# Noise Reduces Foraging Efficiency in Pallid Bats (*Antrozous pallidus*)

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## Abstract

Anthropogenic noise is an emerging global pollutant. Road networks and energy extraction infrastructure are both spatially extensive and rapidly expanding sources of noise. We predict that predators reliant on acoustic cues for hunting are particularly sensitive to louder environments. Here we examined the foraging efficiency of pallid bats (*Antrozous pallidus*) when exposed to played-back traffic and gas compressor station noise in the laboratory. We show that both types of noise at each of five exposure levels (58–76 dBA, 10–640 m from source) and low-level amplifier noise (35 dBA) increase the time required for bats to locate prey-generated sounds by twofold to threefold. The mechanism underlying these findings is unclear and, given the potential landscape-level habitat degradation indicated by our data, we recommend continued research into the effects of noise exposure on acoustically specialized predators.

## Introduction

Anthropogenic noise is a global pollutant (Barber et al. 2010; Slabbekoorn et al. 2010). Noise from transportation networks and energy development is widespread and increasing (Barber et al. 2011; Northrup & Wittemyer 2013). For instance, 83% of land in the continental United States is within ~1 km of a road (Ritters & Wickham 2003) and loud natural gas extraction infrastructure is predicted to increase substantially in coming decades (Copeland et al. 2009). Recent evidence indicates that anthropogenic noise exposure negatively impacts animal communities and behaviors (for a review, see Francis & Barber 2013). However, the effects of noise on predator–prey interactions are less studied (Shannon et al. 2014). Laboratory investigations indicate that two bat species, *Myotis myotis* (Schaub et al. 2008) and *Myotis daubentonii* (Luo et al. 2015), avoid hunting in played-back traffic noise. *M. myotis* also exhibits reduced foraging efficiency in the laboratory when hunting in traffic noise (Siemers & Schaub 2011). One study indicates that the activity levels of bats that echolocate at low frequencies (<35 kHz) are reduced near noisy gas compressor stations (Bunkley et al. 2015).

Here we quantify the foraging efficiency of pallid bats (*Antrozous pallidus*), which glean arthropods using prey-generated sounds (3–20 kHz; Fuzessery et al. 1993), when exposed to played-back traffic and gas compressor station noise in a laboratory experiment. Both types of noise are common throughout this species' range. We predicted that under all traffic and gas compressor noise playbacks pallid bats would experience an increase in search time for prey and a decrease in successful captures. Additionally, we anticipated that broadband and temporally consistent compressor station noise would cause greater deficits than the temporally variable and lower bandwidth traffic stimuli. Finally, we predicted that stimuli replicating noise conditions nearer the source would elicit greater hunting deficits than those of conditions further away, as a result of both increased sound level and broader spectral bandwidth.

## Methods

### Animals and Experimental Design

We mist-netted 12 pallid bats in SE Idaho under Idaho Department of Fish and Game Permit #110615 and held them under Boise State University IACUC proto-

col 006-AC12-006. We followed the husbandry practices outlined by Lollar & Schmidt-French (2002) and kept bats under an inverted light regime (16 h D: 8 h L). We conducted 2 years (six bats each in the summers of 2012 and 2013) of experimental trials in a foam-lined flight room (6.8 × 5.6 × 3.9 m; Fig. 1) outfitted with six speakers (Fig. 1; four Swans (two on each of the long walls), RT2H_A, 1–70 kHz, ±3 dB and two Birds (one on each short wall), 70–25 kHz, ±3 dB) that produced an even sound field (±4 dBA) across an elevated (10 cm) plastic hunting arena (2.4 × 3.6 m). We illuminated the interaction space with LED infrared (IR) lighting (Wildlife Engineering and Raytec) and recorded foraging trials using digital, high-speed, IR cameras (Basler Scout scA640–120 gm, 100 frames/s) streaming to a computer via a National Instruments PCIe-8235 GigE Vision frame grabber and custom LabView software.

Bats were trained to locate insect movement sounds: 5 g of mealworms randomly placed in one of 30 recessed paper-lined bowls equally spaced within the hunting arena (Fig. 1; Audio S1). This stimulus closely resembles natural prey sounds (Goerlitz et al. 2008; Schaub et al. 2008). Mealworms lack ears

(Stehr 1987), and we observed no differences in beetle larvae movement behavior between control and playback conditions. Control bowls contained freeze-dried mealworms comparable to the amount in the bowl with live prey. We covered bowls with plastic screening to prevent access to the mealworms. A freeze-killed mealworm was placed on the screen of the bowl with live prey as a food reward, and mealworm replicas (treated with mealworm scent) were placed on the screens of control bowls, in an attempt to control for olfactory and echoic cues. It took 1–12 days for bats to learn to hunt in this paradigm (Bunkley & Barber 2014).

We remotely released bats into the room from a holding box (Fig. 1b; 30.5 cm square) placed behind a sound-dampening board (1 × 1.25 m, foam-lined) designed to limit sensory information prior to trials. We exposed each bat to a random order of all noise playbacks every day for 15 d. One to three representative tracks were randomly used for each playback (Kroodsma et al. 2001). Before initiating a trial, we played the treatment file for 1 minutes prior to opening the release box. Between trials, we returned bats to the release box for a two-minute washout period.
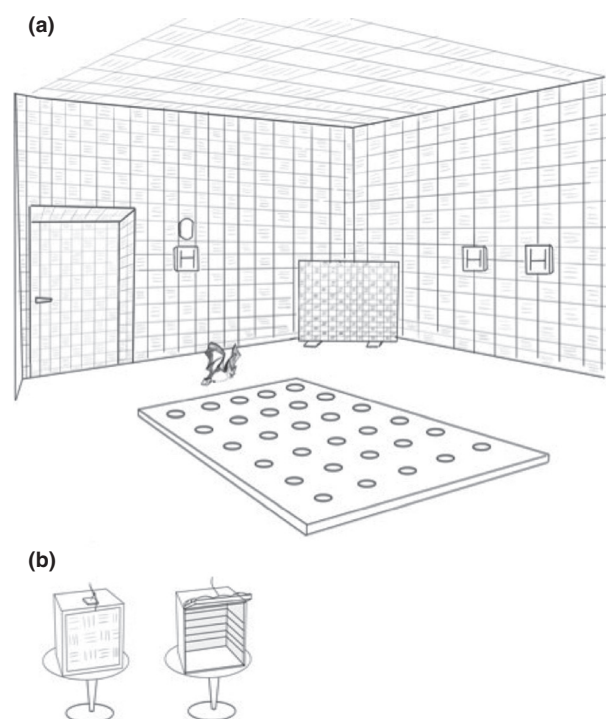


**Fig. 1:** (a) Schematic of the foam-lined flight room and (b) bat release box. A hunting arena was centered in the middle of the room, and an acoustic barrier was positioned in front of the release box – located in the opposite corner of the room as viewed from this perspective. Note the speakers on the room walls.

## Playback Files

We recorded traffic noise (3 minutes integrations) between 07:00 and 09:00 (17–23° C) from I84 near Boise, Idaho at 10, 20, 40, and 160 m from the shoulder (white line) using a Sennheiser ME66 microphone (40–20 000 Hz (±2.5 dB)) and a Roland R05 recorder (96 kHz sample rate) while simultaneously measuring sound level (Larson Davis 824 decibel meter, fast Leq) and vehicle type (video: Panasonic HM-TA20; avg. of 460 cars/trucks, four motorcycles, and nine larger vehicles, such as busses or semi trucks). Preliminary recordings with ultrasonic microphones indicated that our traffic site did not produce ultrasonic frequencies at these distances. Using the same equipment and protocol, we recorded gas compressor station noise at the Gobbler's Knob and Bridger compressor stations in Wyoming (10–12° C) at 40, 50, 60, 80, and 160 m from the edge of the stations. We used dB(A) instead of dB(Z), which would be more ideal for bat hearing ranges (Francis & Barber 2013), due to competing nearby noise sources that prevented the use of dB(Z).

We used 12 playback files (Fig. 2; Table S1) filtered at 1100 and 40 kHz (to remove internal electrical noise in the microphone/recorder and energy outside of pallid bat hearing range and to protect our equipment; Brown et al. 1978). Using a custom MatLab
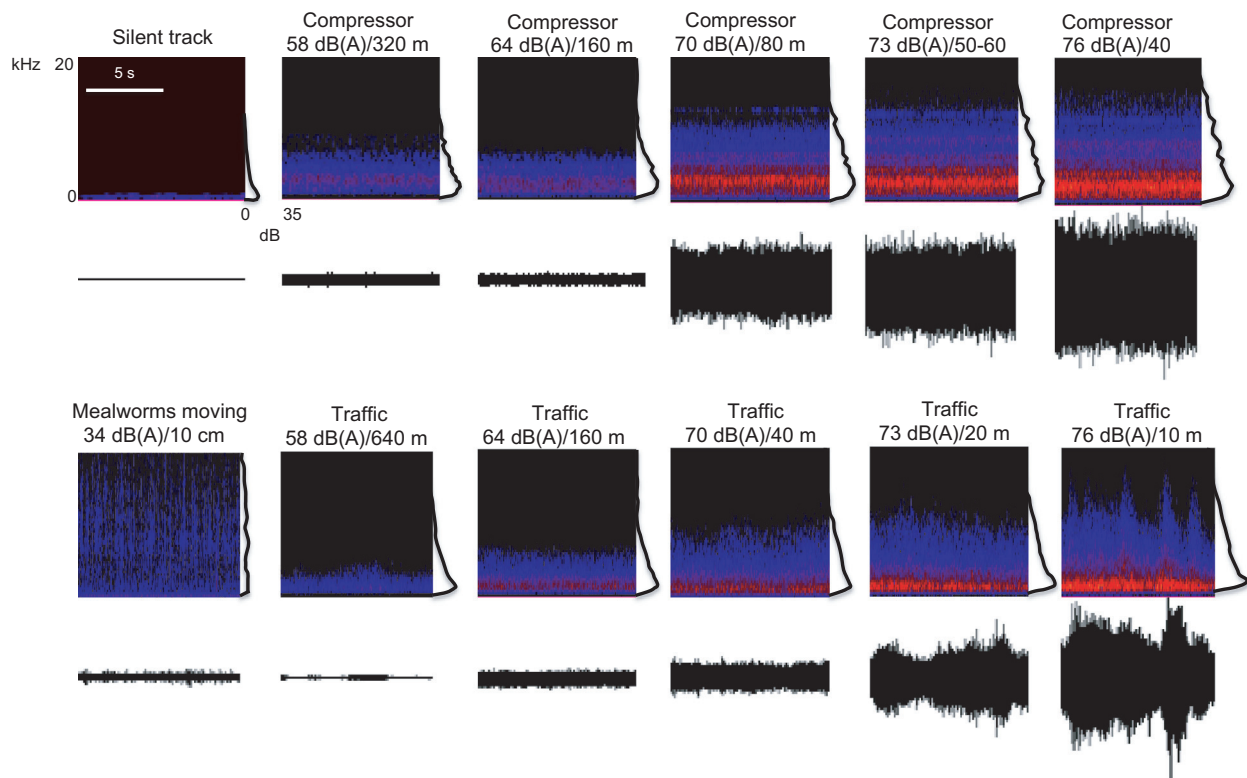
**Fig. 2:** Spectrograms, power spectra, and oscillograms of mealworm movement and playback files recorded in the laboratory. See online supplementary materials for audio clips of the mealworm sounds (Audio S1) and traffic (Audio S2) and compressor (Audio S3) stimuli at 76 dB(A).

program (D. Mennit), we calibrated our playback system so that each 1/3 octave frequency band matched recorded levels. Due to an inability to record noise sources at the 58 dB(A) level as a result of nearby noise sources, we used all other recordings to project 1/3 octave band levels for these playback files. In the second year of trials, we included a silent track as an additional control.

In our second year of data collection, we found that there was added electrical noise in the playbacks due to a faulty amplifier. The equipment failure resulted in a slight increase of energy at 2, 3.5, and 5.5 kHz in all playback files but no increase in the sound level of the noise stimuli due to our calibration procedure. However, as a result the silent track was ~2 dB(A) higher than the ambient control condition.

### Statistical Analyses

We performed all analyses in SAS Institute Inc. (2002–2010) (v9.3) and analyzed the 2 years of search time data separately. For Year 2 data, we also analyzed trial success using logistic regression using Proc Genmod with Generalized Estimating Equations (GEE) for repeated measures. For both years, the search time data were not normally distributed and log transformations failed to normalize the data, but did improve residual distribution. Because analysis of variance is robust to this violation (Schmider et al. 2010), we used the logged data in analyses. We used a repeated measures ANOVA in Proc Mixed that included Playback and Trial Day as two repeated factors and random effects for Bat, Playback*Bat, and Trial Day*Bat. We used Kenward Roger corrections for degrees of freedom because missing data produced an unbalanced ANOVA. We used differences of the least squares means (marginal means) and applied False Discovery Rate corrections for multiple *post hoc* comparisons between playbacks (Ruxton & Beauchamp 2008). To test differences between noise types, we used linear contrasts to compare the log of the search time for all playbacks. We set α to 0.05 and q to 0.05 for False Discovery Rate corrections.

### Results

#### Main Findings

In Year 1, bats were successful at locating prey in 95.8% of trials ($N = 621$). In Year 2, bats were suc-

cessful in 88.5% of trials ($N = 696$). For Year 2, we examined the probability of trial success by playback treatment and found no significant differences ($p > 0.05$; Table S2). In subsequent analyses, we included only successful trials when analyzing the effects of noise playback on search time.

Search time was dependent on playback treatment (Year 1–$F_{6,30.9} = 5.35$, $p < 0.01$, Fig. 3a; Year 2–$F_{7, 29.9} = 10.53$, $p < 0.01$; Fig. 3b), with the ambient control producing shorter search times than all playback types, including the problematic silent track in Year 2, that incorporated additional electrical noise from equipment failure ($p < 0.01$). We found no differences in search time across anthropogenic noise types (traffic vs. compressor station; Year 1–$T_{31.4} = 1.14$, $p = 0.26$; Year 2–$T_{32.2} = -2.00$, $p = 0.05$) or within noise type across sound levels ($p > 0.05$).

### Examination of Data for Carry-Over Effects and Experimental Fatigue or Learning

To examine potential carry-over effects of noise playbacks on subsequent trials, as might be expected by a startle response or temporary auditory threshold shift, we compared trial pairs that had a control (ambient) trial followed by a noise trial or vice versa. The means of the search times for each grouping, before or after noise, did not differ (Year 1: $F_{1,9} = 0.79$, $p = 0.40$ for compressor playbacks and $F_{1,8} = 4.97$, $p = 0.06$ for traffic, 10 and 9 trial pairs compared respectively; Year 2, $F_{1,9} = 1.11$, $p = 0.32$ for compressor playbacks and $F_{1,9} = 0.04$, $p = 0.84$ for traffic, 10 trial pairs compared for each).

While visually inspecting our data, we noticed that the first trial of the day in Year 1 typically had longer search times regardless of playback, likely as a result of bats waking from torpor. Consequently, in Year 2, we allowed bats to fly for 2 minutes under ambient conditions before starting experimental trials, which removed this difference. The analyses we conducted to examine carry-over effects also demonstrate that this difference in first trial duration between years did not influence our conclusions.

To determine whether experience with the playback treatments or the number of days in the experimental paradigm decreased (i.e., learning) or increased (i.e., fatigue) search times, we examined the interaction between playback type and day of trial and found no relationship (Year 1–$F_{84,394} = 0.87$, $p = 0.77$; Year 2–$F_{98,408} = 1.02$, $p = 0.44$); nor was there a relationship between day of trial and search time (Year 1–$F_{14,69.4} = 1.19$, $p = 0.30$; Year 2–$F_{14, 66.2} = 1.33$, $p = 0.21$).
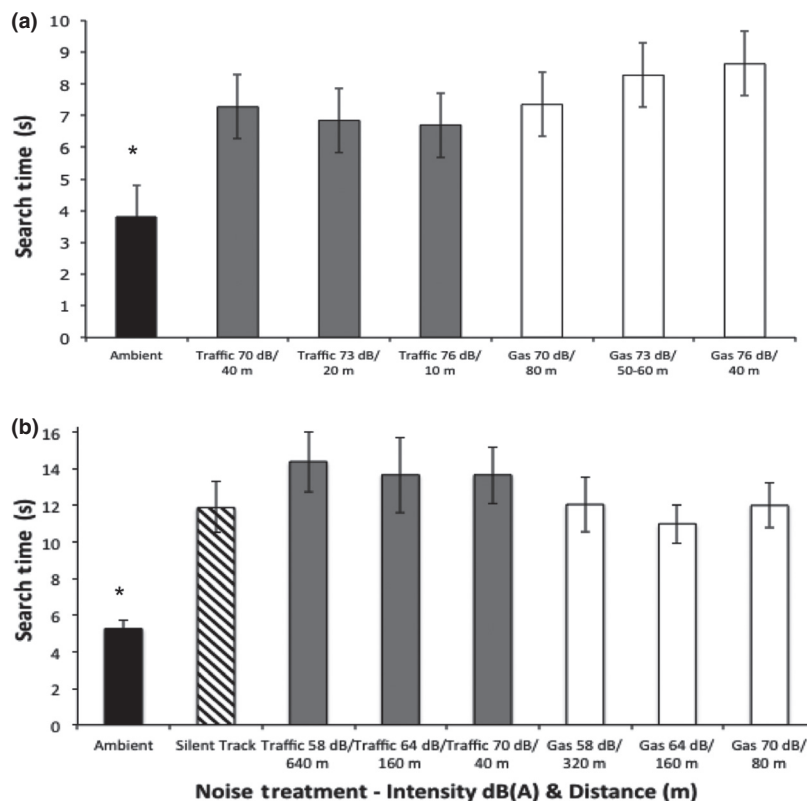


**Fig. 3:** Average raw search time with standard error bars for six bats exposed to seven acoustic conditions in Year 1 (a) and six bats exposed to eight acoustic conditions in Year 2 (b). Asterisks indicate that search time under the ambient control condition was different from all other playback conditions ($p < 0.01$) for each year.

## Discussion

We show that pallid bats experience a twofold to threefold reduction in foraging efficiency when exposed to anthropogenic noise playbacks replicating acoustic conditions as far away as 640 m from a major road and 320 m from a natural gas compressor station. Perhaps most strikingly, low-level noise (35 dBA) resulting from a faulty amplifier also elicited similar deficits in hunting behavior.

Noise might disrupt hunting behavior via (i) acoustic masking, where prey-generated sounds are not fully transduced by the auditory system (Siemers & Schaub 2011), (ii) attentional distraction, where limited processing resources are occupied by the diverting stimulus (Chan et al. 2010), and/or (iii) aversion, that elicits a general avoidance response (Luo et al. 2015). Because the bats in these experiments exerted more search effort in noise, distraction, or masking are the most likely underlying mechanisms (Luo et al. 2015). Previous work has shown that *M. myotis* responds in a dose–response manner to traffic noise exposure, likely driven by acoustic masking (Siemers & Schaub 2011). In this study, masking is not sufficient to explain our data, as bats showed similar performance under a range of stimuli that should vary substantially in their ability to mask prey-generated sounds. We are reluctant to conclude that the bats in our experiment were distracted, as we did not perform the critical test of presenting a noise stimulus that did not spectrally mask prey-generated sounds (Luo et al. 2015). Clearly, further studies are required to understand the mechanistic underpinnings of these and related findings. Given that faulty amplifier noise just 2 decibels above the background of the flight room (33 dBA) resulted in similar search times to loud playbacks (76 dBA), we suggest that the magnetic field in the experimental arena be considered as a potentially important component of hunting deficits (Červený et al. 2011; Svenja et al. 2014).

Foraging search times recorded in the laboratory are likely conservative as compared to hunting in the wild because, under natural conditions, pallid bats must perform multiple tasks simultaneously (e.g., Barber et al. 2003) and often do not have the opportunity to repeatedly investigate prey location (*sensu* Siemers & Schaub 2011). Increased foraging time compounded across an entire night may tax already tight energy budgets and result in reduced fitness or survival. Bats provide a wide range of ecosystem services and currently face multiple threats (Kunz et al. 2011), making an understanding of noise pollution's impact on bat conservation a priority. We recommend continued investigation into the effects of noise on acoustically specialized predators and mitigation of this disturbance.

## Acknowledgements

## Literature Cited

Barber, J. R., Razak, K. A. & Fuzessery, Z. M. 2003: Can two streams of auditory information be processed simultaneously? Evidence from the gleaning bat *Antrozous pallidus*. J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol. **189**, 843—855.

Barber, J. R., Crooks, K. R. & Fristrup, K. M. 2010: The costs of chronic noise exposure for terrestrial organisms. Trends Ecol. Evol. **25**, 180—189.

Barber, J. R., Burdett, C. L., Reed, S. E., Warner, K. A., Formichella, C., Crooks, K. R., Theobald, D. M. & Fistrup, K. M. 2011: Anthropogenic noise exposure in protected natural area: estimating the scale of ecological consequences. Landscape Ecol. **26**, 1281—1295.

Brown, P. E., Grinnell, A. D. & Harrison, J. B. 1978: The development of hearing in the pallid bat, *Antrozous pallidus*. J. Comp. Physiol. **126**, 169—182.

Bunkley, J. P. & Barber, J. R. 2014: An observation of apparent teaching behavior in the pallid bat. *Antrozous pallidus*. West. N. Am. Nat. **74**, 249—252.

Bunkley, J. P., McClure, C. J. W., Kleist, N. J., Francis, C. D. & Barber, J. R. 2015: Anthropogenic noise alters bat activity levels and echolocation calls. Global Ecol. Conserv. **3**, 62—71.

Červený, J., Begall, S., Koubek, P., Nováková, P. & Burda, H. 2011: Directional preference may enhance hunting accuracy in foraging foxes. Biol. Lett. **7**, 355—357, doi:10.1098/rsbl.2010.1145.

Chan, A. A. Y. H., Giraldo-Perez, P., Smith, S. & Blumstein, D. T. 2010: Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. Biol. Lett. **6**, 458—461.

Copeland, H. E., Doherty, K. E., Naugle, D. E., Pocewicz, A. & Kiesecker, J. M. 2009: Mapping oil and gas devel-

opment potential in the US intermountain West and estimating impacts to species. PLoS ONE **4**, e7400.

Francis, C. D. & Barber, J. R. 2013: A framework for understanding noise impacts on wildlife: an urgent conservation priority. Front. Ecol. Environ. **11**, 305—313.

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

Goerlitz, H. R., Greif, S. & 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.

Kroodsma, D. E., Byers, B. E., Goodale, E., Johnson, S. & Liu, W.-C. 2001: Pseudoreplication in playback experiments, revisited a decade later. Anim. Behav. **61**, 1029 —1033.

Kunz, T. H., Torrez, E. B. D., Bauer, D., Lobova, T. & Flemming, T. H. 2011: Ecosystem services provided by bats. Ann. N. Y. Acad. Sci. **1223**, 1—38.

Lollar, A. & Schmidt-French, B. 2002: Captive Care and Medical Reference for the Rehabilitation of Insectivorous Bats, 2nd edn. Bat World Sanctuary, Mineral Wells, TX.

Luo, J., Siemers, B. M. & Koselj, K. 2015: How anthropogenic noise affects foraging. Glob. Change Biol. **21**, 3278—3289. doi: 10.1111/gcb.12997

Northrup, J. M. & Wittemyer, G. 2013: Characterising the impacts of emerging energy development on wildlife, when an eye towards mitigation. Ecol. Lett. **16**, 112—125.

Ritters, K. H. & Wickham, J. D. 2003: How far to the nearest road? Front. Ecol. Environ. **1**, 125—129.

Ruxton, G. D. & Beauchamp, G. 2008: Time for some a priori thinking about post hoc testing. Behav. Ecol. **19**, 690 —693.

SAS Institute Inc. (2002–2010). SAS Software, Version 9.3, Cary, NC.

Schaub, A., Ostwald, J. & Siemers, B. M. 2008: Foraging bats avoid noise. J. Exp. Biol. **211**, 3174—3180.

Schmider, E., Ziegler, M., Danay, E., Beyer, L. & Buhner, M. 2010: Is it really robust? Reinvestigating the robustness of ANOVA against violations of the normal distribution assumption Methodology, **64**, 147—151.

Shannon, G., Angeloni, L. M., Wittemyer, G., Fristrup, K. M. & Crooks, K. R. 2014: Road traffic noise modifies behavior of a keystone species. Anim. Behav. **94**, 135—141.

Siemers, B. M. & Schaub, A. 2011: Hunting at the highway: traffic noise reduces foraging efficiency

in acoustic predators. Proc. Biol. Sci. **278**, 1646—1652.

Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., Ten Cate, C. & Popper, A. N. 2010: A noisy spring: the impact of globally rising underwater sound levels on fish. Trends Ecol. Evol. **25**, 419—427.

Stehr, F. W. 1987: Immature Insects [Vol. 1]. Kendall/Hunt Publishing Co, Dubuque, Iowa.

Svenja, E., Schneider, N.-L., Lefeldt, N., Hein, C. M., Zapka, M., Michalik, A., Elbers, D., Kittel, A., Hore, P. J. & Mouritsen, H. 2014: Anthropogenic electromagnetic noise disrupts magnetic compass orientation in a migratory bird. Nature **509**, 353—356.

## Supporting Information

Additional supporting information may be found in the online version of this article at the publisher's web-site:

**Audio S1**: Mealworm sounds recorded at 10 cm.

**Audio S2**: Traffic noise (76 dBA) playback file.

**Audio S3**: Gas compressor noise (76 dBA) playback file.

**Video S1**: Pallid bat hunting during the ambient control condition.

**Video S2**: Pallid bat hunting during 76 dB(A) traffic playback.

**Video S3**: Pallid bat hunting in the experimental paradigm. For this descriptive high-speed video (Phantom ir300, 1500 fps) multiple simultaneous mealworms were used as rewards; during experiments only a single mealworm reward was presented.

**Table S1**: Summary of noise stimuli: average measured field levels (includes frequencies lower than 1100 Hz), the predicted acoustic propagation loss modeled for line (traffic) and point (compressor) sources (Piercy et al. 1977), calculated intensity levels calibrated for the frequency response of the playback system, and average values of a representative track measured in the flight room. The sound level in the room was ±4 dB for noise playbacks and approximately ±2 dB for the ambient condition and "silent track".

**Table S2**: Probability of success and 95% confidence intervals for each noise playback treatment bats were exposed to in Year 2.