

How anthropogenic noise affects foraging

JINHONG LUO^{1,2}, BJÖRN M. SIEMERS^{1†} and KLEMEN KOSELJ¹

¹Sensory Ecology Group, Max Planck Institute for Ornithology, Eberhard-Gwinner-Straße, 82319 Seewiesen, Germany, ²Jilin Key Laboratory of Animal Resource Conservation and Utilization, Northeast Normal University, 130024 Changchun, China

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.

Keywords: allostatic load, anthrophony, global change, highway noise, *Myotis daubentonii*, noise pollution, road impact, soundscape ecology

Received 27 November 2014; revised version received 17 March 2015 and accepted 4 May 2015

Introduction

With human impact on wildlife increasing globally, there is a pressing need to understand its reach and consequences. However, many human activities have the potential to negatively affect other species by mechanisms that can be hard to detect and can operate at a distance, which makes environmental impact assessments particularly challenging. One such disturbance is anthropogenic noise (i.e., acoustic noise produced by human activities).

Spatial and temporal abundance of anthropogenic noise has increased considerably since the Industrial Revolution in both terrestrial and marine environments (Barber *et al.*, 2010; Slabbekoorn *et al.*, 2010; Simpson *et al.*, 2015). Intense anthropogenic noise is closely linked to urban development, resource extraction or expanding transportation networks. Recent measurements in the USA show that not even the remote wilderness areas are safe from transportation noise and that typical noise levels strongly exceed natural ambient noise levels (Barber *et al.*, 2010; Fristrup, 2015). In addition to the elevated sound pressure level, anthropogenic noise differs strongly from

natural sounds in the frequency composition, spatial distribution and diurnal dynamics (Warren *et al.*, 2006). Anthropogenic noise adversely affects humans and other animals. In humans, it is responsible for sleep disturbance, psychological problems, as well as for higher risks of cardiovascular diseases, tinnitus and cognitive impairments of children (WHO, 2011). In animals, anthropogenic noise has been shown to change or even disrupt a variety of crucial biological processes ranging from communication to foraging or even reproduction (Barber *et al.*, 2010; Brumm, 2010; Kight & Swaddle, 2011; Francis & Barber, 2013). The impacts of anthropogenic noise on animals are not only limited to individuals or populations of single species, but also reach the community level (Francis *et al.*, 2012). Consequently, anthropogenic noise represents a major environmental pollutant of global concern, attracting attention from biologists, resource managers and policy makers (Francis & Barber, 2013).

Foraging is performed virtually by all animal species and is crucial for their survival and reproduction (Lemon, 1991). Anthropogenic noise has recently been shown to impair foraging in different species (L. Quinn *et al.*, 2006; Purser & Radford, 2011; Siemers & Schaub, 2011; Wale *et al.*, 2013). However, it is not yet clear exactly how noise disturbs foraging. Hypotheses of three potential mechanisms of noise disturbance have

Correspondence: Jinhong Luo, tel. +49 89218074367, fax +49 89218074304, e-mail: jluo@orn.mpg.de

[†]Deceased.

been put forward thus far: acoustic masking, reduced attention and noise avoidance.

Acoustic masking is a perceptual process, where surrounding sounds interfere with the detection or recognition of target sound (Moore, 2012). Acoustic masking occurs if the target sound and interfering sounds spectrally and temporally overlap with each other. As a result, acoustic masking can only hinder foraging in animals that find their food by relying on sounds with spectra similar to that of the background noise (Barber *et al.*, 2010; Brumm, 2010; Siemers & Schaub, 2011; Francis & Barber, 2013; Bunkley *et al.*, 2015). Members of many taxa are potentially affected by acoustic masking during foraging, including owls, carnivores, nocturnal primates and many species of bat (Siemers & Schaub, 2011).

Some bats, such as the greater mouse-eared bat (*Myotis myotis*), locate their prey by listening to prey-generated sounds (Arlettaz *et al.*, 2001; Jones *et al.*, 2011) that are produced by the prey and are not to be confused with echoes of bat calls. Prey-generated sounds overlap spectrally with anthropogenic noise (Schaub *et al.*, 2008). A recent study found that traffic noise can deteriorate the foraging performance of the greater mouse-eared bats up to 60 m away from highways (Siemers & Schaub, 2011). Because of the spectral overlap, the authors suggested that a likely mechanism of noise disturbance in this species was acoustic masking.

In contrast to bats using prey-generated sounds, a high proportion of echolocating bat species find their food by broadcasting high-pitched calls and analysing the reflected echoes, that is by echolocation. Because the bulk of anthropogenic noise energy is concentrated at much lower frequencies than the energy of bat echolocation calls (Fig. 2c; see also Siemers & Schaub, 2011), one may be tempted to conclude that such noise cannot mask the reflected prey echoes for these bats. However, traffic noise at 15 m distance from a highway can be as loud as 30 dB SPL (sound pressure level in dB, root mean square relative to 20 μ Pa) at frequencies around 30 kHz, which lies in the frequency range used for echolocation by several bat species (Schaub *et al.*, 2008). Due to the severe transmission loss of ultrasonic sounds in air and the low sound reflection of prey (low target strength), the received echoes by bats are much weaker than the emitted calls (Luo *et al.*, 2014a). Furthermore, high frequency parts of the sound are more sensitive to transmission loss, which means that they get filtered out from the echoes before reaching the bat (Stilz & Schnitzler, 2012). The resulting weak and low-pass-filtered echoes (Fig. 2c) can potentially be masked by anthropogenic noise. The role of acoustic masking as a mechanism of disturbance to foraging bats is, however, still a puzzle that has not been addressed experimentally.

Attention is defined as the allocation of cognitive resources among simultaneous tasks (Anderson, 2009) and is, by definition, limited. Therefore, performance of a task decreases when additional tasks have to be processed. This decrease is stronger and more likely to occur for difficult tasks (Anderson, 2009). For example, walking and chewing gum hardly interfere with each other, whereas using a cell phone while driving leads to a higher risk of car accidents (Lamble *et al.*, 1999). To foraging animals, anthropogenic noise is an additional input that may decrease the available cognitive resources for dealing with foraging tasks (prey detection, localization, decision-making etc.). Therefore, it has the potential to affect many animal species including bats (Dukas & Kamil, 2001; Barber *et al.*, 2003; Dukas, 2004; Chan & Blumstein, 2011). It was proposed that reduced attention deteriorated foraging performance in three-spined sticklebacks exposed to anthropogenic noise (Purser & Radford, 2011).

Anthropogenic noise may also act as a stressor (Wright *et al.*, 2007). In this study, we adopt the definitions proposed by Romero (2004) and refer to a 'stressor' as an unpredictable, noxious stimulus that induces characteristic physiological and behavioural changes, collectively termed a 'stress response'. Behaviourally, a stress response manifests itself as startling, freezing, hiding, avoiding stressors and interruption of foraging (Delaney *et al.*, 1999; Frid & Dill, 2002; Wright *et al.*, 2007; Purser & Radford, 2011; Francis & Barber, 2013). However, because these behaviours can also occur outside of a stress response, they cannot be taken as evidence for it, without showing that they are accompanied by necessary physiological changes (Romero, 2004; Wright *et al.*, 2007). Furthermore, the threshold, at which a minor aversion to stimulus turns into a stress response, is hard if not impossible to define (McEwen & Wingfield, 2003). Therefore, we will use the more general terms 'aversive stimulus' and 'avoidance response' in this study.

It is very difficult to estimate the role of different mechanisms by which anthropogenic noise impairs survival and reproduction, particularly because several of them can operate simultaneously. Ignorance of the underlying mechanism, in turn, hinders the accurate prediction of the damage by noise pollution to wildlife (Francis & Barber, 2013) and can cause planners to underestimate the urgency for conservation measures. Here, we propose a diagnostic framework that can be used to experimentally identify the mechanism of noise disturbance to foragers of any species capable of detecting the noise. We test how the diagnostic framework fulfils this task and ask whether and how anthropogenic noise impairs foraging in Daubenton's bats (*Myotis daubentonii*, Kuhl, 1817), a species that uses

echolocation to find prey (Dietz *et al.*, 2009). We manipulated the presence of spectral overlap and the difficulty of prey detection in a laboratory foraging experiment, to examine our diagnostic predictions.

Diagnostic framework

In the following, we describe the diagnostic framework. It uses the specific characteristics of auditory processes associated with acoustic masking, of cognitive mechanisms that allocate attention, and of avoidance responses to aversive stimuli, to generate testable predictions (Fig. 1).

Acoustic masking makes the task of detecting or recognizing a target sound more difficult. We predict that under the acoustic masking hypothesis, the search effort required for a successful foraging event increases and foraging efficiency decreases only if the noise overlaps spectrally with the sound carrying the prey information. Therefore, the nonoverlapping noise that has to be used in the control treatment should have no effect on foraging.

If noise impairs foraging by reducing the available attention, the effort required for a successful foraging event in noise should be higher than without noise. This effect will only be observable if the foraging task is difficult enough to compete for attention with the noise

(Anderson, 2009). Hence, when designing the experiment, it is important to include foraging tasks with different levels of difficulty. Both the acoustic masking and the reduced attention hypotheses predict an increase in search effort required for a successful foraging event. They can be discriminated from each other by testing whether the noise without spectral overlap has an effect. Namely, if noise limits attention, both overlapping noise and nonoverlapping noise will increase the effort required for a successful foraging event. In contrast, if noise interferes by masking prey information, the nonoverlapping noise should not have an effect.

If noise acts as an aversive stimulus (or even stressor), we predict that animals will avoid the noise source and decrease their foraging activity. Therefore, the effort invested in searching for food should decrease, which distinguishes the effect of noise avoidance from noise-reduced attention and acoustic masking. Foragers may avoid noise directly, but it is conceivable that they may instead avoid the area where foraging is less profitable because noise masks prey information or reduces forager's attention. Such secondary mechanisms of noise disturbance can be revealed using the following predictions. If avoidance behaviour is a response to acoustic masking, a decrease in foraging activity will not occur if the spectral overlap is removed from the noise. If attention overload is causing the avoidance, it

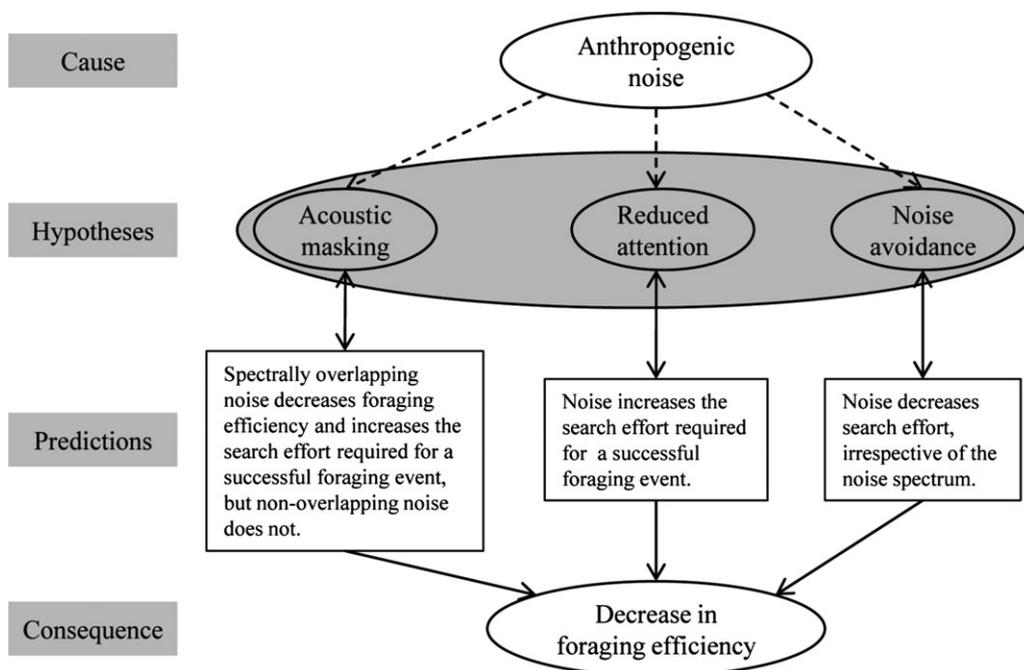


Fig. 1 Diagnostic framework for identifying the mechanism of noise disturbance to foraging animals. The grey ellipse illustrates that several mechanisms may operate at the same time and interact. For example, an avoidance response may also be triggered indirectly as a result of acoustic masking or of reduced attention. Currently, we are not aware of any potential mechanisms not shown in this diagram.

will not take place if the overload is removed by sufficiently reducing the difficulty of the foraging task. Again, the increased search effort required for successful prey capture is a necessary indicator of attention overload and acoustic masking. Note the difference between 'search effort required for a successful prey capture' and 'search effort', with the latter serving to test the noise avoidance hypothesis.

Materials and methods

Animals and housing

Daubenton's bat uses echolocation to detect prey and prefers to forage low above water bodies, trawling prey from the water surface (Dietz *et al.*, 2009). This makes it particularly suitable to test our hypotheses. First, the acoustic prey information available to the bat (echoes) is known, and it is possible to manipulate whether traffic noise spectrally overlaps it or not (Fig. 2c). Second, Daubenton's bat can have a rather small foraging habitat, which allows us to ensnare it homogeneously with noise. Third, prey detection ability in this species is sensitive to the amount of clutter, for example nonprey echoes from vegetation on the water surface (Boonman *et al.*, 1998; Siemers & Schnitzler, 2004), which we used to manipulate the sensory difficulty of foraging to test the reduced attention hypothesis.

Four adult male Daubenton's bats participated in the experiments. The animals were captured in August 2011 in a mist net over the river Eider near Kiel, Germany. The river crosses a highway that lies 2.8 km away from the capture site. Therefore, it is likely that all of the study individuals had experienced traffic noise in the wild before the experiments. The temporary captivity of five Daubenton's bats was licensed by the State Agency for Agriculture, Environment and Rural Areas (LLUR; licence no. 314/5327.74.1.6). The bats were housed, and experiments were conducted at the Max Planck Institute for Ornithology in Seewiesen, Germany (licence no. 515/5327.74.1.6 by Landratsamt Starnberg). Outside the foraging experiments, the bats were held in a mesh tent Tatonka Double Mosquito Dome (length \times width \times height: 2 \times 1.2 \times 1.2 m), in which they were able to fly freely. The tent was placed in a room with regulated temperature (23 °C) and air humidity (70%), with a light regime of 8-h darkness and 16-h light. The bats received their food (mealworms, larvae of beetle *Tenebrio molitor*) during the foraging experiments. On very rare occasions, when a bat had not caught enough, it was fed additional mealworms after the experiment. The diet was supplemented with vitamins, minerals and other essential nutrients. The bats were held in captivity for over 6 months before the start of this experiment, and they adapted well to the captive environment. They also participated in other experiments, in which they caught mealworms from the water surface (Zsebök *et al.*, 2013). The bat keeping facility was located away from the roads, and care was taken that bats did not experience any continuous loud noise in captivity. After the study, bats were released back to the wild at the place of capture.

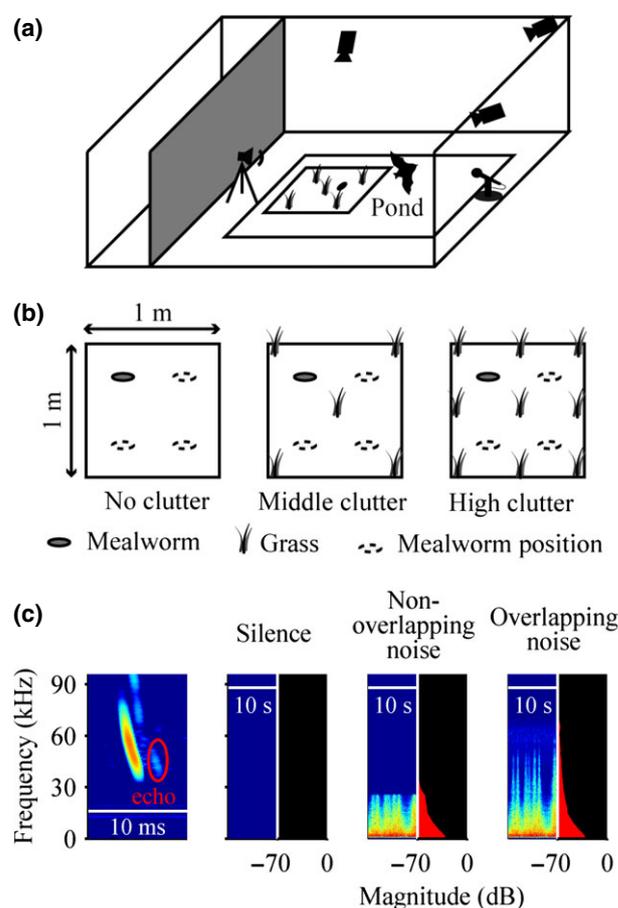


Fig. 2 Experimental setup and playback sounds. (a) Schematic of the flight room (not to scale). Depicted are three cameras for monitoring bat behaviour, loudspeaker for playbacks, microphone and feeding patch in the pond. (b) Clutter levels and possible positions of prey on the feeding patch. (c) Spectrogram of a typical echolocation call of Daubenton's bat and its echo during prey search in the experimental room. Note that the echo is much weaker in amplitude and low-pass-filtered in comparison with the original call. Shown are spectrograms and spectra of traffic noise and silence sequences used for playback. There is no frequency overlap between echoes and nonoverlapping noise.

Experimental setup

We conducted the experiment in a large flight room during the dark phase of the photoperiodic cycle. Walls and ceiling were covered with sound-absorbing foam. We split the flight room into two compartments, one being considerably larger than the other, by hanging a black curtain from the ceiling (Fig. 2a). In the large compartment (length \times width \times height: 5.3 \times 4 \times 3 m), we constructed a quadrangular water pond (length \times width \times depth: 3.8 \times 2.5 \times 0.1 m), where Daubenton's bats could forage naturally by trawling prey from the water surface (Dietz *et al.*, 2009). In the small compartment, the experimenter was able to monitor bat behaviour and record data without disturbing the bats. On each trial, we

offered a mealworm on a 1 × 1 m feeding patch in the pond. We manipulated the level of clutter by adding different amounts of artificial vegetation to the feeding patch (Fig. 2b). We used plastic grass stalks of about 3 mm width in bundles of about 30 stalks each. The bundles were about 2 cm wide at the top and reached about 6 cm out of the water surface. Higher density of vegetation around the mealworm generated more clutter to make prey detection more difficult. In total, there were three clutter levels: no clutter, middle clutter and high clutter. They differed in the number of grass bundles that covered the feeding patch as depicted in Fig. 2b. The mealworm was pinned on a thin metal wire at one of the four possible locations.

Sound recordings were played back to the foraging bat with a loudspeaker (Ultrasonic Dynamic Speaker ScanSpeak, Avisoft, Germany), which was mounted on a tripod placed next to the black curtain for the first 10 days of data collection (Fig. 2a). During the remaining 5 days of data collection, the speaker stood on the opposite side of the feeding patch, next to a microphone used for recording of echolocation calls. In both situations, the loudspeaker was at a height of 0.7 m and at a distance of 1.7 m from the centre of the feeding patch. The location of the speaker was changed to rule out the possibility that foraging performance would decrease due to specific location of the noise source. Echolocation calls were recorded with a custom-built microphone (condenser microphone with a flat response of ± 3 dB between 30 and 120 kHz connected to an A/D converter PCTape, sampling rate 384 kHz, 16-bit depth; Department of Animal Physiology, University of Tübingen, Germany) and stored in a laptop. The foraging behaviour of bats was filmed under infrared (IR) illumination (custom made LED-strobes, 875 nm wavelength, flashing at 50 Hz) with three IR-sensitive cameras (WAT-902H2 Ultimate, Watec, Japan) and DigiProtect computer interface and software (ABUS Security, USBBOX).

Before collecting data, each bat was released in the flight room for about 45 min per day and 6 days per week until it spontaneously learned to catch mealworms from any of the four possible positions at any of the three clutter levels, without acoustic playback. The bats needed less than a week to learn to forage without clutter. We then progressively added artificial vegetation to the patch until bats were able to successfully catch mealworms in all situations. This took about 4 weeks. One of original five bats had to be excluded from the study, because it did not forage in clutter. After the learning phase ended, data collection started. On each experimental day, each bat had the possibility to forage in several blocks of nine one-minute trials. In addition to the three clutter levels, there were three noise treatments (see below). Each trial in a block had a unique combination of clutter and noise treatment of the nine possible pairs. In total, we collected data from three bats on 15 days and from bat CB on 12 days. During a trial, the sound recording was continuously played. The playback was triggered manually, when the bat started to search for a mealworm and therefore lowered its flight height below the height of the loudspeaker (i.e., 0.7 m). In the wild, these bats typically hunt within 0.3 m height above water surface (Kalko & Schnitzler, 1989). There was a delay between the time, when

the experimenter estimated the height of the bat as lower than 0.7 m, and the start of the playback. To account for this delay, we chose to trigger the playback already at 0.7 m instead of 0.3 m. The trial ended either when the bat caught the mealworm, or when the one-minute playback stopped. Between the trials, the experimenter pinned the next mealworm to one of four positions and changed the clutter level of the feeding patch. For each trial, position of the mealworm, clutter level and playback sound were chosen pseudorandomly. This was done as follows. We first randomly generated the order of the three clutter levels in a block. Then we randomly generated the order of the three noise treatments within each of the three clutter levels. The position of the mealworm was randomly selected with the constraint that mealworms did not occur at the same position in two consecutive trials. We stopped the experimental session after the bat had not searched for food for about 15 min (after approximately 20 trials). Overall, each bat participated in 283, 169, 259 or 254 trials, respectively. For numbers of trials per treatment see Fig. 3.

Playback sounds

We used three types of playback sounds, which we refer to as silence, nonoverlapping noise and overlapping noise (Fig. 2c). We assembled them in Adobe Audition 3.0, at a sampling rate of 192 kHz and 16-bit depth. All playback sounds were high-pass-filtered at 1 kHz (digital fast Fourier transform (FFT) filter, 2048 points, Blackman window) to remove low-frequency components probably inaudible to the bats and to avoid damaging the loudspeaker (Siemers & Schaub, 2011).

We assembled playback noise from highway traffic recordings made at 15 m from the Autobahn A8, Stuttgart-Munich, Germany (for details see Schaub *et al.*, 2008). First, we created five overlapping noise sequences by splicing 500 ms long cuts of amplitude peaks that represent the sounds of 43 passing cars and trucks from the original traffic noise recordings. Then, five nonoverlapping noise sequences were created by low-pass-filtering the overlapping noise sequences at 25 kHz (digital FFT filter, 2048 points, Blackman window). The nonoverlapping noise did not spectrally overlap with Daubenton's bats' echolocation calls, whose minimum frequency lies above 28 kHz (Jones & Rayner, 1988). The silence sequence was generated by setting all the samples to zero.

Both types of traffic noise were played back at an amplitude around 76 dB SPL with the instant amplitude ranging 68–84 dB SPL. These sound pressure levels were measured with a SPL meter (Votcraft, SL-400) placed at the centre of the feeding patch at the same height as the loudspeaker to which it was directed. Our SPL meter could only measure sounds of frequencies within 0.25–8 kHz, which is narrower than the full frequency range of the traffic noise (Fig. 2c). However, because traffic noise contains most of its sound energy at lower frequencies, the difference in SPL between the original file and its components <8 kHz was minute. We estimated this measurement error to be 0.15 dB, using a digital low-pass filter (order six Butterworth) with the cut-off frequency at 8 kHz to simulate the frequency sensitivity of the SPL meter. This

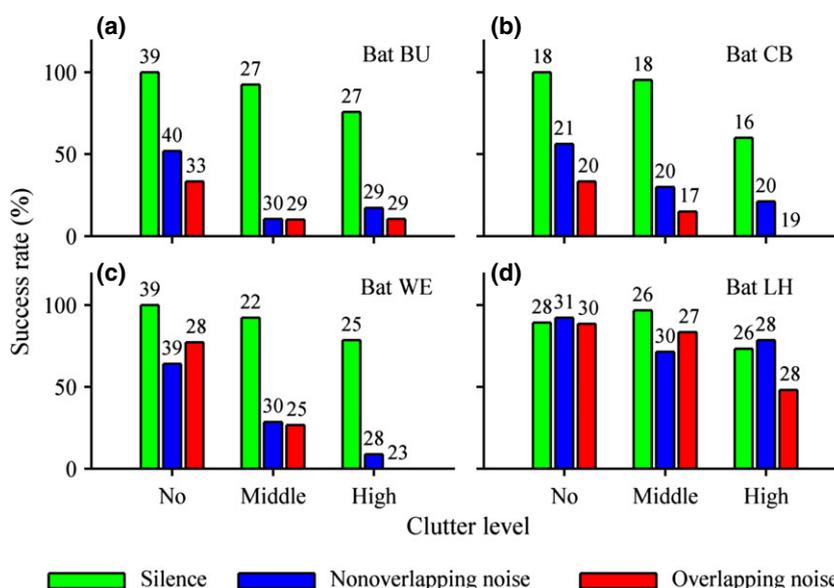


Fig. 3 Overall success rates of individual bats in different noise and clutter treatments. Above each bar is the number of trials from which the success rate was calculated.

assured that the SPL meter underestimated the SPL of the overlapping noise by a negligible amount.

Data analysis

To quantify foraging performance, we measured behavioural parameters that we define as follows. We counted a trial as *successful*, if the bat captured or attacked the mealworm within the one-minute period. The *success rate* was the number of successful trials divided by the number of trials of a bat within the same treatment. The *number of the search flights* was the number of the flight passes in a trial. A flight pass was tallied whenever the bat flew by the feeding patch at the flight height lower than 0.7 m (Video S1, S2). The *number of search flights required for success* equals the *number of search flights* in a *successful* trial. In other words, the *number of search flights required for success* was counted exclusively for trials, in which the bat caught or attacked the food.

Daubenton's bats adjust their echolocation calls to the amount of clutter (Kalko & Schnitzler, 1989), which correlates with the difficulty of prey detection (Siemers & Schnitzler, 2004). Therefore, we measured characteristics of echolocation calls to examine whether clutter had any effect on echolocation performance (see Supporting Information for details).

Statistical analysis

We quantified bats' foraging performance with three dependent variables (i.e. *success rate*, *number of search flights* and *number of search flights required for success*). We modelled these as functions of three explanatory variables: *playback type*, *clutter level* and *individual identity* (if data from all bats were included), using generalized linear models (GLMs) run in SPSS 21.0 (IBM Corp., New York, NY, USA). The *success rate* was

modelled as a binomially distributed number of successful trials within the total trial number using the logit link function. We used Poisson distribution and log link function for *number of search flights* and *number of search flights required for success*. The model fits were examined by subsequent analyses of residuals. These analyses confirmed that residuals were independently and identically distributed. The statistical inferences in all GLMs were based on the log-likelihood ratio test statistic ($-2\ln\Lambda$) used to compare models with and without the tested factor. We examined the effect of *playback type* on *success rate*, on *number of search flights* (as a measure of search effort) and on *number of search flights required for success* (as a measure of difficulty of foraging task) to search for diagnostic characteristics of acoustic masking, avoidance response and reduced attention. In case that acoustic masking or reduced attention decreases foraging success, we expect not only a higher mean number of search flights required for success, but also a higher variance. This is because noise is expected to have differently strong effects on the bats that approach the foraging patch from different directions. To test for both mean and variance effects, we compared the frequency distributions of the mean number of search flights required for success under different treatments using pairwise goodness-of-fit tests. We used a version of Kolmogorov–Smirnov test for this purpose (see Supporting Information for details). This test was also used to examine the effect of clutter level on both the mean number of search flights required for success and on its variation. If clutter increases the difficulty of the foraging task, both distribution parameters are expected to be higher in clutter treatments. The increase in variance is expected, because the negative effect of clutter varies with bat's direction of approach to the patch. All *P* values for pairwise comparisons reported in this study were adjusted with the sequential Dunn–Šidák correction (Sokal & Rohlf, 1994) and are denoted with P_{adj} .

Results

Traffic noise, both overlapping and nonoverlapping type, affected the foraging success of Daubenton's bats. Playback type had a significant effect on success rate (GLM, $-2\ln\Lambda = 289$, $df = 2$, $P < 0.00001$). Success rate was higher in silence than in both overlapping noise and nonoverlapping noise (Fig. 3; *post hoc* comparison of success rate between overlapping noise and silence: mean difference \pm SE = $60 \pm 3.4\%$, $P_{\text{adj}} < 0.00001$; *post hoc* comparison between nonoverlapping noise and silence: mean difference \pm SE = $50 \pm 3.6\%$, $P_{\text{adj}} < 0.00001$). The bats had only slightly lower success rate in the overlapping noise condition than in the nonoverlapping noise condition (mean difference \pm SE = $11 \pm 4.5\%$, $P_{\text{adj}} = 0.019$). The decrease in success rate in noise was not present in all individuals (Fig. 3). Three bats had lower success rate in the noise than in the silence treatments (Fig. 3a,b,c; GLMs, effect of playback type, $-2\ln\Lambda$: 148, 73 and 108, $df = 2$, all $P < 0.00001$). In contrast, success rate of the fourth bat was not affected by noise (Fig. 3d; GLM, effect of play-

back type, $-2\ln\Lambda = 5.09$, $df = 2$, $P = 0.078$). Besides the adverse effect of the nonoverlapping noise, acoustic masking hypothesis was also unsupported by the result that noise did not affect search effort required to capture a prey (next paragraph).

The number of search flights required for success did not differ among silence, nonoverlapping and overlapping noise treatments in any individual (Fig. 4a, GLMs, effect of playback type, $-2\ln\Lambda$: 0.78, 3.07, 1.59, 2.68; $df = 2$, $P = 0.68, 0.22, 0.45, 0.26$). This shows that noise did not noticeably reduce the attention available to foraging bats. In addition, we compared the empirical distributions of the number of search flights required for success with Kolmogorov–Smirnov tests. The results show that in treatments that differed only in playback type and not in clutter level (Supporting Information; green cells in Tables S1, S2), the success probability increased at the same rate with the number of search flights. In other words, noise did not influence the distribution of search effort required for success, which contradicts both reduced attention and acoustic masking hypotheses.

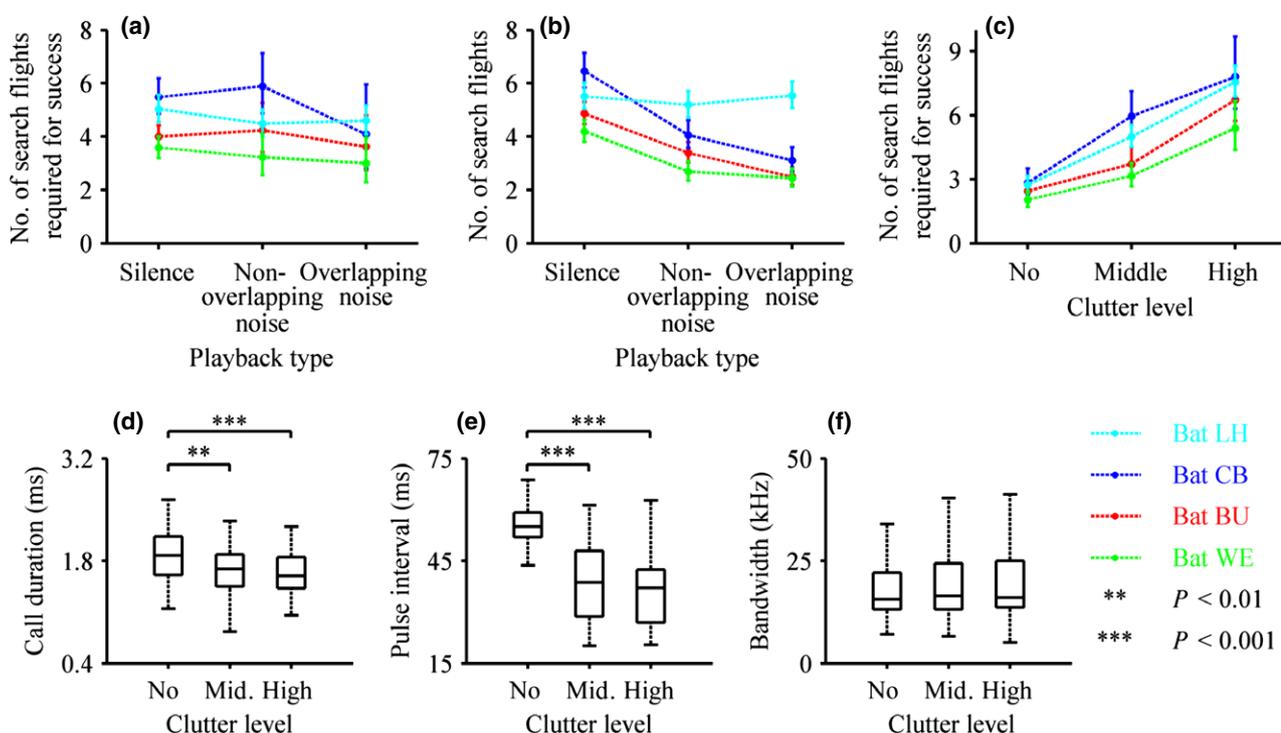


Fig. 4 Effects of traffic noise and vegetation clutter on the search effort and echolocation behaviour of Daubenton's bat. (a–c) Data are presented as marginal means and the 95% confidence intervals. These values were computed within the generalized linear model, while statistically controlling the effects of other factors, that is controlling the effect of clutter level (a,b), and the effect of noise treatment (c). Comparison of corresponding values individual by individual in panels (a) and (b) provides a hint towards understanding the success rate data in Fig. 3. Specifically, if the number of search flights in a treatment (a) is lower than number of search flights required for success (a), the success rate is low. Panels (d–f) show quartiles of echolocation call parameters; data sets pooled from all bats. The lines and stars denote statistically significant differences.

With their echolocation behaviour, bats showed that they indeed perceived denser artificial vegetation as increased clutter. Specifically, in treatments with more vegetation, they produced calls with shorter duration (Fig. 4d, LM, $F_{179,2} = 9.42$, $P = 0.00013$) and shorter inter-pulse interval (Fig. 4e, LM, $F_{179,2} = 40.14$, $P < 0.00001$). Other call parameters did not differ significantly. The search effort data show that the difficulty of the foraging task increased with clutter. The number of search flights required for success increased from no clutter, via middle clutter to high clutter treatments (Fig. 4c, GLM, effect of clutter level, $-2\ln\Lambda = 367$, $df = 2$, $P < 0.00001$). We also found differences in empirical distributions of search effort required for success among treatments that differed in clutter level and not playback type. Under higher clutter levels, bats often exhibited significantly lower rate of growth in the foraging success with increasing number of search flights (Supporting Information; light blue cells in Tables S1 and S2, Fig. S1). The results of the number of search flights required for success confirm that our clutter manipulation was an appropriate way to manipulate the task difficulty as required for testing the reduced attention hypothesis.

On average, bats reduced the foraging activity in the noise treatments. We found that both nonoverlapping noise and overlapping noise reduced the number of search flights (GLM, effect of playback type, $-2\ln\Lambda = 141$, $df = 2$, $P < 0.00001$). Specifically, comparing with the silence treatment, bats made on average 1.3 and 1.7 flights less in nonoverlapping and overlapping noise treatments, respectively (both $P_{\text{adj}} < 0.00001$). The number of search flights in the overlapping noise treatment was significantly lower than in the nonoverlapping noise treatment (mean difference \pm SE = 0.39 ± 0.15 , $P_{\text{adj}} = 0.008$). Three bats had significantly lower number of search flights in the noise treatments than in the silence treatments (Fig. 4b, GLMs, effect of playback type, $-2\ln\Lambda$: 83, 80, 53; $df = 2$, all $P < 0.00001$). Reduced foraging success during noise playback in these three individuals was related to the decreased prey search activity due to noise avoidance. They often abandoned the foraging patch immediately after the noise playback started (Video S2). By contrast, noise did not influence the number of search flights of the fourth individual (Fig. 4b, cyan line; GLM, $-2\ln\Lambda = 1.23$, $df = 2$, $P = 0.54$), which was the same bat that did not experience reduced foraging success (Fig. 3d). The reduction in foraging success due to observed decrease in foraging activity and patch abandonment in those three bats supports the noise avoidance hypothesis.

Discussion

Several studies have pointed out the problem that the different mechanisms by which noise disturbs animals can operate simultaneously and can therefore not be distinguished from each other without ambiguity (Purser & Radford, 2011; Siemers & Schaub, 2011; Francis *et al.*, 2012; Francis & Barber, 2013; Simpson *et al.*, 2015). Here, we developed a diagnostic framework with predictions that discriminate each mechanism from the others. We then implemented it with Daubenton's bats. We found that traffic noise, on average, deteriorated the foraging performance of bats, even without the frequency overlap with prey echoes. However, individual bats differed in their sensitivity to noise, and one individual did not experience any observable disturbance. Due to small sample size, we cannot reach any conclusion concerning how sensitivity to noise may vary in wild populations of echolocating bats. Furthermore, we found that noise did not affect search effort required for prey capture. We conclude that noise avoidance was the mechanism that decreased the foraging efficiency. By this mechanism, noise can adversely affect even those species that do not rely on sounds to find prey. Hence, conservation policies may seriously underestimate the number of species affected and the effect size, by not considering the mechanisms of disturbance. Our framework performed well as a diagnostic tool. With it, we showed that avoidance response was the mechanism of disturbance, whereas we found no support for the remaining mechanisms or joint effects of several mechanisms. The framework can easily be adapted to diagnose the mechanisms and estimate effects of acoustic disturbance in other species.

No effect of acoustic masking observed

The following results show that acoustic masking was not the mechanism of noise disturbance in the foraging Daubenton's bats. First, three bats had a substantially lower foraging success in both overlapping noise and nonoverlapping noise than in silence. The adverse effects of nonoverlapping noise cannot be caused by acoustic masking. The foraging success of the remaining bat was not affected by noise. Such a differential response would have hardly occurred, if a physiological process like acoustic masking had been behind the reduced foraging performance. Namely, sensory physiology of prey detection is not expected to differ among individuals of the same species. Second, neither overlapping noise nor nonoverlapping noise increased search effort required for a successful prey capture.

How does the lack of support for acoustic masking hypothesis by anthropogenic noise apply to wild popu-

lations of bats? Acoustic masking is a hearing physiology phenomenon. It is unlikely to find significant differences in hearing physiology among the bat species that find prey using echolocation system with calls of similar frequency range to those of Daubenton's bats. Hence, despite the low number of individuals on which our results are based, we suggest that a majority of these species will likely not suffer from acoustic masking of their prey echoes by anthropogenic noise. This contradicts the explanation that lower foraging activities of trawling bats close to turbulent water are due to the masking of prey echoes (Mackey & Barclay, 1989). Because water gurgling has a similar spectro-temporal composition to anthropogenic noise (Feng *et al.*, 2006), it is unlikely that it masks the echoes. Recently, ultrasonic deterrents have been developed that playback broadband noise to prevent bats from colliding with wind turbines. The design of these deterrents has usually been guided by the assumption that noise disturbs bats by masking their echolocation calls and echoes (Arnett *et al.*, 2013). However, our study indicates that other mechanisms likely play a more important role in noise disturbance of bats. Moreover, at least some bat species are capable of detecting echoes as low as 35 dB below the white noise level (Griffin & Grinnell, 1958). Considering this and evidence from the present study, we caution that more studies with different species should be conducted to improve our understanding of how anthropogenic or ambient noise mechanistically affect orientation and foraging in bats. Only with such understanding will we be able to efficiently approach the problem of deterring bats from wind power plants and other sources of noise near to protected bat populations. There are two groups of bats, however, that can potentially be sensitive to noise disturbance by acoustic masking. One consists of the species that find food using prey-generated sounds (Siemers & Schaub, 2011) and the other group are the species that use lower frequency echolocation to detect prey (Rydell & Arlettaz, 1994). These groups are interesting candidates for the application of our diagnostic framework in future studies.

No evidence for reduced attention

We did not find any indication that noise reduced attention available to foraging. First, the number of search flights required for success did not increase with the addition of noise, even when the prey capture task was challenging. Second, the probability of prey capture increased at the same rate with the number of search flights in the presence and absence of noise.

To test for the effect of reduced attention, it is necessary that animals are engaged in a challenging task

(Dukas & Kamil, 2001; Dukas, 2004). Is it possible that even prey capture in the high clutter treatment was not difficult enough for the noise to overburden the attention? The following evidence clearly disagrees with this possibility. First, prey detection in Daubenton's bats is more sensitive to clutter interference than that of its congeners (Siemers & Schnitzler, 2004). Second, the Daubenton's bats showed with their echolocation behaviour that they perceived the feeding patch as more cluttered in treatments with denser vegetation. Third and most important, prey capture demanded more effort in the presence of clutter. Specifically, the bats needed on average three times more search flights for a successful prey capture in the high clutter treatment than in the no clutter treatment. We also found that distributions of the number of search flights required for success often differed between treatments that differed only in clutter level (Supporting Information; light blue cells of Tables S1 and S2).

Noise avoidance reduced foraging success

Three of the four bats reduced their foraging effort in both traffic noise and low-pass-filtered traffic noise that did not overlap prey echoes. They often abandoned the feeding patch immediately after the start of the noise playback (Video S2). Consequently, these individuals suffered a reduced foraging success and consumed less food in noise than in silence. By contrast, the fourth bat that did not show avoidance response enjoyed the same success rate in noise and in silence.

The avoidance response in Daubenton's bats could have been caused by noise itself acting as an aversive stimulus. Alternatively, bats could have avoided noise, because it made foraging unprofitable by either masking the prey echoes or reducing the available attention. However, if any of the latter two possibilities would be true, then we would expect a higher search effort required for prey capture in the presence of noise. This was clearly not the case. We showed that noise presence had no effect on the search effort required for successful capture event. Furthermore, the probability of successful capture increased with the number of search flights at equal rates in treatments with or without noise. We can conclude that bats avoided the traffic noise itself, because they were averse to it, which reduced their foraging performance.

The aversive response can have different levels. Stronger aversion can turn into a stress response, which is characterized by both behavioural and physiological changes (e.g. increased heart rate and concentration of steroid hormones; McEwen & Wingfield, 2003; Romero, 2004). We did not measure physiological variables and therefore cannot conclude that noise acted as a stressor.

However, this is a likely possibility. Behaviourally, the stress response to noise has qualitatively the same characteristics as the simple avoidance response and ultimately they have the same consequences for the bats: reduced foraging success and hence reduced fitness (Lemon, 1991). The only difference can be in the magnitude of responses; however, this will matter only in cases where the responses are gradual instead of binary (leave or stay).

Notably, not all Daubenton's bats exhibited avoidance response. One bat did not reduce its search effort and continued foraging in the presence of noise. This result exemplifies individual variation in sensitivity to aversive stimuli. Recent growth in the study of individual variation has shown that many species exhibit strong and consistent inter-individual differences in boldness (Sloan Wilson *et al.*, 1994; Ward *et al.*, 2004). It has also been shown that physiological differences underlying behavioural stress responses are relatively stable (Cohen & Hamrick, 2003; Wright *et al.*, 2007). Because individual variation in response to human disturbance is such a common phenomenon, potentially of high importance to conservation, it calls for further investigation. Another important question to address in the future is to determine the proportion of bats within a population that show noise avoidance behaviour, which cannot be answered by the present experiment due to low number of tested individuals.

To estimate the variation in avoidance response of the wild population of Daubenton's bats, a much larger number of individuals should be tested. Nevertheless, our data show that this variation exists. It would be interesting to compare how populations differ in the proportion of individuals sensitive to anthropogenic noise and how this proportion depends on the traffic concentration in the vicinity of their habitat. Our bats originated from an area with a high road density and have probably all experienced traffic noise in the wild. This suggests that even extensive experience with anthropogenic noise may not necessarily lead to habituation. We cannot judge however, whether the lack of the response to noise treatment in one individual resulted from habituation to traffic noise that took place in the wild, or the individual has ignored the presence of the noise during its entire life. After the bats were released back to the wild, they were radiotracked for a few days. They stayed in the vicinity of the capture site and used different roosts (Frauke Krüger, personal communication). None of them roosted next to the highway. We have no information on relatedness or colony membership of our bats. Due to vicinity of the roosting trees, it is possible that the bats originate from the same colony. It is likely that differences in the

avoidance of anthropogenic noise exist among colony members.

Daubenton's bats had slightly lower success rates in the overlapping than in the nonoverlapping noise treatments. This might be considered an indication of acoustic masking that would take place in addition to the aversive effect in the overlapping noise treatments. However, in that case, we would expect the search effort required for a successful prey capture to be higher in the overlapping noise. This was clearly not the case. A more likely explanation is that overlapping noise was perceived as louder and thus caused a stronger avoidance response than the nonoverlapping noise, despite similar playback amplitudes. The hearing of Daubenton's bats is likely more sensitive to higher frequency components of the noise, because this is the frequency range of their echolocation. Thus, the overlapping noise that contained higher frequency components was probably perceptually louder to the bats and may have caused the stronger avoidance response. This is evidenced by the result that bats invested less effort in foraging during the playback of overlapping noise than nonoverlapping noise.

The sensitivity of bats to anthropogenic noise seems to depend on the behavioural context. Although traffic noise decreases the foraging efficiency of greater mouse-eared bats, the same species sometimes occupies roosts exposed to considerable anthropogenic noise (Schaub *et al.*, 2008). A likely explanation for the tolerance of bats to anthropogenic noise during roosting is the greater sensitivity to other noise stimuli. Roosting bats are often torpid, and it has been shown in the greater mouse-eared bat that colony noise disturbed torpid bats more strongly than traffic noise (Luo *et al.*, 2014b). In our experiments, the noise appeared rather abruptly, because the playback was triggered when a bat started foraging. Noise exposure ended after one minute. Could wild bat populations experience a more continuous noise pollution and therefore respond differently? This seems unlikely, and we argue that exposure to traffic noise by foraging bats is not continuous, but rather acute. First, the amplitude of the traffic noise varies strongly even at a busy highway (Schaub *et al.*, 2008). Second, during the time when bats are foraging, car density becomes lower and thus time intervals between the passing cars are longer. Third, foraging bats, including Daubenton's bat, travel long distances (Parsons & Jones, 2003), which introduces additional variation to noise exposure. However, because of short duration of our study, we cannot judge the consequences of regular noise exposure over years.

Anthropogenic noise can adversely affect more species than expected

So far, studies on effects of anthropogenic noise on animals have often concentrated on species in which noise has an obvious potential to mask information of biological importance (Slabbekoorn & Peet, 2003; Brumm, 2013; Proppe *et al.*, 2013). In bats, research efforts thus focused on species that find prey using prey-generated sounds (Schaub *et al.*, 2008; Siemers & Schaub, 2011; Luo *et al.*, 2014b) that strongly overlap with anthropogenic noise in frequency (Schaub *et al.*, 2008). Here, we show that traffic noise disturbed Daubenton's bats by reducing their foraging activity, despite having no effect on their acoustic prey detection ability. Particularly, even the noise that did not spectrally overlap with the echolocation calls, and thus did not mask their prey echoes, disturbed the bats. This demonstrates that anthropogenic noise can adversely influence a substantially larger number of species than expected judging from spectral composition of noise (see also Hage *et al.*, 2013). These include species that do not rely on sounds for foraging and other behaviours with direct fitness effects. Noise impairment of animal survival and reproduction likely operates through multiple behavioural and ecological channels, making its evaluation a challenging task. We strongly recommend taking this into account and using the precautionary principle, when trying to estimate the effects of noise pollution on wildlife. Environmental impact assessments should also investigate species that may not appear to be affected by anthropogenic noise, when judging from the current knowledge of their sensory ecology.

Acknowledgements

We are grateful to Daniela Schmieder, Erich Koch, Frauke Krüger and Leonie Baier for their help with preparation of the experiment. Frauke Krüger also kindly provided information on the origin of bats and on their habitats. We thank Renate Heckel-Merz for bat husbandry, as well as other colleagues in the Sensory Ecology Group for helpful discussions. Holger Goerlitz, Henrik Brumm and Robert de Bruijn commented on an earlier version of the manuscript. Sue Anne Zollinger improved the language. We acknowledge the anonymous reviewers for their helpful suggestions. The study was supported by the Max Planck Society, the China Scholarship Council and the International Max Planck Research School for Organismal Biology. This paper is dedicated to the memory of Björn, our co-author, mentor and friend, who unexpectedly passed away during its preparation.

References

Anderson JR (2009) *Cognitive Psychology and its Implications*. Worth Publisher, New York.
Arlettaz R, Jones G, Racey PA (2001) Effect of acoustic clutter on prey detection by bats. *Nature*, **414**, 742–745.

Arnett EB, Hein CD, Schirmacher MR, Huso MMP, Szewczak JM (2013) Evaluating the effectiveness of an ultrasonic acoustic deterrent for reducing bat fatalities at wind turbines. *PLoS One*, **8**, e65794.
Barber JR, Razak KA, Fuzessery ZM (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**, 843–855.
Barber JR, Crooks KR, Fristrup KM (2010) The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution*, **25**, 180–189.
Boonman AM, Boonman M, Bretschneider F, Van De Grind WA (1998) Prey detection in trawling insectivorous bats: duckweed affects hunting behaviour in Daubenton's bat, *Myotis daubentonii*. *Behavioral Ecology and Sociobiology*, **44**, 99–107.
Brumm H (2010) Anthropogenic noise: implications for conservation. In: *Encyclopedia of Animal Behavior* (eds Breed MD, Moore J), pp. 89–93. Academic Press, Oxford.
Brumm H (ed.) (2013) *Animal Communication and Noise*. Springer, Berlin, Heidelberg.
Bunkley JP, McClure CJW, Kleist NJ, Francis CD, Barber JR (2015) Anthropogenic noise alters bat activity levels and echolocation calls. *Global Ecology and Conservation*, **3**, 62–71.
Chan AaY-H, Blumstein DT (2011) Attention, noise, and implications for wildlife conservation and management. *Applied Animal Behaviour Science*, **131**, 1–7.
Cohen S, Hamrick N (2003) Stable individual differences in physiological response to stressors: implications for stress-elicited changes in immune related health. *Brain, Behavior, and Immunity*, **17**, 407–414.
Delaney DK, Grubb TG, Beier P, Pater LL, Reiser MH (1999) Effects of helicopter noise on Mexican spotted owls. *Journal of Wildlife Management*, **63**, 60–76.
Dietz C, Helversen OV, Nill D (2009) *Bats of Britain, Europe & Northwest Africa*. A & C Black Publisher, London.
Dukas R (2004) Causes and consequences of limited attention. *Brain, Behavior and Evolution*, **63**, 197–210.
Dukas R, Kamil AC (2001) Limited attention: the constraint underlying search image. *Behavioral Ecology*, **12**, 192–199.
Feng AS, Narins PM, Xu CH *et al.* (2006) Ultrasonic communication in frogs. *Nature*, **440**, 333–336.
Francis CD, Barber JR (2013) A framework for understanding noise impacts on wildlife: an urgent conservation priority. *Frontiers in Ecology and the Environment*, **11**, 305–313.
Francis CD, Kleist NJ, Ortega CP, Cruz A (2012) Noise pollution alters ecological services: enhanced pollination and disrupted seed dispersal. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 2727–2735.
Frid A, Dill L (2002) Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, **6**, 11.
Fristrup KW (2015) Predicting sound and light levels at large spatial scales. In: *Annual Meeting of the American Association for the Advancement of Science*. San Diego. Available at: <https://www.sciencenews.org/article/coast-coast-picture-americas-cacophony-sounds>.
Griffin DR, Grinnell AD (1958) Ability of bats to discriminate echoes from louder noise. *Science*, **128**, 145–147.
Hage SR, Jiang T, Berquist SW, Feng J, Metzner W (2013) Ambient noise induces independent shifts in call frequency and amplitude within the Lombard effect in echolocating bats. *Proceedings of the National Academy of Sciences*, **110**, 4063–4068.
Jones G, Rayner JMV (1988) Flight performance foraging tactics and echolocation in free-living Daubenton's bats *Myotis daubentonii* (Chiroptera: Vespertilionidae). *Journal of Zoology*, **215**, 113–132.
Jones P, Page R, Hartbauer M, Siemers B (2011) Behavioral evidence for eavesdropping on prey song in two Palearctic sibling bat species. *Behavioral Ecology and Sociobiology*, **65**, 333–340.
Kalko EKV, Schnitzler HU (1989) The echolocation and hunting behavior of Daubenton's bat, *Myotis daubentoni*. *Behavioral Ecology and Sociobiology*, **24**, 225–238.
Kight CR, Swaddle JP (2011) How and why environmental noise impacts animals: an integrative, mechanistic review. *Ecology Letters*, **14**, 1052–1061.
Lamble D, Kauranen T, Laakso M, Summala H (1999) Cognitive load and detection thresholds in car following situations: safety implications for using mobile (cellular) telephones while driving. *Accident Analysis & Prevention*, **31**, 617–623.
Lemon WC (1991) Fitness consequences of foraging behaviour in the zebra finch. *Nature*, **352**, 153–155.
Luo J, Koselj K, Zsebik S, Siemers BM, Goerlitz HR (2014a) Global warming alters sound transmission: differential impacts on the prey detection ability of echolocating bats. *Journal of the Royal Society Interface*, **11**, 20130961.
Luo J, Clarin B-M, Borissov IM, Siemers BM (2014b) Are torpid bats immune to anthropogenic noise? *Journal of Experimental Biology*, **217**, 1072–1078.

- Mackey RL, Barclay RMR (1989) The influence of physical clutter and noise on the activity of bats over water. *Canadian Journal of Zoology*, **67**, 1167–1170.
- McEwen BS, Wingfield JC (2003) The concept of allostasis in biology and biomedicine. *Hormones and Behavior*, **43**, 2–15.
- Moore BC (2012) *An Introduction to the Psychology of Hearing*. Emerald Group Publishing Limited, Bingley, UK.
- Parsons KN, Jones G (2003) Dispersion and habitat use by *Myotis daubentonii* and *Myotis nattereri* during the swarming season: implications for conservation. *Animal Conservation*, **6**, 283–290.
- Proppe DS, Sturdy CB, St. Clair CC (2013) Anthropogenic noise decreases urban songbird diversity and may contribute to homogenization. *Global Change Biology*, **19**, 1075–1084.
- Purser J, Radford AN (2011) Acoustic noise induces attention shifts and reduces foraging performance in Three-spined sticklebacks (*Gasterosteus aculeatus*). *PLoS One*, **6**, e17478.
- Quinn JL, Whittingham MJ, Butler SJ, Cresswell W (2006) Noise, predation risk compensation and vigilance in the chaffinch *Fringilla coelebs*. *Journal of Avian Biology*, **37**, 601–608.
- Romero LM (2004) Physiological stress in ecology: lessons from biomedical research. *Trends in Ecology & Evolution*, **19**, 249–255.
- Rydell J, Arlettaz R (1994) Low-frequency echolocation enables the bat *Tadarida teniotis* to feed on tympanate insects. *Proceedings of the Royal Society B: Biological Sciences*, **257**, 175–178.
- Schaub A, Ostwald J, Siemers BM (2008) Foraging bats avoid noise. *Journal of Experimental Biology*, **211**, 3174–3180.
- Siemers BM, Schaub A (2011) Hunting at the highway: traffic noise reduces foraging efficiency in acoustic predators. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 1646–1652.
- Siemers BM, Schnitzler HU (2004) Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. *Nature*, **429**, 657–661.
- Simpson SD, Purser J, Radford AN (2015) Anthropogenic noise compromises antipredator behaviour in European eels. *Global Change Biology*, **21**, 586–593.
- Slabbekoorn H, Peet M (2003) Birds sing at a higher pitch in urban noise. *Nature*, **424**, 267.
- Slabbekoorn H, Bouton N, Van Opzeeland I, Coers A, Ten Cate C, Popper AN (2010) A noisy spring: the impact of globally rising underwater sound levels on fish. *Trends in Ecology & Evolution*, **25**, 419–427.
- Sloan Wilson D, Clark AB, Coleman K, Dearstyne T (1994) Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, **9**, 442–446.
- Sokal R, Rohlf F (1994) *Biometry: the Principles and Practice of Statistics in Biological Research, 2nd edition*. W. H. Freeman, New York.
- Stilz WP, Schnitzler HU (2012) Estimation of the acoustic range of bat echolocation for extended targets. *Journal of the Acoustical Society of America*, **132**, 1765–1775.
- Wale MA, Simpson SD, Radford AN (2013) Noise negatively affects foraging and antipredator behaviour in shore crabs. *Animal Behaviour*, **86**, 111–118.
- Ward AW, Thomas P, Hart PB, Krause J (2004) Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, **55**, 561–568.
- Warren PS, Katti M, Ermann M, Brazel A (2006) Urban bioacoustics: it's not just noise. *Animal Behaviour*, **71**, 491–502.
- WHO (2011) *Burden of Disease from Environmental Noise: Quantification of Healthy Life Years Lost in Europe*. World Health Organization, Geneva.
- Wright AJ, Soto NA, Baldwin AL *et al.* (2007) Anthropogenic noise as a stressor in animals: a multidisciplinary perspective. *International Journal of Comparative Psychology*, **20**, 250–273.
- Zsebök S, Kroll F, Heinrich M, Genzel D, Siemers BM, Wiegrebe L (2013) Trawling bats exploit an echo-acoustic ground effect. *Frontiers in Physiology*, **4**, 65.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Supporting Materials and methods.

Table S1. Noise does not change the search effort required for foraging in Daubenton's bats.

Table S2. Statistics for the tests presented in Table S1.

Fig. S1. Graphical illustration of the relationship between the frequency of successful captures and the number of search flights.

Video S1. An example of foraging behaviour of a bat (WE) in the middle clutter and silence experimental treatment.

Video S2. An example of foraging behaviour of a bat (WE) in the middle clutter and overlapping noise experimental treatment.