

Foraging bats avoid noise

Andrea Schaub, Joachim Ostwald and Björn M. Siemers

10.1242/jeb.037283

There was an error published in *J. Exp. Biol.* **211**, 3174-3180.

In Fig. 2, the values on the *x*-axis (Frequency) were incorrectly labelled as scaling from 10 to 60 kHz.

The correct axis scale is 0 to 50 kHz.

We apologise to all authors and readers for this error.

Foraging bats avoid noise

Andrea Schaub¹, Joachim Ostwald¹ and Björn M. Siemers^{2,*}

¹Zoological Institute, Department of Animal Physiology, University of Tübingen, Auf der Morgenstelle 28, 72076 Tübingen, Germany and ²Max Planck Institute for Ornithology, Sensory Ecology Group, Eberhard-Gwinner-Strasse, 82319 Seewiesen, Germany

*Author for correspondence (e-mail: siemers@orn.mpg.de)

Accepted 14 August 2008

SUMMARY

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.

Key words: environmental noise, anthropogenic noise, traffic noise, foraging, road ecology, *Myotis myotis*, gleaning bats, passive listening, echolocation, masking.

INTRODUCTION

Ambient noise influences the availability and use of acoustic information in animals in many ways. In addition to noises produced by other animals and natural abiotic sources (e.g. wind or running water), anthropogenic noise emissions, such as urban and traffic noise, constitute a major source of ambient noise. The main body of research on the effects of noise on wild animals has concentrated on acoustic communication (for reviews, see Brumm and Slabbekoorn, 2005; Patricelli and Blickley, 2006; Slabbekoorn and Ripmeester, 2008) because noise can mask relevant acoustic signals to potential receivers. Some species of birds, amphibians and dolphins shift the frequency range of their communication signals in an effort to avoid strong overlap with ambient noise (Slabbekoorn and Peet, 2003; Narins et al., 2004; Morisaka et al., 2005; Feng et al., 2006; Slabbekoorn and den Boer-Visser, 2006; Bee and Swanson, 2007). Moreover, some birds also increase their call amplitude when singing in noisy environments, such as a big city (Brumm and Todt, 2002; Brumm, 2004), or shift singing time to less noisy periods (Fuller et al., 2007). Such behavioural flexibility and evolutionary plasticity has allowed individuals and populations, respectively, to cope with natural environmental noise. Indeed, it has enabled them to adapt their communication systems to anthropogenic noise, at least to some degree. However, there are clear indications that noise pollution can negatively affect wild animals (Forman and Alexander, 1998; Forman and Deblinger, 2000; Jaeger et al., 2005). Roadless space is becoming scarce in many places on our planet (Watts et al., 2007) and road influence on wildlife is an important issue. Traffic noise has been suggested

to decrease the occurrence, breeding density and breeding success of birds (Brotons and Herrando, 2001; Fernandez-Juricic, 2001). In marine environments, noise can affect ranging and acoustic behaviours of whales, porpoises and seals (Morton and Symonds, 2002; Koschinski et al., 2003).

Surprisingly, the degree to which noise can influence another crucial behaviour – foraging – has been entirely neglected. Except for a study on noise-increased predator vigilance, which could result in reduced foraging efficiency in chaffinches (Quinn et al., 2006), the present study is the first to address the effects of noise on foraging ability. It is likely that ambient noise does impact an animals’ ability to use acoustic information for foraging because a variety of birds and mammals use sound to find their prey. For example, owls (Konishi, 2003) and insect-eating primates (Goerlitz and Siemers, 2007) listen for rustling sounds produced by moving animals to detect and localize food. Bats represent a special case. While many bats detect and intercept flying insects using echolocation (Griffin, 1958; Kalko, 1995; Siemers and Schnitzler, 2000), others find prey by listening for prey-produced sounds (Marimuthu and Neuweiler, 1987; Faure and Barclay, 1992; Arlettaz et al., 2001; Siemers and Swift, 2006). This strategy of ‘passive listening’ is adopted by bat species specialized to glean arthropods from vegetation or the ground where prey echoes are masked by overlapping, strong background echoes. For such ‘passive listening’ bats, it is conceivable that environmental noise interferes with the detection of prey. As these bats use echolocation for spatial orientation, the reception of relevant echoes could potentially be impaired by noise as well (Griffin and Grinnell, 1958; von Frenckell and Barclay, 1987;

Mackey and Barclay, 1989; Rydell et al., 1999; Spanjer, 2006; Gillam and McCracken, 2007).

In the present study, we assessed the reaction of bats to both anthropogenic and natural ambient noise in a foraging context. The greater mouse-eared bat (*Myotis myotis* Borkhausen 1797) was used as a model species because it belongs to the group of bats that find prey by listening to their rustling sounds (Kolb, 1961; Arlettaz et al., 2001). This species is therefore potentially vulnerable to noise impact on both 'passive listening' and echolocation. Furthermore, greater mouse-eared bats are a highly protected species (European Habitats Directive, Annex II). They are widely distributed (Güttinger et al., 2001; Dietz et al., 2007) and have expansive home ranges (Audet et al., 1991; Arlettaz, 1999; Zahn et al., 2005); therefore, they are highly relevant in virtually all environmental impact assessments for larger highway or railway projects in central and southern Europe. Most projected traffic routes in Europe will cross *M. myotis* foraging areas. The greater mouse-eared bat can serve as a model species to assess noise impact on foraging behaviour in the large and, from a conservation perspective, especially vulnerable (Safi and Kerth, 2004) group of 'passive listening', gleaning bats.

Greater mouse-eared bats roost in caves in southern Europe and typically in large attics in central Europe (Güttinger et al., 2001; Dietz et al., 2007). Colony size ranges from a handful of reproductive females to several thousands of bats. At nightfall, the colony members disperse into individual foraging areas at a distance of 17 km or more from the communal day roost (Güttinger et al., 2001). They listen for ground-running (epigeaic) arthropods by low search flight in habitats with open, accessible ground (Arlettaz, 1996; Güttinger et al., 2001; Pereira et al., 2002). Greater mouse-eared bats land briefly to glean their prey off the ground; carabids and other ground-running beetles, mole-crickets, spiders and lithobiids are important constituents of their diet (Bauerova, 1978; Arlettaz, 1996; Pereira et al., 2002; Siemers and Güttinger, 2006). Siemers and Güttinger recently showed that arthropod taxa and size classes that produce relatively loud rustling sounds when crawling are strongly overrepresented in the diet of greater mouse-eared bats (Siemers and Güttinger, 2006). This finding indicates that acoustic conspicuousness of potential prey could limit the bats' sensory access to food. As acoustic conspicuousness is probably determined by signal-to-noise-ratio, both rustling amplitude and background noise level will influence foraging success, provided they cover the same frequency range. Arthropod rustling sounds are a series of broadband clicks; they contain frequencies of up to 100 kHz and above. The main energy is concentrated between 3 and 40 kHz, however (Goerlitz and Siemers, 2007; Goerlitz et al., 2008).

Environmental noise is generally measured only in the frequency range of human hearing. Often an A-weighting filter is applied, which results in units of dBA sound pressure level and accounts for the frequency response of human hearing. While this approach is obviously correct to assess noise pollution as perceived by humans, it is not appropriate when it comes to other mammals whose hearing ranges extend beyond human range. In the present study, we therefore took 'a bat's perspective' and recorded the frequency spectrum of traffic noise up to 60 kHz.

We then conducted a choice experiment to test whether bats avoid noisy environments. In a large flight room, we constructed two equally profitable foraging compartments. In each trial, noise was played back in one of the compartments. We then measured whether and to what degree it affected foraging effort and foraging success of the bats in this compartment. The aim of this research was to test: (1) if bats will avoid foraging areas with strong noise impact

(hypothesis one); and (2) if the frequency–time structure of the noise will affect its deterring effect (hypothesis two).

MATERIALS AND METHODS

Animals and housing

Seven male greater mouse-eared bats (*Myotis myotis*) were used for experimentation. The animals were captured as juveniles in August 2005 near Freiburg, Germany, for the present investigations under licence from the responsible authority (Regierungspräsidium Freiburg, licence #55-8852.44/1095). Bats were held and tested in specially designed facilities at the University of Tübingen, Tübingen, Germany (approved by Regierungspräsidium Tübingen). They were housed in a flight cage of 2 m × 1.5 m × 2 m (length × width × height) with an inverted light regime [8 h:16 h (darkness:light)]. The bats received food (mealworms – larvae of *Tenebrio molitor* Linnaeus 1758), and water *ad libitum* during the experiments. Their diet was also supplemented with desert locusts (*Schistocerca gregaria* Forskal 1775) once a week and with vitamins and minerals once every four weeks. All seven bats were in good health at the end of the experiments and remained in the Tübingen animal unit thereafter for further investigations of how traffic noise impacts on bat foraging ecology.

Flight room and setup

Bats were tested in a large flight room with dimensions of 13 m × 6 m × 2 m (length × width × height); walls and ceiling were covered with sound-absorbing foam to reduce echoes and reverberations. Two equally sized compartments [2.5 m × 3 m × 2 m (length × width × height)] were constructed by erecting a dividing wall made from PVC and sound-absorbing foam (Fig. 1). Each compartment was equipped with six cylindrical landing platforms (diameter, 40 cm; height, 10 cm). The platforms were arranged in two rows of three, 20 cm apart. Mealworms, as food reward, could be offered on a plastic Petri dish inserted on the centre of the platforms.

A loudspeaker (Swans, RT2H_A; Arcadia, CA, USA) was mounted on the wall at a height of approximately 1.8 m at the rear end of each compartment for the playback of background noise. The speakers were tilted slightly downwards and directed towards the platform array in an attempt to broadcast sound as homogeneously as possible. Test measurements showed maximal variations of 3 dB

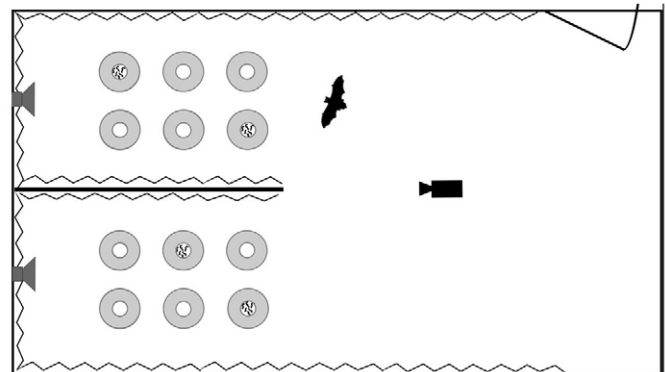


Fig. 1. Schematic representation of the flight room and the experimental setup (not to scale). Each of the two foraging compartments was equipped with a loudspeaker and six landing platforms, two of which contained live mealworms. The room and the division between the compartments were lined with sound-absorbing acoustic foam. A video camera and infrared illumination served to document the bats' behaviour.

in the incident sound pressure levels [SPL (measured 80 cm above the platforms)].

Experimental procedure

In each trial, one compartment was the 'stimulus compartment' where sound was played back and the other compartment was the 'silent compartment' where the loudspeaker was activated but an empty file was played. Sound played back in the stimulus compartment was also audible in the silent compartment. Due to the dividing wall, it was attenuated by 17 dB in comparison with the stimulus compartment (measured at the two platform fields; SdB02 sound level meter, 01dB-Stell, MVI technologies group; Villeurbanne, France). We used four different stimulus types of playback: (1) silence – the loud speaker was activated and an empty file was played back. The silence treatment was a control and served to measure the baseline of the bats' search effort allocation in the two compartments; (2) broadband, digitally generated noise, which served as a broadband control; (3) traffic noise recorded 7.5 m from a highway [30.7 ± 2.5 passing vehicles min^{-1} (mean \pm s.d.)]; and (4) noise recorded from strongly moving reed vegetation (reed bed running alongside a river, which flows across *M. myotis* foraging habitats; bats are known to hunt on meadows adjacent to these reeds; B.M.S., personal observation).

The experiments were divided into three periods of eight days. Different stimuli were used for each period. Each of the four stimuli was presented once on the left side and once on the right side for each bat, resulting in eight experimental conditions per period (i.e. one a day). To factor out day or sequence effects, each bat received a different experimental condition on a given test day (Latin square design). Two out of the six platforms per compartment were continuously baited with 4 g of mealworms, which corresponded to approximately 40 individual larvae. The mealworms produced faint rustling noises with main energy between 3 and 20 kHz, with stronger clicks of up to 50 kHz and above. Measured at 10 cm distance, the loudest peaks ranged from approximately 45 to 62 dB SPL. The mealworm rustling was thus roughly similar to the sounds produced by a carabid beetle (typical greater mouse-eared bat prey) walking on soil, meadow or moist leaf-litter (Goerlitz et al., 2008). Rewards were not placed on the same platform location (front, middle, back) within the two compartments to achieve a homogeneous distribution of the rewarded dishes within the sound field of the speakers. As a result, there were 12 different combinations to choose from. For a balanced design, we used each combination twice within the 24 experimental days, avoiding repeating a dish combination within any of the 8 day periods. The two rewarded dishes of each side were always unrewarded dishes the following day to avoid place conditioning. The assignment of rewarded dishes was independent between the two sides to deter the bats from extracting information from the rewarding scheme of the stimulus compartment from the silent compartment. Platform positions were exchanged between consecutive experiments in order to avoid olfactory labelling on the currently rewarded platforms (scent left from bats of previous session of the day).

Data acquisition started after a 15 day training phase without noise playback in which the bats were accustomed to the flight room. The bats learned to search for prey in the two compartments without much training effort. Bats were tested individually during their natural activity period. After 15 capture events (brief landing on a baited platform, followed by in-flight smacking sounds, which indicate that the bat was chewing food) at a given platform, we removed the remaining prey from this platform. With two baited platforms per compartment, the bats could thus retrieve a maximum

of 30 mealworms from a single compartment per session. The bats were prevented from perching inside the compartments by slowly approaching and gently touching them. To ensure sustained foraging motivation throughout data acquisition, the session was stopped when 45 mealworms had been eaten or 15 min had elapsed. The bats maintained or slightly increased their weight with a daily supply of 45 to 50 mealworms, which was a naturalistic amount of food.

Acquisition and analysis of behavioural data

Experiments were run in the dark and filmed (Sanyo BW CCD camera VCB-3572 IRP, Munich, Germany; Computar lens M0518, Düsseldorf, Germany; Sony recorder GVD1000E, Berlin, Germany) under IR-illumination (custom made IR-strobes) for online display and videotaped for later off-line analysis. For off-line analysis, we used an event-recorder software (Department of Animal Physiology, University of Tübingen) to extract the following parameters: (A) flight time spent in each compartment; (B) number of flights into each compartment. Capture events were counted online and subdivided into; (C) capture events per compartment; and (D) capture events per compartment for the 25 first capture events. The latter measure was introduced because each bat in every session performed at least 25 capture attempts. As a maximum of 30 were allowed per compartment, these first 25 events could be allocated entirely to one compartment, i.e. noise avoidance could be especially pronounced.

The data were normalized and expressed as percentages for display and statistical analysis. Performance of each individual bat was averaged over the three replicas (experimental periods) for a given experimental condition (combination of stimulus type and stimulus compartment position, e.g. 'traffic noise' played in the 'left' compartment) for the statistical analysis. To account for possible individual differences, we used repeated-measures analysis of variance (ANOVA) and *post hoc* paired *t*-tests with sequential Bonferroni correction to test for the influence of playback treatment on the bats' behaviour. To test for possible preferences of the bats for one of the two test compartments, we included stimulus compartment position (left or right) as a factor into the ANOVAs. For testing, percentage data was transformed following Zar (Zar, 1999) ($p' = \arcsin \sqrt{p}$). Tests were run in SPSS 15.0.0 for Windows (SPSS, Inc., Chicago, IL, USA).

Recording, generation and playback of acoustic stimuli

Traffic noise was recorded at a distance of 7.5 m from the centre of the right lane of a highway and 1.5 m in height (Autobahn A8, Stuttgart-Munich, Germany recording location at 48 deg. 37'53.79N and 9 deg. 32'22.36E). We recorded only when it was not raining and when the asphalt was dry. Recordings were taken on windless days; therefore, no wind guard was used (which would have acted as an unwanted low pass filter). Passing vehicles were videotaped to determine vehicle type (car or truck) and to roughly estimate speed. The sound of the cars was picked up with a sensitive, broadband condenser measurement microphone for playback purposes (1/2" low noise Microphone System Type 40HH, G.R.A.S., Holte, Denmark; frequency response ± 1 dB between 0.5 and 10 kHz; ± 8 dB between 10 and 50 kHz, internal noise floor 6.5 dBA re. 20 μ Pa). To ensure a quantitative, broadband analysis of traffic noise, we used a slightly less sensitive but more broadband measurement microphone (G.R.A.S. 1/4" 40BF free field microphone). The microphones were oriented perpendicular to the highway, i.e. we obtained on-axis recordings from passing vehicles. Signals were digitized *via* a custom-built external A/D-converter ('PCTape'; Animal Physiology, University of Tübingen, 16 bit depth,

8×oversampling, digital anti-aliasing; sampling rate 192 kHz) and recorded online onto a laptop computer and stored as wav-files (custom-made recording software). From recordings of the passes of 50 cars and 50 trucks at speeds of approximately 80 km h^{-1} , we selected the loudest 500 ms window (maximum root means square (RMS) amplitude) with a custom Matlab (TheMathWorks, Inc., Natick, MA, USA) routine. To measure the energy distribution over frequency, we computed power spectral densities (PSDs, FFT 256) in Matlab on these 500 ms windows. The average PSDs for these 50 cars and 50 trucks (Fig. 2) show that traffic noise has its main energy clearly within the human audio range but does contain ultrasonic components up to 50 kHz.

We recorded the sound produced by moving vegetation with the above described $1/2''$ microphone and setup. As we faced a prolonged period without wind, we moved bundles of stalks in a dry reed bed by hand in an undulating way in order to simulate wind-induced movement. When the stalks and leaves of the dry reed touched each other, they produced series of broadband click-like and noise-like signals with energy ranging from 0 to frequencies higher than 85 kHz (example in Fig. 3).

All playback files were arranged or generated in Adobe Audition 1.5 (Adobe® Systems, Mountain View, CA, USA). Representative recordings of traffic noise and of moving reed vegetation were used. An empty wav-file (amplitude values of all samples at zero) was generated for the silence treatment. The broadband noise treatment was digitally generated using continuous white noise. The noise spectrum was subsequently altered due to digital filtering, the speaker characteristics and the transmission through air. As a result, the noise spectrum at the platforms was no longer 'white' (i.e. all frequencies at equal amplitude). Higher frequencies were attenuated but were considerably more pronounced than in the traffic noise. All playback files had a sampling rate of 192 kHz, i.e. contained frequencies up to 96 kHz. All files were highpass-filtered at 1 kHz (Adobe Audition; digital FFT filter, 2048 points, Blackman window) to remove sound probably not audible to the bats and to avoid damage to the speaker. The playback amplitude of the digitally generated broadband noise was adjusted in such a way that incident sound measured 80 cm above the platforms had an SPL of 80 dB. This corresponds to the noise level 10–15 m next to a highway as a vehicle passes. The traffic playback files were digitally set at the same RMS sound pressure level for the loudest 500 ms window

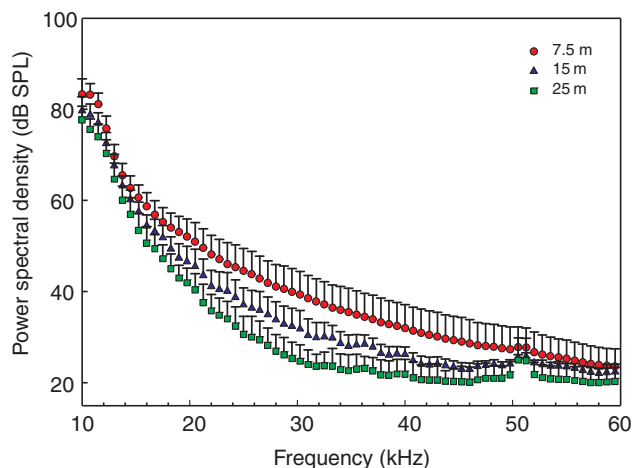


Fig. 2. Mean power spectral densities (PSDs) for 50 cars and 50 trucks recorded at a highway in 7.5 m, 15 m and 25 m distance from the middle of the right lane. Microphone height was 1.5 m. Error bars display the standard deviation.

contained in the playback file (Adobe Audition Analyze). While the broadband noise remained constant at this level, the traffic noise oscillated around this level. The traffic noise would drop when no vehicle was travelling by the recording microphone and would rise in level for periods shorter than 500 ms when a vehicle passed. The playbacks of vegetation movement were set at 12 dB below the broadband noise and the traffic noise files; however, the vegetation movement playbacks were still unnaturally loud or at least corresponding to movement induced by very strong wind as from a human perspective.

Files were played in a continuous loop throughout a trial. They were played back from a laptop through an external D/A-converter (RME Fireface 800 Interface, sampling rate 192 kHz, Haimhausen, Germany), broadband amplifiers (WPA-600 Pro, Conrad Electronics, Hirschau, Germany) and the above mentioned speaker.

RESULTS

There was a clear noise effect on the proportion of flight time allocated to the stimulus compartment (Fig. 4A) (factor stimulus type, $F_{3,18}=27.45$, $P<0.0001$). The bats did not show any preference for either of the two compartments (factor stimulus compartment position, $F_{1,6}=0.03$, $P=0.872$; interaction noise treatment \times compartment position, $F_{3,18}=0.36$, $P=0.786$) when accounting for the influence of stimulus playback. As there was no side preference for any of the behavioural measures (see below), we combined the behavioural data from both compartments for graphic representation (Fig. 4) (averaged within each individual). In the silent treatment, approximately 50% of the flight time was allocated to the stimulus compartment and the remaining 50% to the silent compartment (Fig. 4A). The proportion of search time in the stimulus compartment decreased from the silence treatment *via* traffic and vegetation noise to broadband noise (for pair-wise *post hoc* tests see Fig. 4). In the latter case, only 19% of the flight time was spent in the stimulus compartment and the remaining 81% in the silent compartment (Fig. 4A).

Likewise, there was a clear effect of the type of noise treatment on the percentage of flights into the stimulus compartment (Fig. 4B) (two-way repeated-measures ANOVA, factor stimulus type, $F_{3,18}=24.29$, $P<0.0001$; factor stimulus compartment position, $F_{1,6}=0.23$, $P=0.650$; interaction, $F_{3,18}=0.45$, $P=0.721$). The order of effect magnitude again increased from silence to traffic and vegetation to broadband noise.

The percentage of prey capture events that occurred in the stimulus compartment was affected by the noise treatment. This applies when analysing all capture events per session (maximally 45 per bat) (Fig. 4C) (factor stimulus type, $F_{3,18}=35.41$, $P<0.0001$; factor stimulus compartment position, $F_{1,6}=0.07$, $P=0.805$; interaction, $F_{3,18}=0.50$, $P=0.685$) and even more pronounced when only considering the first 25 capture events per bat and session (Fig. 4D) (factor stimulus type, $F_{3,18}=76.40$, $P<0.0001$; factor stimulus compartment position, $F_{1,6}=0.02$, $P=0.893$; interaction, $F_{3,18}=0.09$, $P=0.962$). The order of stimulus types by effect magnitude was the same as for the two above behavioural measures.

DISCUSSION

Foraging bats avoid noise

Noise treatment clearly affected the foraging effort and foraging success of the bats. When playing back 'silence', the bats, as expected, made equal use of and were equally successful in both compartments. However, when a noise stimulus was present, the bats avoided the stimulus compartment (hypothesis one). Bats allocated more search effort to the silent compartment and less to

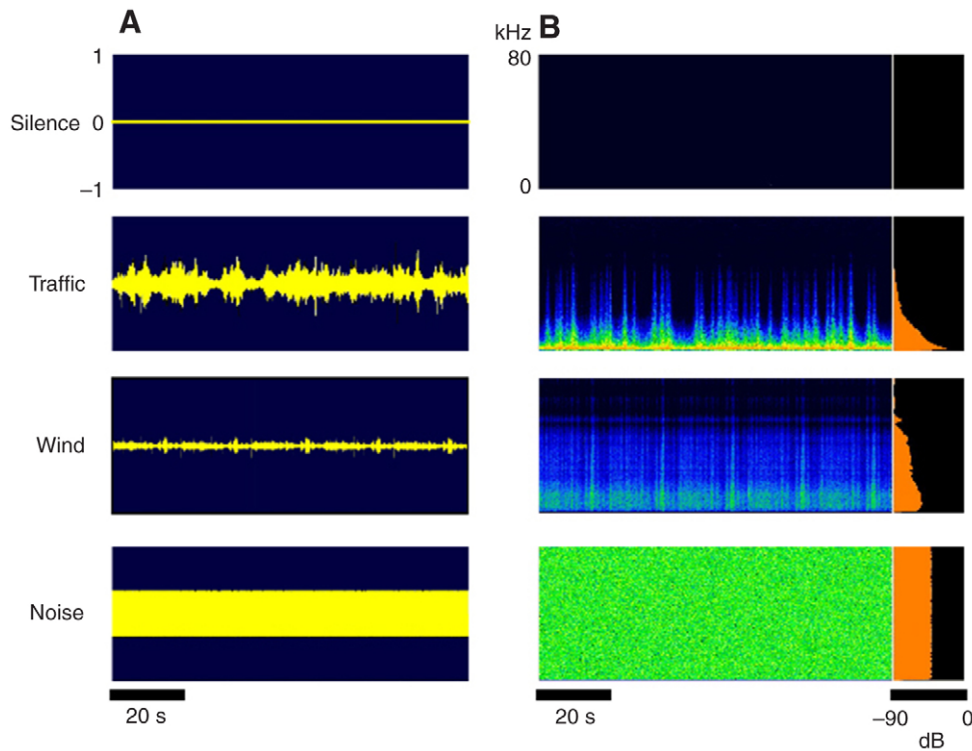


Fig. 3. Examples of the sound files used for playback. (A) Oszillogram, (B) sonogram representation and mean power spectrum.

the stimulus compartment by specifically avoiding foraging areas with strong noise impact. However, avoidance of the stimulus compartment was not complete. Even during the apparently most disturbing broadband noise, the bats still allocated 20% of their time in the compartments to the noisy stimulus compartment.

In the present study, we specifically assessed noise impact on foraging activity. Therefore, we are unable to draw conclusions on

the role environmental noise will play for other bat activities. Bat colonies, including those of greater mouse-eared bats, roost in church towers close to the belfry and sometimes in road and railway bridges (Güttinger et al., 2001). If a church has functional bells, they are in use only for a small proportion of the time. When found in bridges, they typically roost inside the structure of the bridge where high frequency components of traffic noise will be strongly attenuated.

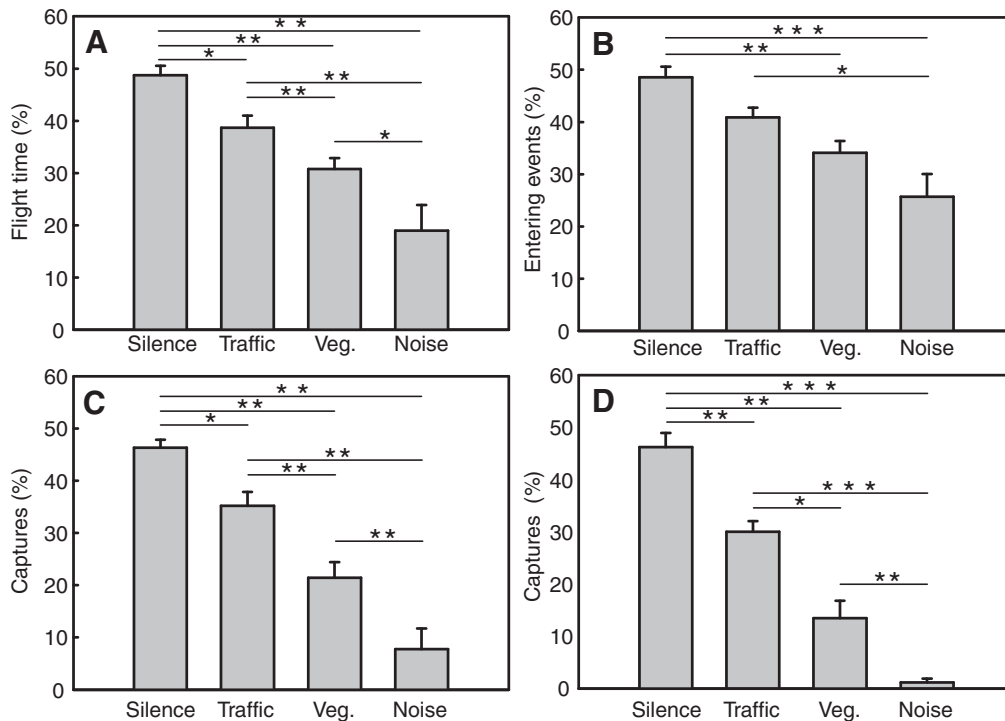


Fig. 4. Influence of noise treatments on foraging behaviour of the mouse eared bats. (A) Percentage of the flight time in the stimulus compartment. (B) Percentage of flights into the stimulus compartment. (C) Percentage of total capture events that occurred in the stimulus compartment. (D) Percentage of the first 25 capture events per session that occurred in the stimulus compartment. Results from repeated-measures ANOVAs for the factors noise treatment and stimulus compartment position are given in the text. As the latter did not have a significant effect on any of the behavioural measures, we combined the behavioural data from both compartments for this graphic representation (averaged within each individual; error bars give the standard error, $N=7$ bats). Asterisks show significant differences revealed in *post hoc* paired *t*-tests for these combined data sets (sequential Bonferroni correction to account for multiple testing). *** $P<0.001$, ** $P<0.01$, * $P<0.05$.

This might reduce traffic noise impact on the bats. Nevertheless, bell tower and bridge-roosting are anecdotal evidence for the ability of bats to cope with considerable background noise in non-foraging situations.

Influence of noise structure

The deterring effect differed between stimuli; it increased from traffic to vegetation to broadband noise. It is interesting to note that the vegetation noise, although set 12 dB below the traffic noise amplitude (still unnaturally loud), had a greater repellent effect than the traffic noise. This supports our second hypothesis, predicting that the frequency–time structure of the noise will affect its deterring intensity. The vegetation noise consisted of a series of transient, broadband signals, not unlike the clicks produced by walking arthropods (Goerlitz and Siemers, 2007; Goerlitz et al., 2008). This similarity to prey sounds might render the vegetation noise an effective masker that reduces the bats' ability to detect insects. Unless shaken by a storm, sounds of naturally wind-moved vegetation will be much less intense than that created in the present study and, hence, will be of less impact for wild bats. Nevertheless, natural noise is likely to affect the foraging efficiency of bats. Behaviour observation and playback experiments suggested that noise from turbulent water could interfere with echo-based prey detection in bats that forage close to, as well as several meters above, water surfaces (von Frenckell and Barclay, 1987; Mackey and Barclay, 1989; Rydell et al., 1999).

The artificial broadband noise in our experiments contained higher frequencies than the traffic noise. It was continuous whereas both traffic and vegetation noise contained short intervals of less intense sound. Both its continuous nature and its content of higher frequencies might in part explain why the broadband noise treatment had the strongest deterrent effect on the bats (see also Huebner and Wiegrebe, 2003).

Reasons for noise avoidance

An unspecific aversive character of noise (Beerda et al., 1998) could be part of the reason why greater mouse-eared bats avoided noisy foraging patches. As these bats do roost in noisy places (see above), it appears more likely, however, that a specific noise-impairment on perception of prey sounds (Huebner and Wiegrebe, 2003; Goerlitz et al., 2008), on echolocation (Griffin and Grinnell, 1958; Rydell et al., 1999; Spanjer, 2006; Gillam and McCracken, 2007) or on both were the reason. Impairment could be caused by the masking of relevant sounds or echoes and by the difficulty of processing several auditory streams simultaneously (Barber et al., 2003). The fact that we did not observe any change in flight ability or landing accuracy argues against a relevant impairment of echolocation. Calls of greater mouse-eared bats are broadband sweeps from between 120 and 70 kHz down to approximately 27 kHz (Boonman and Schnitzler, 2005), i.e. they contain considerable energy above the frequency band covered by the noise playbacks in the present study. The strong effect of the click-like vegetation noise, despite its reduced amplitude, points in the direction of an impairment of the perception of prey rustling-clicks. Further experiments will be needed to verify this explanation and to quantify the conceivable reduction of the ability of bats to detect prey by natural and anthropogenic noise.

Conclusions

Data from the present study 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 the greater mouse-eared bat. The situation, which mimicked the traffic noise treatment, corresponds to a distance of 10–15 m from a highway. Noise intensity and, hence, noise impact will level off with distance. However, it is likely that bats foraging 50 m away from the highway will still be impacted by traffic noise (B.M.S. and A.S., unpublished data). Relatively large areas will be affected and a fitness relevance for natural populations is likely. In addition to distance, the number of passing vehicles will affect the intensity of acoustic habitat degradation. In addition to the greater mouse-eared bats, many other species of bat find their prey predominantly by listening to prey sounds. We therefore assume that acoustic habitat degradation will affect these species in a similar way. This group is especially vulnerable to extinction and is, therefore, of special conservation concern (Safi and Kerth, 2004). In Europe, the potential vulnerable bat species include the lesser mouse-eared bat (*Myotis blythii/oxynathus*), Bechstein's bat (*Myotis bechsteinii*) and all long-eared bats (genus *Plecotus*) (Arlettaz et al., 2001; Swift and Racey, 2002; Siemers and Swift, 2006). In North America, species such as the pallid bat (*Antrozous pallidus*), the long-eared bat (*Myotis evotis*), the Northern long-eared bat (*Myotis septentrionalis*) and possibly the big-eared bats (genus *Corynorhinus*) as well as the little-known spotted bat (*Euderma maculatum*) might also be affected by acoustic habitat degradation (Faure and Barclay, 1992; Fullard and Dawson, 1997; Lacki and Ladeur, 2001; Leslie and Clark, 2002; Barber et al., 2003; Ratcliffe and Dawson, 2003). Interestingly, the reluctance of bats to forage in very noisy environments potentially also brings about conservation benefits. If bats indeed allocate little foraging time to noisy highway margins and highways themselves, the number of potential traffic casualties (Kiefer et al., 1994; Lesinski, 2007) could be reduced. By contrast, aerial hawking bats that detect and track insects by echolocation can be attracted by the high prey abundance associated with anthropogenic habitat alterations, such as streetlights alongside roads (Arlettaz et al., 2000; Avila-Flores and Fenton, 2005) or garbage dumps (Kronwitter, 1988). While this might indicate some dichotomy in how bats from different ecological groups deal with human impact, previous playback experiments indicate that in addition to 'passive listening' bats as shown in the present study, aerial hawking species are also affected and deterred by broadband noise (Mackey and Barclay, 1989; Spanjer, 2006; Szewczak and Arnett, 2006). In the course of environmental impact assessments for highway planning, appropriate preventive measures (noise reduction) or compensatory measures (amelioration of alternative bat foraging habitats) will, according to the respective applicable national and international law, have to be considered. Further research is needed to mechanistically understand the impact of anthropogenic noise on both 'passive listening' gleaning bats and aerial hawking bats, which find prey by echolocation.

We thank Professor Hans-Ulrich Schnitzler for constant support and valuable discussion, Professor Markus Fendt for the event-recorder software, Ingrid Kaipf and Daniela Schmieder for much appreciated help with bat husbandry and video analysis. Amanda Windhof and John Lesku are acknowledged for native speaker language editing; Drs Peter Stitz, Holger Goerlitz and Henrik Brumm for discussion; Brock Fenton as well as an anonymous referee for constructive comments. This research was funded in the framework of a research project commissioned by the German Federal Ministry of Transport, Building and Urban Affairs (FE 02.256/2004/LR 'Quantifizierung und Bewältigung verkehrsbedingter Trennwirkungen auf Arten des Anhangs der FFH-Richtlinie, hier Fledermauspopulationen', subproject Siemers). The responsibility for the contents of this manuscript lies solely with the authors. Data analysis, writing and Open Access were supported by the Max Planck Society. Ministry officers Dr Udo Tegethof and Andreas Wehner-Heil supported us throughout and the project partners Dr Gerald Kerth, Dr Jochen Lüttmann, Jutta Kusenbach, Malte Fuhrmann, Manfred Weißhaar and Birgit Gessner provided discussion.

REFERENCES

- Arllettaz, R.** (1996). Feeding behaviour and foraging strategy of free-living mouse-eared bats, *Myotis myotis* and *Myotis blythii*. *Anim. Behav.* **51**, 1-11.
- Arllettaz, R.** (1999). Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. *J. Anim. Ecol.* **68**, 460-471.
- Arllettaz, R., Godat, S. and Meyer, H.** (2000). Competition for food by expanding pipistrelle bat populations (*Pipistrellus pipistrellus*) might contribute to the decline of lesser horseshoe bats (*Rhinolophus hipposideros*). *Biol. Conserv.* **93**, 55-60.
- Arllettaz, R., Jones, G. and Racey, P. A.** (2001). Effect of acoustic clutter on prey detection by bats. *Nature* **414**, 742-745.
- Audet, D., Krull, D., Marimuthu, G., Sumithran, S. and Singh, J. B.** (1991). Foraging behavior of the Indian false vampire bat, *Megaderma lyra* (Chiroptera, Megadermatidae). *Biotropica* **23**, 63-67.
- Avila-Flores, R. and Fenton, M. B.** (2005). Use of spatial features by foraging insectivorous bats in a large urban landscape. *J. Mammal.* **86**, 1193-1204.
- Barber, J. R., Razak, K. A. and Fuzessery, Z. M.** (2003). Can two streams of auditory information be processed simultaneously? Evidence from the gleaning bat *Antrozous pallidus*. *J. Comp. Physiol.* **189**, 843-855.
- Bauerova, Z.** (1978). Contribution to the trophic ecology of *Myotis myotis*. *Folia Zool.* **27**, 305-316.
- Bee, M. A. and Swanson, E. M.** (2007). Auditory masking of anuran advertisement calls by road traffic noise. *Anim. Behav.* **74**, 1765-1776.
- Beerda, B., Schilder, M. B. H., van Hooff, J., de Vries, H. W. and Mol, J. A.** (1998). Behavioural, saliva cortisol and heart rate responses to different types of stimuli in dogs. *Appl. Anim. Behav. Sci.* **58**, 365-381.
- Boonman, A. and Schnitzler, H. U.** (2005). Frequency modulation patterns in the echolocation signals of two vesperilionid bats. *J. Comp. Physiol.* **191**, 13-21.
- Brotans, L. and Herrando, S.** (2001). Reduced bird occurrence in pine forest fragments associated with road proximity in a Mediterranean agricultural area. *Landsc. Urban Plan.* **57**, 77-89.
- Brumm, H.** (2004). The impact of environmental noise on song amplitude in a territorial bird. *J. Anim. Ecol.* **73**, 434-440.
- Brumm, H. and Slabbekoorn, H.** (2005). Acoustic communication in noise. *Adv. Study Behav.* **35**, 151-209.
- Brumm, H. and Todt, D.** (2002). Noise-dependent song amplitude regulation in a territorial songbird. *Anim. Behav.* **63**, 891-897.
- Dietz, C., von Helversen, O. and Nill, D.** (2007). *Handbuch der Fledermäuse Europas und Nordwestafrikas*. Stuttgart: Franckh-Kosmos Verlags GmbH.
- Faure, P. A. and Barclay, R. M. R.** (1992). The sensory basis of prey detection by the long-eared bat, *Myotis evotis*, and the consequences for prey selection. *Anim. Behav.* **44**, 31-39.
- Feng, A. S., Narins, P. M., Xu, C. H., Lin, W. Y., Yu, Z. L., Qiu, Q., Xu, Z. M. and Shen, J. X.** (2006). Ultrasonic communication in frogs. *Nature* **440**, 333-336.
- Fernandez-Juricic, E.** (2001). Avian spatial segregation at edges and interiors of urban parks in Madrid, Spain. *Biodivers. Conserv.* **10**, 1303-1316.
- Forman, R. T. T. and Alexander, L. E.** (1998). Roads and their major ecological effects. *Annu. Rev. Ecol. Syst.* **29**, 207-231.
- Forman, R. T. T. and Deblinger, R. D.** (2000). The ecological road-effect zone of a Massachusetts (USA) suburban highway. *Conserv. Biol.* **14**, 36-46.
- Fullard, J. H. and Dawson, J. W.** (1997). The echolocation calls of the spotted bat *Euderma maculatum* are relatively inaudible to moths. *J. Exp. Biol.* **200**, 129-137.
- Fuller, R. A., Warren, P. H. and Gaston, K. J.** (2007). Daytime noise predicts nocturnal singing in urban robins. *Biol. Lett.* **3**, 368-370.
- Gillam, E. H. and McCracken, G. F.** (2007). Variability in the echolocation of *Tadarida brasiliensis*: effects of geography and local acoustic environment. *Anim. Behav.* **74**, 277-286.
- Goerlitz, H. R. and Siemers, B. M.** (2007). Sensory ecology of prey rustling sounds: acoustical features and their classification by wild Grey Mouse Lemurs. *Funct. Ecol.* **21**, 143-153.
- Goerlitz, H. R., Greif, S. and Siemers, B. M.** (2008). Cues for acoustic detection of prey: insect rustling sounds and the influence of walking substrate. *J. Exp. Biol.* **211**, 2799-2806.
- Griffin, D. R.** (1958). *Listening in the Dark*. New Haven: Yale University Press.
- Griffin, D. R. and Grinnell, A. D.** (1958). Ability of bats to discriminate echoes from louder noise. *Science* **128**, 145-147.
- Güttinger, R., Zahn, A., Krapp, F. and Schober, W.** (2001). *Myotis myotis*-Großes Mausohr, Großmausohr. In *Handbuch der Säugetiere Europas*, vol. 4/I: Fledertiere I (ed. F. Krapp). Wiebelsheim: Aula-Verlag.
- Huebner, M. and Wiegrebe, L.** (2003). The effect of temporal structure on rustling-sound detection in the gleaning bat, *Megaderma lyra*. *J. Comp. Physiol. A* **189**, 337-346.
- Jaeger, J. A. G., Bowman, J., Brennan, J., Fahrigh, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B. and von Toschanowitz, K. T.** (2005). Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. *Ecol. Modell.* **185**, 329-348.
- Kalko, E. K. V.** (1995). Insect pursuit, prey capture and echolocation in pipistrelle bats (*Microchiroptera*). *Anim. Behav.* **50**, 861-880.
- Kiefer, A., Merz, H., Rackow, W., Roer, H. and Schlegel, D.** (1994). Bats as traffic casualties in Germany. *Myotis* **32-33**, 215-220.
- Kolb, A.** (1961). Sinnesleistungen Einheimischer Fledermaeuse Bei Der Nahrungssuche Und Nahrungsauswahl Auf Dem Boden Und In Der Luft. *Z. Vgl. Physiol.* **44**, 550-564.
- Konishi, M.** (2003). Coding of auditory space. *Ann. Rev. Neurosci.* **26**, 31-55.
- Koschinski, S., Culik, B. M., Henriksen, O. D., Tregenza, N., Ellis, G., Jansen, C. and Kathe, G.** (2003). Behavioural reactions of free-ranging porpoises and seals to the noise of a simulated 2 MW windpower generator. *Mar. Ecol. Prog. Ser.* **265**, 263-273.
- Kronwitter, F.** (1988). Population structure, habitat use and activity patterns of the noctule bat, *Nyctalus noctula* Schreb., 1774 (Chiroptera: Vespertilionidae) revealed by radio-tracking. *Myotis* **26**, 23-85.
- Lacki, M. J. and Ladeur, K. M.** (2001). Seasonal use of lepidopteran prey by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*). *Am. Midl. Nat.* **145**, 213-217.
- Lesinski, G.** (2007). Bat road casualties and factors determining their number. *Mammalia* **71**, 138-142.
- Leslie, D. M. and Clark, B. S.** (2002). Feeding habits of the endangered Ozark big-eared bat (*Corynorhinus townsendii ingens*) relative to prey abundance. *Acta Chiropt.* **4**, 173-182.
- Mackey, R. L. and Barclay, R. M. R.** (1989). The influence of physical clutter and noise on the activity of bats over water. *Can. J. Zool.* **67**, 1167-1170.
- Marimuthu, G. and Neuweiler, G.** (1987). The use of acoustical cues for prey detection by the Indian false vampire bat, *Megaderma lyra*. *J. Comp. Physiol.* **160**, 509-515.
- Morisaka, T., Shinohara, M., Nakahara, F. and Akamatsu, T.** (2005). Effects of ambient noise on the whistles of Indo-Pacific bottlenose dolphin populations. *J. Mammal.* **86**, 541-546.
- Morton, A. B. and Symonds, H. K.** (2002). Displacement of *Orcinus orca* (L.) by high amplitude sound in British Columbia, Canada. *ICES J. Mar. Sci.* **59**, 71-80.
- Narins, P. M., Feng, A. S., Lin, W. Y., Schnitzler, H. U., Denzinger, A., Suthers, R. A. and Xu, C. H.** (2004). Old World frog and bird, vocalizations contain prominent ultrasonic harmonics. *J. Acoust. Soc. Am.* **115**, 910-913.
- Patricelli, G. L. and Blickley, J. L.** (2006). Avian communication in urban noise: causes and consequences of vocal adjustment. *Auk* **123**, 639-649.
- Pereira, M. J. R., Rebelo, H., Rainho, A. and Palmeirim, J. M.** (2002). Prey selection by *Myotis myotis* (Vespertilionidae) in a Mediterranean region. *Acta Chiropt.* **4**, 183-193.
- Quinn, J. L., Whittingham, M. J., Butler, S. J. and Cresswell, W.** (2006). Noise, predation risk compensation and vigilance in the chaffinch *Fringilla coelebs*. *J. Avian Biol.* **37**, 601-608.
- Ratcliffe, J. M. and 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. *Anim. Behav.* **66**, 847-856.
- Rydell, J., Miller, L. A. and Jensen, M. E.** (1999). Echolocation constraints of Daubenton's bat foraging over water. *Funct. Ecol.* **13**, 247-255.
- Safi, K. and Kerth, G.** (2004). A comparative analysis of specialization and extinction risk in temperate-zone bats. *Conserv. Biol.* **18**, 1293-1303.
- Siemers, B. M. and Güttinger, R.** (2006). Prey conspicuousness can explain apparent prey selectivity. *Curr. Biol.* **16**, R157-R159.
- Siemers, B. M. and Schnitzler, H. U.** (2000). Natterer's bat (*Myotis nattereri* Kuhl, 1818) hawks for prey close to vegetation using echolocation signals of very broad bandwidth. *Behav. Ecol. Sociobiol.* **47**, 400-412.
- Siemers, B. M. and Swift, S. M.** (2006). Differences in sensory ecology contribute to resource partitioning in the bats *Myotis bechsteinii* and *Myotis nattereri* (Chiroptera: Vespertilionidae). *Behav. Ecol. Sociobiol.* **59**, 373-380.
- Slabbekoorn, H. and den Boer-Visser, A.** (2006). Cities change the songs of birds. *Curr. Biol.* **16**, 2326-2331.
- Slabbekoorn, H. and Peet, M.** (2003). Ecology: birds sing at a higher pitch in urban noise-Great tits hit the high notes to ensure that their mating calls are heard above the city's din. *Nature* **424**, 267-267.
- Slabbekoorn, H. and Ripmeester, E. A. P.** (2008). Birdsong and anthropogenic noise: implications and applications for conservation. *Mol. Ecol.* **17**, 72-83.
- Spanjer, G. R.** (2006). Responses of the big brown bat, *Eptesicus fuscus*, to a proposed acoustic deterrent device in a lab setting: a report submitted to the Bats and Wind Energy Cooperative and the Maryland Department of Natural Resources. Austin, Texas, USA: Bat Conservation International. <http://www.batsandwind.org/pdf/detlab2006.pdf>
- Swift, S. M. and Racey, P. A.** (2002). Gleaning as a foraging strategy in Natterer's bat *Myotis nattereri*. *Behav. Ecol. Sociobiol.* **52**, 408-416.
- Szewczak, J. M. and Arnett, E. B.** (2006). An acoustic deterrent with the potential to reduce bat mortality from wind turbines. *Bat Res. News* **47**, 151-152.
- von Frenczell, B. and Barclay, R. M. R.** (1987). Bat activity over calm and turbulent water. *Can. J. Zool.* **65**, 219-222.
- Watts, R. D., Compton, R. W., McCammon, J. H., Rich, C. L., Wright, S. M., Owens, T. and Ouren, D. S.** (2007). Roadless space of the conterminous United States. *Science* **316**, 736-738.
- Zahn, A., Haselbach, H. and Güttinger, R.** (2005). Foraging activity of central European *Myotis myotis* in a landscape dominated by spruce monocultures. *Mamm. Biol.* **70**, 265-270.
- Zar, J. H.** (1999). *Biostatistical Analysis*. Upper Saddle River, NJ: Pearson Education.