomly selected crevices. At the landscape scale, aspect of the hillside was important, with autumn roosts typically facing north–northwest. Autumn roosts fell into 2 categories: those used for a few days (transient roosts) and those used for 7 days and presumed to be hibernacula. Temperature regimes in the presumed hibernacula appear to provide optimal conditions for use of winter torpor, whereas transient roosts may offer passive rewarming and energy savings for bats still active in early autumn. Elevational segregation of sexes also was documented in our region, with a preponderance of females found at lower elevations and males at higher elevations in summer. Sex ratios at higher elevations became even in autumn. Use of short elevational migrations and selection of hibernation sites in rock crevices may be a common overwintering strategy of insectivorous bats of western North America.

Neumann, I. & Schuller, G., 1991. Spectral and temporal gating mechanisms enhance the clutter rejection in the echolocating bat, *Rhinolophus rouxi*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*,169(1), pp.109–116.

Abstract: Doppler shift compensation behaviour in horseshoe bats, *Rhinolophus rouxi*, was used to test the interference of pure tones and narrow band noise with compensation performance. The distortions in Doppler shift compensation to sinusoidally frequency shifted echoes (modulation frequency: 0.1 Hz, maximum frequency shift: 3 kHz) consisted of a reduced compensation amplitude and/or a shift of the emitted frequency to lower frequencies (Fig. 1). Pure tones at frequencies between 200 and 900 Hz above the bat's resting frequency (RF) disturbed the Doppler shift compensation, with a maximum of interference between 400 and 550 Hz (Fig. 2). Minimum duration of pure tones for interference was 20 ms and durations above 40 ms were most effective (Fig. 3). Interfering pure tones arriving later than about 10 ms after the onset of the echolocation call showed markedly reduced interference (Fig. 4). Doppler shift compensation was affected by pure tones at the optimum interfering frequency with sound pressure levels down to -48 dB rel the intensity level of the emitted call (Figs. 5, 6). Narrow bandwidth noise (bandwidth from ±100 Hz to ±800 Hz) disturbed Doppler shift compensation at carrier frequencies between -250 Hz below and 800 Hz above RF with a maximum of interference between 250 and 500 Hz above resting frequency (Fig. 7). The duration and delay of the noise had similar influences on interference with Doppler shift compensation as did pure tones (Figs. 8, 9). Intensity dependence for noise interference was more variable than for pure tones (-32 dB

to -45 dB rel emitted sound pressure level, Fig. 10). The temporal and spectral gating in Doppler shift compensation behaviour is discussed as an effective mechanism for clutter rejection by improving the processing of frequency and amplitude transients in the echoes of horseshoe bats.

Neuweiler, G., 1989. Foraging ecology and audition in echolocating bats. *Trends in Ecology & Evolution*, 4(6), pp.160–166.

Abstract: The types of echolocation signal and the auditory capacities of echolocating Guts are adapted to specific acoustical constraints of the foraging areas. Bats hunting insects above the canopy use low frequencies for echolocation; this is an adaptation to prey detection over long distances. Bats foraging close to and within foliage avoid masking of insect echoes by specializing on "fluttering target" detection. "Gleaning" bats are adapted to the auditory detection of very faint noises generated by ground-dwelling prey, and are capable of analysing fine changes in the echo spectrum, which may indicate a stationary prey changing its posture on a su6strate. This review of recent research demonstrates that, in bats, foraging ecology and audition are intricately interrelated and interdependent.

Neuweiler, G., 1990. Auditory adaptations for prey capture in echolocating bats. *Physiological Review*, 70, pp.615-641.

No abstract

Neuweiler, G., Singh, S. & Sripathi, K., 1984. Audiograms of a south Indian bat community. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology* A, 154, pp.133-142.

Abstract: Audiograms are recorded from 1 non-echolocating and 9 echolocating sympatrically living bat species of South India. These species are *Cynopterus sphinx* (non-echolocating), *Tadarida aegyptiaca*, *Taphozous melanopogon*, *T. kachhensis*, *Rhinopoma hardwickei*, *Pipistrellus dormeri*, *P. mimus*, *Hipposideros speoris*, *H. bicolor* and *Megaderma lyra*. In R. hardwickei a highly sensitive frequency range was found which is narrowly tuned to the frequency band of the bat's CF [constant frequency]-echolocation call (32-35 kHz, Fig. 3). In hipposiderids a filter narrowly tuned to the frequency of the CF-part of the CF-FM [frequency modulated] echolocation sounds (137.5 kHz in H. speoris and 151.5 kHz in H. bicolor) could be recorded from deeper parts of IC [inferior colliculus]. In the echolocating species the best frequency of the audiograms closely matched with that frequency range in the echolocation calls containing most energy. In bat species foraging flying prey best frequencies of audiograms and height of preferred foraging areas are inversely related, i.e. bat species hunting high above canopy have lower best frequencies than those foraging close to or within canopy. A hypothesis is forwarded explaining how fluttering target detection by CF echolocation might have evolved from long distance echolocation by pure tone signals.

Nicholls, B. & Racey, P.A., 2009. The aversive effect of electromagnetic radiation on foraging bats: a possible means of discouraging bats from approaching wind turbines. *PloS One*, 4(7), p.e6246.

Abstract: Large numbers of bats are killed by collisions with wind turbines and there is at present no accepted method of reducing or preventing this mortality. Following our demonstration that bat activity is reduced in the vicinity of large air traffic control and weather

radars, we tested the hypothesis that an electromagnetic signal from a small portable radar can act as a deterrent to foraging bats. From June to September 2007 bat activity was compared at 20 foraging sites in northeast Scotland during experimental trials (radar switched on) and control trials (no radar signal). Starting 45 minutes after sunset, bat activity was recorded for a period of 30 minutes during each trial and the order of trials were alternated between nights. From July to September 2008 aerial insects at 16 of these sites were sampled using two miniature light-suction traps. At each site one of the traps was exposed to a radar signal and the other functioned as a control. Bat activity and foraging effort per unit time were significantly reduced during experimental trials when the radar antenna was fixed to produce a unidirectional signal therefore maximising exposure of foraging bats to the radar beam. However, although bat activity was significantly reduced during such trials, the radar had no significant effect on the abundance of insects captured by the traps.

Nicholls, B. & Racey, P.A., 2009. The aversive effect of electromagnetic radiation on foraging bats: a possible means of discouraging bats from approaching wind turbines. *PloS One*, 4(7), p.e6246.

Abstract: Large numbers of bats are killed by collisions with wind turbines and there is at present no accepted method of reducing or preventing this mortality. Following our demonstration that bat activity is reduced in the vicinity of large air traffic control and weather radars, we tested the hypothesis that an electromagnetic signal from a small portable radar can act as a deterrent to foraging bats. From June to September 2007 bat activity was compared at 20 foraging sites in northeast Scotland during experimental trials (radar switched on) and control trials (no radar signal). Starting 45 minutes after sunset, bat activity was recorded for a period of 30 minutes during each trial and the order of trials were alternated between nights. From July to September 2008 aerial insects at 16 of these sites were sampled using two miniature light-suction traps. At each site one of the traps was exposed to a radar signal and the other functioned as a control. Bat activity and foraging effort per unit time were significantly reduced during experimental trials when the radar antenna was fixed to produce a unidirectional signal therefore maximising exposure of foraging bats to the radar beam. However, although bat activity was significantly reduced during such trials, the radar had no significant effect on the abundance of insects captured by the traps.

Nicholls, J.A. & Goldizen, A.W., 2006. Habitat type and density influence vocal signal design in satin bowerbirds. *The Journal of Animal Ecology*, 75(2), pp.549–58.

Abstract: 1. This study provided a thorough test of the acoustic adaptation hypothesis using a within-species comparison of call structure involving a wide range of habitat types, an objective measure of habitat density and direct measures of habitat-related attenuation. 2. The structure of the bower advertisement call of the satin bowerbird was measured in 16 populations from throughout the species' range and related to the habitat type and density at each site. Transmission of white noise, pure tones and different bowerbird dialects was measured in five of six habitat types inhabited by satin bowerbirds. 3. Bowerbird advertisement call structure converged in similar habitats but diverged among different habitats; this pattern was apparent at both continent-wide and local geographical scales. Bowerbirds' call structures differed with changes in habitat density, consistent with the acoustic adaptation hypothesis. Lower frequencies and less frequency modulation were utilized in denser habitats such as rainforest and higher frequencies and more frequency modulation were used in the more open eucalypt-dominated

habitats. 4. The white noise and pure tone transmission measurements indicated that different habitats varied in their sound transmission properties in a manner consistent with the observed variation in satin bowerbird vocalizations. 5. There was no effect of geographical proximity of recording locations, nor was there the predicted inverse relationship between frequency and body size. 6. These findings indicate that the transmission qualities of different habitats have had a major influence on variation in vocal phenotypes in this species. In addition, previously published molecular data for this species suggest that there is no effect of genetic relatedness on call similarity among satin bowerbird populations.

Nilsson, M.E., Andéhn, M. & Leśna, P., 2008. Evaluating roadside noise barriers using an annoyance-reduction criterion. *The Journal of the Acoustical Society of America*, 124(6), pp.3561–7.

Abstract: A common indicator of effectiveness for roadside noise barriers is the reduction in A-weighted sound pressure level (L_A). The present experimental study considered alternative indicators using an annoyance-reduction criterion. A large number of 8 s experimental sounds were created from binaural recordings conducted at various distances from a highway at a location with a 4.6 m high roadside barrier (barrier sounds) and at a location along the same road with no barrier (nonbarrier sounds). Eighteen listeners scaled the annoyance of the experimental sounds with the method of magnitude estimation. The barrier sounds recorded 10-45 m from the road and nonbarrier sounds recorded 50-200 m from the road were of similar (L_A). Despite this, the barrier sounds were found to be more annoying than the nonbarrier sounds. The annoyance difference corresponded to approximately a 3 dB increase in (L_A) and was mainly related to the barrier sounds' higher relative level of low-frequency sound. This suggests that (L_A) reduction may not be a valid indicator of the annoyance reduction caused by a noise barrier. The loudness level (ISO 532B) and a low-frequency corrected sound pressure level (L_A^*) were found to be better than (L_A) as indicators of the barrier's annoyance-reduction efficiency.

Norberg, U.M.L. & Norberg, R.A., 2012. Scaling of wingbeat frequency with body mass in bats and limits to maximum bat size. *The Journal of Experimental Biology*, 215, pp.711–22.

Abstract: The ability to fly opens up ecological opportunities but flight mechanics and muscle energetics impose constraints, one of which is that the maximum body size must be kept below a rather low limit. The muscle power available for flight increases in proportion to flight muscle mass and wingbeat frequency. The maximum wingbeat frequency attainable among increasingly large animals decreases faster than the minimum frequency required, so eventually they coincide, thereby defining the maximum body mass at which the available power just matches up to the power required for sustained aerobic flight. Here, we report new wingbeat frequency data for 27 morphologically diverse bat species representing nine families, and additional data from the literature for another 38 species, together spanning a range from 2.0 to 870 g. For these species, wingbeat frequency decreases with increasing body mass as $M_b^{-0.26}$. We filmed 25 of our 27 species in free flight outdoors, and for these the wingbeat frequency varies as $M_b^{-0.30}$. These exponents are strikingly similar to the body mass dependency $M_b^{-0.27}$ among birds, but the wingbeat frequency is higher in birds than in bats for any given body mass. The downstroke muscle mass is also a larger proportion of the body mass in birds. We applied these empirically based scaling functions for wingbeat frequency in bats to biomechanical theories about how the power required for flight and the power available converge as animal size increases. To this end we estimated the muscle mass-specific power required for the largest flying extant bird (12-16

kg) and assumed that the largest potential bat would exert similar muscle mass-specific power. Given the observed scaling of wingbeat frequency and the proportion of the body mass that is made up by flight muscles in birds and bats, we estimated the maximum potential body mass for bats to be 1.1-2.3 kg. The largest bats, extinct or extant, weigh 1.6 kg. This is within the range expected if it is the bat characteristic flight muscle mass and wingbeat frequency that limit the maximum body mass in bats. It is only a tenth the mass of the largest flying extant bird.

Novick, A., 1977. Acoustic orientation. In: Wimsatt, W.A. (ed) Biology of bats, vol 3. Academic, New York, pp 73-287.

No Abstract

O'Farrell, M. & Studier, E., 1970. Fall metabolism in relation to ambient temperatures in three species of *Myotis*. *Comparative Biochemistry and Physiology*, 35, pp.697–703.

Abstract: 1. A zone of thermoneutrality exists for adult female *Myotis thysanodes* in early September in an ambient temperature range of 32.5-34.5°C with minimum metabolism of 1.74 cm3/g per hr. 2. A transition from a homeothermic to a non-homeothermic metabolism to ambient temperature relation is evident by late September in adult female *M. thysanodes*. 3. In early September, some adult female *M. yumanensis* exhibit a homeothermic metabolism to ambient temperature relation while others exhibit a non-homeothermic relation. 4. In early September, adult *M. ludfugus occultus* of both sexes exhibit a non-homeothermic relation. 5. At ambient temperatures above 32.5°C, metabolism in *M. thysanodes* increases at a significantly more rapid rate than in *M. lucifugus occultus*. 6. A critical thermal maximum ambient temperature of 44.5°C has been found for each of these three species.

O'Farrell, M.J., Studier, E.H. & Ewing, W.G., 1971. Energy utilization and water requirements of captive *Myotis thysanodes* and *Myotis lucifugus* (Chiroptera). *Comparative Biochemistry and Physiology Part A: Physiology*, 39(3), pp.549–552.

Abstract: Ten captive *Myotis thysanodes* ingested an average of 5.05 kcal/ day and egested 0.47 kcal/day with a mean energy utilization of 90.8 per cent. 2. One captive *M. lucifugus* ingested 4.15 kcal/day and egested 0.37 kcal/day with an energy utilization of 91.2 per cent. 3. *M. thysanodes* gained an average of 2.77 cm^3/day of water and lost an average of 2.86 cm^3/day. This represents a water turnover of almost half the total body water. 4. The *M. lucifugus* gained 1.97 cm^3/day of water and lost at least 1.47 cm^3/ day representing a water turnover of about one third of the total body water. 5. It is suggested that for small mammals in general that the energy utilization approaches or exceeds 90 per cent efficiency.

Ogahalai, J.S., 2015. Figure of Organ of Corti. Online: http://www.neurophys.wisc.edu/auditory/johc.html

No abstract.

O'Keefe, J.M., Loeb, S., Lanham, J.D. & Hill Jr., H.S., 2009. Macrohabitat factors affect day roost selection by eastern red bats and eastern pipistrelles in the southern Appalachian Mountains, USA. *Forest Ecology and Management*, 257(8), pp.1757–1763.

Abstract: Although roost sites are critically important to bats, we have few data on macrohabitat factors that affect roost selection by foliage-roosting bats. Such data are needed so that forest managers can make informed decisions regarding conservation of bat roosts. Our objective was to examine roost selection by nonreproductive eastern pipistrelles (*Perimyotis subflavus*) and red bats (*Lasiurus borealis*) in a dense deciduous forest undergoing low-intensity timber management in the southern Appalachian Mountains of western North Carolina, USA. During May to August 2004–2006, we radiotracked eight red bats and seven pipistrelles to roosts for 1–14 days (red bat $\tilde{x}$ = 4.11 days, n = 19 roosts; pipistrelles, $\tilde{x}$ = 7 days, n = 15 roosts). We compared roost and random trees or points using paired-sample t-tests for tree and microhabitat characters and logistic regression models of one to three variables for macrohabitat characters. Neither red bats nor pipistrelles selected roosts based on tree or microhabitat characteristics. Red bats used a wide range of stand ages and conditions and, based on our most plausible models for macrohabitat variables, roosted closer than expected ($\tilde{x}$ = 70.6 m) to linear openings such as gated roads. Pipistrelles only used stands 72 years in age and roosted closer than expected ($\tilde{x}$ = 185.6 m) to nonlinear openings and at elevations lower than expected ($\tilde{x}$ = 882 m). Combined evidence of multiple variables indicated that pipistrelles preferred to roost close to streams. Our results indicate that land managers in the southern Appalachians should maintain a diversity of age classes to provide roosting habitat for both species, and that pipistrelles in particular may benefit from retention of mature stands or buffer zones near perennial streams. Furthermore, non-reproductive red bats and pipistrelles may prefer to roost near openings to minimize commuting costs when openings comprise a small proportion of a densely forested landscape.

Obrist, M. & Fenton, M., 1993. What ears do for bats: a comparative study of pinna sound pressure transformation in Chiroptera. *Journal of Experimental Biology*, 152, pp.119–152.

Abstract: Using a moveable loudspeaker and an implanted microphone, we studied the sound pressure transformation of the external ears of 47 species of bats from 13 families. We compared pinna gain, directionality of hearing and interaural intensity differences (IID) in echolocating and non-echolocating bats, in species using different echolocation strategies and in species that depend upon prey-generated sounds to locate their targets. In the Pteropodidae, two echolocating species had slightly higher directionality than a non-echolocating species. The ears of phyllostomid and vespertilionid species showed moderate directionality. In the Mormoopidae, the ear directionality of *Pteronotus parnellii* clearly matched the dominant spectral component of its echolocation calls, unlike the situation in three other species. Species in the Emballonuridae, Molossidae, Rhinopomatidae and two vespertilionids that use narrow-band search-phase echolocation calls showed increasingly sharp tuning of the pinna to the main frequency of their signals. Similar tuning was most evident in Hipposideridae and Rhinolophidae, species specialized for flutter detection via Doppler-shifted echoes of high-duty-cycle narrowband signals. The large pinnae of bats that use prey-generated sounds to find their targets supply high sound pressure gain at lower frequencies. Increasing domination of a narrow spectral band in echolocation is reflected in the passive acoustic properties of the external ears (sharper directionality). The importance of IIDs for lateralization and horizontal localization is discussed by comparing the behavioural directional performance of bats with their bioacoustical features.

Obrist, M. & Wenstrup, J., 1998. Hearing and hunting in red bats (*Lasiurus borealis*, Vespertilionidae): audiogram and ear properties. *The Journal of Experimental Biology*, 201, pp.143–154.

Abstract: We examined aspects of hearing in the red bat (*Lasiurus borealis*) related to its use of biosonar. Evoked potential audiograms, obtained from volume-conducted auditory brainstem responses, were obtained in two bats, and the sound pressure transformation of the pinna was measured in three specimens. Field-recorded echolocation signals were analysed for comparison. The fundamental sonar search calls sweep from 45 to 30 kHz (peak energy at 35 kHz), approach-phase calls sweep from 65 to 35 kHz (peak 40 kHz) and terminal calls sweep from 70 to 30 kHz (peak 45 kHz). The most sensitive region of the audiogram extended from 10 kHz to 45–55 kHz, with maximum sensitivity as low as 20 dB SPL occurring between 25 and 30 kHz. A relative threshold minimum occurred between 40 and 50 kHz. With increasing frequency, the acoustic axis of the pinna moves upwards and medially. The sound pressure transformation was noteworthy near 40–45 kHz; the acoustic axis was closest to the midline, the -3dB acceptance angles showed local minima, and the pinna gain and interaural intensity difference were maximal. These results are related to the known echolocation and foraging behavior of this species and match the spectral components of approach- and final-phase calls. We conclude that coevolution with hearing prey has put a higher selective pressure on optimizing localization and tracking of prey than on improving detection performance.

Ortega, Y.K. and D.E. Capen. 1999. Effects of forest roads on habitat quality for ovenbirds in a forested landscape. *Auk*, 116, pp.937-946.

Abstract: Numerousstu dies have reported lower densities of breeding Ovenbirds (*Seiurus aurocapillus*) adjacent to forest edges. However, none of these studies has considered hab-itat use and reproductive success to address mechanisms underlying the observed pattern, and most were conducted in fragmented landscapes and ignored juxtapositions of forest with narrow openings such as roads. We studied the influence of forest roads on Ovenbird density in an extensively forested region of Vermont, evaluating habitat use and reproductive success relative to mechanisms proposed to explain the density-edge relationship. Territory densities on seven study plots were 40% lower within edge areas (0 to 150 m from unpaved roads) than within interior areas (150 to 300 m from roads). We simulated the distribution of Ovenbird territories and concluded that passive displacement, where birds perceive hab-itat interfaces as boundaries and limit their territories entirely to forest habitat, did not ac-count for the observed density-edge pattern. Territory size was inversely related to distance from roads, providing an alternative explanation for reduced densities near edges and sug-gesting that habitat quality was higher away from roads. Pairing success was lower within edge areas than within interior zones, but the difference was not statistically significant. The proportion of males that produced fledglings did not differ between edge and interior areas. We conclude that habitat quality for Ovenbirds may be lower within 150 m of unpaved roads in extensive forested landscapes, affecting territory density and possibly reproductive suc-cess.

Park, T.J. & Dooling, R.J., 1991. Sound localization in small birds: absolute localization in azimuth. *Journal of Comparative Psychology*, 105(2), pp.125–33.

Abstract: Nine small birds of 3 species (*Melopsittacus undulatus*, *Serinus canarius*, and *Poephila guttata*) were trained in an operant procedure to fly to sound sources for food reward.

The angle between the 2 sound sources was varied on a session-by-session basis, and threshold (i.e., minimum resolvable angle) was taken as the angle that corresponded to a performance level of 75% correct. In all, thresholds were calculated for pure tones of 5 different frequencies, noise bands of 3 different spectral compositions, and species-specific contact or distance calls recorded from each of the 3 species. Thresholds for both simple and complex stimuli were larger than 25 degrees. There were statistically significant species differences for each stimulus set, but these differences were not correlated with species differences in head size. Birds with 1 ear plugged performed as well as binaural birds in this task. Birds deafened in 1 ear, however, performed at chance.

Parris, K.M. & Schneider, A., 2008. Impacts of traffic noise and traffic volume on birds of roadside habitats. *Ecology and Society*, 14(1), p.29.

Abstract: Roadside habitats are important for a range of taxa including plants, insects, mammals, and birds, particularly in developed countries in which large expanses of native vegetation have been cleared for agriculture or urban development. Although roadside vegetation may provide suitable habitat for many species, resident animals can be exposed to high levels of traffic noise, visual disturbance from passing vehicles, and the risk of collision with cars and trucks. Traffic noise can reduce the distance over which acoustic signals such as song can be detected, an effect known as acoustic interference or masking. Studies from the northern hemisphere show that the singing behavior of birds changes in the presence of traffic noise. We investigated the impact of traffic noise and traffic volume on two species of birds, the Grey Shrike-thrush (*Colluricincla harmonica*) and the Grey Fantail (*Rhipidura fuliginosa*), at 58 roadside sites on the Mornington Peninsula, southeastern Australia. The lower singing Grey Shrike-thrush sang at a higher frequency in the presence of traffic noise, with a predicted increase in dominant frequency of 5.8 Hz/dB of traffic noise, and a total effect size of 209 Hz. In contrast, the higher singing Grey Fantail did not appear to change its song in traffic noise. The probability of detecting each species on a visit to a site declined substantially with increasing traffic noise and traffic volume, with several lines of evidence supporting a larger effect of traffic noise. Traffic noise could hamper detection of song by conspecifics, making it more difficult for birds to establish and maintain territories, attract mates and maintain pair bonds, and possibly leading to reduced breeding success in noisy roadside habitats. Closing key roads during the breeding season is a potential, but untested, management strategy to protect threatened bird species from traffic noise and collision with vehicles at the time of year when they are most vulnerable to their impacts. Other management options include reducing the speed and/or volume of traffic on such roads to an acceptably low level. Ours is the first study to investigate the effect of traffic noise on the singing behavior of birds in the southern hemisphere.

Parsons, S. & Jones, G., 2000. Acoustic identification of twelve species of echolocating bat by discriminant function analysis and artificial neural networks. *Journal of Experimental Biology*, 203, pp.2641–2656.

Abstract: We recorded echolocation calls from 14 sympatric species of bat in Britain. Once digitised, one temporal and four spectral features were measured from each call. The frequency–time course of each call was approximated by fitting eight mathematical functions, and the goodness of fit, represented by the mean-squared error, was calculated. Measurements were taken using an automated process that extracted a single call from background noise and measured all variables without intervention. Two species of *Rhinolophus* were easily identified

from call duration and spectral measurements. For the remaining 12 species, discriminant function analysis and multilayer back propagation perceptrons were used to classify calls to species level. Analyses were carried out with and without the inclusion of curve-fitting data to evaluate its usefulness in distinguishing among species. Discriminant function analysis achieved an overall correct classification rate of 79 % with curve-fitting data included, while an artificial neural network achieved 87 %. The removal of curve fitting data improved the performance of the discriminant function analysis by 2 %, while the performance of a perceptron decreased by 2 %. However, an increase in correct identification rates when curve-fitting information was included was not found for all species. The use of a hierarchical classification system, whereby calls were first classified to genus level and then to species level, had little effect on correct classification rates by discriminant function analysis but did improve rates achieved by perceptrons. This is the first published study to use artificial neural networks to classify the echolocation calls of bats to species level. Our findings are discussed in terms of recent advances in recording and analysis technologies, and are related to factors causing convergence and divergence of echolocation call design in bats.

Pater, L.L., Grubb, T.G. & Delaney, D.K., 2009. Recommendations for improved assessment of noise impacts on wildlife. *Journal of Wildlife Management*, 73(5), pp.788–795.

Abstract: Research to determine noise impacts on animals benefits from methodology that adequately describes the acoustical stimulus as well as the resulting biological responses. We present acoustical considerations and research techniques that we have found to be useful. These include acoustical definitions and noise measurement techniques that conform to standardized acoustical practice and advice for controlled experimentation to supplement behavioral observation. Specific considerations include characteristics of noise stimulus, selection of noise metrics, use of frequency-weighting algorithms tailored to a specific animal species, selection and placement of noise measurement equipment, and methods for documenting animal responses. We also present arguments for measuring the noise stimulus at the location and time of each response observation. Our purpose is to recommend some baseline terminology, metrics, and techniques prerequisite to effective assessment of noise impacts on terrestrial wildlife whenever and wherever potential conflicts arise.

Patricelli, G.L. & Blickley, J.L., 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. *Auk*, 123, pp.639–649.

No abstract

Patriquin, K.J. & Barclay, R.M.R., 2003. Foraging by bats in cleared, thinned and unharvested boreal forest. *Journal of Applied Ecology*, 40(4), pp.646–657.

Abstract: 1. Modern silvicultural methods employ various styles of selective harvesting in addition to traditional clear-cutting. This can create a mosaic of patches with different tree densities that may influence habitat use by foraging bats. Use of forest patches may also vary among bat species due to variation in their manoeuvrability. Apart from studies investigating use of clear-cuts, few have tested for differences in use of forest patches by bats, or for differences among bat species. 2. We investigated the influence of various harvesting regimes, which created forest patches of different tree densities, on habitat selection by foraging bats in the boreal mixed-wood forest of Alberta, Canada. We also tested for variation in habitat selection among

species related to differences in body size and wing morphology. 3. Over two summers we assessed habitat use by bats using ultrasonic detectors to count the echolocation passes of foraging bats. We measured activity in three forest types and four tree densities, ranging from intact (unharvested) forests to clear-cuts. 4. Smaller, more manoeuvrable, species (*Myotis* spp.) were less affected by tree density than the larger, less manoeuvrable, *Lasionycteris noctivagans*. Two *Myotis* spp. differed in their habitat use. *Myotis lucifugus*, an aerial insectivore, preferred to forage along the edge of clear-cuts, while *M. septentrionalis*, a species that gleans prey from surfaces, did not forage in clear-cuts but preferred intact forest. 5. The largest species in our study, *L. noctivagans*, preferred clear-cuts and avoided intact patches. There were therefore differences in habitat selection by foraging bats among the species in our study area, and these were correlated with size and wing morphology. 6. Synthesis and applications. Our results suggest that, in the short term, thinning has minimal effect on habitat use by bats. They also indicate that silvicultural methods have different immediate effects on different species of bats that may be obscured if the community is studied as a single entity. Management for forest-dwelling bats must take such species-specific effects into consideration. Harvesting that creates a mosaic of patches with different tree densities is likely to satisfy the requirements of more species than a system with less diverse harvesting styles.

Pearl, D.L. & Fenton, M.B., 1996. Can echolocation calls provide information about group identity in the little brown bat (*Myotis lucifugus*)? *Canadian Journal of Zoology*, 74(12), pp.2184–2192.

Abstract: We studied the potential for colony-specific echolocation calls at maternity colonies of little brown bats, *Myotis lucifugus*, in Chautauqua County, New York. By analyzing echolocation calls recorded from free-flying bats returning to their roosts before dawn and those of known individuals in a captive setting, we tested for structural differences in the echolocation calls among maternity colonies. There were significant differences in the structure of the echolocation calls among the maternity colonies in both data sets, but the nature of these differences may depend on the setting in which the echolocation calls were produced. The echolocation calls of volant juveniles differed from those of adult females. Colony-specific echolocation calls could facilitate group and site recognition in microchiropteran bats.

Pearson, O.P., Koford, M.P. & Pearson, A. K., 1952. Reproduction of the lump-nosed bat (*Corynorhinus rafinesquei*) in California. *Journal of Mammalogy*, 33, pp.273-320.

No abstract

Pedersen, S., 1998. Morphometric analysis of the chiropteran skull with regard to mode of echolocation. *Journal of Mammalogy*, 79, pp.91–103.

Abstract: I compared simple morphometric data with cephalometric data on the angular arrangements of the facial and neural components of the skull of bats. The morphological dichotomy between oral and nasal emission of the echolocation pulse in the Microchiroptera is presumably under strong selective pressure to provide an acoustical horn for efficient emission of the echolocative call. Cephalometric and morphometric data compliment each other in the distinction between oral and nasal baupliiane. However, fine taxonomic resolution provided by morphometric data is subject to the otherwise plastic functional matrix of the head conforming to the acoustical axis of the skull.

Penna, M., Pottstock, H. & Velasquez, N. 2005. Effect of natural and synthetic noise on evoked vocal responses in a frog of the temperate austral forest. *Animal Behaviour*, 70, pp.639-651.

Abstract: Animals using sound communication have developed different strategies to overcome noise interference, but studies have rarely examined animals behaving in their natural environments. Males of the leptodactylid frog *Eupsophus calcaratus* exposed to natural noises of wind, rain, creek and sea surf and to a band-pass noise encompassing the main spectral components of the conspecific advertisement call increased their call rate in the presence of noises of moderate level, and this effect was particularly strong for the band-pass noise. Frogs exposed to band-pass noise of different intensities increased their call rate in response to exposures of 66–78 dB RMS sound pressure level. Call duration followed similar trends, but the effects of noise exposure on this measure of evoked vocal response were not as strong as those on call rate. The vocal responsiveness of males of this species in the presence of noise denotes adaptations to cope with high interference, in spite of the relatively simple acoustic environment of the austral temperate forest.

Perry, R.W., 2013. A review of factors affecting cave climates for hibernating bats in temperate North America. *Environmental Reviews*, 21(1), pp.28–39.

Abstract: The fungal pathogen *Geomyces destructans*, which causes white-nose syndrome in bats, thrives in the cold and moist conditions found in caves where bats hibernate. To aid managers and researchers address this disease, an updated and accessible review of cave hibernacula and cave microclimates is presented. To maximize energy savings and reduce evaporative water loss during winter, most temperate vespertilionid bats in North America select caves with temperatures between 2 and 10 °C, with 60%–100% relative humidity. Generally, the temperature in caves is similar to the mean annual surface temperature (MAST) of a region, which varies by latitude, altitude, and topography. However, MAST for most areas where caves are found in eastern North America is well above 10 °C. Thus, various factors cause cold-air infiltration that reduces temperatures of these caves during winter. These factors include depth of cave, topographic setting, airflow patterns, cave configuration, and water infiltration. Factors affecting humidity, condensation, and evaporation are also addressed. In areas where MAST is above or below the thermal requirements of *Geomyces destructans*, many caves used by bats as hibernacula may still provide favorable sites for optimal growth of this fungus.

Pettit, T.W. & Wilkins, K.T., 2012. Canopy and edge activity of bats in a quaking aspen (*Populus tremuloides*) forest. *Canadian Journal of Zoology*, 90(7), pp.798–807.

Abstract: Characteristics of edges affect the behavior of species that are active in and near edges. Forest canopies may provide edge-like habitat for bats, though bat response to edge orientation has not been well examined. We sampled bat activity in quaking aspen (*Populus tremuloides* Michx.) forest canopies and edges in Heber Valley, Utah, during summer 2009 using Anabat detectors. Categorization and regression tree (CART) analysis of echolocation characteristics (e.g., frequency, duration) identified two guilds based on characteristic frequency (i.e., high- and low-frequency guilds). We used linear regression to compare characteristics of canopy and edge vegetation (e.g., tree height, diameter at breast height) to bat activity levels. Activity levels of high-frequency bats did not respond differentially to edge vegetation; low-frequency bat activity seemed to respond to canopy height. Activity levels of high-frequency bats

were significantly greater than low-frequency bats in both edges and canopies. We detected significantly more bat activity in forest edges than in forest canopies, indicating the importance of edges to bats in forests.

Pfalzer, G. & Kusch, J., 2003. Structure and variability of bat social calls: implications for specificity and individual recognition. *Journal of Zoology*, 261(1), pp.21–33.

Abstract: Communication sounds or "social calls" of 16 European bat species (Chiroptera, Vespertilionidae) were recorded at a range of roost and foraging sites. A comparative analysis of more than 5400 individual calls for general structures and for inter- as well as intraspecific variability resulted in 50 types of calls, which differed by their specific structure and by the calling species. These types could be grouped into four different general types of calls, according to the kind and complexity of their structure, independent of the calling species. Distinct types of calls seem to have similar functions in different bat species. One general type may be used predominantly in female–infant interactions as an isolation or direction call, which serves as mutual recognition. This type of social call was also used in "tandem flights" of pairs of bats, which might increase individual knowledge of roost sites and foraging success. A second type was used in mate attraction, and a further one in an aggressive context. The fourth one was used by hindered or distressed bats. The group of "aggressive" calls is least variable, but the complex mating calls and isolation calls are very diverse. Species-specific sound structures were identified, which allowed a computational species distinction. The measured inter-individual variability of social calls should be significant for their functions in individual recognition. So, beyond common features concerning the frequency structure of bat social calls, interspecific differences, as well as the intraspecific variability of details of sonagraphic parameters, should elucidate the specific functions of the calls.

Pierson, E.D. & Rainey, W.E., 1998. Habitat use and foraging behavior of Townsend's big-eared bat (*Corynorhinus townsendii*) in coastal California. California Department of Fish and Game, Bird and Mammal Conservation Program Report 96-7:1–49.

No abstract

Pirrera, S., De Valck, E. & Cluydts, R., 2010. Nocturnal road traffic noise: A review on its assessment and consequences on sleep and health. *Environment International*, 36(5), pp.492–8.

Abstract: Research on the impact of nocturnal road traffic noise on sleep and the consequences on daytime functioning demonstrates detrimental effects that cannot be ignored. The physiological reactions due to continuing noise processing during night time lead to primary sleep disturbances, which in turn impair daytime functioning. This review focuses on noise processing in general and in relation to sleep, as well as methodological aspects in the study of noise and sleep. More specifically, the choice of a research setting and noise assessment procedure is discussed and the concept of sleep quality is elaborated. In assessing sleep disturbances, we differentiate between objectively measured and subjectively reported complaints, which demonstrates the need for further understanding of the impact of noise on several sleep variables. Hereby, mediating factors such as noise sensitivity appear to play an important role. Research on long term effects of noise intrusion on sleep up till now has mainly

focused on cardiovascular outcomes. The domain might benefit from additional longitudinal studies on deleterious effects of noise on mental health and general well-being.

Pohl, N.U., Slabbekoorn, H., Klump, G.M. & Langemann, U., 2009. Effects of signal features and environmental noise on signal detection in the great tit*, Parus major*. *Animal Behaviour*, 78(6), pp.1293–1300.

Abstract: Environmental noise caused by human activities may hamper acoustic communication in animals. Field studies in urban environments suggest that birds may alter their communicative behaviour in response to noise, but there is little experimental evidence for a detrimental effect of urban noise on perception. We investigated the masking effects of urban noise on signal detection using operant tests with great tits in the laboratory. We compared masking effects induced by urban noise, woodland noise and a typical dawn chorus, including a variety of singing birds. Maskers were presented at their natural sound pressure level and masking conditions were compared to a silent no-masker condition. The signals to be detected were composed of artificial sinusoids and noise bands mimicking signal features of natural great tit song elements. Both masker condition and signal feature significantly affected signal detection in the captive great tits. Deteriorated auditory thresholds in woodland and urban noise required the signal to be on average 12 dB and 18 dB louder than in the no-masker condition, respectively. The dawn chorus masker showed the most dramatic shift in auditory threshold of about 29 dB. Signals with the sound energy concentrated within a narrow frequency range were on average easier to detect than signals spread over a wide frequency range. Our perceptual results provide insight into how birds may counteract negative masking effects by singing song elements with specific features.

Pollak, G.D., 1988. Time is traded for intensity in the bat's auditory system. *Hearing Research*, 36(2-3), pp.107–124.

Abstract: Disparities in time and intensity are the two chief cues animals use for localizing a sound source in space. Echolocating bat belonging to the family Molossidae emit brief, ultrasonic signals for orientation that sweep downward about an octave over the duration of the pulse. Due to acoustic shadowing and the directional properties of the ears, pronounced interaural intensity disparities are created that vary as a function of azimuth. However. due to the small headwidth of these animals azimuthal changes create small interaural time disparities that are at most 30 µs. The experiments in this report are concerned with the binaural processing of time and intensity disparities using brief FM signals that simulate the animal's natural echolocation calls. Binaural neurons receiving excitation from one ear and inhibition from the other (E-l neurons) were recorded from the inferior colliculus of Mexican free-tailed hats. The majority of units sampled were highly sensitive for temporal disparities of 100-300 µs. and a few had significant changes in discharge probability when interaural time was changed by 10-20 µs. However, all E-I neurons were also sensitive to intensity disparities. With only one exception, all E-l neurons traded time for intensity. On the average, each decibel difference in intensity could be compensated for by advancing or delaying the Inhibitory sound by 47 µs. The main conclusion is that the auditory system processes interaural disparities by transforming level difference at the two ears into latency differences. Thus the discharge probabrlity of each binaural neuron is determined largely by the arrival times of the discharges from the excitatory and inhibitory ears. In view of the substantial time-intensity trading ratios, the small interaural time disparities produced by azimuthal locations off the midline play no role in shaping the

response properties of these neurons. Specific examples of how time-intensity trades can translate into a high spatial selectivity are presented.

Poussin, C. & Simmons, J., 1982. Low-frequency hearing sensitivity in the echolocating bat, *Eptesicus fuscus*. *The Journal of the Acoustical Society of America* 72(2), pp.340–342.

Abstract: Echolocating bats of the species *Eptesicus fuscus* use sound at frequencies of 10 to 100 kHz for sonar or for acoustic social communication, and they hear these ultrasonic frequencies very well. *Eptesicus* also has a lower-frequency region of auditory sensitivity from 200 Hz to 5 kHz. They may use these lower frequencies to detect and identify insect prey by passive hearing of the insect's own sounds. The hearing of *Eptesicus* at low frequencies is tuned to 0.7 to 1.3 kHz, indicating that some specialization of the auditory system, perhaps in the external or middle ear, underlies the capacity to hear these lower frequencies. The results also suggest some specific role for low frequency hearing in the bat's life, and it is know that *Eptesicus* orients toward the sounds produced by insects under natural conditions.

Press, A., Kalcounis-jlippell, M.C. & Brigham, R.M., 2005. Tree roost selection by bats : an empirical synthesis using. *Wildlife Society Bulletin*, 33(3), pp.1123–1132.

Abstract: Over the past 2 decades, we have begun to accumulate a basic understanding of the roosting and foraging ecology of temperate insectivorous bats in forests. As our under- standing improves, it is not surprising there should be attempts at synthesizing our knowledge to prioritize future research directions (e.g., Hayes 2003, Miller et al. 2003). Miller et al. (2003) reviewed results of 56 papers (1980-2001) and concluded that current data were unreliable because of small sample sizes, the short-term nature of studies, pseudoreplication, inferences beyond the scale of data collected, study design, and limitations of bat detectors and statistical analyses. Our concern is that this type of narrative synthesis that highlights limitations ignores any quantitative patterns that may exist. In this study we assess whether general patterns in North American bat use of roost trees and stand characteristics are robust enough to distill from the published literature. We used a series of meta-analyses on the same set of studies cited by Miller et al. (2003) to assess whether limitations of the current data warrant exclusion of bats from management recommendations. We used a second series of meta-analyses incorporating more recent data to determine the best current synthesis of knowledge on bat use of forests for roosting. In a third and fourth series of meta-analyses, we separated studies done on bats roosting in cavities versus roosting in foliage. In general, we found that, relative to other trees in the forest, the roost trees of bats were tall with large DBH in stands with open canopy and high snag density. In contrast, roost trees of bats did not differ from random trees with respect to live-tree density. The main differences we detected between foliage- and cavity-roosting bats were in percent canopy cover and distance to water. The roost trees of cavity-roosting species had more open canopies and were closer to water than random trees. Our results clearly show that significant patterns can be detected from the literature when data sets are combined using a meta-analytic approach.

Price, M.A., Attenborough, K. & Heap, W., 1988. Sound attenuation through trees: Measurements and models. *Journal of the Acoustical Society of America*, 84(5), pp.1836–1844.

Abstract: Measurements obtained at three British woodlands for the frequency-dependent attenuation of broadband sound with distance under neutral atmospheric conditions are compared with the predictions of a model obtained by summing the separate contributions of the ground, the trunks and branches, and the foliage. The two latter contributions are predicted by an empirically modified multiple scattering approach. The principal features of the measured spectra, vis., the low-frequency peak in excess attenuation below 500 Hz and a gradual increase of attenuation with frequency above 1 kHz, are predicted in a tolerable fashion by the composite model, as are the observed differences in acoustic propagation in the three different woodland areas.

Proppe, D.S., Sturdy, C.B. & St Clair, C.C., 2013. Anthropogenic noise decreases urban songbird diversity and may contribute to homogenization. *Global Change Biology*, 19(4), pp.1075–84.

Abstract: More humans reside in urban areas than at any other time in history. Protected urban green spaces and transportation greenbelts support many species, but diversity in these areas is generally lower than in undeveloped landscapes. Habitat degradation and fragmentation contribute to lowered diversity and urban homogenization, but less is known about the role of anthropogenic noise. Songbirds are especially vulnerable to anthropogenic noise because they rely on acoustic signals for communication. Recent studies suggest that anthropogenic noise reduces the density and reproductive success of some bird species, but that species which vocalize at frequencies above those of anthropogenic noise are more likely to inhabit noisy areas. We hypothesize that anthropogenic noise is contributing to declines in urban diversity by reducing the abundance of select species in noisy areas, and that species with low-frequency songs are those most likely to be affected. To examine this relationship, we calculated the noise-associated change in overall species richness and in abundance for seven common songbird species. After accounting for variance due to vegetative differences, species richness and the abundance of three of seven species were reduced in noisier locations. Acoustic analysis revealed that minimum song frequency was highly predictive of a species' response to noise, with lower minimum song frequencies incurring greater noise-associated reduction in abundance. These results suggest that anthropogenic noise affects some species independently of vegetative conditions, exacerbating the exclusion of some songbird species in otherwise suitable habitat. Minimum song frequency may provide a useful metric to predict how particular species will be affected by noise. In sum, mitigation of noise may enhance habitat suitability for many songbird species, especially for species with songs that include low-frequency elements.

Psyllakis, J.M. & Brigham, R.M., 2006. Characteristics of diurnal roosts used by female *Myotis* bats in sub-boreal forests. *Forest Ecology and Management*, 223(1-3), pp.93–102.

Abstract: Incorporating biodiversity objectives into industrial forest activities is a required part of sustainable management initiatives. In many temperate forest environments, bats represent a large portion of the vertebrate species diversity, but for most locations we lack basic data regarding habitat needs. We describe characteristics of diurnal roost trees and stands used by radio-tagged bats in the sub-boreal forest of central British Columbia. We tracked 12 female *Myotis lucifugus*, 2 *M. volans*, and 1 *M. septentrionalis* to 33-day-roosts and found 4 additional roosts by random observations and inspecting cavities for guano. The 37 roosts occurred primarily in two species of trees, lodgepole pine (*Pinus contorta*; n = 18) and trembling aspen (*Populus tremuloides*; n = 17). In lodgepole pine, trees were in early stages of decay and bats

roosted under bark, usually alone. Trembling aspen more typically contained groups of roosting bats (henceforth communal roosts; n = 14 trees). Communal roosts were all in vertical cracks that were formed from a combination of trauma causing a wood scar and decay fungi. Other species of trees used as roosts included black cottonwood (*P. balsamifera*; n = 1) and hybrid white spruce (*Picea glauca x engelmannii*; n = 1).We constructed logistic regression models for conifer and deciduous roosts used by *M. lucifugus* and *M. volans* to determine selection characteristics. Results from our analyses suggest that in sub-boreal forests, management of bat habitat should focus on the maintenance of: (1) mature stands; (2) individual lodgepole pine trees with exfoliating bark, few missing limbs, and free of potential obstructions to roost entrance; (3) large diameter trembling aspen, with long vertical cracks, in stands with fewer stems per hectare. No roosts were located in cavities excavated by woodpeckers, which implies that in our study area management plans that incorporate bats as secondary cavity users may not be sufficient to maintain populations.

Pu, J. & Wei, L., 2012. Prediction of the traffic noise around newly constructed highways. 2012 International Conference on Information Management, Innovation Management and Industrial Engineering, pp.519–522.

Abstract: For more accurate prediction on the impact of noise of highways under construction and newly constructed highways on the nearby environment, and to find effective way to protect sensitive points near these highways, models suitable for the construction period and operation period were established according to the modes of noise influence on the environment and China's "Specifications of environmental impact evaluation on road construction projects". The models were used for the evaluation of noise level and environmental impact on the section from Cangzhou to Qiantong of BeijingShanghai highway, in construction and operation periods. The results show that in the highway construction period, noise may decrease to the standard level at 100 m away from the construction site in the daytime, while at night it needs 400 m to reach the same level. Results for the operation periods show that there are four acoustic environment sensitive points along the main line. These results indicated that the models can used to predict the impact of the ambient noise of highway construction projects.

Puechmaille, S.J., Borissov, I.M., Zsebok, S., Allegrini, B., Hizem, M., Kuenzel, S., Schuchmann, M., Teeling, E.C. & Siemers, B.M., 2014. Female mate choice can drive the evolution of high frequency echolocation in bats: a case study with *Rhinolophus mehelyi*. *PloS One*, 9(7), p.e103452.

Abstract: Animals employ an array of signals (i.e. visual, acoustic, olfactory) for communication. Natural selection favours signals, receptors, and signalling behaviour that optimise the received signal relative to background noise. When the signal is used for more than one function, antagonisms amongst the different signalling functions may constrain the optimisation of the signal for any one function. Sexual selection through mate choice can strongly modify the effects of natural selection on signalling systems ultimately causing maladaptive signals to evolve. Echolocating bats represent a fascinating group in which to study the evolution of signalling systems as unlike bird songs or frog calls, echolocation has a dual role in foraging and communication. The function of bat echolocation is to generate echoes that the calling bat uses for orientation and food detection with call characteristics being directly related to the exploitation of particular ecological niches. Therefore, it is commonly assumed that echolocation has been shaped by ecology via natural selection. Here we demonstrate for the first

time using a novel combined behavioural, ecological and genetic approach that in a bat species, *Rhinolophus mehelyi*: (1) echolocation peak frequency is an honest signal of body size; (2) females preferentially select males with high frequency calls during the mating season; (3) high frequency males sire more off-spring, providing evidence that echolocation calls may play a role in female mate choice. Our data refute the sole role of ecology in the evolution of echolocation and highlight the antagonistic interplay between natural and sexual selection in shaping acoustic signals.

Pye, A., 1966. The structure of the cochlea in Chiroptera. I. Microchiroptera: Emballonuroidea and Rhinolophoides. *Journal of Morphology*, 118, pp.495-510.

Abstract: The structure of the ears, especially of the cochleae, has been examined in two superfamilies, i.e. Emballonuroidea and Rhinolophoidea of the Microchiroptera. An intra-vitam fixation method was used and gave good histological preparations. The following features of the cochlea have been measured: the general size of the cochlea, the width and thickness of the basilar membrane, the size of the spiral ligament and the height of the cells of Claudius. The interpretation of measurements is discussed in relation to the nature of ultrasonic sounds produced by bats. It is concluded that functional interpretation of specific cochlear modifications cannot be assessed at present.

Pye, A., 1970. The structure of the cochlea in Chiroptera. A selection of Microchiroptera from Africa. *Journal of Zool. Lond*., 162, pp.335-343.

Abstract: Various measurements have been made on the cochleae of some insectivorous African Microchiroptera, including representatives from all the three superfamilies, the Emballonuroidea, Rhinolophoidea and Vespertilionoidea. Their ultrasonic pulses have been recorded and correlations between the structure of the cochlea and the pulses have been attempted. The most extreme measurements are found in the Rhinolophoidea, confirming earlier results in other species.

Pye, J.D. & Roberts, L.H., 1970. Ear movements in a hipposiderid bat. *Nature* 225, 285-286.

No abstract

Radford, A.N., Kerridge, E. & Simpson, S.D., 2014. Acoustic communication in a noisy world: can fish compete with anthropogenic noise? *Behavioral Ecology*, 25, pp.1022–1030.

Abstract: Anthropogenic (man-made) noise has changed the acoustic environment both on land and underwater and is now recognized as a pollutant of international concern. Increasing numbers of studies are assessing how noise pollution affects animals across a range of scales, from individuals to communities, but the topic receiving the most research attention has been acoustic communication. Although there is now an extensive literature on how signalers might avoid potential masking from anthropogenic noise, the vast majority of the work has been conducted on birds and marine mammals. Fish represent more than half of all vertebrate species, are a valuable and increasingly utilized model taxa for understanding behavior, and provide the primary source of protein for >1 billion people and the principal livelihoods for hunderds of millions. Assessing the impacts of noise on fish is therefore of clear biological, ecological, and

societal importance. Here, we begin by indicating why acoustic communication in fish is likely to be impacted by anthropogenic noise. We then use studies from other taxa to outline 5 main ways in which animals can alter their acoustic signaling behavior when there is potential masking due to anthropogenic noise and assess evidence of evolutionary adaptation and behavioral plasticity in response to abiotic and biotic noise sources to consider whether such changes are feasible in fish. Finally, we suggest directions for future study of fish acoustic behavior in this context and highlight why such research may allow important advances in our general understanding of the impact of this global pollutant.

Radle, A.L., 2007. The Effect Of Noise On Wildlife: A Literature Review. Online: http://wfae.proscenia.net/library/articles/radle_effect_noise_wildlife.pdf

Abstract: Noise pollution, as it effects humans, has been a recognized problem for decades, but the effect of noise on wildlife has only recently been considered a potential threat to animal health and long-term survival. Research into the effects of noise on wildlife, which has been growing rapidly since the 1970s, often presents conflicting results because of the variety of factors and variables that can effect and/or interfere with the determination of the actual effects that human-produced noise is having on any given creature. Both land and marine wildlife have been studied, especially in regards to noise in the National Parks System and the onslaught of human- made cacophony in the oceans from military, commercial and scientific endeavors. Most researchers agree that noise can effect an animal's physiology and behavior, and if it becomes a chronic stress, noise can be injurious to an animal's energy budget, reproductive success and long-term survival. Armed with this understanding it should follow that humans would attempt to minimize the threat to wildlife by reducing the amount of noise that they are exposed to in natural areas; but this has not been the situation. Natural areas continue to be degraded by human-made noise, wildlife continues to suffer from these disturbances, and to date the majority of the debate revolves around the egocentric demands of people to either produce more noise in nature (through motorized recreation, scientific research, military exercises etc.) or experience natural areas in the absence of anthropogenic noise. Neither side has adequately addressed the issue from the biocentric view of wildlife and the known, or as yet undiscovered, damage that our increasingly noisy human-altered environment is inflicting upon them.

Ramasindrazana, B., Goodman, S.M., Schoeman, M.C. & Appleton, B., 2011. Identification of cryptic species of *Miniopterus* bats (Chiroptera: Miniopteridae) from Madagascar and the Comoros using bioacoustics overlaid on molecular, genetic and morphological characters. *Biological Journal of the Linnean Society*, 104(2), pp.284–302.

Abstract: The number of *Miniopterus* bat species on Madagascar and the nearby Comoros islands (Malagasy region) has risen from four to 11. These recently described cryptic taxa have been differentiated primarily based on molecular markers and associated a posteriori morphological characters that corroborate the different clades. Members of this Old World genus are notably conservative in morphology across their range. Several sites on Madagascar hold up to four small-bodied taxa of this genus that are morphologically similar to one another, although they can be distinguished based on the tragus, an ear structure associated with echolocation. *Miniopterus* often emit species specific calls. In the present study, we analyze the bioacoustics of the 11 species of *Miniopterus* currently recognized from the Malagasy region, with an initial identification of the 87 recorded and collected individuals based on molecular markers and

certain morphological characters. In most cases, bioacoustic parameters differentiate species and have taxonomic utility. *Miniopterus griveaudi* populations, which occur on three islands (Madagascar, Anjouan, and Grande Comore), showed no significant differences in peak echolocation frequencies. After running a discriminant function analysis based on five bioacoustic parameters, some mismatched assignments of Malagasy species were found, which include allopatric sister-taxa and sympatric, phylogenetically not closely-related species of similar body size. Because the peak echolocation frequencies of two species (*Miniopterus sororculus* and *Miniopterus aelleni*) were independent of body size, they were acoustically distinguishable from cryptic sympatric congeners. The small variation around the allometric relationship between body size and peak echolocation frequency of Malagasy *Miniopterus* species suggests that intraspecific communication rather than competition or prey detection may be the driver for the acoustic divergence of these two species. Our well-defined echolocation data allow detailed ecological work to commence aiming to test predictions about the relative roles of competition, prey availability, and social communication on the evolution of echolocation in Malagasy *Miniopterus* species.

Rambaldini, D.A. & Brigham, R.M., 2008. Torpor use by free-ranging pallid bats (*Antrozous pallidus*) at the northern extent of their range. *Journal of Mammalogy*, 89(4), pp.933–941.

Abstract: Torpor minimizes energy expenditure and water loss during periods of inclement weather, low prey availability, or both, and appears especially important in harsh environments such as deserts. We investigated use of torpor by free-ranging adult male pallid bats (*Antrozous pallidus*) at the northern limit of their range in the semiarid Okanagan Valley in British Columbia, Canada. We predicted that males would use torpor frequently during the active season and that ambient temperature (T_a) as well as nutritional condition (body condition index [BCI]) would affect torpor use. We expected roost microclimate to be conducive to daily heterothermy given that roosts had cool morning temperatures that increased in the afternoon. We used temperature-sensitive radiotransmitters to measure skin temperature (T_{skin}) of 8 bats from June to August 2003. Seven individuals used torpor each day (n = 54 tracking days) but not at night. Torpor duration increased as mean daytime Ta decreased albeit the relationship differed between individuals. There was no significant effect of individual on the relationship between minimum T_{skin} during torpor and T_a. BCI was significantly and inversely correlated with torpor bout duration. Mean daytime temperatures in rock crevice roosts approached 30°C and fluctuated less than T_a.

Rambaldini, D.A. & Brigham, R.M., 2011. Pallid bat (*Antrozous pallidus*) foraging over native and vineyard habitats in British Columbia, Canada. *Canadian Journal of Zoology*, 89(9), pp.816–822.

Abstract: Optimal foraging theory predicts organisms will forage in habitats providing the most profitable prey. Human alterations to ecosystems may affect predators' foraging activity by changing landscape features, prey types, and prey availability. Assessing the selection of foraging habitats in a heterogeneous landscape can provide data to improve land management and conservation policies. In Canada, the pallid bat (*Antrozous pallidus* (LeConte, 1856); Vespertilionidae) is listed as threatened partly because of loss or modification of shrub–steppe habitat. Our purpose was to determine if vineyards provide a suitable surrogate for foraging habitat relative to native habitat. We used pitfall traps to compare prey abundance in each habitat

and analyzed faeces to assess diet composition. Over 24 nights, we surveyed both habitats for foraging bats. Bats foraged over vineyards, but we recorded significantly more foraging activity over native habitat. We collected over 2000 arthropods in pitfall traps and found significantly more in native habitat compared with vineyards. Species eaten by pallid bats were present in both habitats. Scarab beetles (Coleoptera: Scarabidae) and Jerusalem crickets (Orthopthera: Stenopelmatidae) represented the principal prey. The use of vineyards by pallid bats for foraging suggests that while they are adapting to a changing landscape, reduced prey abundance in vineyards may negatively affect them over the long term.

Ramprashad, F., Landolt, J.P., Money, K.E., Clark, D. & Laufer, J., 1979. A morphometric study of the cochlea of the little brown bat (*Myotis lucifugus*). *Journal of Morphology*, 160, pp.345-358.

Abstract: A detailed morphometric study of the basilar membrane was made from serial sections and graphic reconstructions of the cochlea of three little brown bats. Four distinct morphometric changes were observed within the basilar membrane. First, between 0-1.4 mm from the basal end of the cochlea, there is a rapid increase in width and cross-sectional area of the basilar membrane. Secondly, between 1.4-2.5 mm, there is little change in width of the basilar membrane (its cross-sectional area is at its greatest in this region). Thirdly, between 2.7-3.1 mm, there is a sudden decrease in cross-sectional area concomitant with an increase in the width of the basilar membrane. Finally, between 3.1 mm and the apex, there is a gradual decrease in cross-sectional area concomitant with an increase in the width of the basilar membrane. The magnitudes of the cross-sectional areas of the scalae media and vestibuli decrease from base to apex, but this is not true for the scala tympani. The cross-sectional area of the scala tympani appears to decrease from the base to 0.7 mm, then it increases up to 1.4 mm, and then it decreases to the apex. These morphometric changes in the basilar membrane of the little brown bat are compared to those in other echolocating and non-echolocating mammals. The significance of these changes is discussed in relation to the range of hearing in the little brown bat.

Randall, L.A., Barclay, R.M.R., Reid, M.L. & Jung, T.S., 2011. Recent infestation of forest stands by spruce beetles does not predict habitat use by little brown bats (*Myotis lucifugus*) in southwestern Yukon, Canada. *Forest Ecology and Management*, 261(11), pp.1950–1956.

Abstract: Insect outbreaks affect forest structure which may have significant effects on the habitat of other animals. Forest-dwelling insectivorous bats are likely affected by associated changes in the abundance of roost trees and insect prey, altered foraging and flying efficiency, and predation risk. We examined the short term effects (3-13 years post-infestation) of an outbreak of spruce beetles (*Dendroctonus rufipennis*) on the habitat use of little brown bats (*Myotis lucifugus*) in the boreal forest of the southwestern Yukon, Canada. We measured bat activity, using Anabat II bat detectors, in 90 forested stands that had experienced from 0 to 90% tree mortality due to spruce beetles. We used generalized linear models to assess whether bat activity varied with tree mortality, season, tree density, canopy closure, or distance to the nearest lake or town. Bat activity did not vary significantly with tree mortality, season, or canopy closure, but decreased with increasing tree density. Bat activity was significantly greater in areas close to both the nearest lake and nearest town, and was low in areas that were far from either. Our results indicate that in the short term, habitat use by little brown bats was not related to the

severity of spruce beetle infestation, but suggest that in the long-term, bats may be positively affected by decreased tree density as beetle-killed trees fall down.

Rasmussen, K.B., 1985. On the effect of terrain profile on sound propagation outdoors. *Journal of Sound and Vibration*, 98(1), pp.35–44.

Abstract: Various models describing outdoor sound propagation over wedge barriers and three sided barriers are described. The starting point is the approximate solution for diffraction by a hard wedge given by Kouyoumjian and Pathak [l]. This solution is extrapolated to cover the finite impedance case by employing arguments originating from Jonasson [2]. The Kbuyoumjian and Pathak solution is also used in connection with the calculation method originating from Pierce [3] for diffraction by a three-sided barrier. The theoretical results are compared with measured data for sound propagation over grass-covered earth berms, from a loudspeaker source. Calculated and measured results for a road traffic noise situation involving an earth berm are also presented.

Rasmussen, K.B., 1990. Approximate formulae for short-distance outdoor sound propagation. *Applied Acoustics*, 29(4), pp.313–324.

Abstract: A number of asymptotic approximations to sound propagation from a point source over level ground have been developed over the years and, since it is difficult to determine their accuracy in practical situations, some numerical tests are performed. The influence of propagation within the ground itself, i.e. so-called extended reaction, is also investigated. Finally, a new empirical approximation that is simple to use is introduced as a consequence of the low efficiency of the mathematically rigorous solutions. The empirical solution is accurate for distances below approximately 200 m.

Rasmussen, S., Glickman, G., Norinsky, R., Quimby, F.W. & Tolwani, R.J., 2009. Construction noise decreases reproductive efficiency in mice. *Journal of the American Association for Laboratory Animal Science*, 48(4), pp.363–370.

Abstract: Excessive noise is well known to impair rodent health. To better understand the effect of construction noise and to establish effective noise limits during a planned expansion of our vivarium, we analyzed the effects of construction noise on mouse gestation and neonatal growth. Our hypothesis was that high levels of construction noise would reduce the number of live births and retard neonatal growth. Female Swiss Webster mice were individually implanted with 15 B6CBAF1/J embryos and then exposed to 70- and 90-dBA concrete saw cutting noise samples at defined time points during gestation. In addition, groups of mice with litters were exposed to noise at 70, 80, or 90 dBA for 1 h daily during the first week after parturition. Litter size, birth weight, incidence of stillborn pups, and rate of neonatal weight gain were analyzed. Noise decreased reproductive efficiency by decreasing live birth rates and increasing the number of stillborn pups.

Ratcliffe, J.M. & Dawson, J.W., 2003. Behavioural flexibility: the little brown bat, *Myotis lucifugus*, and the northern long-eared bat, *M. septentrionalis* , both glean and hawk prey. *Animal Behaviour*, 66(5), pp.847–856.

Abstract: We present behavioural data demonstrating that the little brown bat, *Myotis lucifugus*, and the northern long-eared bat, *M. septentrionalis*, can glean prey from surfaces and take prey

on the wing. Our data were collected in a large outdoor flight room mimicking a cluttered environment. We compared and analysed flight behaviours and echolocation calls used by each species of bat when aerial hawking and gleaning. Our results challenge the traditional labelling of *M. lucifugus* as an obligate aerial-hawking species and show that *M. septentrionalis*, which is often cited as a gleaning species, can capture airborne prey. As has been shown in previous studies, prey-generated acoustic cues were necessary and sufficient for the detection and localization of perched prey. We argue that the broadband, high-frequency, downward sweeping, frequency-modulated calls used by some bats when gleaning prey from complex surfaces resolve targets from background. First, because calls of lower frequency and narrower bandwidth are sufficient for assessing a surface before landing, and second, because there are few, if any, simple surfaces in nature from which substrate-gleaning behaviours in wild bats would be expected.

Ratcliffe, J.M., Jakobsen, L., Kalko, E.K. &Surlykke, A., 2011. Frequency alternation and an offbeat rhythm indicate foraging behavior in the echolocating bat, *Saccopteryx bilineata. Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 197(5), pp.413–23.

Abstract: The greater sac-winged bat, *Saccopteryx bilineata* (Emballonuridae), uses two distinct echolocation call sequences: a "monotonous" sequence, where bats emit ~48 kHz calls at a relatively stable rate, and a frequency-alternating sequence, where bats emit calls at ~45 kHz (low-note call) and ~48 kHz (high-note call). The frequencies of these low-high-note pairs remain stable within sequences. In Panama, we recorded echolocation calls from S. bilineata with a multi-microphone array at two sites: one a known roosting site, the other a known foraging site. Our results indicate that this species (1) only produces monotonous sequences in non-foraging contexts and, at times, directly after emitting a feeding buzz and (2) produces frequency-alternating sequences when actively foraging. These latter sequences are also characterized by an unusual, offbeat emission rhythm. We found significant positive relationships between (1) call intensity and call duration and (2) call intensity and distance from clutter. However, these relationships were weaker than those reported for bats from other families. We speculate on how call frequency alternation and an offbeat emission rhythm might reflect a novel strategy for prey detection at the edge of complex habitat in this ancient family of bats.

Ratcliffe, J.M., Raghuram, H., Marimuthu, G., Fullard, J.H. & Fenton, M.B., 2005. Hunting in unfamiliar space: echolocation in the Indian false vampire bat, *Megaderma lyra*, when gleaning prey. *Behavioral Ecology and Sociobiology*, 58(2), pp.157–164.

Abstract: The literature suggests that in familiar laboratory settings, Indian false vampire bats (*Megaderma lyra*, family Megadermatidae) locate terrestrial prey with and without emitting echolocation calls in the dark and cease echolocating when simulated moonlit conditions presumably allow the use of vision. More recent laboratory-based research suggests that *M. lyra* uses echolocation throughout attacks but at emission rates much lower than those of other gleaning bats. We present data from wild-caught bats hunting for and capturing prey in unfamiliar conditions mimicking natural situations. By varying light level and substrate complexity we demonstrated that hunting *M. lyra* always emit echolocation calls and that emission pat terns are the same regardless of light/substrate condition and similar to those of other wild-caught gleaning bats. Therefore, echoic information appears necessary for this species

when hunting in unfamiliar situations, while, in the context of past research, echolocation may be supplanted by vision, Spatial memory or both in familiar spaces.

Razak, K. & Fuzessery, Z., 2002. Functional organization of the pallid bat auditory cortex: emphasis on binaural organization. *Journal of Neurophysiology*, 87, pp.72–86.

Abstract: This report maps the organization of the primary auditory cortex of the pallid bat in terms of frequency tuning, selectivity for behaviorally relevant sounds, and interaural intensity difference (IID) sensitivity. The pallid bat is unusual in that it localizes terrestrial prey by passively listening to prey-generated noise transients (1–20 kHz), while reserving high-frequency (30 kHz) echolocation for obstacle avoidance. The functional organization of its auditory cortex reflects the need for specializations in echolocation and passive sound localization. Best frequencies were arranged tonotopically with a general increase in the caudolateral to rostromedial direction. Frequencies between 24 and 32 kHz were under-represented, resulting in hypertrophy of frequencies relevant for prey localization and echolocation. Most neurons (83%) tuned 30 kHz responded preferentially to broadband or band-pass noise over single tones. Most neurons (62%) tuned 30 kHz responded selectively or exclusively to the 60- to 30-kHz downward frequency-modulated (FM) sweep used for echolocation. Within the low-frequency region, neurons were placed in two groups that occurred in two separate clusters: those selective for low- or high-frequency band-pass noise and suppressed by broadband noise, and neurons that showed no preference for band-pass noise over broadband noise. Neurons were organized in homogeneous clusters with respect to their binaural response properties. The distribution of binaural properties differed in the noise- and FM sweep-preferring regions, suggesting task-dependent differences in binaural processing. The low-frequency region was dominated by a large cluster of binaurally inhibited neurons with a smaller cluster of neurons with mixed binaural interactions. The FM sweep-selective region was dominated by neurons with mixed binaural interactions or monaural neurons. Finally, this report describes a cortical substrate for systematic representation of a spatial cue, IIDs, in the low-frequency region. This substrate may underlie a population code for sound localization based on a systematic shift in the distribution of activity across the cortex with sound source location.

Razak, K.A. & Fuzessery, Z.M., 2007. Development of functional organization of the pallid bat auditory cortex. *Hearing Research*, 228(1-2), pp.69–81.

Abstract: The primary auditory cortex is characterized by a tonotopic map and a clustered organization of binaural properties. The factors involved in the development of overlain representation of these two properties are unclear. We addressed this issue in the auditory cortex of the pallid bat. The adult pallid bat cortex contains a systematic relationship between best frequency (BF) and binaural properties. Most neurons with BF<30 kHz are binaurally inhibited (EO/I), while most neurons with BF>30 kHz are monaural (EO). As in other species, binaural properties are clustered. The EO/I cluster contains a systematic map of interaural intensity difference (IID) sensitivity. We asked if these properties are present at the time the bat acquires its full audible range (postnatal day [P] 15). Tonotopy, relationship between BF and binaural properties, and the map of IID sensitivity are adult-like at P15. However, binaural facilitation is only observed in pups older than P25. Frequency selectivity shows a BF-dependent sharpening during development. Thus, overlain representation of binaural properties and tonotopy in the pallid bat cortex is remarkably adult-like at an age when the full audible range is first present, suggesting an experience-independent development of overlapping feature maps.

Read, J., Jones, G. & Radford, A. N., 2013. Fitness costs as well as benefits are important when considering responses to anthropogenic noise. *Behavioral Ecology*, 25(1), pp.4–7.

Abstract: Trade-offs lie at the heart of behavioral ecology, with our ultimate understanding of many behaviors reliant on an assessment of both fitness benefits and costs. However, the rapidly expanding research literature on the impacts of anthropogenic noise (a recently recognized global pollutant) tends to focus on the benefits likely to be accrued by any resulting behavioral adaptations or plasticity. In particular, although studies investigating acoustic communication (the topic receiving the most attention to date) invariably discuss, and occasionally attempt to measure, the perceived benefits in terms of reduced masking that might arise from vocal adjustments by signalers, only rarely are the potential fitness costs even mentioned. The bias toward benefits prevents a full understanding of the consequences of anthropogenic noise, including the implications for population viability and community structure. Here, we argue for a greater consideration of fitness costs, outline a number of specific examples (reduced transmission distances, increased risk of predation/parasitism, altered energy budgets, loss of vital information), make suggestions about how to move forward, and showcase why a balanced view is as crucial in this field as any other aspect of behavioral ecology.

Reichard, J.D., Prajapai, S.I., Austad, S.N., Keller, C. & Kunz, T.H., 2010. Thermal windows on Brazilian free-tailed bats facilitate thermoregulation during prolonged flight. Integrative and comparative biology, 50(3), pp.358–70.

Abstract: The Brazilian free-tailed bat (*Tadarida brasiliensis*) experiences challenging thermal conditions while roosting in hot caves, flying during warm daylight conditions, and foraging at cool high altitudes. Using thermal infrared cameras, we identified hot spots along the flanks of free-ranging Brazilian free-tailed bats, ventral to the extended wings. These hot spots are absent in syntopic cave myotis (*Myotis velifer*), a species that forages over relatively short distances, and does not engage in long-distance migration. We hypothesized that the hot spots, or "radiators," on Brazilian free-tailed bats may be adaptations for migration, particularly in this long-distance, high-flying species. We examined the vasculature of radiators on Brazilian free-tailed bats with transillumination to characterize the unique arrangements of arteries and veins that are positioned perpendicular to the body in the proximal region of the wing. We hypothesized that these radiators aid in maintaining heat balance by flushing the uninsulated thermal window with warm blood, thereby dissipating heat while bats are flying under warm conditions, but shunting blood away and conserving heat when they are flying in cooler air at high altitudes. We also examined fluid-preserved specimens representing 122 species from 15 of 18 chiropteran families and radiators appeared present only in species in the family Molossidae, including both sedentary and migratory species and subspecies. Thus, the radiator appears to be a unique trait that may facilitate energy balance and water balance during sustained dispersal, foraging, and long-distance migration.

Reijniers, J. & Peremans, H., 2010. On population encoding and decoding of auditory information for bat echolocation. *Biological Cybernetics*, 102(4), pp.311–26.

Abstract: In this article, we study the neural encoding of acoustic information for FM-bats (such as *Eptesicus fuscus*) in simulation. In echolocation research, the frequency-time sound representation as expressed by the spectrogram is often considered as input. The rationale behind this is that a similar representation is present in the cochlea, i.e. the receptor potential of the inner

hair cells (IHC) along the length of the cochlea, and hence similar acoustic information is relayed to the brain. In this article, we study to what extent the latter assumption is true. The receptor potential is converted into neural activity of the synapting auditory nerve cells (ANC), and information might be lost in this conversion process. Especially for FM-bats, this information transmission is not trivial: in contrast to other mammals, they detect short transient signals, and consequently neural activity can only be integrated over very limited time intervals. To quantify the amount of information transmitted we design a neural network-based algorithm to reconstruct the IHC receptor potentials from the spiking activity of the synapting auditory neurons. Both the receptor potential and the resulting neural activity are simulated using Meddis' peripheral model. Comparing the reconstruction to the IHC receptor potential, we quantify the information transmission of the bat hearing system and investigate how this depends on the intensity of the incoming signal, the distribution of auditory neurons, and previous masking stimulation (adaptation). In addition, we show how this approach allows to inspect which spectral features survive neural encoding and hence can be relevant for echolocation.

Reynolds, R.P., Kinard, W.L., Degraff, J.J., Leverage, N. & Norton, H. N., 2010. Noise in a Laboratory Animal Facility from the Human and Mouse Perspectives. *Journal of the American Association for Laboratory Animal Science*, 49(5), pp.592–597.

Abstract: The current study was performed to understand the level of sound produced by ventilated racks, animal transfer stations, and construction equipment that mice in ventilated cages hear relative to what humans would hear in the same environment. Although the ventilated rack and animal transfer station both produced sound pressure levels above the ambient level within the human hearing range, the sound pressure levels within the mouse hearing range did not increase above ambient noise from either noise source. When various types of construction equipment were used 3 ft from the ventilated rack, the sound pressure level within the mouse hearing range was increased but to a lesser degree for each implement than were the sound pressure levels within the human hearing range. At more distant locations within the animal facility, sound pressure levels from the large jackhammer within the mouse hearing range decreased much more rapidly than did those in the human hearing range, indicating that less of the sound is perceived by mice than by humans. The relatively high proportion of low-frequency sound produced by the shot blaster, used without the metal shot that it normally uses to clean concrete, increased the sound pressure level above the ambient level for humans but did not increase sound pressure levels above ambient noise for mice at locations greater than 3 ft from inside of the cage, where sound was measured. This study demonstrates that sound clearly audible to humans in the animal facility may be perceived to a lesser degree or not at all by mice, because of the frequency content of the sound.

Roberts, C. 2009. Construction noise and vibration impact on sensitive premises. *Proceedings of Acoustics, Australian Acoustical Society*. Online: http://www.acoustics.asn.au/conference_proceedings/AAS2009/papers/p11.pdf

Abstract: Construction noise and vibration must be considered an essential part of the development of any transportation facility. Road and tunnel construction is often conducted in close proximity to residential and commercial premises and should be predicted, controlled and monitored in order to avoid excessive noise and vibration impacts. Construction noise and vibration can threaten a project's schedule if not adequately analysed and if the concerns of the community are not addressed and incorporated.

Rodhouse, T.J., Vierling, K.T. & Irvine, K.M., 2011. A practical sampling design for acoustic surveys of bats. *The Journal of Wildlife Management*, 75(5), pp.1094–1102.

Abstract: Acoustic surveys are widely used for describing bat occurrence and activity patterns and are increasingly important for addressing concerns for habitat management, wind energy, and disease on bat populations. Designing these surveys presents unique challenges, particularly when a probabilistic sample is required for drawing inference to unsampled areas. Sampling frame errors and other logistical constraints often require survey sites to be dropped from the sample and new sites added. Maintaining spatial balance and representativeness of the sample when these changes are made can be problematic. Spatially balanced sampling designs recently developed to support aquatic surveys along rivers provide solutions to a number of practical challenges faced by bat researchers and allow for sample site additions and deletions, support unequal-probability selection of sites, and provide an approximately unbiased local neighborhood-weighted variance estimator that is efficient for spatially structured populations such as is typical for bats. We implemented a spatially balanced design to survey canyon bat (*Parastrellus hesperus*) activity along a stream network. The spatially balanced design accommodated typical logistical challenges and yielded a 25% smaller estimated standard error for the mean activity level than the usual simple random sampling estimator. Spatially balanced designs have broad application to bat research and monitoring programs and will improve studies relying on model-based inference (e.g., occupancy models) by providing flexibility and protection against violations of the independence assumption, even if design-based estimators are not used. Our approach is scalable and can be used for pre- and post-construction surveys along wind turbine arrays and for regional monitoring programs.

Rogers, D.S., Belk, M.C., Gonzalez, M.W. & Coleman, B.L., 2006. Patterns of habitat use by bats along a riparian corridor in northern Utah. *The Southwestern Naturalist*, 51(1), pp.52–58.

Abstract: We examined patterns of habitat use within a community of bats along the Provo River in Heber Valley, Utah. The landscape was divided into 5 habitat categories: riparian forest, wetland, agricultural field, edge, and a habitat restoration site. We used Anabat II bat detectors to record the number of echolocation calls per night within each habitat type as an index of bat activity. Echolocation calls were classified into foraging guilds based on acoustic traits, and we analyzed activity by entire community and by the 4 guilds related to habitat type and environmental variables. Activity was not significantly related to moon phase, average temperature, or day of the season. Activity by the entire bat community was significantly higher in riparian forest and edge habitats compared to other habitat types. Activity of the "'high'" *Myotis* guild was significantly greater in the riparian forest, edge habitats, and in the restored habitat site. Similarly, activity by the "'low'" *Myotis* guild was significantly higher in riparian forest and edge habitats. In contrast to the *Myotis* guilds, activity of molossids was significantly higher in agricultural fields compared to other habitats. Activity by the "'low'" *Eptesicus* guild did not vary significantly among habitats.

Ross, Z., Kheirbek, I., Clougherty, J.E., Ito, K., Matte, T., Markowitz, S. & Eisl, H., 2011. Noise, air pollutants and traffic: continuous measurement and correlation at a high-traffic location in New York City. *Environmental Research*, 111(8), pp.1054–63.

Abstract: BACKGROUND: Epidemiological studies have linked both noise and air pollution to common adverse health outcomes such as increased blood pressure and myocardial infarction. In urban settings, noise and air pollution share important sources, notably traffic, and several recent studies have shown spatial correlations between noise and air pollution. The temporal association between these exposures, however, has yet to be thoroughly investigated despite the importance of time series studies in air pollution epidemiology and the potential that correlations between these exposures could at least partly confound statistical associations identified in these studies. METHODS: An aethelometer, for continuous elemental carbon measurement, was co-located with a continuous noise monitor near a major urban highway in New York City for six days in August 2009. Hourly elemental carbon measurements and hourly data on overall noise levels and low, medium and high frequency noise levels were collected. Hourly average concentrations of fine particles and nitrogen oxides, wind speed and direction and car, truck and bus traffic were obtained from nearby regulatory monitors. Overall temporal patterns, as well as day-night and weekday-weekend patterns, were characterized and compared for all variables. RESULTS: Noise levels were correlated with car, truck, and bus traffic and with air pollutants. We observed strong day-night and weekday-weekend variation in noise and air pollutants and correlations between pollutants varied by noise frequency. Medium and high frequency noise were generally more strongly correlated with traffic and traffic-related pollutants than low frequency noise and the correlation with medium and high frequency noise was generally stronger at night. Correlations with nighttime high frequency noise were particularly high for car traffic (Spearman rho=0.84), nitric oxide (0.73) and nitrogen dioxide (0.83). Wind speed and direction mediated relationships between pollutants and noise. CONCLUSIONS: Noise levels are temporally correlated with traffic and combustion pollutants and correlations are modified by the time of day, noise frequency and wind. Our results underscore the potential importance of assessing temporal variation in co-exposures to noise and air pollution in studies of the health effects of these urban pollutants.

Roux, D.S. Le & Waas, J.R., 2012. Do Long-Tailed Bats Alter Their Evening Activity in Response to Aircraft Noise? *Acta Chiropterologica*, 14(1), pp.111–120.

Abstract: Human-generated noise may alter animal activity patterns and mask vocal signals. We used field-based observations and a playback experiment to investigate whether aircraft activity and noise alter the evening activity of New Zealand long-tailed bats (*Chalinolobus tuberculatus*) — a cryptic threatened species. Low-altitude aircraft activity temporally overlapped bat activity near the runway of an international airport, but was unlikely to mask echolocation pulses as aircraft noise was most intense at ≤ 10 kHz. There was no statistically significant difference in mean bat activity during and after overflights compared with pre-aircraft activity. The experiment revealed that playback stimuli (aircraft passes and two controls: silent tracks and blackbird (*Turdus merula*) calls) differed in their effect on bat activity at two sites, one with low and one with high aircraft activity. Simulated aircraft noise and silent tracks reduced bat activity when compared with blackbird calls ($P < 0.05$). Bats may have found it easier to detect observers during the playback of silent tracks (sampling involved walking circuits with hand-held detectors), and may have reduced activity to a perceived threat. This result suggests that broadcasted aircraft noise is no more disturbing than researcher presence during playback trials. Evidence for a site × playback stimuli interaction ($P = 0.054$) suggests that bats at the site with high aircraft activity may have habituated to aircraft noise. Both correlative and experimental

data suggests that aircraft activity and noise may not have major impacts on long-tailed bat activity.

Ruczynski, I., Kalko, E.K. V & Siemers, B.M., 2007. The sensory basis of roost finding in a forest bat, *Nyctalus noctula*. *The Journal of Experimental Biology*, 210, pp.3607–15.

Abstract: Tree cavities are a critical resource for most forest-dwelling bats. Yet, it is not known how bats search for new sites and, in particular, find entrances to cavities. Here, we evaluated the importance of different sensory channels for the detection of tree roosts by the noctule bat *Nyctalus noctula*. Specifically, we tested the role of three non-social cues (echo information, visual information and temperature-related cues) and two social sensory cues (conspecific echolocation calls and the presence of bat olfactory cues). We set up an experiment in a flight room that mimicked natural conditions. In the flight room, we trained wild-caught bats kept in captivity for a short while to find the entrance to an artificial tree cavity. We measured the bats' hole-finding performance based on echolocation cues alone and then presented the bat with one of four additional sensory cues. Our data show that conspecific echolocation calls clearly improved the bats' performance in finding tree holes, both from flying (long-range detection) and when they were crawling on the trunk (short range detection). The other cues we presented had no, or only weak, effects on performance, implying that detection of new cavities from a distance is difficult for noctules if no additional social cues, in particular calls from conspecifics, are present. We conclude that sensory constraints strongly limit the effectiveness of finding new cavities and may in turn promote sociality and acoustic information transfer among bats. As acoustic cues clearly increased the bats' detection performance, we suggest that eavesdropping is an important mechanism for reducing the costs of finding suitable roosts.

Ruczyński, I., Kalko, E.K. V. & Siemers, B.M., 2009. Calls in the Forest: A comparative approach to how bats find tree cavities. *Ethology*, 115, pp.167–177.

Abstract: Although tree cavities are a particularly critical resource for forest bats, how bats search for and find new roosts is still poorly known. Building on a recent study on the sensory basis of roost finding in the noctule (Ruczynski et al. 2007), here we take a comparative approach to how bats find roosts. We tested the hypothesis that species' flight abilities and echolocation call characteristics play important roles in how well and by which cues bats find new tree roosts. We used the very manoeuvrable, faintly echolocating brown long-eared bat (*Plecotus auritus*) and the less manoeuvrable, louder Daubenton's bat (*Myotis daubentonii*) as study species. The species are sympatric in European temperate forests and both roost in tree cavities. We trained bats in short-term captivity to find entrances to tree cavities and experimentally manipulated the sensory cues available to them. In both species, cue type influenced the search time for successful cavity detection. Visual, olfactory and temperature cues did not improve the bats' performance over the performance by echolocation alone. Eavesdropping on conspecific echolocation calls played back from inside the cavity decreased search time in Daubenton's bat (*M. daubentonii*), underlining the double function of echolocation signals – orientation and communication. This was not so in the brown long-eared bat (*P. auritus*) that has low call amplitudes. The highly manoeuvrable *P. auritus* found cavities typically from flight and the less manoeuvrable *M. daubentonii* found more entrances during crawling. Comparison with the noctule data from Ruczynski et al. (2007) indicates that manoeuvrability predicts the mode of cavity search. It further highlights the importance of call amplitude for eavesdropping and cavity detection in bats.

Russ, J., Jones, G., Mackie, I.J. & Racey, P.A., 2004. Interspecific responses to distress calls in bats (Chiroptera: Vespertilionidae): a function for convergence in call design? *Animal Behaviour*, 67, pp.1005–1014.

Abstract: Distress calls were recorded from three sympatric species of pipistrelle bat (*Pipistrellus nathusii*, *P. pipistrellus* and *P. pygmaeus*) in England and Northern Ireland. At foraging sites, we conducted playback experiments, consisting of experimental distress call sequences from each species and control sequences of random noise and sound recorded with no bats present. We measured response by simultaneously recording ultrasound during playbacks and counting the echolocation pulses above a predetermined threshold which were then identified to species. All three species responded to each other's calls. The number of recorded echolocation pulses of all species increased eight-fold, on average, during the playback of distress call sequences compared with the playback of ultrasonic noise, and four-fold compared with the playback of silence. In a separate playback experiment, the number of echolocation pulses of *P. pygmaeus* increased 14-fold during the playback of distress calls of four endemic species of bat from Madagascar (*Emballonura atrata*, *Myotis goudoti*, *Miniopterus majori* and *M. manavi*) compared with the playback of silence. This increased response might have been caused by the high calling rates of the Malagasy species. Distress calls of *P. nathusii*, *P. pipistrellus* and *P. pygmaeus* were structurally convergent, consisting of a series of downward-sweeping, frequency-modulated elements of short duration and high intensity with a relatively strong harmonic content. Selection may favour convergence in the structure of distress calls among bat species, if attracting heterospecifics increases the chance of repelling predators by mobbing.

Russo, D., Jones, G. & Arlettaz, R., 2007. Echolocation and passive listening by foraging mouse-eared bats *Myotis myotis* and *M. blythii*. *The Journal of Experimental Biology*, 210(Pt 1), pp.166–76.

Abstract: The two sibling mouse-eared bats, *Myotis myotis* and *M. blythii*, cope with similar orientation tasks, but separate their trophic niche by hunting in species-specific foraging microhabitats. Previous work has shown that both species rely largely on passive listening to detect and glean prey from substrates, and studies on other bat species have suggested that echolocation is ;switched off' during passive listening. We tested the hypothesis that mouse-eared bats continuously emit echolocation calls while approaching prey. Echolocation may be needed for orientation while simultaneously listening for prey. Because these sibling species forage in different microhabitats and eat different prey, we also compared their echolocation behaviour and related it to their ecology. Both species used echolocation throughout prey approach, corroborating a functional role for echolocation during gleaning. Captive bats of both species emitted similar orientation calls, and pulse rate increased during prey approach. Between the search to approach phases, call amplitude showed a sudden, dramatic drop and bats adopted ;whispering echolocation' by emitting weak calls. Whispering echolocation may reduce the risks of masking prey-generated sounds during passive listening, the mouse-eared bats' main detection tactic; it may also avoid alerting ultrasound-sensitive prey. In several cases *M. myotis* emitted a loud buzz made of 2-18 components when landing. We hypothesise that the buzz, absent in *M. blythii* at least when gleaning from the same substrate, is used to assess the distance from ground and refine the landing manoeuvre. Our findings have implications for niche

separation between sibling species of echolocating bats, support a role for echolocation during passive listening and suggest a functional role for buzzes in landing control.

Ryals, B.M., Dooling, R.J., Westbrook, E., Dent, M.L., MacKenzie, A. & Larsen, O.N., 1999. Avian species differences in susceptibility to noise exposure. *Hearing Research*, 131, 71–88.

Abstract: Previous studies of hair cell regeneration and hearing recovery in birds after acoustic overstimulation have involved relatively few species. Studies of the effects of acoustic overexposure typically report high variability. Though it is impossible to tell, the data so far also suggest there may be considerable species differences in the degree of damage and the time course and extent of recovery. To examine this issue, we exposed four species of birds (quail, budgerigars, canaries, and zebra finches) to identical conditions of acoustic overstimulation and systematically analyzed changes in hearing sensitivity, basilar papilla morphology, and hair cell number. Quail and budgerigars showed the greatest susceptibility to threshold shift and hair cell loss after overstimulation with either pure tone or bandpass noise, while identical types of overstimulation in canaries and zebra finches resulted in much less of a threshold shift and a smaller, more diffuse hair cell loss. All four species showed some recovery of threshold sensitivity and hair cell number over time. Canary and zebra finch hearing and hair cell number recovered to within normal limits while quail and budgerigars continued to have an approximately 20 dB threshold shift and incomplete recovery of hair cell number. In a final experiment, birds were exposed to identical wide-band noise overstimulation under conditions of artificial middle ear ventilation. Hair cell loss was substantially increased in both budgerigars and canaries suggesting that middle ear air pressure regulation and correlated changes in middle ear transfer function are one factor influencing susceptibility to acoustic overstimulation in small birds.

Rydell, J., Entwistle, A. & Racey, P.A., 1996. Timing of foraging flights of three species of bats in relation to insect activity and predation risk. *Oikos*, 76(2), p.243.

Abstract: The flight activity of three species of insectivorous bats and their prey was studied in north-east Scotland (57'N) during summer 1993. Aerial insects of sizes taken by bats were more abundant during the day than during the night, but the highest abundance usually occurred around dusk, partly reflecting increased flight of dipterans. In contrast, the flight activity of moths, mainly Geometridae and Pyralidae, was greatest around midnight. Two species of aerial-hawking bats, *Pipistrellus pipistrellus* and *Myotis daubentonii*, which feed primarily on small flying insects, mainly Diptera, emerged from their roosts 15-30 min after sunset, during or after the dusk peak in insect activity, and subsequently foraged as their food was declining in abundance. In contrast, the foliage gleaning bat *Plecotus auritus*, which feeds primarily on moths, did not emerge until about one hour after sunset, but while the activity of its main prey was increasing. The two aerial-hawking bats therefore seem to be constrained from exploiting most of the evening peak in aerial insect abundance, presumably because earlier emergence would result in higher predation risk at the higher light levels. *P. auritus* may have less to gain by emerging early, since it can feed on moths and non-flying prey independently of the activity of small insects at dusk. The conclusions have implications for the conservation of bats and their habitats particularly at high latitudes. Protective tree cover may allow earlier evening emergence of bats and therefore provide access to more food.

Samarra, F.I.P., Klappert, K., Brumm, H. & Miller, P., 2009. Background noise constrains communication: acoustic masking of courtship song in the fruit fly *Drosophila montana*. *Behaviour*, 146(12), pp.1635–1648.

Abstract: *Drosophila montana* males produce a courtship song that is a prerequisite for mating to occur and which females use to select mates. Here we show that *D. montana* female responses to courtship song decreased in the presence of high levels of noise within the same frequency band as the courtship song, but not in equivalent noise levels in an adjacent higher frequency band. This suggests that high noise levels overlapping the frequency band of the song impair signal detection, but that a mechanism for frequency filtering exists that reduces the influence of noise in adjacent frequency bands. Although the acoustic environment of this species in the wild is not known, some potential sources of noise are discussed. Nevertheless, our findings show that background noise (biotic or abiotic) within the same frequency band as the courtship song of *D. montana* can mask it, suggesting that environmental noise might affect mate choice and thereby may influence the evolution of this courtship signalling system.

Sändig, S., Schnitzler, H.-U. & Denzinger, A., 2014. Echolocation behaviour of the big brown bat (*Eptesicus fuscus*) in an obstacle avoidance task of increasing difficulty. The *Journal of Experimental Biology*, 217(Pt 16), pp.2876–84.

Abstract: Four big brown bats (*Eptesicus fuscus*) were challenged in an obstacle avoidance experiment to localize vertically stretched wires requiring progressively greater accuracy by diminishing the wire-to-wire distance from 50 to 10 cm. The performance of the bats decreased with decreasing gap size. The avoidance task became very difficult below a wire separation of 30 cm, which corresponds to the average wingspan of *E. fuscus*. Two of the bats were able to pass without collisions down to a gap size of 10 cm in some of the flights. The other two bats only managed to master gap sizes down to 20 and 30 cm, respectively. They also performed distinctly worse at all other gap sizes. With increasing difficulty of the task, the bats changed their flight and echolocation behaviour. Especially at gap sizes of 30 cm and below, flight paths increased in height and flight speed was reduced. In addition, the bats emitted approach signals that were arranged in groups. At all gap sizes, the largest numbers of pulses per group were observed in the last group before passing the obstacle. The more difficult the obstacle avoidance task, the more pulses there were in the groups and the shorter the within-group pulse intervals. In comparable situations, the better-performing bats always emitted groups with more pulses than the less well-performing individuals. We hypothesize that the accuracy of target localization increases with the number of pulses per group and that each group is processed as a package.

Saunders, J.C., Dear, S. P. & Schneider, M.E., 1985. The anatomical consequences of acoustic injury: A review and tutorial. *The Journal of the Acoustical Society of America*, 78, pp.833 - 860.

Abstract: The anatomic consequences of acoustic overstimulation are explored in this presentation, and attention is directed toward issues where improvements in technology and empirical observation are needed before further advances in our understanding can be achieved. Gains have been made in the last decade in appreciating sound-induced cochlear injury, but there is now a need to evaluate not only cochlear pathology but also the functional state of the surviving structures. There is a wealth of information about the susceptibility of inner or outer hair cells to acoustic injury; however, the etiology of this injury is not yet fully understood. In

addition, current ideas concerning the effects of noise on hair-cell stereocilia, hair-cell synapses, the cochlear vascular supply, and the central auditory pathways are in a state of flux and are either undergoing revision or emerging. Other issues, such as the basis of temporary or permanent threshold shift at the cellular level, and the individual differences in susceptibility to injury are in need of a fresh approach. It would seem that the time is now ripe to review our knowledge, recognize its gaps, and develop testable hypotheses concerning the mechanisms of acoustic injury to the ear.

Schaub, A., Ostwald, J. & Siemers, B.M., 2008. Foraging bats avoid noise. *The Journal of Experimental Biology*, 211(Pt 19), pp.3174–80.

Abstract: Ambient noise influences the availability and use of acoustic information in animals in many ways. While much research has focused on the effects of noise on acoustic communication, here, we present the first study concerned with anthropogenic noise and foraging behaviour. We chose the greater mouse-eared bat (*Myotis myotis*) as a model species because it represents the especially vulnerable group of gleaning bats that rely on listening for prey rustling sounds to find food (i.e. "passive listening"). In a choice experiment with two foraging compartments, we investigated the influence of background noise on foraging effort and foraging success. We tested the hypotheses that: (1) bats will avoid foraging areas with particularly loud background noise; and (2) the frequency-time structure of the noise will determine, in part, the degree to which it deters bats. We found a clear effect of the type of noise on the allocation of foraging effort to the compartments and on the distribution of prey capture events. When playing back silence, the bats made equal use of and were equally successful in both compartments. In the other three treatments (where a non-silent sound was played back), the bats avoided the playback compartment. The degree to which the background noise deterred bats from the compartment increased from traffic noise to vegetation movement noise to broadband computer-generated noise. Vegetation noise, set 12 dB below the traffic noise amplitude, had a larger repellent effect; presumably because of its acoustic similarity with prey sounds. Our experimental data suggest that foraging areas very close to highways and presumably also to other sources of intense, broadband noise are degraded in their suitability as foraging areas for such "passive listening" bats.

Schmidt, S., Hanke, S. & Pillat, J., 2000. The role of echolocation in the hunting of terrestrial prey - new evidence for an underestimated strategy in the gleaning bat, *Megaderma lyra*. *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology*, 186(10), pp.975–988.

Abstract: The observation that gleaning bats detect prey by its noises, together with difficulties in recording their faint sonar calls, have led some authors to conclude that gleaning bats may not use echolocation in certain hunting situations. In particular, it is conjectured that echolocation plays no role in the classification and tracking of prey. In the present study, we show that the gleaning bat, *Megaderma lyra*, is able to find silent and motionless prey on the ground. The significance of sonar for catching a variety of terrestrial prey is established in a standardized situation. Sonar calls were found to be emitted during all stages, i.e. approach, hovering above the prey, and return to the roost, of every hunting flight. The harmonic pattern of the calls differed significantly between these stages, calls with three or more prominent components prevailing during hovering. Bats identified prey and rejected dummies while hovering above

them. During this state, increased call rates and reduced call durations were found. Echolocation activity during, and the duration of, the hovering phase depended on prey type, in particular on prey movement. The prey-dependent shifts in sonar activity, the broadband call structure with an emphasis on higher harmonics, and a systematic shift of the calls' peak frequencies during hovering, are discussed as adaptations to identifying prey by sonar.

Schmidt, S. & Thaller, J., 1994. Temporal auditory summation in the echolocating bat, *Tadarida brasiliensis*. *Hearing Research*, 77, pp.125–134.

Abstract: Auditory thresholds improve with increasing signal duration within the maximum integration time of the auditory system, a phenomenon called temporal summation. The temporal summation function is a basic characteristic of particular relevance for bat sonar, as it determines the ability to detect targets with short echolocation calls. Temporal summation was studied in 6 Mexican free-tailed bats (*Tadarida brasiliensis*) in a forced two-choice behavioural test. Masked auditory thresholds for 40-kHz test tone pulses with durations between 2 ms and 400 ms were determined in broadband noise of two different spectrum levels (-18 dB, + 17 dB). At both masker levels, thresholds decreased by considerably more than 10 dB per decade of duration. The time constants of the summation functions, which are a measure of the maximum integration time, shortened significantly with increasing masker level from 62 ms to 14 ms. The steep summation functions are only partly accounted for by spectral splatter. This suggests that the bats are capable of a neural overintegration of sound intensity. Finally, it is shown that such short time constants are typical for echolocating animals, and the implications of the found summation functions for echolocation are considered.

Schmieder, D.A., Kingston, T., Hashim, R. & Siemers, B.M., 2012. Sensory constraints on prey detection performance in an ensemble of vespertilionid understorey rain forest bats. *Functional Ecology*, 26(5), pp.1043–1053.

Abstract: 1. Bats evolved different strategies to find prey close to vegetation. Previous studies on European bats of the genus *Myotis* (Vespertilionidae) revealed an association between echolocation call bandwidth and the ability to find and capture prey close to vegetation. Here, we investigated whether the role of call bandwidth in prey detection is a more general principle in bat sensory ecology. We focused on eight palaeotropical species of the vespertilionid subfamilies Kerivoulinae and Murininae, as they also achieve very broad bandwidths with the first harmonic of their echolocation calls. 2. All species emitted calls of bandwidths broader than 90 kHz with extremely high start frequencies (max. 230 kHz), and all of five experimentally tested species were able to catch prey closer than 6 cm, occasionally even closer than 2•5 cm, to a standardized vegetation-like background. The performance and call data corroborate the hypothesis that bats with very broadband calls and high-frequency components have access to prey very close to vegetation and establish this as a more general principle in bat sensory ecology. 3. In a second experiment, we questioned whether echolocation is the only sensory cue used by the bats to find prey. Echo-acoustic prey dummies that did not smell or taste like arthropods and did not produce any sounds or movement were presented to all five species. In 80 of 83 cases, the bats caught or attempted to catch the dummy, indicating that the bats used only echo-acoustic information for prey detection and recognition in our experiments. 4. We then tested whether the sensory difficulty in finding prey close to clutter constrains the bats' attacks on prey – or whether flight manoeuvrability may be limiting – by manipulating the echo reflection properties of the background. The bats were able to find prey very slightly, but significantly closer to a

background with lower echo reflection (an easier sensory task), which corroborates the limiting role of sensory performance. 5. While silent, motionless prey close to and in vegetation will be accessible to these specialists, it will go undetected by other bats. This scenario supports the idea that sensory specialization mediates resource access and niche separation ("sensory niche partitioning").

Schnitzler, H.-U. & Kalko, E.K. V., 2001. Echolocation by Insect-Eating Bats. *BioScience*, 51(7), p.557.

No abstract

Schnitzler, H.-U., Moss, C.F. & Denzinger, A., 2003. From spatial orientation to food acquisition in echolocating bats. *Trends in Ecology & Evolution*, 18(8), pp.386–394.

Abstract: Field research on echolocation behavior in bats has emphasized studies of food acquisition, and the adaptive value of sonar signal design has been considered largely in the context of foraging. However, echolocation tasks related to spatial orientation also differ among bats and are relevant to understanding signal structure. Here, we argue that the evolution of echolocation in bats is characterized by two key innovations: first, the evolution of echolocation for spatial orientation and, second, a later transition for prey acquisition. This conceptual framework calls for a new view on field data from bats orienting and foraging in different types of habitats. According to the ecological constraints in which foraging bats operate, four distinct functional groups or guilds can be defined. Within each group, signal design and echolocation behavior are rather similar.

Schöner, C.R., Schöner, M.G. & Kerth, G., 2010. Similar is not the same: Social calls of conspecifics are more effective in attracting wild bats to day roosts than those of other bat species. *Behavioral Ecology and Sociobiology*, 64(12), pp.2053–2063.

Abstract: Many bat species regularly need to find new day roosts as they require numerous shelters each breeding season. It has been shown that bats exchange information about roosts among colony members, and use echolocation and social calls of conspecifics in order to find roosts. However, it is unclear if wild bats discriminate between social calls of conspecifics and other bat species while searching for roosts. Furthermore, the extent that bats are attracted to potential roosts by each of these two call types is unknown. We present a field experiment showing that social calls of conspecifics and other bat species both attract bats to roosts. During two summers, we played back social calls of Bechstein's bats (*Myotis bechsteinii*) and Natterer's bats (*Myotis nattereri*) from different bat boxes that can serve as roosts for these species. All experimental bat boxes were monitored with infrared video to identify the approaching bat species. Three species (*M. bechsteinii*, *M. nattereri*, and *Plecotus auritus*) approached the boxes significantly more often during nights when bat calls were played compared to nights without playbacks. Bechstein's bats and Natterer's bats were both more attracted to social calls of conspecifics than of the other species, whereas *P. auritus* did not discriminate between calls of either *Myotis* species. Only Bechstein's bats entered experimental boxes and only at times when calls from conspecifics were played. Our findings show that wild bats discriminate between social calls of conspecifics and other bat species although they respond to both call types when searching for new roosts.

Schroeder, J., Nakagawa, S., Cleasby, I. R. & Burke, T., 2012. Passerine birds breeding under chronic noise experience reduced fitness. *PloS One*, 7(6).

Abstract: Background: Fitness in birds has been shown to be negatively associated with anthropogenic noise, but the underlying mechanisms remain obscure. It is however crucial to understand the mechanisms of how urban noise impinges on fitness to obtain a better understanding of the role of chronic noise in urban ecology. Here, we examine three hypotheses on how noise might reduce reproductive output in passerine birds: (H1) by impairing mate choice, (H2) by reducing territory quality and (H3) by impeding chick development. Methodology/Principal Findings: We used long-term data from an island population of house sparrows, Passer domesticus, in which we can precisely estimate fitness. We found that nests in an area affected by the noise from large generators produced fewer young, of lower body mass, and fewer recruits, even when we corrected statistically for parental genetic quality using a cross-fostering set-up, supporting H3. Also, individual females provided their young with food less often when they bred in the noisy area compared to breeding attempts by the same females elsewhere. Furthermore, we show that females reacted flexibly to increased noise levels by adjusting their provisioning rate in the short term, which suggests that noise may be a causal factor that reduces reproductive output. We rejected H1 and H2 because nestbox occupancy, parental body mass, age and reproductive investment did not differ significantly between noisy and quiet areas. Conclusions/Significance: Our results suggest a previously undescribed mechanism to explain how environmental noise can reduce fitness in passerine birds: by acoustically masking parent–offspring communication. More importantly, using a cross-fostering set-up, our results demonstrate that birds breeding in a noisy environment experience significant fitness costs. Chronic noise is omnipresent around human habitation and may produces similar fitness consequences in a wide range of urban bird species.

Schuchmann, M., Puechmaille, S.J. & Siemers, B.M., 2012. Horseshoe Bats Recognise the Sex of Conspecifics from Their Echolocation Calls. *Acta Chiropterologica*, 14(1), pp.161–166.

Abstract: Echolocation calls produced by bats contain information on the emitter that could be used in social interactions. Nevertheless, little is known about the whether such information actually is being used by bats. Here we tested the ability of two horseshoe bat species (*Rhinolophus mehelyi* and *R. euryale*; n = 20 each) to discriminate conspecific male from conspecific female echolocation calls and vice versa. Behavioural data from a habituation-discrimination paradigm revealed that both species were able to recognize the sex of conspecifics from their calls, providing evidence that cues on the sex of the emitter are encoded in echolocation signals. While our data support that the sex-specific acoustic cues are not (just) the horseshoe bats' constant-frequency call part, their nature remains enigmatic. This is the second study to show that bats can recognize the caller's gender from echolocation calls and the first to do so for "high-duty-cycle bats"; those that use calls with a prominent constant-frequency (CF) component.

Schuchmann, M. & Siemers, B.M., 2010. Behavioral evidence for community-wide species discrimination from echolocation calls in bats. *The American Naturalist*, 176(1), pp.72–82.

Abstract: Recognizing species identity is crucial for many aspects of animal life and is often mediated by acoustic signals. Although most animals are able to distinguish acoustic signals of

their own species from other sympatrically occurring species, it is yet unknown whether animals can distinguish among acoustic signals of different closely related sympatric species. In this context, echolocating bats are a particularly interesting model system: their echolocation system evolved primarily for spatial orientation and foraging, but recent studies indicate that echolocation also has an important communicative function. Yet, the role of echolocation calls for species discrimination and thus potentially for interspecific communication has not been investigated. Using a behavioral discrimination assay, we found that two species of wild horseshoe bats could discriminate calls of their own species from those of three sympatric congeneric species. We further show that the bats were able to discriminate between echolocation calls of different congeneric species from the local community. In both cases, discrimination ability was high despite strong overlap of species' call frequency bands. This study provides the first experimental evidence for species discrimination based on echolocation calls. On a more general level, it shows for the first time that animals can distinguish among acoustic signals of different closely related and ecologically similar species from their local community.

Schwartz, C., Tressler, J., Keller, H., Manzant, M., Ezell, S. & Smotherman, M., 2007. The tiny difference between foraging and communication buzzes uttered by the Mexican free-tailed bat, *Tadarida brasiliensis*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 193(8), pp.853–63.

Abstract: Echolocating insectivorous bats consummate prey captures using a distinct vocal motor pattern commonly known as the terminal or feeding buzz, which is widely considered a fixed motor pattern executed independently of auditory feedback influences. The Mexican free-tailed bat, *Tadarida brasiliensis*, offers an opportunity to explore the role of sensory feedback in buzzing because they emit similar buzzes both in flight during foraging and while stationary as communication sounds. Here we compared the spectral and temporal patterns of foraging and communication buzzes to address whether or not auditory feedback may influence buzz patterns. We found that while foraging buzzes uttered in open space were composed of generic FM calls, communication buzzes were composed of an adapted CF-FM call similar to the call type used by *T. brasiliensis* when navigating in confined spaces. This provides the first evidence that some bats can make significant context-dependent changes in the spectral parameters of calls within their buzz. We also found that inter-pulse intervals, but not call durations, were different within the two buzz types. These observations indicate that though a common pattern generator hierarchically organizes all buzzes, *T. brasiliensis* retains a significant capacity to adapt the spectral and temporal patterns of elements within its buzzes.

Seong, J.C., Park, T.H., Ko, J.H., Chang, S.I., Kim, M., Holt, J.B. & Mehdi, H.R., 2011. Modeling of road traffic noise and estimated human exposure in Fulton County, Georgia, USA. *Environment International*, 37(8), pp.1336–41.

Abstract: Environmental noise is a major source of public complaints. Noise in the community causes physical and socio-economic effects and has been shown to be related to adverse health impacts. Noise, however, has not been actively researched in the United States compared with the European Union countries in recent years. In this research, we aimed at modeling road traffic noise and analyzing human exposure in Fulton County, Georgia, United States. We modeled road traffic noise levels using the United States Department of Transportation Federal Highway Administration Traffic Noise Model implemented in SoundPLAN®. After analyzing noise levels

with raster, vector and façade maps, we estimated human exposure to high noise levels. Accurate digital elevation models and building heights were derived from Light Detection And Ranging survey datasets and building footprint boundaries. Traffic datasets were collected from the Georgia Department of Transportation and the Atlanta Regional Commission. Noise level simulation was performed with 62 computers in a distributed computing environment. Finally, the noise-exposed population was calculated using geographic information system techniques. Results show that 48% of the total county population [N=870,166 residents] is potentially exposed to 55 dB(A) or higher noise levels during daytime. About 9% of the population is potentially exposed to 67 dB(A) or higher noises. At nighttime, 32% of the population is expected to be exposed to noise levels higher than 50 dB(A). This research shows that large-scale traffic noise estimation is possible with the help of various organizations. We believe that this research is a significant stepping stone for analyzing community health associated with noise exposures in the United States.

Sgro, M.P. & Wilkins, K.T., 2003. Roosting behavior of the Mexican free-tailed bat (*Tadarida brasiliensis*) in a highway overpass. *Western North American Naturalist*, 63(3), pp.366–373.

Abstract: A colony of Mexican free-tailed bats (*Tadarida brasiliensis*) roosting in an interstate highway overpass in Belton, Bell County, Texas, was studied weekly from 28 June to 21 November 1996 (except for the week of 4 July). We examined 2 aspects of roosting behavior: site-specific fidelity to locations within the roost and gender-related segregation within the roost. Colony estimates based on guano production showed a marked decrease in the number of bats from 19 to 26 July; many of these departing bats were adult females. No female bats sampled after this interval were pregnant. Male bats outnumbered females on nearly all sampling occasions. Throughout the study, one section of the roost was dominated by males, ranging from 83% to 100% of total bats. The majority of bats recaptured at least once were faithful to specific locations within the roost, and more than 70% of bats recaptured multiple times were faithful to specific roost location

Shapiro, A.D., 2010. Recognition of individuals within the social group: signature vocalizations. In Handbook of Mammalian Vocalization - An Integrative Neuroscience Approach. *Handbook of Behavioral Neuroscience*. Elsevier, pp. 495–503.

Abstract: Signature vocalizations contain sufficiently unique spectral and/or temporal identity to allow conspecifics to differentiate between individuals. Experimental assessment of signature content relies on: (1) accurate discrimination of vocalizations according to individual callers using human observers and statistical methods; (2) playback experiments with conspecifics in captivity or in the wild. Signature vocalizations are often acquired through social and vocal learning. Functions for such signals include individual recognition (e.g., between parents and offspring, mating pairs, territorial rivals) and the mediation of social interactions. Signature cues are likely to be subtle, and their analysis is likely to benefit from the use of new data collection technologies and human speech recognition techniques.

Shaw, N.A., 1988. The auditory evoked potential in the rat - a review. *Prog. Neurobiol*., 31, pp.19-45.

No abstract

Sherwin, R., Stricklan, D., & Rogers., 2000. Roosting affinities of Townsend's Big-eared Bats (*Corynorhinus townsendii*) in northern Utah. *Journal of Mammalogy,* 81, pp.939-947.

Abstract: We surveyed abandoned mines, caves, and bridges to identify habitat preferences of day-roosting Townsend's big-eared bat (*Corynorhinus townsendii*) in northern Utah. Of 820 sites surveyed (676 mines, 39 caves, and 105 bridges), 196 (23.9%) were occupied by *C. townsendii*. Caves were the most frequently used type of roost (84.6%), 21.2% of abandoned mines were used as day roosts, and no bridges were used. Bats occupied mines and caves at lower available elevations (1,350–2,440 m), which were associated with sagebrush–grass steppe, juniper woodlands, and mountain brush vegetation. In general, roosts with single low (<1.5 m height) entrances were more likely to be occupied than those with multiple or tall entrances. Day roosts typically were subject to little disturbance by humans. Aspect and width of entrance, stability and complexity of interior, presence of multiple entrances, length of tunnel, amount of internal air flow, presence of multiple levels, and presence of internal water were not associated significantly with occupancy; however, maternity colonies tended to be located in large complex sites with multiple openings.

Shier, D.M., Lea, A.J., & Owen, M.A., 2012. Beyond masking: Endangered Stephen's kangaroo rats respond to traffic noise with foot drumming. *Biological Conservation*, 150(1), 53–58.

Abstract: On-road vehicles have become a pervasive source of low frequency noise in both urban environments and natural protected areas. Because many species rely on low-frequency signals to communicate with conspecifics, they are likely to be especially vulnerable to signal masking and the concomitant biological effects associated with exposure to traffic noise. Here, we show that the spectral characteristics of traffic noise overlap extensively with footdrumming signals of the endangered Stephens' kangaroo rat (*Dipodomys stephensi*; SKR). Playbacks of footdrumming overlaid with experimental and control background noises indicate that traffic noise masks and may mimic footdrumming signals. SKR showed no response to footdrumming playbacks overlaid with traffic noise. Yet, traffic noise itself may mimic footdrumming and prompt a false response in SKR – playbacks of traffic noise alone and footdrumming overlaid with control sounds elicited similar behavioral responses. These results provide the first evidence that anthropogenic noise may function as a deceptive signal to wildlife, causing animals to engage in false responses that may be energetically and biologically costly. More broadly, these results indicate that anthropogenic noise can have multiple, concurrent effects. For SKR, the combined effects of communication disruption and signal deception may further tax already endangered populations. Roads and road margins on and off reserves serve as dispersal corridors and refugia for SKR and other semifossorial taxa; these areas may therefore function as ecological traps if anthropogenic roadway noise negatively affects population persistence.

Shimozawa, T., Sun, X. & Jen, P. H., 1984. Auditory space representation in the superior colliculus of the big brown bat, *Eptesicus fuscus*. *Brain Research*, 311, 289–296.

Abstract: The auditory response areas of 123 superior collicular (SC) units of *Eptesicus fuscus* were studied under free-field acoustic stimulus conditions. A stimulus was delivered from a loudspeaker placed 14 cm in front of a bat. The best frequency of a unit was determined by

changing the stimulus frequency until the minimum threshold was measured. A best frequency stimulus was then delivered as the loudspeaker was moved across the auditory space to determine the response center of the auditory response area of each unit. The response center was defined as the direction at which the unit had its lowest minimum threshold. The stimulus intensity was then raised 2–20 dB above the lowest minimum threshold of the unit and the response area for each stimulus intensity was determined.

Shiori, Y., Hiryu, S., Watanabe, Riquimaroux, H., & Watanabe, Y., 2009. Pulse-echo interaction in free-flying horseshoe bats, *Rhinolophus ferrumequinum nippon*. *The Journal of the Acoustical Society of America*, 126(3), pp.EL80–5.

Abstract: Because horseshoe bats emit a long-duration pulse, the returning echo temporally overlaps with the emitted pulse during echolocation. Here, the pulse-echo interaction that horseshoe bats actually experience during flight was examined using onboard telemetry sound recordings. Doppler-shifted returning echoes produced beats in the amplitude patterns of constant-frequency components. Bats shortened the pulse duration with target distance, but the overlap duration was at least 8 ms within the approach phase. The computations suggest that the phase difference in slowly amplitude-modulated sound (the beat signal) provides a useful cue for target localization.

Shirley, M.D.F., Armitage, V.L., Barden, T.L., Gough, M., Lurz, P.W.W., Oatway, D.E., South, A.B., & Rushton, W.P., 2001. Assessing the impact of a music festival on the emergence behaviour of a breeding colony of Daubenton's bats (*Myotis daubentonii*). *Journal of Zoology*, 254(3), pp.367–373.

Abstract: The emergence of Daubenton's bats *Myotis daubentonii* from a priory in the north of England was recorded to assess the impact of an annual music festival. Bat emergence was related to measured environmental variables using generalized linear modelling. The temperatures inside and outside the priory were significant predictors of the numbers of bats emerging. Sunset time was a significant predictor of the time of bat emergence. The timing of bat emergence was significantly later during the music festival, but there was no significant difference in the number of bats emerging. The bats left the priory up to 47 min later on festival nights than one would expect them to emerge in the absence of the festival. The results on the patterns of bat emergence were used to make recommendations regarding the timing of the music festival in the following year to minimize detrimental impacts on the bat colony.

Shump, K.A. & Shump, A.U., 1980. Comparative insulation in Vespertilionid bats. *Comparative Biochemistry and Physiology Part A: Physiology*, 66, pp.351–354.

Abstract: l. Physical insulation was examined in five North American bats: *Lusiurus borealis*, *Lasiurus cinereus*, *Myotis lucifugus*, *Myotis keenii*, and *Eptesicus fuscus*. 2. *Lasiurus* were more insulated than the other three species, which appears to be related to the habits of these species; lasiurines are solitary, occupying tree roosts, whereas *Myotis* and *Eptesicus* species are colonial and commonly occur in environmentally protected roosts, buildings and caves. 3. Seasonal changes were found to occur in insulation with winter pelts being more insulative than summer ones.

Siemers, B.M. & Schaub, A., 2011. Hunting at the highway: traffic noise reduces foraging efficiency in acoustic predators. *Proceedings. Biological sciences / The Royal Society*, 278(1712), pp.1646–52.

Abstract: Noise pollution from human traffic networks and industrial activity impacts vast areas of our planet. While anthropogenic noise effects on animal communication are well documented, we have very limited understanding of noise impact on more complex ecosystem processes, such as predator-prey interactions, albeit urgently needed to devise mitigation measures. Here, we show that traffic noise decreases the foraging efficiency of an acoustic predator, the greater mouse-eared bat (*Myotis myotis*). These bats feed on large, ground-running arthropods that they find by listening to their faint rustling sounds. We measured the bats' foraging performance on a continuous scale of acoustically simulated highway distances in a behavioural experiment, designed to rule out confounding factors such as general noise avoidance. Successful foraging bouts decreased and search time drastically increased with proximity to the highway. At 7.5 m to the road, search time was increased by a factor of five. From this increase, we predict a 25-fold decrease in surveyed ground area and thus in foraging efficiency for a wild bat. As most of the bats' prey are predators themselves, the noise impact on the bats' foraging performance will have complex effects on the food web and ultimately on the ecosystem stability. Similar scenarios apply to other ecologically important and highly protected acoustic predators, e.g. owls. Our study provides the empirical basis for quantitative predictions of anthropogenic noise impacts on ecosystem processes. It highlights that an understanding of the effects of noise emissions and other forms of "sensory pollution" are crucially important for the assessment of environmental impact of human activities.

Siemers, B.M. & Swift, S.M., 2005. Differences in sensory ecology contribute to resource partitioning in the bats *Myotis bechsteinii* and *Myotis nattereri* (Chiroptera: Vespertilionidae). *Behavioral Ecology and Sociobiology*, 59(3), pp.373–380.

Abstract: Coexisting animal species frequently differ in resource use in at least one niche dimension and thus avoid competition. While a range of morphological differences that lead to differentiation in animals' mechanical access to food have been identified, the role of sensory differences in within-guild niche differentiation has received less attention. We tested the hypothesis that differences in sensory access to prey contribute to resource partitioning between potentially competing species using two sympatric, similar-sized, congeneric bat species as a model system. Nursery colonies of Natterer's bat (*Myotis nattereri*) and Bechstein's bat (*Myotis bechsteinii*) roost in bat boxes in the same orchard and forage in forests and orchards nearby. In observations and behavioural experiments with freshly captured *M. bechsteinii*, we showed that individuals are able to hunt using prey-generated sound alone. In contrast, *M. nattereri* rarely uses prey-generated sound, but instead is able to find prey by echolocation very close to vegetation. In accordance with these behavioural data, we showed that *M. bechsteinii* has significantly larger ears than *M. nattereri*, providing it with superior detection and localization abilities for relatively low-frequency prey rustling sounds. We hypothesized that these differences in sensory ecology of the two syntopic, congeneric species would contribute to resource partitioning, so that *M. bechsteinii* would find more noisy prey taxa, possibly hidden in vegetation, by listening for prey sounds, while *M. nattereri* would have better access to still prey using echolocation or associative learning. Analysis of faecal samples collected on the same nights from bat boxes occupied by each species corroborated this prediction. The diets of the two

species differed significantly, reflecting their different prey perception techniques and thereby supporting the hypothesis that differences in sensory ecology contribute to niche differentiation.

Simmons, J.A., 1989. A view of the world through the bat's ear: The formation of acoustic images in echolocation. *Cognition*, 33, pp.155-199.

Abstract: Echolocating bats perceive objects as acoustic images derived from echoes of the ultrasonic sounds they emit. They can detect, track, identify, and intercept flying insects using sonar. Many species, such as the big brown bat, *Eptesicus fuscus*, emit frequency-modulated sonar sounds and perceive the distance to targets, or target range, from the delay of echoes. For *Eptesicus*, a pointtarget's image has a sharpness along the range axis that is determined by the acuity of echo-delay perception, which is about 10 ns under favorable conditions. The image as a whole has a fine range structure that corresponds to the cross-correlation function between emissions and echoes. A complex target - which has reflecting points, called "glints", located at slightly different distances and reflects echoes containing overlapping components with slightly different delays - is perceived in terms of its range profile. The separation of the glints along the range dimension is encoded by the shape of the echo spectrum created by interference between overlapping echo components. However, *Eptesicus* transforms the echo spectrum back into an estimate of the original delay separation of echo components. The bat thus converts spectral cues into elements of an image expressed in terms of range. The absolute range of the nearest glint is encoded by the arrival time of the earliest echo component, and the spectrally spectrally encoded range separation of additional glints is referred to this time-encoded reference range for the image as a whole. Each individual glint is represented by a cross-correlation function for its own echo component, the nearest of which is computed directly from arrival-time measurements while further ones are computed by transformation of the echo spectrum. The bat then sums the cross-correlation functions for multiple glints to form the entire image of the complex target. Range and shape are two distinct features of targets that are separately encoded by the bat's auditory system, but the bat perceives unitary images that require fusion of these features to create a synthetic psychological dimension of range. The bat's use of cross-correlation-like images reveals neural computations that achieve fusion of stimulus features and offers an example of high-level operations involved in the formation of perceptual "wholes".

Simmons, J.A. & Dear, S.P., 1991. Computational representations of sonar images in bats. *Current Biology*, 1(3), pp.174–176.

No abstract

Simmons, J., Fenton, M. & O'Farrell, M., 1979. Echolocation and pursuit of prey by bats. *Science*, 203(4375), pp.16–21.

No abstract

Simmons, J. & Kick, S., 1984. Physiological mechanisms for spatial filtering and image enhancement in the sonar of bats. *Annual Review of Physiology*, 46, pp.599–614.

No abstract

Simmons, J. & Kick, S., 1988. Clutter interference along the target range axis in the echolocating bat, *Eptesicus fuscus*. *The Journal of the Acoustical Society of America*, 84, pp.551–559.

Abstract: The sensitivity of the echolocating bat, *Eptesicus fuscus*, for detection of a sonar target is impaired by the presence of additional targets located at similar distances. At a range of 50 cm, sensitivity to one target declines if the range separation to the other targets is smaller than 8-9 cm. This loss of sensitivity is an example of clutter interference along the range axis, created by simultaneous masking of one set of echoes by another. Echoes that fall within an experimentally defined critical range band may sum together to contribute collectively to detection in that band. Echoes falling into separate bands may be detected independently. Acoustic glints within a band appear to be grouped together to be perceived as a single range-extended target of complex structure. Range bands may thus define what a "target" is by specifying within-target and between-target differences in range. The width of critical range bands appears to depend upon target range, with wider bands at greater ranges.

Simmons, J., Kick, S. & Lawrence, B., 1984. Echolocation and hearing in the mouse-tailed bat, *Rhinopoma hardwickei*: acoustic evolution of echolocation in bats. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 154, pp.347–356.

Abstract: 1. Mouse-tailed bats (*Rhinopoma hardwickei*) use short-duration, multiple-harmonic, constant-frequency (CF) or slightly frequency-modulated (FM) signals for echolocation of flying insect prey. The frequency components are 18-20 kHz (first harmonic), 36-40 kHz (second harmonic), 56 60kHz (third harmonic), and 75 80 kHz (fourth harmonic). The second harmonic is the strongest component, with the third harmonic 2 to 10 dB weaker, and the first and fourth harmonics about I0 to 20 dB weaker than the second. 2. The bat's hearing, as indicated by N 4 auditory evoked potentials, is moderately sharply tuned to the second harmonic, broadly sensitive to the first harmonic and to lower frequencies, and moderately sensitive to the third and fourth harmonics. The degree of tuning is sufficient to indicate some specialized function for the second harmonic, perhaps in the task of detecting targets at maximum range, since this is the lowest of the strong harmonics and least affected by atmospheric attenuation. These bats probably do not perform the Doppler compensation response even though their hearing is tuned. 3. The pattern of emission of sonar sounds (repetition rate, duration) during interception of prey is similar to that observed in most other species of bats. The signals are emitted at repetition rates of 10-20/s during the search stage, 20M0/s during the approach stage, and about 100/s during the terminal stage of the pursuit process. The sonar sounds emitted during the search stage are 6-10 ms long, during the approach stage they are 2-4 ms long, and during the terminal stage they are less than I ms long. 4. The principal acoustic dimension of echolocation sounds that relates to perception of targets is signal bandwidth, which *Rhinopoma hardwickei* manipulates throughout the pursuit process by shortening the duration of its sonar sounds and also by slightly broadening the FM sweeps in its terminal-stage sounds. The onset-time of the long, search-stage sounds and the longer, early approach- stage sounds is more abrupt than for the shorter, late approach-stage and the short terminal- stage sounds. This apparently deliberate transient beginning broadens the signal's bandwidth at the onset relative to the narrower bandwidth prevailing for the rest of the CF harmonic structure which follows. In the shorter sounds, which are emitted during the late approach stage and terminal stage, the onset is more gradual, but the duration (the envelope) and

the offset-time are now short enough that the bandwidth of the signal as a whole is increased. The bandwidth is manipulated primarily by these changes in signal envelope and secondarily by the increased FM sweep-width in the terminal stage. 5. Except for duration these signals are relatively inflexible and suggestive of a primitive kind of echolocation in which only one dimension **is** changed to achieve qualities which most other species of bats obtain by changing a variety of signal dimensions simultaneously. The abrupt signal onsets may be an indication that multiple-harmonic CF and FM echolocation sounds evolved from click-like echolocation sounds of the type emitted by *Rousettus* and some terrestrial mammals.

Simmons, J.A., Neretti, N., Intrator, N., Altes, R.A., Ferrangamo, M.J. & Sanderson, M.I., 2004. Delay accuracy in bat sonar is related to the reciprocal of normalized echo bandwidth, or Q. *Proceedings of the National Academy of Sciences of the United States of America*, 101(10), pp.3638–43.

Abstract: Big brown bats (*Eptesicus fuscus*) emit wideband, frequency-modulated biosonar sounds and perceive the distance to objects from the delay of echoes. Bats remember delays and patterns of delay from one broadcast to the next, and they may rely on delays to perceive target scenes. While emitting a series of broadcasts, they can detect very small changes in delay based on their estimates of delay for successive echoes, which are derived from an auditory time/frequency representation of frequency-modulated sounds. To understand how bats perceive objects, we need to know how information distributed across the time/frequency surface is brought together to estimate delay. To assess this transformation, we measured how alteration of the frequency content of echoes affects the sharpness of the bat's delay estimates from the distribution of errors in a psychophysical task for detecting changes in delay. For unrestricted echo frequency content and high echo signal-to-noise ratio, bats can detect extremely small changes in delay of about 10 ns. When echo bandwidth is restricted by filtering out low or high frequencies, the bat's delay acuity declines in relation to the reciprocal of relative echo bandwidth, expressed as Q, which also is the relative width of the target impulse response in cycles rather than time. This normalized-time dimension may be efficient for target classification if it leads to target shape being displayed independent of size. This relation may originate from cochlear transduction by parallel frequency channels with active amplification, which creates the auditory time/frequency representation itself.

Simmons, J.A., Saillant, P.A., Wotton, J.M., Haresign, T., Ferragamo, M.J. & Moss, C.F., 1995. Composition of biosonar images for target recognition by echolocating bats. *Neural Networks*, 8(7-8), pp.1239–1261.

Abstract: Echolocating bats can recognize flying insects as sonar targets in a variety of different acoustic situations ranging from open spaces to dense clutter. Target classification must depend on perceiving images whose dimensions can tolerate intrusion of additional echoes from other objects, even echoes arriving at about the same time as those from the insect, without disrupting image organization. The big brown bat, *Eptesicus fuscus*, broadcasts FM sonar sounds in the 15-100 kHz band and perceives the arrival-time of echoes with an accuracy of 10-15 ns and a two point resolution of 2 µs, which suggests that perception of fine detail on the dimension of echo delay or target range is the basis for reconstructing complex acoustic scenes and recognizing targets that are embedded in these scenes. The directionality of the bat's sonar sound is very broad, making it impossible to isolate echoes from individual targets merely by aiming the head and ears at one object instead of another. Consequently, segregation of targets must depend on

isolating their echoes as discrete events along the axis of delay. That is, the bat's images must correspond to impulse responses of target scenes. However, the bat's sonar broadcasts are several milliseconds long, and the integration time of echo reception is about 350 µs, so perception of separate delays for multiple echoes only a few microseconds apart requires deconvolution of spectrally-complex echoes that overlap and interfere with each other within the 350 µs integration time. The bat's auditory system encodes the FM sweeps of transmissions and echoes as half-wave-rectified, magnitude-unsquared spectrograms, and then registers the time that elapses between each frequency in the broadcast and the echo, effectively correlating the spectrograms. The interference patterns generated by overlap of multiple echoes are then used to modify these delay estimates by adding fine details of the delay structure of echoes. This is equivalent to transformation of the spectrograms into the time domain, or deconvolution of echo spectra by spectrogram correlation and transformation (SCAT). However, while deconvolution overcomes integration time, the bat's receiving antennas reverberate for about 100 µs, smearing the echoes upon arrival. The bat overcomes this problem by receiving echoes from different directions than the transmitted sound, which radiates from the mouth. The broad range of antenna reverberations common to the emission and echoes thus cancel out, leaving only narrow elevation-dependent differences, which in fact appear in the bat's images. The SCAT algorithms successfully recreate images comparable to those perceived by the bat and provide for classification of targets from their glint structure in different situations.

Simmons, J.A. & Simmons, A.M., 2011. Bats and frogs and animals in between: evidence for a common central timing mechanism to extract periodicity pitch. *Journal of comparative physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 197(5), pp.585–94.

Abstract: Widely divergent vertebrates share a common central temporal mechanism for representing periodicities of acoustic waveform events. In the auditory nerve, periodicities corresponding to frequencies or rates from about 10 Hz to over 1,000 Hz are extracted from pure tones, from low-frequency complex sounds (e.g., 1st harmonic in bullfrog calls), from mid-frequency sounds with low-frequency modulations (e.g., amplitude modulation rates in cat vocalizations), and from time intervals between high-frequency transients (e.g., pulse-echo delay in bat sonar). Time locking of neuronal responses to periodicities from about 50 ms down to 4 ms or less (about 20-300 Hz) is preserved in the auditory midbrain, where responses are dispersed across many neurons with different onset latencies from 4-5 to 20-50 ms. Midbrain latency distributions are wide enough to encompass two or more repetitions of successive acoustic events, so that responses to multiple, successive periods are ongoing simultaneously in different midbrain neurons. These latencies have a previously unnoticed periodic temporal pattern that determines the specific times for the dispersed on-responses.

Simmons, J.A., Wotton, J.M., Ferrangamo, M.J. & Moss, C.F., 2002. Transformation of external-ear spectral cues into perceived delays by the big brown bat, *Eptesicus fuscus*. *The Journal of the Acoustical Society of America,* 111(6), p.2771.

Abstract: The external-ear transfer function for big brown bats (*Eptesicus fuscus*) contains two prominent notches that vary from 30 to 55 kHz and from 70 to 100 kHz, respectively, as sound-source elevation moves from 240 to 110 degrees. These notches resemble a higher-frequency version of external-ear cues for vertical localization in humans and other mammals. However, they also resemble interference notches created in echoes when reflected sounds overlap at short

time separations of 30–50 ms. Psychophysical experiments have shown that bats actually perceive small time separations from interference notches, and here we used the same technique to test whether external-ear notches are recognized as a corresponding time separation, too. The bats' performance reveals the elevation dependence of a time-separation estimate at 25–45 ms in perceived delay. Convergence of target-shape and external-ear cues onto echo spectra creates ambiguity about whether a particular notch relates to the object or to its location, which the bat could resolve by ignoring the presence of notches at external-ear frequencies. Instead, the bat registers the frequencies of notches caused by the external ear along with notches caused by the target's structure and employs spectrogram correlation and transformation (SCAT) to convert them all into a family of delay estimates that includes elevation.

Slabbekoorn, H., Ellers, J. & Smith, T.B., 2002. Birdsong and sound transmission: The benefits of reverberations. *The Condor*, 104, pp.564–573.

Abstract: Animal vocalizations used for long-distance communication are shaped by acoustic properties of the environment. Studies of the relationship between signal design and sound transmission typically focus on habitat-induced limitations due to signal attenuation and degradation. However, signal design may not entirely be explained by habitat limitations, but rather by beneficial consequences of reverberations. Narrow-frequency bandwidth notes (NFB notes) are pure notes that change little in frequency, and are typical for many bird species living in dense tropical forests. In contrast to frequency-modulated notes, we show that reverberations lead to a longer and louder signal after transmission for NFB notes. Furthermore, playback experiments to territorial males of an African passerine indicated that longer notes led to a stronger behavioral response. These results suggest that reverberations may benefit signal efficiency depending on the signal design, and add new insight into the selection pressures imposed on acoustic signals by the environment.

Slabbekoorn, H. & Peet, M. 2003. Ecology: birds sing at a higher pitch in urban noise. *Nature*, 424, p.267.

No abstract

Slabbekoorn, H. & Ripmeester, E.A.P., 2008. Birdsong and anthropogenic noise: implications and applications for conservation. *Molecular Ecology*, 17(1), pp.72–83.

Abstract: The dramatic increase in human activities all over the world has caused, on an evolutionary time scale, a sudden rise in especially low-pitched noise levels. Ambient noise may be detrimental to birds through direct stress, masking of predator arrival or associated alarm calls, and by interference of acoustic signals in general. Two of the most important functions of avian acoustic signals are territory defence and mate attraction. Both of these functions are hampered when signal efficiency is reduced through rising noise levels, resulting in direct negative fitness consequences. Many bird species are less abundant near highways and studies are becoming available on reduced reproductive success in noisy territories. Urbanization typically leads to homogenization of bird communities over large geographical ranges. We review current evidence for whether and how anthropogenic noise plays a role in these patterns of decline in diversity and density. We also provide details of a case study on great tits (Parus major), a successful urban species. Great tits show features that other species may lack and make them unsuitable for city life. We hypothesize that behavioural plasticity in singing behaviour

may allow species more time to adapt to human-altered environments and we address the potential for microevolutionary changes and urban speciation in European blackbirds (*Turdus merula*). We conclude by providing an overview of mitigating measures available to abate noise levels that are degrading bird breeding areas. Bird conservationists probably gain most by realizing that birds and humans often benefit from the same or only slightly modified measures.

Sleep, D.J.H. & Brigham, R.M., 2003. An experimental test of clutter tolerance in bats. *Journal of Mammalogy*, 84(1), pp.216–224.

Abstract: To examine the effects of spatially complex habitat (i.e., cluttered) and prey availability on habitat selection by bats, we constructed 3-dimensional "'clutter cones'" and monitored activity of free-ranging bats in them. Cones were paired with cones of equal clutter density and size in which we placed ultraviolet (UV) light sources to attract nocturnal insects and hence increase prey availability. We tested predictions arising from resource-partitioning experiments in previous works from laboratories and the field. Activity by bats of all sizes was unaffected by density of clutter, and activity by small-sized bats at all UV-illuminated sites increased significantly, whereas activity by large-sized bats was unaffected. Also, *Myotis* lucifugus did not negotiate clutter densities as complex as those in previous laboratory work. This suggests that habitat complexity is likely one means by which foraging areas are partitioned between those bats that can exploit them (i.e., smaller species) and those that cannot and that cluttered habitats are avoided except when they may serve a purpose such as an energetic benefit. Although behavioral studies conducted in the laboratory serve to obtain data on ultimate capabilities, differences between results from the laboratory and the field suggest that an animal's behavior may be specific to its present environment.

Smotherman, M. & Metzner, W., 2003. Effects of echo intensity on Doppler-shift compensation behavior in horseshoe bats. *Journal of Neurophysiology*, 89(2), pp.814–21.

Abstract: Echolocating horseshoe bats respond to flight-speed induced shifts in echo frequency by adjusting the frequency of subsequent calls. Under natural conditions, Doppler effects may force the frequency of a returning echo several kilohertz above the original emission frequency. By lowering subsequent call frequencies, the bat can return echo frequencies to within a narrow spectral bandwidth to which its highly specialized auditory system is most sensitive. While Doppler-shift compensation (DSC) behavior specifically refers to frequency compensation, other parameters of the returning echo, such as delay, duration, and interaural time and intensity differences have been shown to influence DSC performance. Understanding the nature of these influences has already led to a better appreciation of the neurophysiology of DSC. Here we provide a quantitative analysis of the effects of a prominent feature of the returning echo, its intensity, on DSC performance in horseshoe bats. Although DSC performance generally tolerates echo attenuation up to approximately 40 dB relative to the outgoing emission intensity, a systematic decline in DSC performance can be observed over this range. Generally, the effects of echo attenuation are characterized by a reduction in 1) the overall amount of compensation relative to the size of the shift in echo frequency and 2) the rate at which the bat responds to perceived echo shifts. These effects appear to be the consequence of a systematic shift in the range of echo frequencies capable of inducing DSC behavior. In particular, the reference frequency (the minimum shift in echo frequency that will elicit DSC behavior) appears to be highly sensitive to echo intensity. Every 10-dB reduction in echo intensity shifts the reference upward nearly 250 Hz. Our results indicate that, even at the highest intensity levels, relatively

minor changes in echo intensity critically influence frequency compensation during normal DSC. We conclude with a discussion of how these results might impact echolocation behavior of horseshoe bats under natural and experimental conditions.

Smotherman, M. & Metzner, W., 2003. Fine control of call frequency by horseshoe bats. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology,* 189(6), pp.435–46.

Abstract: The auditory system of horseshoe bats is narrowly tuned to the sound of their own echoes. During flight these bats continuously adjust the frequency of their echolocation calls to compensate for Doppler-effects in the returning echo. Horseshoe bats can accurately compensate for changes in echo frequency up to 5 kHz, but they do so through a sequence of small, temporally-independent, step changes in call frequency. The relationship between an echo's frequency and its subsequent impact on the frequency of the very next call is fundamental to how Doppler-shift compensation behavior works. We analyzed how horseshoe bats control call frequency by measuring the changes occurring between many successive pairs of calls during Doppler-shift compensation and relating the magnitude of these changes to the frequency of each intervening echo. The results indicate that Doppler-shift compensation is mediated by a pair of (echo)frequency-specific sigmoidal functions characterized by a threshold, a slope, and an upper limit to the maximum change in frequency that may occur between successive calls. The exact values of these parameters necessarily reflect properties of the underlying neural circuitry of Doppler-shift compensation and the motor control of vocalization, and provide insight into how neural feedback can accommodate the need for speed without sacrificing stability.

Smotherman, M., Zhang, S. & Metzner, W., 2003. A Neural basis for auditory feedback control of vocal pitch. *Journal of Neuroscience,* 23(4), pp.1464–1477.

Abstract: Hearing one's own voice is essential for the production of correct vocalization patterns in many birds and mammals, including humans. Bats, for instance, adjust temporal, spectral, and intensity parameters of their echolocation calls by precisely monitoring the characteristics of the returning echo signals. However, neuronal substrates and mechanisms for auditory feedback control of vocalizations are still mostly unknown in any vertebrate. We used echolocating horseshoe bats to investigate the role of the midbrain and hindbrain tegmentum for the control of call frequencies in response to changing auditory feedback. These bats accurately control the frequency of their echolocation calls through auditory feedback both when the bat is at rest [resting frequency (RF)] and when it is flying and compensating for changes in echo frequency caused by flight-induced Doppler shifts [Doppler shift compensation (DSC)].We iontophoretically injected various GABAergic and glutamatergic transmitter agonists and antagonists into the brainstem tegmentum. We found that within the parabrachial nuclei and the immediately adjacent tegmentum, excitatory effects caused by application of the glutamate agonist AMPAor the GABAA antagonist bicuculline raised RF and the frequency of calls emitted during DSC. Bicuculline application routinely blocked DSC altogether. Alternately, inhibitory effects caused by application of either the GABAA agonist muscimol or the AMPA antagonist CNQX lowered call frequencies emitted at rest and during DSC. Such an audio–vocal feedback mechanism might share basic aspects with audio–vocal feedback controlling the pitch of vocalizations in other mammals, including the involuntary response to "pitch-shifted feedback" in humans.

Snider, E.A., Cryan, P.M. & Wilson, K.R., 2013. Roost selection by western long-eared myotis (*Myotis evotis*) in burned and unburned piñon–juniper woodlands of southwestern Colorado. *Journal of Mammalogy*, 94(3), pp.640–649.

Abstract: All 16 species of bats known to occur in western Colorado are found at Mesa Verde National Park (MVNP) in the southwestern United States. Since 1996, wildfires have burned more than 70% of MVNP (.15,000 ha), potentially altering food and roosting resources for bats. During the summers of 2006–2007, we investigated roost use by reproductive female western long-eared myotis (*Myotis evotis*). We located 33 bat roosts in rock crevices and 1 in a juniper snag. All but 2 of the roosts were in unburned habitat. Bats roosted alone or in small groups (3 individuals) and switched roosts frequently (1–7 roosts per bat, median = 1.5 roosts per bat, SE - 0.5 roosts per bat). We compared occupied roosts with randomly selected unoccupied crevices and used an information theoretic approach to determine which variables were most important in determining roost use at microhabitat and landscape scales. At the microhabitat scale, maternity roosts were higher above the ground and deeper than random, unoccupied rock crevices. At the landscape scale, roosts were closer to water and farther from burned habitat than random crevices, providing reproductive female *M. evotis* with the best opportunities to drink and forage for insects. Tree roosts are apparently not a vital resource for reproductive female *M. evotis* during the summer months at our study site, presumably because of the extensive availability of rock crevices. Understanding site-specific roosting behavior is important for proper management of bat populations because differences can exist between geographic regions, even among areas with similar plant communities.

Solick, D.I. & Barclay, R.M.R., 2006. Thermoregulation and roosting behaviour of reproductive and nonreproductive female western long-eared bats (*Myotis evotis*) in the Rocky Mountains of Alberta. *Canadian Journal of Zoology*, 84(4), pp.589–599.

Abstract: Entering torpor can yield significant energy savings for temperate-zone bats but can be costly for reproductive females by slowing fetal development and reducing milk production. We studied western long-eared bats (*Myotis evotis* (H. Allen, 1864)) in the Rocky Mountains of Alberta to test the hypothesis that different costs of torpor result in different patterns of thermoregulation and roosting behaviour for reproductive and nonreproductive females. We radio-tracked bats to monitor body temperatures and locate roosts. We took roost measurements and inserted temperature data loggers to measure roost microclimate. Bats entered torpor frequently, but nonreproductive females spent longer periods in torpor, had lower minimum body temperatures, and entered deep torpor more often than reproductive females did, supporting the hypothesis that entering torpor is more costly for reproductive individuals. Roosts were located mainly in rock fields on steep, open, south-facing slopes. Reproductive females roosted in crevices between rocks located above or on the surface of the ground. Roosts warmed rapidly and reached warm daytime temperatures. Females roosted alone during pregnancy but formed small colonies within roosts during lactation when ambient conditions were cooler. Clustering may reduce thermoregulatory costs for both adults and young. Nonreproductive females roosted mainly along in crevices in the ground. These roosts had cooler, more stable microclimates, allowing females to enter deeper bouts of torpor and remain torpid longer.

Speakman, J.R., Webb, P.I. & Racey, P.A., 1991. Effects of disturbance on the energy expenditure of hibernating bats. *The Journal of Applied Ecology*, 28(3), p.1087.

Abstract: (1) We investigated the effects of a range of stimuli, associated with disturbance by visitors to caves, on the energy expenditure of hibernating bats. (2) Twenty-five individual bats of six species were exposed to 206 separate applications of non-tactile stimuli (head torch, photographic flash, sound, speech, temperature increase). This resulted in only nine significant increases in energy expenditure (4.4%). In contrast, nineteen out of nineteen tactile stimuli, applied to ten individuals of four species, resulted in significant increases in energy expenditure. The difference in frequency of response to the two types of stimulation was highly significant. (3) The extra energy expended by bats in a response following a non-tactile stimulation was low (mean=49 J). Tactile stimulation resulted in much greater energy expenditure (mean= 2038 J). (4) Neither the degree nor the frequency of response to non-tactile stimulation was affected by species, body mass, ambient temperature, season, or metabolic rate during torpor. Degree of response to tactile stimulation increased significantly with increasing body mass. (5) Energy expenditure during torpor (pre-stimulation) was significantly affected by temperature in Natterer's bat (*Myotis nattereri* Kuhl), Daubenton's bat (*Myotis daubentoni* Kuhl), brown long-eared bats (*Plecotus auritus* L.), and by body mass in these species and pipistrelles (*Pipistrellus pipistrellus* Schreber). The mean energy expenditure across all species was 6.17mW. (6) By combining the measured energy expenditure in torpor before stimulation with the increase in energy requirements which accompanied non-tactile and tactile disturbance, the mean maximum reduction in potential duration of hibernation resulting from a non-tactile disturbance which elicited a significant response was 4.5h, and was 104h for each tactile disturbance. (7) Each non-tactile disturbance was predicted to decrease fat stores by 0001 g. Each tactile disturbance was predicted to decrease fat stores by 005 g.

Stahlschmidt, P. & Brühl, C.A., 2012. Bats as bioindicators - the need of a standardized method for acoustic bat activity surveys. *Methods in Ecology and Evolution*, 3, pp.503–508.

Abstract: 1. The species-rich group of bats fills a wide range of ecological niches and provides ecosystem services like pest control. Bats are known to be sensitive to environmental stressors and could, therefore, be used in assessing ecosystem quality. To use bats as bioindicators, a standardized bat survey method needs to be established as the existing approaches vary in their methodology, and results are, therefore, often not comparable. 2. Generally, there are two different acoustic bat survey methods: the transect walk and the stationary measurement. By conducting transect surveys and simultaneously using several stationary systems, we measured bat activity within a homogeneous habitat and evaluated which method assessed the spatial bat activity patterns with highest precision. Also the survey tool – the detectors themselves – can be grouped into devices with two different methods of triggering the recording of ultrasonic signals: actively by a fieldworker or automatically by a built-in recording control algorithm of the detector. We measured bat activity simultaneously and side by side with both methods for direct comparison. 3. Our results indicate that the transect survey fails to represent the heterogeneous bat activity patterns in a homogeneous landscape. Furthermore, errors occur based on the subjective hearing of the active triggering of the data recording by the human operator. 4. The application of several stationary and automatic sampling systems has the highest potential for standardized acoustic bat surveys. The general use of such an approach would enable us to understand bat activity at landscape scale and could lead to an improvement of bats as bioindicators.

Sterbing-D'Angelo, S., Chdha, M., Chiu, C., Falk, B., Zian, W., Barcelo, J., Zook, J.M. Moss, C.F., 2011. Bat wing sensors support flight control. *Proceedings of the National Academy of Sciences of the United States of America,* 108(27), pp.11291–6.

Abstract: Bats are the only mammals capable of powered flight, and they perform impressive aerial maneuvers like tight turns, hovering, and perching upside down. The bat wing contains five digits, and its specialized membrane is covered with stiff, microscopically small, domed hairs. We provide here unique empirical evidence that the tactile receptors associated with these hairs are involved in sensorimotor flight control by providing aerodynamic feedback. We found that neurons in bat primary somatosensory cortex respond with directional sensitivity to stimulation of the wing hairs with low-speed airflow. Wing hairs mostly preferred reversed airflow, which occurs under flight conditions when the airflow separates and vortices form. This finding suggests that the hairs act as an array of sensors to monitor flight speed and/or airflow conditions that indicate stall. Depilation of different functional regions of the bats' wing membrane altered the flight behavior in obstacle avoidance tasks by reducing aerial maneuverability, as indicated by decreased turning angles and increased flight speed.

Stilz, W. & Schnitzler, H., 2012. Estimation of the acoustic range of bat echolocation for extended targets. *The Journal of the Acoustical Society of America,* 132, pp.1765–1775.

Abstract: Extended natural structures of the bat environment such as trees, meadows, and water surfaces were ensonified in distances from 1 to 20 m and the echoes recorded using a mobile ultrasonic sonar system. By compensating the atmospheric attenuation, the attenuation of the reflected echo caused by diffraction, energy absorption of the target, and two-way-geometric spreading was calculated for each distance. For each target type the attenuation of the compensated echo sound pressure level was fitted over distance using a linear function which yields simple laws of reflection loss and geometric spreading. By adding to this function again variable atmospheric attenuation, the overall attenuation of a signal reflected from these targets can be estimated for various conditions. Given the dynamic range of a sonar system, the acoustic maximum detection distance can thus be estimated. The results show that the maximum range is dominantly limited by atmospheric attenuation. Energy loss in the reflecting surface is more variable than geometric spreading loss and accounts for most of the differences between the ensonified targets. Depending on atmospheric conditions, echolocation frequency, and the dynamic range of the sonar system, the maximum range for extended backgrounds such as a forest edge can be as short as 2.4 m.

Suga, N., 1990. Cortical computational maps for auditory imaging. *Neural Networks*. 3, pp.3-21.

Abstract:The mustached bat emits complex biosonar signals (pulses) and listens to echoes for orientation and hunting flying insects. Different types of biosonar information are conveyed by different parameters characterizing pulse-echo pairs. For example, range information is conveyed by echo delay, while velocity information is carried by Doppler shift. At the auditory periphery, frequency is expressed by the anatomical location along the basilar membrane and also along the array of ganglion cells, while amplitude and time (duration of signals and interval between signals) are not expressed by anatomical locations, but by discharge rate and the temporal pattern of nerve discharges, respectively. In the auditory cortex, however, not only frequency but also other informationbearing parameters (IBPs) such as echo delay and Doppler shift are

systematically expressed by anatomical locations. That is, the IBPs are mapped. These computational maps greatly depend upon subcortical signal processing. The subcortical auditory nuclei create delay lines and multipliers (or AND gates) for processing range (echo delay) information, and also create level-tolerant frequency tuning and multipliers (or AND gates) for processing velocity (Doppler shift) information. These multipliers are called FM-FM or CF/ CF combinationsensitive neurons, respectively. Signal processing in the auditory system is parallel-hierarchical. The neurophysiological studies of the bat's auditory system provide an excellent data base for computational models.

Sümer, S., Denzinger, A. & Schnitzler, H. U., 2009. Spatial unmasking in the echolocating big brown bat, *Eptesicus fuscus*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 195, pp.463-472.

Abstract: Masking affects the ability of echolocating bats to detect a target in the presence of clutter targets. It can be reduced by spatially separating the targets. Spatial unmasking was measured in a two-alternative-forced-choice detection experiment with four Big Brown Bats detecting a wire at 1 m distance. Depth dependent spatial unmasking was investigated by the bats detecting a wire with a diameter of 1.2 mm in front of a masker with a threshold distance of 11 cm behind the wire. For angle dependent spatial unmasking the masker was turned laterally, starting from its threshold position at 11 cm. With increasing masker angles the bats could detect thinner wires with diameters decreasing from 1.2 mm (target strength −36.8 dB) at 0° to 0.2 mm (target strength −63.0 dB) at 22°. Without masker, the bats detected wire diameters of 0.16 mm (target strength −66.2 dB), reached with masker positions beyond 23° (complete masking release). Analysis of the sonar signals indicated strategies in the echolocation behavior. The bats enhanced the second harmonics of their signals. This may improve the spatial separation between wire and masker due to frequency-dependent directionality increase of sound emission and echo reception.

Sun, J. W. C. & Narins P., 2005. Anthropogenic sounds differentially affect amphibian call rate. *Biological Conservation*, 121, pp.419–427.

Abstract: The effects of airplane flyby noise and playbacks of low-frequency motorcycle sounds on calling activity were examined in a mixed-species anuran calling assemblage in central Thailand. In response to these stimuli, three of the most acoustically active pond-edge species (*Microhyla butleri*, *Rana nigrovittata* and *Kaloula pulchra*) significantly decreased their calling rate. Yet under the identical stimulus regime, *Rana taipehensis* consistently increased its calling rate. Moreover, during the occasional natural lulls in the chorus in which males collectively stop calling, resulting in a conspicuous reduction in chorus intensity, calls of *R. taipehensis* would appear to emerge from the background noise. These results suggest that man-made acoustic interference may affect anuran chorus behavior either directly by modulating call rates of the chorus participants or indirectly, by suppressing calling behavior of one set of species which in turn stimulates calling in other species. The results of our playback experiment coupled with the natural calling behavior of these species support the latter hypothesis.

Surlykke, A., Ghose, K. & Moss, C.F., 2009. Acoustic scanning of natural scenes by echolocation in the big brown bat, *Eptesicus fuscus*. *The Journal of Experimental Biology*, 212(Pt 7), pp.1011–20.

Abstract: Echolocation allows bats to orient and localize prey in complete darkness. The sonar beam of the big brown bat, *Eptesicus fuscus*, is directional but broad enough to provide audible echo information from within a 60-90 deg. cone. This suggests that the big brown bat could interrogate a natural scene without fixating each important object separately. We tested this idea by measuring the directional aim and duration of the bat's sonar beam as it performed in a dual task, obstacle avoidance and insect capture. Bats were trained to fly through one of two openings in a fine net to take a tethered insect at variable distances behind the net. The bats sequentially scanned the edges of the net opening and the prey by centering the axis of their sonar beam with an accuracy of approximately 5 deg. The bats also shifted the duration of their sonar calls, revealing sequential sampling along the range axis. Changes in duration and directional aim were correlated, showing that the bat first inspected the hole, and then shifted its gaze to the more distant insect, before flying through the net opening. Contrary to expectation based on the sonar beam width, big brown bats encountering a complex environment accurately pointed and shifted their sonar gaze to sequentially inspect closely spaced objects in a manner similar to visual animals using saccades and fixations to scan a scene. The findings presented here from a specialized orientation system, echolocation, offer insights into general principles of active sensing across sensory modalities for the perception of natural scenes.

Surlykke A., and Kalko, E.K.V., 2008. Echolocating bats cry out loud to detect their prey. *PloS One*, 3, p.e2036

Abstract: Echolocating bats have successfully exploited a broad range of habitats and prey. Much research has demonstrated how time-frequency structure of echolocation calls of different species is adapted to acoustic constraints of habitats and foraging behaviors. However, the intensity of bat calls has been largely neglected although intensity is a key factor determining echolocation range and interactions with other bats and prey. Differences in detection range, in turn, are thought to constitute a mechanism promoting resource partitioning among bats, which might be particularly important for the species-rich bat assemblages in the tropics. Here we present data on emitted intensities for 11 species from 5 families of insectivorous bats from Panamá hunting in open or background cluttered space or over water. We recorded all bats in their natural habitat in the field using a multi-microphone array coupled with photographic methods to assess the bats' position in space to estimate emitted call intensities. All species emitted intense search signals. Output intensity was reduced when closing in on background by 4–7 dB per halving of distance. Source levels of open space and edge space foragers (Emballonuridae, Mormoopidae, Molossidae, and Vespertilionidae) ranged between 122–134 dB SPL. The two Noctilionidae species hunting over water emitted the loudest signals recorded so far for any bat with average source levels of ca. 137 dB SPL and maximum levels above 140 dB SPL. In spite of this ten-fold variation in emitted intensity, estimates indicated, surprisingly, that detection distances for prey varied far less; bats emitting the highest intensities also emitted the highest frequencies, which are severely attenuated in air. Thus, our results suggest that bats within a local assemblage compensate for frequency dependent attenuation by adjusting the emitted intensity to achieve comparable detection distances for prey across species. We conclude that for bats with similar hunting habits, prey detection range represents a unifying constraint on

the emitted intensity largely independent of call shape, body size, and close phylogenetic relationships.

Surlykke, A. & Moss, C., 2000. Echolocation behavior of big brown bats, *Eptesicus fuscus*, in the field and the laboratory. *The Journal of the Acoustical Society of America* 108(5), pp.2419–2429.

Abstract: Echolocation signals were recorded from big brown bats, *Eptesicus fuscus*, flying in the field and the laboratory. In open field areas the interpulse intervals (IPI) of search signals were either around 134 ms or twice that value, 270 ms. At long IPI's the signals were of long duration (14 to 18–20 ms), narrow bandwidth, and low frequency, sweeping down to a minimum frequency (F_{min}) of 22–25 kHz. At short IPI's the signals were shorter (6–13 ms), of higher frequency, and broader bandwidth. In wooded areas only short (6–11 ms) relatively broadband search signals were emitted at a higher rate (avg. IPI5122 ms) with higher F_{min} (27–30 kHz). In the laboratory the IPI was even shorter (88 ms), the duration was 3–5 ms, and the F_{min} 30– 35 kHz, resembling approach phase signals of field recordings. Excluding terminal phase signals, all signals from all areas showed a negative correlation between signal duration and F_{min} , i.e., the shorter the signal, the higher was F_{min}. This correlation was reversed in the terminal phase of insect capture sequences, where F_{min} decreased with decreasing signal duration. Overall, the signals recorded in the field were longer, with longer IPI's and greater variability in bandwidth than signals recorded in the laboratory.

Surlykke, A., Pedersen, S.B. & Jakobsen, L., 2009. Echolocating bats emit a highly directional sonar sound beam in the field. *Proceedings. Biological sciences / The Royal Society*, 276, pp.853–60.

Abstract: Bats use echolocation or biosonar to navigate and find prey at night. They emit short ultrasonic calls and listen for reflected echoes. The beam width of the calls is central to the function of the sonar, but directionality of echolocation calls has never been measured from bats flying in the wild. We used a microphone array to record sounds and determine horizontal directionality for echolocation calls of the trawling Daubenton's bat, *Myotis daubentonii*, flying over a pond in its natural habitat. *Myotis daubentonii* emitted highly directional calls in the field. Directionality increased with frequency. At 40 kHz half-amplitude angle was 25 degrees , decreasing to 14 degrees at 75 kHz. In the laboratory, *M. daubentonii* emitted less intense and less directional calls. At 55 kHz half-amplitude angle was 40 degrees in the laboratory versus 20 degrees in the field. The relationship between frequency and directionality can be explained by the simple piston model. The model also suggests that the increase in the emitted intensity in the field is caused by the increased directionality, focusing sound energy in the forward direction. The bat may increase directionality by opening the mouth wider to emit a louder, narrower beam in the wild.

Suthers, R. & Summers, C., 1980. Behavioral audiogram and masked thresholds of the megachiropteran echolocating bat, *Rousettus*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 136, pp.227-233.

Summary: 1. A behavioral auditory threshold obtained by operant conditioning of the megachiropteran bat, *Rousettus aegyptiacus*, is described. 2. The auditory threshold in quiet has a maximum sensitivity between 8 and 10 kHz, separated by an 8 to 10 dB rise from a second

more sharply tuned peak at 20 kHz (Fig. 2). The minimum mean threshold is 44 dB SPL at 10 kHz. No response was obtained to sounds below 1 kHz or above 30 kHz. 3. The amount of masking produced by the presence of broad band noise with a spectrum level of 31.7 dB SPL varies between a minimum at 2 kHz of 10.1 dB and a maximum at 20 kHz of 21.9 dB (Fig. 2). 4. The critical ratio is smallest (29 dB) at 8 kHz. It increases gradually at higher frequencies in a manner similar to other mammals studied, but is unusual in rising very steeply at lower frequencies (Fig. 3). 5. The masked threshold at 12 kHz increases only about 11 dB when the stimulus duration is decreased from 250 ms to 2 ms (Fig. 4). 6. The acoustic orientation of *Rousettus* is discussed in relation to these psychophysical data.

Swift, S.M. & Racey, P., 2002. Gleaning as a foraging strategy in Natterer's bat *Myotis nattereri*. *Behavioral Ecology and Sociobiology*, 52(5), pp.408–416.

Abstract: Natterer's bats, *Myotis nattereri*, continued to emit echolocation calls while gleaning non-flying arthropods, and made little use of prey-generated sound as a cue to locate them. Feeding buzzes were recorded during most attacks. In contrast, brown long-eared bats, *Plecotus auritus*, in parallel experiments stopped echolocating during the hovering phase of gleaning attacks, did not emit feeding buzzes and used prey-generated sound as a cue to find food. In uncluttered foraging situations, *M. nattereri* were able to locate prey by echolocation alone, but in clutter they may have combined it with associative learning, and may also have gleaned prey after being attracted to food sources by feeding buzzes from conspecifics. Both in a flight room and in the wild, Natterer's bats foraged using a sequence of low searching flight, hovering, capture, using the interfemoral membrane and prey consumption at a perch or on the wing. They also landed and pursued prey by quadrupedal locomotion. Their diet consisted mainly of medium-sized (5-15 mm body length) arthropods, particularly dungflies, spiders, beetles and harvestmen, active on plant surfaces at night, some of which could only have been captured by gleaning. Moths were eaten in relatively small quantities, suggesting that the bats were unable to hear their fluttering sounds or that tympanate moth species could detect the bats' approach and take avoiding action. In the same area, moths formed the major component of the diet *of P. auritus*, reflecting the different foraging techniques of the two bat species.

Swystun, M.B., Lane, J.E. & Brigham, R.M., 2007. Cavity roost site availability and habitat use by bats in different aged riparian cottonwood stands. *Acta Chiropterologica*, 9(1), pp.183–191.

Abstract: Riparian forests provide important roosting habitat, abundant prey and access to drinking water for many bat species but to date there has been little research on the differential quality of habitats within riparian areas. We quantified the density of potential roost cavities in three age classes (i.e., young: ca. 20 years, mature: ca. 60 years, and old: ca. 100 years) of riparian cottonwood (*Populus deltoides*) forest stands. Bat activity was also sampled using acoustic detectors in one representative stand of each age class. Stands were situated along an 80 km stretch of the Missouri River in southeastern South Dakota and northwestern Iowa, USA. We predicted the highest density of potential roosts and the highest activity of bats to occur in the oldest age class. Contrary to our predictions, and previous work in aspen dominated upland sites, we found that the density of potential roosts was not significantly different between mature and old stands. However, there were no potential roosts in young stands. Data from guano traps verified the use of a number of cavities in both mature and old stands. Both commuting and foraging activities were highest in the mature, relative to the old and young stand. In total, our

data indicate that mature and old stands represent high quality roosting habitat, with the mature being used preferentially for commuting and foraging. Trees in the oldest stands, however, are nearing the end of their lifespan and falling. Younger cohorts must therefore be retained for future recruitment of natural cavities.

Sygna, K., Aasvang, G.M., Aamodt, G., Oftedal, B. & Krog, N.H., 2014. Road traffic noise, sleep and mental health. *Environmental Research*, 131, pp.17–24.

Abstract: This study examines the relationship between road traffic noise, self-reported sleep quality and mental health. The study is cross-sectional and based on data from a survey conducted in Oslo, Norway, in 2000. Psychological distress (Hopkins Symptom Checklist, HSCL-25) was measured along with self-reported somatic health, sleep quality, noise sensitivity and socioeconomic variables. Questionnaire data were combined with modeled estimates of noise exposure. The total study sample consisted of 2898 respondents. After adjustment for potential confounders and stratifying for sleep quality, we found a positive, but not statistically significant association between noise exposure and symptoms of psychological distress among participants with poor sleep quality (slope=0.06, 95% CI: -0.02 to 0.13, per 10 dB increase in noise exposure). In the same sleep quality group, we found a borderline statistically significant association between noise exposure and a symptom level indicating a probable mental disorder (HSCL≥1.55) (odds ratio=1.47, 95% CI: 0.99-1.98, per 10 dB increase in noise exposure). We found no association between road traffic noise and mental health among subjects reporting good and medium sleep quality. The results suggest that road traffic noise may be associated with poorer mental health among subjects with poor sleep. Individuals with poor sleep quality may be more vulnerable to effects of road traffic noise on mental health than individuals with better sleep quality.

Szewczak, J. M., 2011. Acoustic deterrence of bats: A guidance document. A report submitted to the California Department of Transportation, Sacramento, Ca.

No abstract

Szewczak, J.M. & Arnett, E.B., 2006. Preliminary field test results of a potential acoustic deterrent to reduce bat mortality from wind turbines. An investigative report submitted to the Bats and Wind Cooperative. Bat Conservation International. Austin Texas.

No abstract

Szewczak, J.M. & Arnett, E.B., 2008. Field test results of a potential acoustic deterrent to reduce bat mortality from wind turbines. An investigative report submitted to the Bats and Wind Cooperative. Bat Conservation International. Austin Texas.

No abstract

Takahashi, E., Hyomoto, K., Riquimaroux, H., Watanabe, Y., Ohta, T. & Hiryu, S., 2014. Adaptive changes in echolocation sounds by *Pipistrellus abramus* in response to artificial jamming sounds. *The Journal of Experimental Biology*, 217(Pt 16), pp.2885–91.

Abstract: The echolocation behavior of *Pipistrellus abramus* during exposure to artificial jamming sounds during flight was investigated. Echolocation pulses emitted by the bats were

recorded using a telemetry microphone mounted on the bats' backs, and their adaptation based on acoustic characteristics of emitted pulses was assessed in terms of jamming-avoidance responses (JARs). In experiment 1, frequency-modulated jamming sounds (3 ms duration) mimicking echolocation pulses of *P. abramus* were prepared. All bats showed significant increases in the terminal frequency of the frequency-modulated pulse by an average of 2.1-4.5 kHz when the terminal frequency of the jamming sounds was lower than the bats' own pulses. This frequency shift was not observed using jamming frequencies that overlapped with or were higher than the bats' own pulses. These findings suggest that JARs in *P. abramus* are sensitive to the terminal frequency of jamming pulses and that the bats' response pattern was dependent on the slight difference in stimulus frequency. In experiment 2, when bats were repeatedly exposed to a band-limited noise of 70 ms duration, the bats in flight more frequently emitted pulses during silent periods between jamming sounds, suggesting that the bats could actively change the timing of pulse emissions, even during flight, to avoid temporal overlap with jamming sounds. Our findings demonstrate that bats could adjust their vocalized frequency and emission timing during flight in response to acoustic jamming stimuli.

Tanaka, S. & Shiraishi, B., 2008. Wind effects on noise propagation for complicated geographical and road configurations. *Applied Acoustics*, 69(11), pp.1038–1043.

Abstract: Outdoor propagation from roads is influenced by wind, temperature and humidity. It is necessary to predict wind effects to simulate long-term environmental noise accurately. Noise levels have been measured in conjunction with wind speed and wind direction measurements. These noise levels showed noticeable daily changes. Excess attenuations of noise levels were found to depend on the vector wind (U_{vec}). By relating the vector wind and observed sound attenuations under all wind conditions, the influence of wind can be more accurately predicted for purposes of simulating noise propagation.

Taylor, C., 2013. A highway, a wetland and 250,000 bats. Bay Nature July 25, 2013. Online: http://baynature.org/2013/07/25/yolo-bats/

No abstract

Teeling, E.C., 2009. Hear, hear: the convergent evolution of echolocation in bats? *Trends in Ecology & Evolution*, 24(7), pp.351–4.

Abstract: The evolutionary history of laryngeal echolocation is controversial, and little is known about the molecular mechanisms that underlie this sense. A recent paper by Li and colleagues is one of the first studies to identify and sequence a gene involved in echolocation in bats -Prestin, the so-called mammalian hearing gene. Phylogenetic analyses show evidence for positive selection acting on this gene in the echolocating lineages and support the convergent evolution of laryngeal echolocation in bats.

Thomas, D.W., 1988. The distribution of bats in different ages of Douglas-fir forests. *The Journal of Wildlife Management*, 52(4), p.619.

Abstract: I examined the distribution of activity of bats in different-age Douglas-fir (P*seudotsuga menziesii*) stands in the Pacific Northwest. Bat activity was higher ($P < 0.05$) in old-growth forests than in mature or young tree stands. In the southern Washington Cascades, old-growth stands had 2.65-5.67 x higher bat activity than younger stands. In the Oregon Coast

Range, old-growth stands had 2.54-9.75 x higher bat activity. Feeding activity was low in all forest stands and activity by bats occurred during the first 15 minutes of the evening, indicating that bats use old-growth forests only for roosting. Reproductive females were not captured at sites >300 m elevation in the Washington Cascades, but were common at elevations >300 m in the Oregon Coast Range. Reductions in old-growth forests may have a more severe impact on populations of breeding bats in the Oregon Coast Range than in the Washington Cascades.

Thomas, D.W., 1995. Hibernating bats are sensitive to nontactile human disturbance. *Journal of Mammalogy,* 76, pp.940-946.

Abstract: I measured natural baseline activity and the response of hibernating bats to human presence in a hibernaculum containing ca. 1,300 bats of the species Myotis lucifugus and Myotis septentrionalis. Infrared detectors registered baseline flight movements in the hibernaculum over 62 days in January to March and over 8 days in April, when no observer was present, and they also registered the increase in flight movements following six visits of 1-2 h each to the hibernaculum. Visits to the mine resulted in a dramatic increase in flight activity of bats beginning within 30 min of the visit, peaking 1.0-7.5 h later, and remaining significantly above baseline level for 2.5-8.5 h. These results show that, contrary to previously published studies, hibernating bats are sensitive to nontactile stimuli and arouse and fly following human visits. To avoid increased mortality due to the premature depletion of fat reserves, human visits to hibernacula should be kept to a minimum.

Tressler, J. & Smotherman, M.S., 2009. Context-dependent effects of noise on echolocation pulse characteristics in free-tailed bats. *Journal of comparative physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology,* 195(10), pp.923–34.

Abstract: Background noise evokes a similar suite of adaptations in the acoustic structure of communication calls across a diverse range of vertebrates. Echolocating bats may have evolved specialized vocal strategies for echolocating in noise, but also seem to exhibit generic vertebrate responses such as the ubiquitous Lombard response. We wondered how bats balance generic and echolocation-specific vocal responses to noise. To address this question, we first characterized the vocal responses of flying free-tailed bats (*Tadarida brasiliensis*) to broadband noises varying in amplitude. Secondly, we measured the bats' responses to band-limited noises that varied in the extent of overlap with their echolocation pulse bandwidth. We hypothesized that the bats' generic responses to noise would be graded proportionally with noise amplitude, total bandwidth and frequency content, and consequently that more selective responses to band-limited noise such as the jamming avoidance response could be explained by a linear decomposition of the response to broadband noise. Instead, the results showed that both the nature and the magnitude of the vocal responses varied with the acoustic structure of the outgoing pulse as well as non-linearly with noise parameters. We conclude that free-tailed bats utilize separate generic and specialized vocal responses to noise in a context-dependent fashion.

Turbill, C., Körtner, G. & Geiser, F., 2003. Natural use of heterothermy by a small, tree-roosting bat during summer. *Physiological and Biochemical Zoology: PBZ,* 76(6), pp.868–76.

Abstract: Little is known about the use of heterothermy by wild bats during summer, especially for tree-roosting species. Because thermal conditions within tree roosts can fluctuate widely with

ambient temperature, which affects thermoregulatory energy expenditure during diurnal roosting, we measured skin temperatures of free-ranging male *Nyctophilus geoffroyi* (8 g) to quantify the relation between summer torpor use and roost thermal conditions. Bats roosted under bark on the northern (sunny) side of trees and entered torpor every day, usually near sunrise. Bats exhibited two bouts of torpor on most days: the first occurred in the morning, was terminated by partially passive rewarming, and was followed by a period of normothermy during the warmest part of the day; a second torpor bout occurred in the late afternoon, with arousal near sunset. On the warmest days, bats had only a single, short morning bout. On the coolest days, bats remained torpid throughout the day, and one 2-d bout was observed. Thus, presumably owing to their poorly insulated roosts and the high energetic cost of normothermy at temperatures below 30 degrees C, the extent and timing of heterothermy was closely related to the cycle of diurnal temperatures. Our study indicates that torpor use is important for energy maintenance during summer diurnal roosting of *N. geoffroyi* and likely of other small, tree-roosting bats.

Übernickel, K., Tschapka, M. & Kalko, E.K. V., 2013. Selective eavesdropping behaviour in three neotropical bat species. *Ethology*, 119, pp.66–76.

Abstract: Knowledge of interspecies information transfer in mammals is scarce compared with other taxa. We investigated whether eavesdropping on echolocation calls of bats may be used by sympatric bats with similar feeding ecology. We performed playback experiments with three free-ranging neotropical bat species, broadcasting search phase calls or feeding buzzes of conspecifics and heterospecifics belonging either to the same or to another bat family. Both the greater fishing bat *Noctilio leporinus* and the lesser bulldog bat *Noctilio albiventris* (Noctilionidae) reacted with repeated approaches in response to playbacks of search phase calls and feeding buzzes from conspecifics and also to congeneric feeding buzzes. *Noctilio leporinus* also were attracted by search phase calls from its sister species *N. albiventris*. In contrast, the sac-winged bat *Saccopteryx bilineata* (Emballonuridae) did not react to any playback sequences presented. Our results support the existence of eavesdropping behaviour for both species of *Noctilio*. We suggest that information transfer via eavesdropping may depend mainly on species-specific traits, including foraging style and social behaviour (territoriality, group foraging), and on distribution and density of prey. Call design had only a minor influence on the reaction.

Ulanovsky, N., Fenton, M. B., Tsoar, A. & Korine, C. 2004. Dynamics of jamming avoidance in echolocating bats. *Proceedings of the Royal Society of London, Series B*, 271, pp.1467-1475.

Abstract: Animals using active sensing systems such as echolocation or electrolocation may experience interference from the signals of neighbouring conspecifics, which can be offset by a jamming avoidance response (JAR). Here, we report JAR in one echolocating bat (*Tadarida teniotis*: Molossidae) but not in another (*Taphozous perforatus*: Emballonuridae) when both flew and foraged with conspecifics. In *T. teniotis*, JAR consisted of shifts in the dominant frequencies of echolocation calls, enhancing differences among individuals. Larger spectral overlap of signals elicited stronger JAR. *Tadarida teniotis* showed two types of JAR: (i) for distant conspecifics: a symmetric JAR, with lower- and higher-frequency bats shifting their frequencies downwards and upwards, respectively, on average by the same amount; and (ii) for closer conspecifics: an asymmetric JAR, with only the upper-frequency bat shifting its frequency upwards. In comparison, 'wave-type' weakly electric fishes also shift frequencies of discharges in a JAR, but unlike *T. teniotis*, the shifts are either symmetric in some species or asymmetric in

others. We hypothesize that symmetric JAR in T. teniotis serves to avoid jamming and improve echolocation, whereas asymmetric JAR may aid communication by helping to identify and locate conspecifics, thus minimizing chances of mid-air collisions.

Ulanovsky, N. & Moss, C.F., 2008. What the bat's voice tells the bat's brain. *Proceedings of the National Academy of Sciences of the United States of America,* 105(25), pp.8491–8.

Abstract: For over half a century, the echolocating bat has served as a valuable model in neuroscience to elucidate mechanisms of auditory processing and adaptive behavior in biological sonar. Our article emphasizes the importance of the bat's vocal-motor system to spatial orientation by sonar, and we present this view in the context of three problems that the echolocating bat must solve: (i) auditory scene analysis, (ii) sensorimotor transformations, and (iii) spatial memory and navigation. We summarize our research findings from behavioral studies of echolocating bats engaged in natural tasks and from neurophysiological studies of the bat superior colliculus and hippocampus, brain structures implicated in sensorimotor integration, orientation, and spatial memory. Our perspective is that studies of neural activity in freely vocalizing bats engaged in natural behaviors will prove essential to advancing a deeper understanding of the mechanisms underlying perception and memory in mammals.

U.S. Department of Transportation (USDOT)., 2011. Highway Traffic Noise Analyses and Abatement Guidance. U.S. Department of Transportation, Federal Highway Administration, Office of Environment and Planning, Noise and Air Quality Branch, Washington, D.C. Online: https://www.fhwa.dot.gov/environment/noise/regulations_and_guidance/analysis_and_abatement_guidance/revguidance.pdf

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U.S. Fish and Wildlife Service (USFWS 2006). Transmittal of Guidance: Estimating the effects of auditory and visual disturbance to northern spotted owls and marbled murrelets in northwestern California. Arcata Fish and Wildlife Office, Arcata California. Online: http://calfire.ca.gov/resource_mgt/downloads/EstimatingAuditoryAndVisualDisturbanceEffectsOnMAMUAndNSO.pdf.

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Valdez, E.W. & Cryan, P.M., 2009. Food habits of the hoary bat (*Lasiurus cinereus*) during spring migration through New Mexico. *The Southwestern Naturalist*, 54(2), pp.195–200.

Abstract: Hoary bats (*Lasiurus cinereus*) exhibit continental patterns of migration that are unique to bats, but details about their behaviors during migration are lacking. We captured 177 hoary bats in spring and early summer 2002 as individuals migrated through the Sandia Mountains of north-central New Mexico. Our results support earlier observations of asynchronous timing of migration between sexes of *L. cinereus* during spring, with females

preceding males by ca. 1 month. We provide the first evidence that hoary bats may travel in dispersed groups, fly below the tree canopy along streams, and feed while migrating during spring. Analysis of guano revealed that diet of *L. cinereus* consisted mostly of moths, with more than one-half of samples identified as Noctuidae and Geometridae. We observed a late-spring decline in consumption of moths that might be related to seasonal changes in abundance of prey, differential selection of prey by bats, or sampling bias. We suspect that spring migration of L. *cinereus* through New Mexico temporally coincides with the seasonal abundance of moths.

Van Beers, R.J., Wolpert, D.M. & Haggard, P., 2002. When feeling is more important than seeing in sensorimotor adaptation. *Current Biology*, 12(10), pp.834–837.

Abstract: Perception and action are based on information from multiple sensory modalities. For instance, both vision and proprioception provide information about hand position, and this information is integrated to generate a single estimate of where the hand is in space. Classically, vision has been thought to dominate this process, with the estimate of hand position relying more on vision than on proprioception [1]. However, an optimal integration model [2] that takes into account the precision of vision and proprioception predicts that the weighting of the two senses varies with direction and that the classical result should only hold for specific spatial directions. Using an adaptation paradigm, we show that, as predicted by this model, the visual proprioceptive integration varies with direction. Variation with direction was so strong that, in the depth direction, the classical result was reversed: the estimate relies more on proprioception than on vision. These results provide evidence for statistically optimal integration of information from multiple modalities.

Vanderelst, D., Jonas, R. & Herbert, P., 2012. The furrows of Rhinolophidae revisited. *Journal of the Royal Society, Interface / the Royal Society*, 9(70), pp.1100–3.

Abstract: Rhinolophidae, a family of echolocating bats, feature very baroque noseleaves that are assumed to shape their emission beam. Zhuang & Muller (Zhuang & Muller 2006) have proposed, based on finite element simulations, that the furrows present in the noseleaves of these bats act as resonance cavities. Using *Rhinolophus rouxi* as a model species, they reported that a resonance phenomenon causes the main beam to be elongated at a particular narrow frequency range. Virtually filling the furrows reduced the extent of the main lobe. However, the results of Zhuang & Muller are difficult to reconcile with the ecological background of *R. rouxi*. In this report, we replicate the study of Zhuang & Muller, and extend it in important ways: (i) we take the filtering of the moving pinnae into account, (ii) we use a model of the echolocation task faced by Rhinolophidae to estimate the effect of any alterations to the emission beam on the echolocation performance of the bat, and (iii) we validate our simulations using a physical mock-up of the morphology of *R. rouxi*. In contrast to Zhuang & Muller, we find the furrows to focus the emitted energy across the whole range of frequencies contained in the calls of *R. rouxi* (both in simulations and in measurements). Depending on the frequency, the focusing effect of the furrows has different consequences for the estimated echolocation performance. We argue that the furrows act to focus the beam in order to reduce the influence of clutter echoes.

Vanderelst, D., Mey, F.D., Peremans, H., Geipel, G., Kalko, E. & Firzlaff, U., 2010. What noseleaves do for FM bats depends on their degree of sensorial specialization. *PloS One*, 5(8), p.e11893.

Abstract: BACKGROUND: Many bats vocalizing through their nose carry a prominent noseleaf that is involved in shaping the emission beam of these animals. To our knowledge, the exact role of these appendages has not been thoroughly investigated as for no single species both the hearing and the emission spatial sensitivities have been obtained. In this paper, we set out to evaluate the complete spatial sensitivity of two species of New World leaf-nosed bats: *Micronycteris microtis* and *Phyllostomus discolor*. From an ecological point of view, these species are interesting as they belong to the same family (Phyllostomidae) and their noseleaves are morphologically similar. They differ vastly in the niche they occupy. Comparing these species allows us to relate differences in function of the noseleaf to the ecological background of bat species. METHODOLOGY/PRINCIPAL FINDINGS: We simulate the spatial sensitivity of both the hearing and the emission subsystems of two species, *M. microtis* and *P. discolor*. This technique allows us to evaluate the respective roles played by the noseleaf in the echolocation system of these species. We find that the noseleaf of *M. microtis* focuses the radiated energy better and yields better control over the emission beam. CONCLUSIONS: From the evidence presented we conclude that the noseleaves serve quantitatively different functions for different bats. The main function of the noseleaf is to serve as an energy focusing mechanism that increases the difference between the reflected energy from objects in the focal area and objects in the periphery. However, despite the gross morphological similarities between the noseleaves of the two Phyllostomid species they focus the energy to a different extent, a capability that can be linked to the different ecological niches occupied by the two species.

Vanderelst, D., Reijniers, J., Firzlaff, U. Peremans, H., 2011. Dominant glint based prey localization in horseshoe bats: a possible strategy for noise rejection. *PLoS Computational Biology*, 7(12), p.e1002268.

Abstract: Rhinolophidae or Horseshoe bats emit long and narrowband calls. Fluttering insect prey generates echoes in which amplitude and frequency shifts are present, i.e. glints. These glints are reliable cues about the presence of prey and also encode certain properties of the prey. In this paper, we propose that these glints, i.e. the dominant glints, are also reliable signals upon which to base prey localization. In contrast to the spectral cues used by many other bats, the localization cues in Rhinolophidae are most likely provided by self-induced amplitude modulations generated by pinnae movement. Amplitude variations in the echo not introduced by the moving pinnae can be considered as noise interfering with the localization process. The amplitude of the dominant glints is very stable. Therefore, these parts of the echoes contain very little noise. However, using only the dominant glints potentially comes at a cost. Depending on the flutter rate of the insect, a limited number of dominant glints will be present in each echo giving the bat a limited number of sample points on which to base localization. We evaluate the feasibility of a strategy under which Rhinolophidae use only dominant glints. We use a computational model of the echolocation task faced by Rhinolophidae. Our model includes the spatial filtering of the echoes by the morphology of the sonar apparatus of *Rhinolophus rouxii* as well as the amplitude modulations introduced by pinnae movements. Using this model, we evaluate whether the dominant glints provide Rhinolophidae with enough information to perform localization. Our simulations show that Rhinolophidae can use dominant glints in the echoes as carriers for self-induced amplitude modulations serving as localization cues. In particular, it is shown that the reduction in noise achieved by using only the dominant glints outweighs the information loss that occurs by sampling the echo.

Vanderelst, D., Reijniers, J., Steckel, J. & Peremans, H., 2011. Information generated by the moving pinnae of *Rhinolophus rouxi*: tuning of the morphology at different harmonics. PloS One, 6(6), p.e20627.

Abstract: Bats typically emit multi harmonic calls. Their head morphology shapes the emission and hearing sound fields as a function of frequency. Therefore, the sound fields are markedly different for the various harmonics. As the sound field provides bats with all necessary cues to locate objects in space, different harmonics might provide them with variable amounts of information about the location of objects. Also, the ability to locate objects in different parts of the frontal hemisphere might vary across harmonics. This paper evaluates this hypothesis in *R. rouxi*, using an information theoretic framework. We estimate the reflector position information transfer in the echolocation system of *R. rouxi* as a function of frequency. This analysis shows that localization performance reaches a global minimum and a global maximum at the two most energetic frequency components of *R. rouxi* call indicating tuning of morphology and harmonic structure. Using the fundamental the bat is able to locate objects in a large portion of the frontal hemisphere. In contrast, using the 1st overtone, it can only locate objects, albeit with a slightly higher accuracy, in a small portion of the frontal hemisphere by reducing sensitivity to echoes from outside this region of interest. Hence, different harmonic components provide the bat either with a wide view or a focused view of its environment. We propose these findings can be interpreted in the context of the foraging behaviour of *R. rouxi*, i.e., hunting in cluttered environments. Indeed, the focused view provided by the 1st overtone suggests that at this frequency its morphology is tuned for clutter rejection and accurate localization in a small region of interest while the finding that overall localization performance is best at the fundamental indicates that the morphology is simultaneously tuned to optimize overall localization performance at this frequency.

Vater, M. & Kössl, M., 2011. Comparative aspects of cochlear functional organization in mammals. *Hearing Research*, 273(1-2), pp.89–99.

Abstract: This review addresses the functional organization of the mammalian cochlea under a comparative and evolutionary perspective. A comparison of the monotreme cochlea with that of marsupial and placental mammals highlights important evolutionary steps towards a hearing organ dedicated to process higher frequencies and a larger frequency range than found in non-mammalian vertebrates. Among placental mammals, there are numerous cochlear specializations which relate to hearing range in adaptation to specific habitats that are superimposed on a common basic design. These are illustrated by examples of specialist ears which evolved excellent high frequency hearing and echolocation (bats and dolphins) and by the example of subterranean rodents with ears devoted to processing low frequencies. Furthermore, structural functional correlations important for tonotopic cochlear organization and predictions of hearing capabilities are discussed.

Vater, M. & Siefer, W., 1995. The cochlea of *Tadarida brasiliensis*: specialized functional organization in a generalized bat. *Hearing Research*, 91, pp.178–195.

Abstract: *Tadarida brasiliensis mexicana* employs a broad-band sonar system at frequencies between 8l) and 20 kHz and is characterized by non-specialized hearing capabilities. The cochlear frequency map was determined with extracellular horseradish peroxidase tracing in relation to quantitative morphological data obtained with light, scanning and transmission

electron microscopy. These data reveal distinct species characteristic specializations clearly separate from the patterns observed in other bats with either broad-band or narrow-band sonar systems. The basilar membrane (BM) is coiled to 2.5 turns and about 12 mm long. Its thickness and width only change within the extreme basal and apical ends. The frequency range from about 30 to 80 kHz is represented in the lower basal turn with a typically mammalian mapping coefficient of about 3 mm/octave. This region exhibits morphological features correlated with non-specialized processing of high frequencies. (1) The BM is radially segmented by thickenings of pars tecta and pars pectinata. (2) The 3 rows of outer hair cells (OHCs) have similar morphology. Between 35 and 86% distance from base, frequencies between 30 and 12 kHz are represented with a slightly expanded mapping coefficient of about 6 mm/octave. In analogy to previous work, this cochlea region is termed "acoustic fovea". It includes the frequency range of maximum sensitivity and sharpest tuning (21-27 kHz) but also frequencies below the sonar signals. The fovea is characterized by several morphological specializations. (1) The BM features a continuous radial thickening mainly composed of hyaline substance. (2) There is an increased number of layers of tension fibroblasts in the spiral ligament. (3) There are morphological differences in the arrangements of stereocilia bundles among the 3 rows of OHCs. The transitions between non-specialized and specialized cochlear regions occur gradually within a distance of about 600 µm. The gradients in stereocilia length of both receptor cell types and the gradations in length of the OHC bodies match specialized aspects of the frequency map.

Veselka, N., McGuire, L.P., Dzal, Y.A., Hooton, L.A. & Fenton, M.B., 2013. Spatial variation in the echolocation calls of the little brown bat (*Myotis lucifugus*). *Canadian Journal of Zoology*, 91, pp.795–801.

Abstract: We studied spatial variation in echolocation call structure of the little brown bat (*Myotis lucifugus* (LeConte, 1831)) by analysing calls recorded from free-flying individuals at 1 site in Haida Gwaii, British Columbia, 1 site in Chautaqua, New York, and 20 sites along the Hudson River, New York. We controlled for factors that are often thought to lead to interspecific variation in echolocation calls (habitat, ontogeny, presence of conspecifics, recording techniques, ambient conditions), which allowed us to focus on the effect of spatial scale on call structure. As predicted, we found that at small scales (up to 1 km), there was significant geographic variation, likely owing to roost-specific signatures and group foraging activities. At intermediate scales (2–500 km), we found no differences in call structure, suggesting that populations within this area are part of a single hibernating and breeding population. Finally, echolocation call structure differed at the continental scale (>1000 km) likely because of little genetic exchange among sampled populations. Our results highlight the importance of considering the magnitude of spatial scale when examining variation in echolocation call structure.

Voigt, C.C., Behr, O., Caspers, B., von Helversen, O., Knornschild, M., Mayer, F. & Nagy, M., 2008. Songs, scents, and senses: sexual selection in the greater sac-winged bat, *Saccopteryx bilineata*. *Journal of Mammalogy*, 89(6), pp.1401–1410.

Abstract: Like many other mammals, *Saccopteryx bilineata* exhibits a polygynous mating system, in which each male defends a group of females called a harem. Colonies consist of several harems, and nonharem males roost adjacent to harems. Unlike most other mammals, females disperse from their natal colony and most juvenile males remain in it. Thus, colonies consist of patrilines, which promotes intense local mate competition. Females are in estrus during a few weeks at the end of the rainy season. Mating is most likely initiated by females and

preceded by intense courtship displays of males. Forty percent of colony males do not sire any offspring during their tenure in the colony, whereas a few males can sire up to 6 offspring in a single year. Males use olfactory, visual, and acoustic signals for courtship, and they demonstrate territory ownership by scent marks, low frequency calls, and visual displays. Harem males sire on average more offspring than do nonharem males but produce only 30% of the offspring within their own harem territory, with 70% being sired by other harem males or nonharem males. Reproductive success of males increases with decreasing size, fluctuating asymmetry, and fundamental frequency of territorial calls. In addition, females that are closely related to the harem holder are more likely to mate with other males than with the harem holder. Sexual selection in *S. bilineata* is most likely influenced by intense local mate competition caused by scarce roosts and the patrilineal organization of colonies.

Voigt, C.C. & Lewanzik, D., 2012. "No cost of echolocation for flying bats" revisited. *Journal of comparative physiology. B, Biochemical, systemic, and environmental physiology*, 182(6), pp.831–40.

Abstract: Echolocation is energetically costly for resting bats, but previous experiments suggested echolocation to come at no costs for flying bats. Yet, previous studies did not investigate the relationship between echolocation, flight speed, aerial manoeuvres and metabolism. We re-evaluated the "no-cost" hypothesis, by quantifying the echolocation pulse rate, the number of aerial manoeuvres (landings and U-turns), and the costs of transport in the 5 g insectivorous bat *Rhogeessa io* (Vespertilionidae). On average, bats (n = 15) travelled at 1.76 ± 0.36 m s^{-1} and performed 11.2 ± 6.1 U-turns and 2.8 ± 2.9 ground landings when flying in an octagonal flight cage. Bats made more U-turns with decreasing wing loading (body weight divided by wing area). At flight, bats emitted 19.7 ± 2.7 echolocation pulses s−1 (range 15.3-25.8 pulses s^{-1}), and metabolic rate averaged 2.84 ± 0.95 ml CO_2 min^{-1}, which was more than 16 times higher than at rest. Bats did not echolocate while not engaged in flight. Costs of transport were not related to the rate of echolocation pulse emission or the number of U-turns, but increased with increasing number of landings; probably as a consequence of slower travel speed when staying briefly on ground. Metabolic power of flight was lower than predicted for *R. io* under the assumption that energetic costs of echolocation call production is additive to the aerodynamic costs of flight. Results of our experiment are consistent with the notion that echolocation does not add large energetic costs to the aerodynamic power requirements of flight in bats.

Voigt-Heucke, S.L., Taborsky, M. & Dechmann, D.K.N., 2010. A dual function of echolocation: bats use echolocation calls to identify familiar and unfamiliar individuals. *Animal Behaviour*, 80(1), pp.59–67.

Abstract: Bats use echolocation for orientation during foraging and navigation. However, it has been suggested that echolocation calls may also have a communicative function, for instance between roost members. In principle, this seems possible because echolocation calls are species specific and known to differ between the sexes, and between colonies and individuals for some species. We performed playback experiments with lesser bulldog bats, *Noctilio albiventris*, to which we presented calls of familiar/unfamiliar conspecifics, cohabitant/noncohabitant heterospecifics and ultrasonic white noise as a control. Bats reacted with a complex repertoire of social behaviours and the intensity of their response differed significantly between stimulus categories. Stronger reactions were shown towards echolocation calls of unfamiliar conspecifics

than towards heterospecifics and white noise. To our knowledge, this is the first time that bats have been found to react to echolocation calls with a suite of social behaviours. Our results also provide the first experimental evidence for acoustical differentiation by bats between familiar and unfamiliar conspecifics, and of heterospecifics. Analysis of echolocation calls confirmed significant individual differences between echolocation calls. In addition, we found a nonsignificant trend towards group signatures in echolocation calls of *N. albiventris*. We suggest that echolocation calls used during orientation may also communicate species identity, group affiliation and individual identity. Our study highlights the communicative potential of sonar signals that have previously been categorized as cues in animal social systems.

Vonhof, M.J. & Barclay, R.M.R., 1996. Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. *Canadian Journal of Zoology*, 74(10), pp.1797–1805.

Abstract: We used radiotelemetry to examine the roost-site preferences of four species of tree-roosting bats *(Eptesicus fuscus*, *Lasionycteris noctivagans*, *Myotis evotis*, and *M. volans*) in southern British Columbia, Canada, by radio-tracking bats to their day roosts. We found a total of 21 roost trees: 14 roosts were beneath loose bark, 5 were in cavities excavated by woodpeckers, and 2 were in natural cavities. Entrance height increased with tree height, but roost entrances tended to be situated below the level of the canopy. Of the 22 tree and site variables examined, only 3 significantly discriminated between roost trees and available trees: tree height, distance to the nearest available tree, and percent canopy closure. Bats preferred tall trees associated with low percent canopy closure and a short distance to the nearest available tree. Bats roosted in western white pine, and to a lesser extent ponderosa pine and western larch, in intermediate stages of decay more often than would be expected at random. Bats switched roosts frequently. The distance between Subsequent roost trees was short, suggesting a degree of fidelity to a particular group of trees or area of forest. The number of days of rain during the roosting period significantly influenced the number of days spent in a particular roost, and thus ambient conditions may restrict the frequency with which bats can switch roosts.

Vonhof, M.J. & Barclay, R.M.R., 1997. Use of tree stumps as roosts by western long-eared bats. *Journal of Wildlife Management*, 61(3), pp.674–684.

Abstract: We report for the first time widespread use of loose bark on stumps in clearcuts as roosting sites by bats. We first discovered stump-roosting behaviour during the summer of 1993 when a radiotagged female western long-eared bat (*Myotis evotis*) roosted beneath loose bark on 4 separate stumps. During the summer of 1994 we searched for stump roosts in 11 south-facing clearcuts in the West Arm Demonstration Forest near Nelson, British Columbia. Nineteen roosts in 17 different stumps were located in 3 of the 11 clearcuts searched. Males and females accounted for 10 and 9 of the 19 roosts. Within clearcuts, bats selected large-diameter stumps, and tended to roost in southwest facing cavities. Temperatures of roost cavities were intermediate between those within randomly selected cavities and ambient temperatures. Temperatures within randomly selected cavities were significantly warmer than ambient temperatures, while those within roosts were not. Cavity temperature was related negatively to stump diameter, and cavities on the south side of stumps were relatively warm. We conclude that bats chose to roost in clearcuts to gain thermal benefits through increased exposure to sunlight and reflective heat, but within these clearcuts close stumps that provided relatively cooler and more stable temperatures, presumably to avoid heat stress. Bats selected clearcuts with high

proportions of uncluttered stumps, and stumps in clearcuts used by bats provided deeper cavities relatively far away from neighboring shrubs. Bats roosting in clearcuts may be subject to a trade-off between increased energetic savings and increased predation risk.

Vonhof, M.J. & Gwilliam, J.C., 2007. Intra- and interspecific patterns of day roost selection by three species of forest-dwelling bats in southern British Columbia. *Forest Ecology and Management*, 252(1-3), pp.165–175.

Abstract: We examined intra- and interspecific patterns of roost-site selection by females of three species of forest-dwelling bats (silver-haired, *Lasionycteris noctivagans*; big brown, *Eptesicus fuscus*; and California, *Myotis californicus*) in the Pend d'Oreille Valley in southern British Columbia. Roost-sites were located by outfitting reproductive and non-reproductive female bats with radio-transmitters and tracking them during the daytime. The tree and site characteristics of roost trees used by each bat species were then compared to those of randomly available trees with cavities, as well as to each other, using logistic regression. All three bat species selected roosts that were taller than cavity trees, and the majority of roost trees were emergent or canopy trees. In addition, tree species and the type of cavity were important predictors of whether trees were used as roosts in both intra- and interspecific analyses. The majority of silver-haired and big brown bat roost trees were in hollows in live trembling aspen trees (*Populus tremuloides*), but both species used small numbers of roosts on conifer snags. In contrast, the majority of California bat roosts were beneath loose bark on conifer snags, particularly Douglas-fir (*Pseudotsuga menziesii*), in intermediate stages of decay. In general, site characteristics were only weak predictors of differences between roost and random trees, and roost trees used by the three bat species, but roost trees were found in patches with lower percent canopy closure and greater density of available trees. These results suggest that while all three species of forest-dwelling bats use large trees, within this restricted range of trees there is considerable variation among species in the types of cavities and the tree species used. Maintaining stands containing mature trembling aspen is necessary to provide silver-haired and big brown bats with suitable roosting opportunities, but to meet the needs of California bats, areas rich in conifer snags must be protected. Thus, unique management strategies or silvicultural practices may be required to maintain suitable habitat for all bat species in a given area.

Wadsworth, J. & Moss, C., 2000. Vocal control of acoustic information for sonar discriminations by the echolocating bat, *Eptesicus fuscus*. *The Journal of the Acoustical Society of America*, 107(4), pp.2265–2271.

Abstract: This study aimed to determine whether bats using frequency modulated (FM) echolocation signals adapt the features of their vocalizations to the perceptual demands of a particular sonar task. Quantitative measures were obtained from the vocal signals produced by echolocating bats (*Eptesicus fuscus*) that were trained to perform in two distinct perceptual tasks, echo delay and Doppler-shift discriminations. In both perceptual tasks, the bats learned to discriminate electronically manipulated playback signals of their own echolocation sounds, which simulated echoes from sonar targets. Both tasks utilized a single-channel electronic target simulator and tested the bat's in a two-alternative forced choice procedure. The results of this study demonstrate changes in the features of the FM bats' sonar sounds with echolocation task demands, lending support to the notion that this animal actively controls the echo information that guides its behavior.

Walker, V., Peremans, H. & Hallam, J., 1998. One tone, two ears, three dimensions: A robotic investigation of pinnae movements used by rhinolophid and hipposiderid bats. *The Journal of the Acoustical Society of America*, 104(1), pp.569–579.

Abstract: Bats, which echolocate using broadband calls, are believed to employ the passive acoustic filtering properties of the head and pinnae to provide spectral cues which encode 3-D target angle. Microchiropteran species whose calls consist of a single, constant frequency harmonic (i.e., some species in the families Rhinolophidae and Hipposideridae) may create additional acoustic localization cues via vigorous pinna movements. In this work, two types of echolocation cues generated by moving a pair of receivers aboard a model sensor head are investigated. In the first case, it is supposed that a common 3-D echolocation principle employed by all bats is the creation of alternative viewing perspectives, and that constant frequency ~CF! echolocators use pinna movement rather than morphology to alter the acoustic axes of their perceptual systems. Alternatively, it is possible rhinolophids and hipposiderids move their ears to create dynamic cues—in the form of frequency and amplitude modulations—which vary systematically with target elevation. Here the use of binaural and monaural timing cues derived from amplitude modulated echo envelopes are investigated. In this case, pinna mobility provides an echolocator with a mechanism for creating dramatic temporal cues for directional sensing which, unlike interaural timing differences, do not degrade with head size.

Walsh, S.A., Barrett, P.M., Milner, A.C., Manley, G. & Witmer, L.M., 2009. Inner ear anatomy is a proxy for deducing auditory capability and behaviour in reptiles and birds. *Proceedings. Biological sciences / The Royal Society*, 276(1660), pp.1355–60.

Abstract: Inferences of hearing capabilities and audition-related behaviours in extinct reptiles and birds have previously been based on comparing cochlear duct dimensions with those of living species. However, the relationship between inner-ear bony anatomy and hearing ability or vocalization has never been tested rigorously in extant or fossil taxa. Here, micro-computed tomographic analysis is used to investigate whether simple endosseous cochlear duct (ECD) measurements can be fitted to models of hearing sensitivity, vocalization, sociality and environmental preference in 59 extant reptile and bird species, selected based on their vocalization ability. Length, rostrocaudal/mediolateral width and volume measurements were taken from ECD virtual endocasts and scaled to basicranial length. Multiple regression of these data with measures of hearing sensitivity, vocal complexity, sociality and environmental preference recovered positive correlations between ECD length and hearing range/mean frequency, vocal complexity, the behavioural traits of pair bonding and living in large aggregations, and a negative correlation between ECD length/rostrocaudal width and aquatic environments. No other dimensions correlated with these variables. Our results suggest that ECD length can be used to predict mean hearing frequency and range in fossil taxa, and that this measure may also predict vocal complexity and large group sociality given comprehensive datasets.

Wang, L.C.H. & Wolowyk, M.W., 1988. Torpor in mammals and birds. *Canadian Journal of Zoology*, 66(1), pp.133–137.

Abstract: Torpor in mammals and birds is characterized by a periodic lowering of the set point for body temperature regulation to achieve a hypometabolic state for energy and water conservation. Torpor may be seasonal (hibernation, estivation) or nonseasonal (nocturnal

hypothermia, daily torpor) and, depending on the depth and duration of the torpor, energy savings from 10 to 88 % may be achieved. Despite the different patterns of torpor, recent studies have demonstrated a physiological homology between sleep and torpor, suggesting a continuum in energy conservation in times of inactivity. The physiological and biochemical adaptations for torpor are many, including both species-specific and seasonally dependent aspects. Two examples are discussed. In terms of cardiac function, differences exist among species in the maintenance of resting and action potentials at low temperatures, whereas seasonal differences exist for dependence of trans-sarcolemmal calcium flux in excitation- contraction coupling. With respect to ionic regulation, the ability of red blood cells to maintain high intracellular K^+ and low intracellular Na^+ and Ca_2^+ at low temperatures is species-specific and not seasonally dependent. The competence for intracellular Ca_2^+ regulation (i.e., active calcium pump) at low temperatures appears to be a key feature that allows the hibernator's cells to function continually despite the prolonged and profound depression of body temperature during hibernation.

Warnecke, M. [n.d.] Acoustic echoflow and target-clutter discrimination in the flying big brown bat. Department of Psychological and Brain Sciences Comparative Neural Systems and Behavior Lab, Johns Hopkins University. Baltimore, MD. Online: http://pbs.jhu.edu/research/moss/research/ElaProject.

No abstract

Warnecke, M., Bates, M. E. & Simmons, J.A., 2012. Spatial release from electronic clutter masking in FM bat echolocation. *The Journal of the Acoustical Society of America*, 132, p.1978.

Abstract: Big brown bats (Eptesicus fuscus) use biosonar to navigate and locate objects in their surroundings. During natural foraging, they often encounter echoes returned by a target of interest located to the front while other, often stronger, clutter echoes are returned from objects, such as vegetation, located to the sides or above. Nevertheless, bats behave as if they do not suffer interference from this clutter. Using a two-choice delay discrimination procedure, bats were tested for the masking effectiveness of clutter echoes on target echoes when the target echoes were delivered from the bat's front while clutter echoes were delivered from 90° overhead, a direction of lowpass filtering by the external ears. When clutter echoes are presented from the front at the same delay as target echoes, detection performance declines and clutter masking occurs. When the clutter echoes are presented at the same delay but from overhead, discrimination performance is unaffected and no masking occurs. Thus there is masking release for simultaneous off-axis lowpass clutter compared to masking by simultaneous clutter from the front. The bat's performance for simultaneous target and clutter echoes indicates a new role for the mechanism that separates overlapping echoes by decomposing the bat's auditory time-frequency representation.

Warren, P.S., Matti, M., Errmann, M. & Brazel, A., 2006. Urban bioacoustics: it's not just noise. *Animal Behaviour*, 71(3), pp.491–502.

Abstract: The acoustic environment has a major influence in shaping animal communication systems. Humans, particularly in cities, profoundly alter the acoustic structure of their environment. Recent articles have identified effects of noise on animal communication and behaviour. These studies, however, serve to highlight the surprising dearth of research on the

behavioural responses of animals to altered acoustic environments. We argue that noise is not the only aspect of urban bioacoustics that researchers should explore. In addition to elevated noise levels, urban areas are characterized by a spatial heterogeneity in noise levels, predictable diurnal variation in noise levels and the existence of many vertical reflective surfaces. All of these characteristics have parallels in natural environments. We suggest that cities are a fruitful area for future research on the evolution of animal communication systems, with more general implications for conservation in human-altered environments.

Waser, P.M. & Brown, C.H., 1986. Habitat acoustics and primate communication. *American Journal of Primatology*, 10(2), pp.135–154.

Abstract: The acoustic characteristics of three tropical habitats were investigated to determine how they might constrain the structure of primate signals. Ambient noise was measured, along with signal attenuation and aspects of signal degradation (reverberation, amplitude fluctuations, and pulse train modulation depth). These measures allowed estimation of the effects of habitat acoustics on the distances over which calls would be audible (the "active space") and over which primates could reliably transmit amplitude modulated or pulse-coded information.

Washington Department of Transportation (WSDOT), 2013. 7.0 Construction Noise Impact Assessment. In Washington Department of Transportation Advanced Training Manual: Biological Assessment Preparation for Transportation Projects. pp. 7.1 –7.55.

No abstract

Washington Department of Transportation (WSDOT) 2015. Biological Assessment Preparation Advanced Training Manual version 02-2014. Updated version in In Biological Assessment Preparation Advanced Training Manual version 02-2015. Online: http://www.wsdot.wa.gov/Environment/Biology/BA/BAguidance.htm

No abstract

Waters, D.A. & Jones, G., 1995. Echolocation call structure and intensity in five species of insectivorous bats. *The Journal of Experimental Biology*, 198, pp.475–89.

Abstract: Echolocation call intensity was measured in the laboratory for five species of British insectivorous bats in free flight and in the hand. All species showed similar call intensities of between 80 and 90 dB peSPL (peak equivalent SPL) at 1 m during flight except *Plecotus auritus*, whose call intensity was between 68 and 77 dB peSPL at 1 m. Calls from stationary bats were about 13 dB less intense than calls during flight. A method is proposed to measure the root mean square (rms) amplitude of echolocation calls and, hence, to calculate the energy flux density of the call. The constant-frequency calls of *Rhinolophus hipposideros* have energy flux densities approximately ten times higher than those of bats using frequency-modulated calls as a result of their longer durations and lower crest factors. It is argued that the low-intensity calls of *P. auritus* allow it to approach tympanate moths more closely before triggering their escape response.

Weinbeer, M. & Kalko, E.K. V., 2007. Ecological niche and phylogeny: the highly complex echolocation behavior of the trawling long-legged bat, *Macrophyllum macrophyllum*. *Behavioral Ecology and Sociobiology*, 61(9), pp.1337–1348.

Abstract: Bats produce echolocation signals that reflect the sensory tasks they perform. In open air or over water, bats encounter few or no background echoes (clutter). Echo location of such bats is the primary cue for prey perception and varies with the stage of approach to prey, typically comprising search, approach, and terminal group calls. In contrast, bats that glean stationary food from rough surfaces emit more uniform calls without a distinct terminal group. They use echolocation primarily for orientation in space and mostly need additional sensory cues for finding food because clutter echoes overlap strongly with food echoes. *Macrophyllum macrophyllum* is the only Neotropical leaf nosed bat (Phyllostomidae) that hunts in clutter-poor habitat over water. As such, we hypothesized that, unlike all other members of its family, but similar to other trawling and aerial insectivorous bats, *M. macrophyllum* can hunt successfully by using only echolocation for prey perception. In controlled behavioral experiments on Barro Colorado Island, Panama, we confirmed that echolocation alone is sufficient for finding prey in *M. macrophyllum*. Furthermore, we showed that pattern and structure of echolocation signals in *M. macrophyllum* are more similar to aerial and other trawling insectivorous bats than to close phylogenetic relatives. Particularly unique among phyllostomid bats, we found distinct search, approach, and terminal group calls in foraging *M. macrophyllum*. Call structure, however, consisting of short, multiharmonic, and steep frequency-modulated signals, closely resembled those of other phyllostomid bats. Thus, echolocation behavior in *M. macrophyllum* is shaped by ecological niche as well as by phylogeny.

Wenstrup, J.J., 1984. Auditory sensitivity in the fish-catching bat, *Noctilio leporinus*. *Journal of comparative physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 155, 91–101.

Summary: 1. Behavioral and auditory brainstem response (ABR) audiograms are described for the fish-catching bat,Noctilio leporinus, which uses short constant frequency/frequency modulated (short-CF/FM) sonar pulses with a CF component of 56–59 kHz, followed by an FM sweep down to 28–32 kHz. Social communication signals contain the frequencies found in sonar pulses, but may extend to lower frequencies (16 kHz). 2. Behavioral thresholds, obtained by operant conditioning in three bats, display maximum sensitivity in the region of the bats' CF sonar component, but show good sensitivity (thresholds less than 10 dB SPL) between 32 and 57 kHz. Below 24 to 32 kHz, sensitivity declined at a rate of 35 to 45 dB/octave. No response was obtained below 1 kHz. 3. The most prominent feature of the behavioral audiogram is an abrupt increase in threshold above 56 to 58 kHz, with an initial roll-off as high as 550 dB/octave. A threshold ‘plateau’ exists between 64 and 96 kHz, but sensitivity declines rapidly above 96 kHz. No response was obtained above 120 kHz. 4. ABR audiograms were obtained in two animals in which behavioral thresholds had been measured previously. These display a broadly tuned peak of maximum sensitivity at 24 kHz and a more sharply tuned sensitivity peak in the region between 56 and 59 kHz. No responses were obtained below 1 kHz or above 96 kHz. 5. Differences in the shape of the behavioral and ABR threshold curves are discussed. It is suggested that the two sensitivity peaks in the ABR may result from a disproportionately large representation of frequencies corresponding to social communication signals (24 kHz) and the bat's CF sonar pulse (56 to 59 kHz). 6. The behavioral audiogram ofN. leporinus is compared to those of other bats, and functional implications are discussed.

Wermundsen, T. & Siivonen, Y., 2009. Seasonal variation in use of winter roosts by five bat species in south-east Finland. *Central European Journal of Biology*, 5(2), pp.262–273.

Abstract: We studied seasonal variation in the use of winter roosts by five bat species (*Eptesicus nilssonii*, *Myotis brandtii*/*mystacinus*, *Myotis daubentonii* and *Plecotus auritus*) in south-east Finland during the winters of 2003/2004 and 2004/2005. At the beginning of the bat hibernation season all species used higher temperatures and humidity than by the season's end. Hibernacula were at their coldest in mid-hibernation season and became warmer towards the end of the season. However, no species hibernated in warmer locations at the end of the season than in mid-season. Results suggest that bats tend to use different strategies throughout the hibernation season, minimizing the cost of hibernation early in the season by hibernating in warmer locations and minimizing energy expenditure later in the season by hibernating in colder locations. *M. brandtii/mystacinus* were found in locations with stable temperature and humidity, moving to increasingly stable conditions (chambers, crevices, clusters, ceiling) towards spring. All other species hibernated in more variable microclimates throughout the hibernation season.

West, M., Walkden, F. & Sack, R. a., 1989. The acoustic shadow produced by wind speed and temperature gradients close to the ground. *Applied Acoustics*, 27(3), pp.239–260.

Abstract: The residue solutions of Pierce and of Berry & Daigle for predicting sound pressure in a shadow region are described A new ray based procedure for obtaining the average sound speed gradient required in both solutions is shown to improve the accuracy of predicted peak pressures.

Western Bat Working Group., 2015. Western Bat Species. Online: http://wbwg.org/western-bat-species/.

No abstract

Wever, E.G. & Vernon, J.A., 1961. The protective mechanisms of the bat's ear. *Ann. Otol. Rhinol. Ixyngol.* 70, pp.5-18.

No abstract

Wiley, R.H. & Richards, D.G., 1978. Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology*, 3(1), pp.69–94.

Abstract: 1. Acoustic communication requires not only detection of the signal but also discrimination of differences among signals by the receiver. Attenuation and degradation of acoustic signals during transmission through the atmosphere will impose limits on acoustic communication. Attenuation of sound during atmospheric transmission results primarily from atmospheric absorption, ground attenuation, scattering of a sound beam, and deflection of sound by stratified media. For maximum range of detection, therefore, animals should favor optimal positions in their habitat and optimal weather conditions. Frequency-dependent attenuation seems not to differ consistently among major classes of terrestrial habitats, such as forests and fields. Increased scattering of higher frequencies from vegetation in forests is in part matched by scattering from micrometerological heterogeneities in the open. 2. In addition to frequency-dependent attenuation, two kinds of degradation during atmospheric transmission will limit a receiver's ability to resolve differences among acoustic signals: the accumulation of irregular amplitude fluctuations from nonstationary heterogeneities, often atmospheric turbulence, and reverberation. Both types of degradation affect temporal patterns of amplitude or intensity modulation more than patterns of frequency modulation. Both effects should increase with

carrier frequency, as they depend on the relationship between wavelength and the dimensions of scattering heterogeneities. Irregular amplitude fluctuations are more severe in open habitats and primarily mask low frequencies of amplitude modulation; reverberations are more severe in forested habitats and primarily mask high frequencies of amplitude modulation and rapid, repetitive frequency modulation. This difference between forested and open habitats could explain previous reports that birds in the undergrowth of tropical forests avoid rapid frequency modulation in their long-range vocalizations. 3. Maximum range of detection is probably not the primary selection pressure on many animal vocalizations, even for territorial advertisement, except perhaps in tropical forests. Instead, acoustic signals might incorporate features that degrade predictably with range to permit a receiver to estimate the signaler's distance. Future investigations might explore the propagation of animal vocalizations in relation to the usual spacing of animals in their habitat. Features that encode different kinds of information, such as individual and species identity, might propagate to different distances. 4. Measurements of the transmission of sound in natural environments have often not controlled several important parameters. First, the effects of ground attenuation and scattering are not linear with range; consequently measurements of excess attenuation over different ranges in the same environment might differ. Second, the directionality of speakers and microphones will affect measurements of attenuation and reverberations in scattering environments. Third, as stationary waves shift with frequency, any single microphone placement will lie in a null for some frequencies and in a maximum for others.

predicted based on data from other groups of bats.

Willis, C.K.R. & Brigham, R.M., 2005. Physiological and ecological aspects of roost selection by reproductive female hoary bats (*Lasiurus cinereus*). *Journal of Mammalogy*, 86(1), pp.85–94.

Abstract: Most recent research on the roosting habits of temperate, forest-living bats has focused on species that use enclosed cavities, but less has been done to address roosting by foliage-living species, which are assumed to have more flexible roost requirements. Numerous studies have suggested that bats select roosts on the basis of microclimate, yet few have tested this hypothesis empirically and none have addressed the use of foliage roosts in this context. We used radiotelemetry to locate roost sites of reproductive female hoary bats (*Lasiurus cinereus*) then compared a variety of physical features of these trees with randomly selected nonroost trees. We also recorded ambient temperature and wind speed at roost and nonroost sites to test the hypothesis that physical features associated with foliage roosts provide energetic benefits. Hoary bats selected roost sites on the southeast side of mature white spruce trees (*Picea glauca*; X orientation 158.666.38 SSE). Roost trees were more likely than random trees to be the same height as the surrounding forest canopy; had less canopy cover facing out from the tree in the direction of the roost branch; and had lower forest density on their southeast side. Wind speed was significantly lower at roosts sites compared with opposite sides of the same trees, presumably due to increased protection from prevailing westwinds. Incorporating an estimate of convective cooling due to wind, we predicted daily thermal energy expenditure for normothermic bats and found that selected roost sites provided statistically significant energy savings (up to 1.606 0.99 kJ/day) relative to the predicted expenditures if bats had roosted on the opposite sides of trees. Our results provide direct evidence that hoary bats select forest roosts on

the basis of microclimate and suggest that roost requirements of foliage-roosting species may be more specific than has been previously assumed.

Willis, C. & Lane, J., 2005. Thermal energetics of female big brown bats (*Eptesicus fuscus*). *Canadian Journal of Zoology*, 83, pp.871–879.

Abstract: We investigated thermoregulation and energetics in female big brown bats, *Eptesicus fuscus* (Beauvois, 1796). We exposed bats to a range of ambient temperatures (T_a) and used open-flow respirometry to record their metabolic responses. The bats were typically thermoconforming and almost always entered torpor at T_as below the lower critical temperature T_{lc} of 26.7 °C. Basal metabolic rate (BMR, 16.98 ± 2.04 mL O_2 h^{-1}, mean body mass = 15.0 ± 1.4 g) and torpid metabolic rate (TMR, 0.460 ± 0.207 mL O_2 h^{-1}, mean body mass = 14.7 ± 1.3 g) were similar to values reported for other vespertilionid bats of similar size and similar to a value for *E. fuscus* BMR calculated from data in a previous paper. However, we found that big brown bats had a lower T_{lc} and lower thermal conductance at low T_a relative to those measured in the previous study. During torpor, the minimum individual body temperature (T_b) that we recorded was 1.1 °C and the bats began defending minimum T_b at T_a of approximately 0 °C. BMR of big brown bats was 76% of that predicted for bats based on the relationship between BMR and body mass. However, the Vespertilionidae have been under-represented in previous analyses of the relationship between BMR and body mass in bats. Our data, combined with data for other vespertilionids, suggest that the family may be characterized by a lower BMR than that

Wilson, D.R., 2014. Animal communication: keep your wings off my food! *Current biology* : CB, 24(8), pp.R319–21.

Abstract: When foraging, male big brown bats produce ultrasonic social calls. The calls repel rival bats from the caller and its prey, and increase the caller's foraging success during their high-speed aerial excursions.

Wilson, J.M. & Barclay, R.M.R., 2006. Consumption of caterpillars by bats during an outbreak of western spruce budworm. *The American Midland Naturalist*, 155(1), pp.244–249.

Abstract: We investigated the diets of insectivorous bats (Chiroptera: Vespertilionidae) in forests with high densities of western spruce budworm (*Choristoneura occidentalis*, Lepidoptera: Tortricidae), in southern interior British Columbia, Canada. Caterpillars as potential prey were more common and widespread than previously reported. Caterpillar consumption by bats was more frequent where *C. occidentalis* larvae were more abundant, suggesting that the caterpillars being eaten were *C. occidentalis*. The frequency of caterpillar consumption was similar for *Myotis evotis*, which gleans prey from vegetation, and for other bat species that forage primarily by aerial-hawking. We suggest that caterpillars hanging by silk threads were captured by bats that foraged aerially.

Wilson, J.P. & Bruns, V., 1983. Middle-ear mechanics in the CF-bat *Rhinolophus ferrumequinum*. *Hearing Research*, 10(1), pp.1–13.

Abstract: The acoustic vibrations of the eardrum at the umbo and of the stapes have been measured in the greater horseshoe bat. The displacement amplitude response of the eardrum shows a second-order low-pass characteristic, typical of a lumped mass and stiffness system with

a resonance frequency of about 55 kHz. The effective mass was calculated to be about 8 pg. and the specific stiffness 40x 10^6 dyne/cm^3. which is one hundred times greater than guinea pig. The measured level ratio appears to be greater (3x-5x) than the geometric ratio (2x) probably due to flexing of the manubrium. The umbo-stapes phase lag exceeds 1 cycle at high frequencies. suggesting a system of at least four reactances. This is not consistent with the relatively slight change in lever ratio with frequency. One possibility for reconciling the two results is that the distributed mass and stiffness of the ossicles act as a transmission line for transverse vibrations. There is no evidence for a sharply peaked middle-ear response (although it is more sharply tuned than some species), nor for resonant absorption by the cochlea in the region of 83 kHz - the "constant" frequency of this bat. The eardrum shows theoretically optimal matching to the air at 55 kHz and is reasonably efficient from 15 kHz to at least 110 kHz.

Wojciechowski, M.S., Jefimow, M. & Tegowska, E., 2007. Environmental conditions, rather than season, determine torpor use and temperature selection in large mouse-eared bats (*Myotis myotis*). *Comparative biochemistry and physiology. Part A, Molecular & integrative physiology*, 147(4), pp.828–40.

Abstract: We tested whether food availability, thermal environment and time of year affect torpor use and temperature selection in the large mouse-eared bat (*Myotis myotis*) in summer and winter. Food-deprived bats were torpid longer than bats offered food ad libitum. Bats placed in a gradient of low (0 °C - 25 °C) ambient temperatures (T_a) spent more time in torpor than bats in a gradient of high (7 °C - 43 °C) T_a's. However, we did not observe seasonal variations in the use of torpor. Moreover, even when food deprived in winter, bats never entered prolonged torpor at T_a's characteristic of their natural hibernation. Instead, bats preferred shallow torpor at relatively high T_a, but they always maintained a difference between body and ambient temperatures of less than 2 °C. Calculations based on respirometric measurements of metabolic rate showed that food deprived bats spent less energy per unit of time in torpor than fed individuals, even when they entered torpor at higher T_a's. We conclude that T_a likely serves as a signal of food availability and daily torpor is apparently an adaptation to unpredictable changes in food availability, such as its decrease in summer or its increase in winter. Thus, we interpret hibernation to be a second step in the evolution of heterothermy in bats, which allows survival in seasonal environments.

Wolf, S. & Shaw, W., 2002. Roost selection of bridges by bats in an urban area. Arizona Game and Fish Department Heritage Grant (U98007), Final Report, October 2002.

Abstract: Selection of appropriate roosts is crucial to the survival and reproduction of bats. In Tucson, Arizona, bridges seem to be an important source of roost sites for the crevice dwelling species able to live in urban environments. We studied bats that use bridges in the Tucson metropolitan area to provide information to wildlife managers for bat management and conservation. We studied 43 bridges that were constructed with crevices between concrete beams creating potential for roost sites. We found bats in 81% of these bridges and identified 8 species: *Tadarida brasiliensis*, *Eptesicus fuscus*, *Pipistrellus hesperus*, *Antrozous pallidus*, *Lasionycteris noctivagans*, *Myotis velifer*, *M. californicus*, and *M. yumanensis*. We conducted monthly surveys January through December 1999 to follow changes in abundance and diversity and identify maternity colonies. We identified some characteristics of bridges that are correlated with the presence of bats, such as adjacent land use, crevice width, crevice depth, and bridge height. State, county, and city departments of transportation can use study results to make engineering decisions that will benefit bats or minimize negative effects on bats using bridges.

Wotton, J., Jenison, R. & Hartley, D., 1997. The combination of echolocation emission and ear reception enhances directional spectral cues of the big brown bat, *Eptesicus fuscus*. *The Journal of the Acoustical Society of America*, 101(3), pp.1723–1733.

Abstract: The acoustic information used by bats is produced by a combination of the properties of the sound emission and the reception at the eardrum. The potential localization cues used by bats can only be fully revealed when the magnitude spectra of the emission and the external ear are convolved to produce the echolocation combination magnitude spectra. The spatially dependent changes in the magnitude spectra of the echolocation combination *of Eptesicus fuscus* are described. The emission and external ear magnitude spectra act together to enhance the potential localization cues. In the echolocation combination, the spectral peaks are sharpened and there is greater contrast in intensity between peaks and notches when compared to the spectra of the ear alone. The spectral localization cues in the echolocation combination appear to be restricted to a cone of space of approximately 630°.

Wright, G.S., Wilkinson, G.S. & Moss, C.F., 2011. Social learning of a novel foraging task by big brown bats (*Eptesicus fuscus*). *Animal behaviour*, 82, pp.1075–1083.

Abstract: Acquiring information via observation of others can be an efficient way to respond to changing situations or learn skills, particularly for inexperienced individuals. Many bat species are gregarious, yet few studies have investigated their capacity for learning from conspecifics. We tested whether big brown bats (*Eptesicus fuscus*) can learn a novel foraging task by interacting with knowledgeable conspecifics. In experimental trials 11 naïve bats (7 juveniles, 4 adults) interacted freely with trained bats that were capturing tethered mealworms, while in control trials 11 naïve bats (7 juveniles, 4 adults) flew with untrained bats. Naïve bats were then assessed for their ability to capture tethered mealworms. While no bat in the control group learned the task, a significant number of experimental bats, including juveniles with little or no experience foraging, showed evidence of learning. Eighty-two per cent of experimental bats and 27% of control bats directed feeding buzzes (echolocation calls associated with prey capture) at the mealworm. Furthermore, seven experimental bats (64%) showed evidence of learning by attacking and/or capturing the mealworm, while no bat in the control group attacked or captured the prey. Analyses of high-speed stereo video recordings revealed increased interaction with demonstrators among bats attacking or capturing the mealworm. At the time they displayed evidence of learning, bats flew closer together during feeding buzzes than during other portions of trials. Our results demonstrate that social interaction with experienced bats, and listening to feeding buzzes in particular, may play an integral role in development of foraging skills in bats.

Wright, G.S., Wilkinson, G.S. & Moss, C.F., 2014. Social calls predict foraging success in big brown bats. *Current Biology*, 24, pp.885–889.

Abstract: Animals foraging in the dark are engaged simultaneously in prey pursuit, collision avoidance, and interactions with conspecifics, making efficient nonvisual communication essential. A variety of birds and mammals emit food-associated calls that inform, attract, or repel conspecifics (e.g.,). Big brown bats (*Eptesicus fuscus*) are insectivorous aerial hawkers that may forage near conspecifics and are known to emit social calls (e.g.,). Calls recorded in a foraging setting might attract (e.g.,) or repel conspecifics and could denote territoriality or food claiming. Here, we provide evidence that the "frequency-modulated bout" (FMB), a social call emitted only by male bats (exclusively in a foraging context), is used to claim food and is individually

distinct. Bats were studied individually and in pairs in a flight room equipped with synchronized high-speed stereo video and audio recording equipment while sex and experience with a foraging task were experimentally manipulated. Male bats emitting the FMB showed greater success in capturing prey. Following FMB emission, interbat distance, diverging flight, and the other bat's distance to the prey each increased. These findings highlight the importance and utility of vocal communication for a nocturnal animal mediating interactions with conspecifics in a fast-paced foraging setting.

Wund, M.A., 2005. Learning and the development of habitat-specific bat echolocation. *Animal Behaviour*, 70(2), pp.441–450.

Abstract: Bats use echolocation calls that are suited for foraging in particular habitats. Many generalist bats alter their call design patterns as they move between open and spatially complex areas. This plasticity probably allows them to respond to the perceptual challenges posed by different structural environments. I tested the hypothesis that bats learn to produce these habitat-specific calls. I recorded the echolocation calls and foraging success of 14 juvenile little brown bats, *Myotis lucifugus*, as they foraged repeatedly in a large flight arena in two habitat treatments: open space and cluttered space. Calls were plastic across habitats. Furthermore, as bats gained experience, their foraging performance improved significantly in both open and cluttered habitat treatments. These improvements were related to changes in echolocation behaviour within the open habitat, which is consistent with the hypothesis that bats learn to produce more efficient calls in the open. Although the bats changed some aspects of their calls in the cluttered treatment, their use of space in the arena was the best predictor of foraging success. Bats that foraged in the centre of the arena were more successful. When bats switched habitat treatments, performance in the open was not affected by previous experience in the cluttered treatment. Bats that had previously experienced the open treatment, however, tended to use a more "open-area" call when foraging in cluttered space. This result is discussed in light of habitat selection in young *M. lucifugus*.

Wund, M.A., 2006. Variation in the echolocation calls of little brown bats (*Myotis lucifugus*) in response to different habitats. *American Midland Naturalist* 156(1), pp.99–108.

Abstract: Among different bat species, echolocation call structure varies predictably according to habitat use. Much of this interspecific variation in echolocation calls reflects the physical constraints of sound propagation and echo formation in open versus spatially complex habitats. Bats must use calls that are suitable for detecting obstacles and prey in a particular setting; thus, bats that use similar habitats and catch similar prey produce similar calls. The same can be true for variation in echolocation calls within a single species that uses a variety of habitats. I recorded the echolocation calls and habitat use of a habitat generalist bat, *Myotis lucifugus* in order to determine whether the echolocation calls of *M. lucifugus* vary predictably across habitats, and if call variation is the result of individual flexibility in habitat use and echolocation behavior. I found that *M. lucifugus* used calls with higher frequencies, shorter durations and steeper frequency modulation in cluttered habitats than in open habitats. This type of call is consistent with a short-range target-detection strategy whereas the lower frequencies, longer call durations and shallower frequency modulation of bats in open habitats are consistent with longer-range target detection strategies. Furthermore, radiotelemetry indicated that individuals routinely foraged in different habitats. Taken together, these results suggest that call variation across habitats is the result of individual plasticity in echolocation behavior.

Wunder, L. & Carey, A.B., 1996. Use of the Forest Canopy by Bats. *Northwest Science*, 70, pp.79–85.

Abstract: Of the 15 species of bats in the Pacific Northwest, 11 are known to make regular use of the forest canopy for roosting, foraging, and reproduction. This paper reviews roosting requirements, foraging, and the importance of landscape-scale factors to canopy=using species in the Northwest. Many northwest bats use several different types of tree roosts. Common roosting sites are in cavities, crevices, and foliage. Factors that may be important in roost site selection include microclimate, roost structure, crown architecture, canopy tree age and species, bark characteristics, foliage density, and stand and landscape composition. Some representative Pacific Northwest cavity- and crevice/bark-roosting species include the little brown bat (*Myotis lucifugus*), silver-haired bat (*Lasionycteris noctivagans*), and long-legged bat (*M. volans*). Only two Pacific Northwest species are known to roost in foliage. Several species forage in forest gaps, along forest edges, or in riparian areas. Long-eared (*M. evotis*) and Keen's (*M. keenii*) bats may forage within the forest canopy, although foraging behavior of these species in the Pacific Northwest is not well documented. Stand- and landscape-scale complexity may be important in providing bats with the abundance and diversity of roost foraging, and hibernation sites they require.

Xie, D. & Henson, Jr, O.H., 1998. Tonic efferent-induced cochlear damping in roosting and echolocating mustached bats. *Hearing Research*, 124, pp.60–68.

Abstract: The activity of the medial olivocochlear (MOC) efferent system in mustached bats, *Pteronotus p. parnellii*, was studied by monitoring changes in the mechanical properties of the cochlea. The changing properties were expressed by the decay time (DT) of cochlear microphonic potentials produced by transient-induced ringing (Henson et al., 1995). Tape-recorded roost noise (biosonar and communication sounds) produced sudden, marked decreases in DT when presented to the contralateral ear of animals adapted to the quiet. When the animals were first removed from their roosts the DT was relatively short (1.2 - 1.5 ms) but this gradually lengthened by about 0.5 - 1.0 ms as they rested in a quiet chamber. The time required to reach a stable, quiet-adapted state after noise exposure varied with SPL and exposure time; in many experiments recovery was in the range of 90 - 120 min. When quiet-adapted bats were isolated and allowed to fly and echolocate for 20 min, the DTs measured within a few minutes after the end of the flight were also short and only slowly returned to longer preflight values. The administration of a single dose of gentamicin, which blocks MOC effects, greatly reduced the amount of suppression (damping) observed after periods of noise and echolocation sound exposure. We conclude that tonic MOC activity is induced by the natural vocalizations and roost noise and this activity probably regulates and protects the highly resonant cochlear partition.

Xinde, S. & Jen, P., 1987. Pinna position affects the auditory space representation in the inferior colliculus of the FM bat, *Eptesicus fuscus*. *Hearing Research*, 21, pp.207–219.

Abstract: Using free-field acoustic stimulus conditions, we studied the auditory space representation in the inferior colliculus (IC) of the big brown bat, *Eptesicus fuscus*, under different puma positions. Stimuli were delivered from a loudspeaker placed 14 cm in front of the bat to determine the best frequency (BF) of an isolated neuron. A BF stimulus was then delivered as the loudspeaker was moved across the frontal auditory space of the bat to locate the response center of the neuron. At the response center, the neuron has its lowest minimum threshold (MT).

The stimulus was then raised 5-dB above the lowest MT to measure the spatial response area. Both response center and spatial response area of each neuron were measured under different pinna positions. Variation in the response center and MT of each neuron under different pinna positions was determined and a possible reason for this variation was discussed. The variation in auditory space representation in the IC due to variation in pinna position is presented. We suggest that during echolocation a bat could make changes in its pinna position to create additional binaural disparity for accurate target localization.

Yates, M. & Muzika, R., 2006. Effect of forest structure and fragmentation on site occupancy of bat species in Missouri Ozark forests. *Journal of Wildlife Management*, 70(5), pp.1238–1248.

Abstract: Changes in structure and arrangement of forests may influence the distribution of bat communities by affecting roosting and foraging habitat. Using Anabat bat detectors, we determined presence of bat species at 316 sample plots in southeastern Missouri, USA, through qualitative identification of echolocation calls collected. We used maximum-likelihood estimation techniques incorporating detection probabilities into estimation of site occupancy by species of bats. We compared a priori models at 2 geographic scales using information theoretic methods. At the local-site scale, eastern pipistrelle (*Pipistrellus subflavus*) and red bat (*Lasiurus borealis*) occupancy was most influenced by structural characteristics of forested areas, whereas Indiana bats (*Myotis sodalis*) were influenced most by density of large-diameter snags that could provide roosting habitat. At the landscape scale, occupancy of Indiana bats was directly related to amount of nonforested land cover. Northern long-eared bat (*M. septentrionalis*) occupancy was inversely related to edge. These data describe implications of forest fragmentation and provide information that can be used when integrating forest-management practices into bat conservation.

Yovel, Y., Falk, B., Moss, C.F. & Ulanovsky, N., 2011. Active control of acoustic field-of-view in a biosonar system. *PLoS Biology*, 9(9), p.e1001150.

Abstract: Active-sensing systems abound in nature, but little is known about systematic strategies that are used by these systems to scan the environment. Here, we addressed this question by studying echolocating bats, animals that have the ability to point their biosonar beam to a confined region of space. We trained Egyptian fruit bats to land on a target, under conditions of varying levels of environmental complexity, and measured their echolocation and flight behavior. The bats modulated the intensity of their biosonar emissions, and the spatial region they sampled, in a task-dependant manner. We report here that Egyptian fruit bats selectively change the emission intensity and the angle between the beam axes of sequentially emitted clicks, according to the distance to the target, and depending on the level of environmental complexity. In so doing, they effectively adjusted the spatial sector sampled by a pair of clicks-the "field-of-view." We suggest that the exact point within the beam that is directed towards an object (e.g., the beam's peak, maximal slope, etc.) is influenced by three competing task demands: detection, localization, and angular scanning-where the third factor is modulated by field-of-view. Our results suggest that lingual echolocation (based on tongue clicks) is in fact much more sophisticated than previously believed. They also reveal a new parameter under active control in animal sonar-the angle between consecutive beams. Our findings suggest that acoustic scanning of space by mammals is highly flexible and modulated much more selectively than previously recognized.

Yovel, Y., Melcon, M.L., Franz, M. O., Denzinger, A. & Schnitzler, H., 2009. The voice of bats: how greater mouse-eared bats recognize individuals based on their echolocation calls. *PLoS Computational Biology*, 5(6), p.e1000400.

Abstract: Echolocating bats use the echoes from their echolocation calls to perceive their surroundings. The ability to use these continuously emitted calls, whose main function is not communication, for recognition of individual conspecifics might facilitate many of the social behaviours observed in bats. Several studies of individual-specific information in echolocation calls found some evidence for its existence but did not quantify or explain it. We used a direct paradigm to show that greater mouse-eared bats (*Myotis myotis*) can easily discriminate between individuals based on their echolocation calls and that they can generalize their knowledge to discriminate new individuals that they were not trained to recognize. We conclude that, despite their high variability, broadband bat-echolocation calls contain individual-specific information that is sufficient for recognition. An analysis of the call spectra showed that formant-related features are suitable cues for individual recognition. As a model for the bat's decision strategy, we trained nonlinear statistical classifiers to reproduce the behaviour of the bats, namely to repeat correct and incorrect decisions of the bats. The comparison of the bats with the model strongly implies that the bats are using a prototype classification approach: they learn the average call characteristics of individuals and use them as a reference for classification.

Zhou, X. & Jen, P., 2002. The effect of sound duration on rate–amplitude functions of inferior collicular neurons in the big brown bat, *Eptesicus fuscus*. *Hearing Research*, 166, pp.124–135.

Abstract: During echolocation, the amplitude and duration of echo pulses of the big brown bat, *Eptesicus fuscus*, covary throughout the entire course of hunting. The purpose of this study was to examine if variation in sound duration might affect the amplitude selectivity of inferior collicular (IC) neurons of this bat species under free-field stimulation conditions. A family of rate-amplitude functions of each IC neuron was obtained with different sound durations. The effect of sound duration on the neuron's amplitude selectivity was then studied by examining the type, best amplitude, dynamic range and slope of each rate-amplitude function. The rate - amplitude functions of 83 IC neurons determined with different sound durations were either monotonic, saturated or nonmonotonic. Neurons with monotonic rate-amplitude functions had the highest best amplitude, largest dynamic range but smallest slope. Neurons with non-monotonic rate-amplitude functions had the lowest best amplitude, smallest dynamic range but largest slope. The best amplitude, dynamic range and slope of neurons with saturated rate-amplitude functions were intermediate between these two types. Rate-amplitude functions of one group (47, 57%) of IC neurons changed from one type to another with sound duration and one-third of these neurons were tuned to sound duration. As a result, the best amplitude, dynamic range, and slope also varied with sound duration. However, rate-amplitude functions of the other group (36, 43%) of IC neurons were hardly affected by sound duration and two-thirds of these neurons were tuned to sound duration. Biological relevance of these findings in relation to bat echolocation is discussed.

Zhao, J. & Qin, Q., 2014. Highway traffic noise prediction based on *GIS Q*, 9158, p.915810.

Abstract: Before building a new road, we need to predict the traffic noise generated by vehicles. Traditional traffic noise prediction methods are based on certain locations and they are not only

time-consuming, high cost, but also cannot be visualized. Geographical Information System (GIS) can not only solve the problem of manual data processing, but also can get noise values at any point. The paper selected a road segment from Wenxi to Heyang. According to the geographical overview of the study area and the comparison between several models, we combine the JTG B03-2006 model and the HJ2.4-2009 model to predict the traffic noise depending on the circumstances. Finally, we interpolate the noise values at each prediction point and then generate contours of noise. By overlaying the village data on the noise contour layer, we can get the thematic maps. The use of GIS for road traffic noise prediction greatly facilitates the decision-makers because of GIS spatial analysis function and visualization capabilities. We can clearly see the districts where noise are excessive, and thus it becomes convenient to optimize the road line and take noise reduction measures such as installing sound barriers and relocating villages and so on.

Zhuang, Q., Want, X., Li, M., Mao, J. & Wang, F., 2012. Noseleaf pit in Egyptian slit-faced bat as a doubly curved reflector. *EPL* (*Europhysics Letters*), 97(4), p.44001.

Abstract: Noseleaves in slit-faced bats have been hypothesized to affect the sonar beam. Using numerical methods, we show that the pit in the noseleaf of an Egyptian slit-faced bat has an effect on focusing the acoustic near field as well as shaping the radiation patterns and hence enhancing the directionality. The underlying physical mechanism suggested by the properties of the effect is that the pit acts as a doubly curved reflector. Thanks to the pit the beam shape is overall directional and more selectively widened at the high end of the biosonar frequency range to improve spatial coverage and detectability of targets.

Zurcher, A. a., Sparks, D.W. & Bennett, V.J., 2010. Why the bat did not cross the road? *Acta Chiropterologica*, 12(2), pp.337–340.

Abstract: Roadways are nearly ubiquitous parts of the modern landscape, but their impact on bats remain relatively unknown. We studied the influence of vehicular traffic on the behaviour of commuting bats near the Indianapolis International Airport. A previous study at this site documented that Indiana bats (*Myotis sodalis*) were much more likely to cross roads with low traffic volumes. One potential interpretation of this result is that bats perceive motor vehicles as a threat and exhibit avoidance behaviour whether or not the bats are in immediate danger. To test this hypothesis, we observed 211 cases of bats approaching roads that bisected their commuting routes. Information recorded at the time included the presence or absence of vehicles, the height the bat was flying, whether a bat reversed course prior to crossing the road and if so the distance from the road or vehicle (if present) when it altered its direction, and finally the speed, type and relative level of noise emitted by vehicles. Results revealed that bats were more than twice as likely to reverse course when vehicles were present as opposed to their absence. When automobiles were present 60% of bats exhibited avoidance behaviour, reversing course at an average of 10 m from a vehicle. Conversely, when no automobiles were present, only 32% of bats reversed their course and 68% crossed the road. The height a bat flew, speed of the vehicle, type of vehicle or level of noise emitted by vehicles had no effect on the likelihood of bats reversing course. These data support the hypothesis that bats perceive vehicles as a threat and display anti-predator avoidance behaviour in response to their presence.

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