



Original Article

Does bat response to traffic noise support the misleading cue hypothesis?

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Received 8 March 2019; revised 18 July 2019; editorial decision 22 July 2019; accepted 27 July 2019.

The world has become a noisier place due to the increase in urbanization. Noise is generally considered an impediment, altering an animal's behavior through masking or distraction. But noise can also provide useful information about the environment. For animals that rely on natural environmental noise as an indicator of favorable foraging conditions, increasing levels of anthropogenic noise might mislead informed decision-making. Bats use rain noise, a natural environmental cue, to delay their emergence from the roost, presumably to avoid sensory and metabolic costs associated with foraging in heavy rain. Here we tested the “misleading cue hypothesis,” asking whether traffic noise is mistaken for rain noise by bats. Given the acoustic similarity between rain noise and traffic noise, we predicted that bats would confuse the two. We conducted a playback experiment using rain, traffic, and ambient noise at natural roosts of common big-eared bats (*Micronycteris microtis*, Phyllostomidae) and recorded bat emergence behavior. In contrast to their response to rain noise, the bats did not delay roost emergence in response to traffic noise. Thus, we found that bats were able to discriminate between traffic noise and rain noise and were not misled by similarity in acoustic parameters in the two noise types, when emerging from their roost. Emerging bats did show more exploration flights during traffic noise than during rain noise, but not during ambient noise, suggesting that they perceive traffic noise as a novel acoustic cue. Our data provide new insights into perception of traffic noise by bats.

Key words: anthropogenic noise, bats, evolutionary trap, *Micronycteris microtis*, misleading cues, traffic noise

INTRODUCTION

The world is becoming increasingly noisy due to human activities related to industry and transportation (Chepesiuk 2005). The sounds from motorized vehicles such as planes, trains, and automobiles transmit over vast distances and are thus exposing large areas to increased noise levels. We are becoming increasingly aware that noise levels from anthropogenic activities can have detrimental effects on both terrestrial and aquatic species (Barber et al. 2010; Slabbekoorn et al. 2010; Kight and Swaddle 2011).

Anthropogenic noise affects a wide range of behavioral, physiological, and cognitive mechanisms in animals (Kight and Swaddle 2011; Francis and Barber 2013; Swaddle et al. 2015). Birds, for example, adjust their songs in response to increased noise levels to restore communication ability (Slabbekoorn and Peet 2003; Patricelli

and Blickley 2006; Slabbekoorn and den Boer-Visser 2006; Halfwerk and Slabbekoorn 2009). Population studies have repeatedly shown that different species, for example, birds and crickets, exposed to anthropogenic noise experience reduced reproductive success and abundance (birds: Bayne et al. 2008; Francis et al. 2009; Halfwerk et al. 2011; crickets: Bent et al. 2018).

Foraging behavior, crucial for survival and reproduction of animals, is known to be impaired by anthropogenic noise in a broad range of species (Barber et al. 2010; Purser and Radford 2011; Siemers and Schaub 2011; Wale et al. 2013). For example, bats, fish, and crabs have been shown to forage less effectively when exposed to high levels of background noise (Purser and Radford 2011; Wale et al. 2013; Gomes et al. 2016). Vespertilionid bats avoid noisy foraging areas when possible (Mackey and Barclay 1989; Schaub et al. 2008).

Currently, there are three main hypotheses proposed through which anthropogenic noise can impede foraging: 1) acoustic masking, 2) reduced attention, and 3) noise avoidance (reviewed in Luo et al. 2015).

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1. Acoustic masking occurs when there is a spectral and/or temporal overlap between signals or cues of interest and the background noise that impedes an individual's detection of biologically relevant stimuli (Brumm and Slabbekoorn 2005).
2. The additional sensory input from anthropogenic noise can also interfere with the attention of an animal during foraging due to a decrease in available cognitive resources necessary to process foraging information (Chan et al. 2010).
3. Finally, the two perceptual mechanisms above might simply cause animals to avoid noisy areas, even though these areas may contain prey (e.g., Schaub et al. 2008) and may thus reduce their foraging success (for further examples, refer to Luo et al. 2015).

Animals often have long evolutionary histories with their environments and tend to be highly tuned to respond to specific environmental cues (e.g., see review Watts et al. 2019). With rapid anthropogenic change, however, adaptive responses to known environmental cues can quickly become maladaptive (reviewed in Schlaepfer et al. 2002). One example is the timed migratory behavior of long-distance migrating birds and the constrained adaptation to climate change based on their arrival time determined breeding date based on day length rather than on temperature (Both and Visser 2001). The long-distance migrating pied fly catcher has advanced the date of laying due to an increase of the temperature during spring arrival time (Both and Visser 2001). But the timing of the spring migration is determined by day length in this species (Both and Visser 2001). The decision for when to start migrating becomes maladaptive, as the cue for migrating is day length rather than temperature. As another example, mayflies key in on horizontally polarized light as an indicator of favorable oviposition sites (i.e., water surfaces). With the proliferation of asphalt roads, however, the previously adaptive response of ovipositing on a horizontally polarized light surface can incur a strong fitness consequence (Kriska et al. 1998). Likewise, sensory pollution, such as artificial light and traffic noise can provide cues that share stimulus properties with natural cues and therefore mislead animals (Velilla and Halfwerk 2019).

The noise of rainfall can be a salient environmental cue, reliably indicating unfavorable foraging conditions. Bats in their roosts use rain as an informational cue to decide whether and when to forage (Geipel, Smeekes, et al. 2019). Traffic noise has similar acoustic properties as rain noise. Acoustic cues that long signified unfavorable foraging conditions (i.e., the sounds of heavy downpours) could be confused with new anthropogenic noises—the sounds of traffic from large highways. As such, bats could be misled into making poor decisions, for example, delaying roost emergence when in fact conditions were favorable for foraging. Here, we ask whether bats are misled by the sound of traffic noise, falling into the evolutionary trap of delaying in their roosts unnecessarily, thus potentially losing foraging opportunities and incurring fitness costs. To test this “misleading cue hypothesis,” we quantified the roost emergence behavior of the common big-eared bat (*Micronycteris microtis*; Phyllostomidae) in the rainforests of Panama. *Micronycteris microtis* is a gleaning insectivorous bat species that finds and catches its prey using echolocation (Geipel, Jung, et al. 2013; Geipel, Steckel, et al. 2019). This species emerges from its roost around sunset for its first hunting flight, but delays its natural emergence time in the presence of rain noise, thus avoiding unfavorable foraging conditions associated with sensory and metabolic costs (Geipel, Smeekes, et al. 2019). We predict that if traffic noise acts as a misleading cue, it will induce the same response as rain noise, that is, delaying time of emergence from the roost. To our knowledge, this is one of the first

tests introducing traffic noise to naive free-living bats that have not been exposed to traffic noise before.

METHODS

Study species and roost locations

We conducted playback experiments from November 2016 to March 2017 at the entrances of nine natural *M. microtis* (Miller, 1898) roosts around Gamboa (9°07'11.5"N, 79°41'55.3"W) and along Pipeline Road in Soberanía National Park in Panamá. The bats roost in concrete water drainage pipes close to unpaved forest roads, with approximately zero to at most 20 cars passing per day. We visually checked each roost for *M. microtis* occupancy the morning before the first night of the experiment and verified bat presence every evening before stating the playbacks. *Micronycteris microtis* shows a high roost fidelity with groups of the same individuals staying in the same roost for many years (Geipel et al., in preparation) and has a very small home range (Van De Sand 2004). The experiment at each roost took four consecutive nights. It never rained during the playback periods or prior the playback on the respective day. All experiments adhere to ABS/ASAB guidelines for ethical treatment of animals and were approved by the Government of Panamá (Ministerio de Ambiente permit SE/A-94-16 and SE/A-6-17) and the Smithsonian Tropical Research Institute (STRI IACUC protocol 2016-0101-2019).

Noise recordings and stimuli preparation

Using an ultrasound microphone (CM16/CPMA, Avisoft Bioacoustics, Glienicke, Germany; frequency response: ± 6 dB between 5 and 150 kHz; frequency range: 2 and 200 kHz), recording interface (UltraSoundGate 116Hm, Avisoft Bioacoustics; sampling rate: 500 kHz, resolution: 16 bit, frequency response: -3 dB), and laptop (Lenovo ThinkPad 11e, Lenovo, Beijing, China), we recorded three different noise types: ambient, traffic, and rain. We simultaneously measured sound pressure levels (SPLs) each minute using an SPL-meter (Digital Sound Level Meter 33-2055, RadioShack Corporation, Fort Worth, TX, set to A-weighting, fast and max). Ten-minute ambient noise recordings were made at eight forest locations around Gamboa and on Pipeline Road between 17:00 and 19:15 (around sunset). We included an ambient noise treatment into our experiment to ensure that amplitude alone was not driving behavioral changes in the bats. From each 10-min ambient noise recording, we randomly chose a 5-min segment that did not contain any unusual extraneous noise, and used these 5-min segments for our playback experiments. Five-minute traffic noise recordings were made between 11:45 and 17:00 at nine locations in Panamá City at approximately 15 m distance from the edges of major roads, with hundreds of cars, trucks, and other noisy vehicles passing per minute. We specifically recorded in areas of Panamá City with heavy moving traffic, but not in areas with such intense traffic that cars were stopped. Ten-minute rain noise recordings were made during heavy downpours at three forest locations around Gamboa and on Pipeline Road between 14:30 and 0:15. We protected the recording equipment from rain with an umbrella (canopy span: approx. 120 cm) covered with thick acoustic foam (approx. 1–5 cm) to avoid noise originating from the impact of the raindrops on the umbrella. From these 10-min rain recordings, we selected a 5-min segment that contained the most intense rainfall we were able to record.

We then randomly assigned these 5-min recordings (one ambient, one traffic, and one rain noise) to each of our nine roosts.

Due to the frequency response of our recording equipment, we had to amplify frequencies below 10 kHz to compensate for the lower sensitivity of the microphone in the 1–10 kHz range using SASLab Pro software (version 5.2.09, Avisoft Bioacoustics). We applied a filter with intensities that were inversely related to the sensitivity curve of our microphone. Each audio file was resampled at 192 kHz, normalized to -3.0 dB in Audacity® version 2.1.2 (<https://audacityteam.org/>), and looped to create a 1.5 h playback file. We tested the acoustic quality of our noise stimuli within a bat roost by conducting a playback experiment at an empty roost (see [Supplementary Material](#)). Power spectra and spectrograms of the noise treatments can be found in [Figure 1](#) and short sound examples in [Supplementary Audio A1–A3](#).

Experimental setup

We placed an ultrasound speaker (Ultrasonic Dynamic Speaker Scanspeak, frequency response: -12 dB between 5 and 80 kHz, frequency range: 1 and 120 kHz via UltraSoundGate Player 116, frequency range: 1 and 180 kHz; and UltraSoundGate Player BL Light, frequency response: ±6 dB between 5 and 75 kHz, frequency range: 1 and 125 kHz; Avisoft Bioacoustics) approximately 1 m in front of each of the two roost entrances of the drainage pipes, not obstructing the bats’ flight path. Stimuli were broadcasted from a laptop (ThinkPad L450, Lenovo) connected to the speakers via USGH-Recorder software (version 4.2, Avisoft Bioacoustics). Bat emergence behavior was recorded with infrared cameras (Panasonic hx-a1m, Panasonic, Kadoma, Japan, 60fps) combined with custom-built infrared lights positioned 1 m to the side of the roost entrance.

Each experiment started with one night of baseline observations, during which no sound was broadcasted (hereafter referred to as baseline). On the following three nights, roosts were exposed

to traffic, rain, or ambient noise stimuli in a randomized order. We started noise playback and video recording 30 min prior to sunset, as *M. microtis* emerged around sunset. Playback lasted until an hour after sunset, while video recording continued for an additional 30 min, in case the bats only started emerging after the noise playbacks would have stopped. All stimuli were broadcasted at 77.2 ± 0.14 (mean \pm SE) dB at 10 cm from the entrance of the roost (Digital Sound Level Meter 33-2055, RadioShack, set to C-weighting, fast and max), amplitude levels comparable to those of the loud rain and traffic noise we measured in our recordings.

Behavioral observations

Recorded videos were scored with Solomon Coder (version beta 17.03.22, <https://solomoncoder.com/>). We noted the time that each individual emerged from the roost (example for a bat emergence, see [Supplementary Video S1](#)) and determined the maximum number of bats that left the roost during the treatment (see [Supplementary Table S2](#)). For the maximum number of bats, we counted each bat leaving the roost and each bat that entered the roost. The number of the entering bats was subtracted from the number of emerging bats to get the maximum number of bats that left the roost to forage. We then calculated the emergence time of the median bat (MBE), defined as the moment the median numbered bat left the roost (based on the maximum number of emerged bats on the baseline night). For example, if the maximum number of emerged bats was 15 during baseline, then the eighth bat was the median number for that specific roost. Subsequently, during following treatment nights, we took the time that the eighth bat emerged from the roost as our MBE time. For roosts with an even number of bats, the MBE was the average of the two mid-most bats. For example, if the maximum bats emerged would be

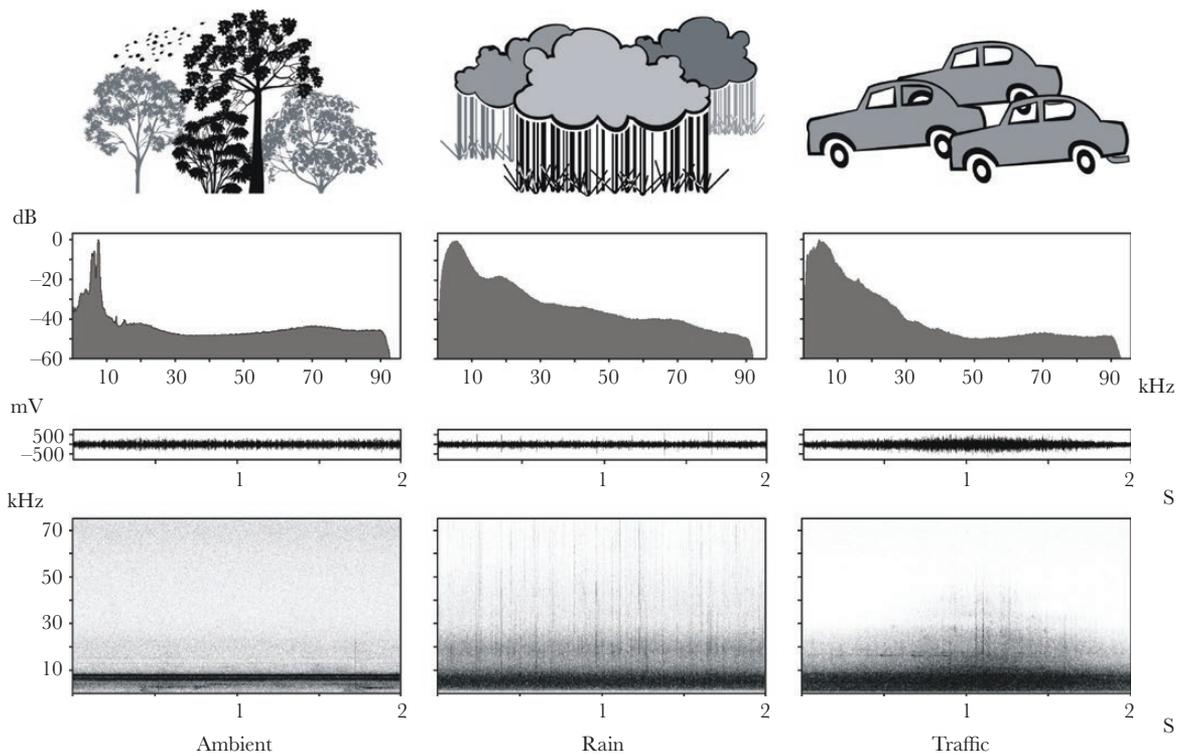


Figure 1 Power spectra, amplitude envelopes, and spectrograms of representative examples of sound files used for the playback treatments: ambient, rain and traffic noise. Icon illustrations by Damond Kylo.

12, then the MBE would be the average of the emergence times of the sixth and seventh bat.

One of the roosts (D34) had a larger number of bats entering the roost than the number of bats leaving during traffic noise playback. Since this was a very unusual pattern compared to the other roosts, and because this pattern meant that the median bat was never reached in this treatment, we omitted the traffic noise data point for this roost out of any further analyses. Another roost (Tele08) had a maximum number of 15 bats. Therefore, the median bat would be the eighth bat. However, during traffic noise, the maximum number of emerged bats was 7. Therefore, the seventh bat was taken as the median bat for this trial.

Upon emergence from the roost, bats often took short exploration flights, re-entering the roost within a few seconds (for detailed description of this behavior, see Geipel, Smeekes, et al. 2019). We defined these “exploration flights” as instances when the bat emerged and re-entered the roost within 2 s, staying in close proximity of the roost (visible on the video recording; e.g., Supplementary Video S2). The duration of these exploration flights were usually very short, on the order of 0.5 s.

Statistical analysis

We analyzed the emergence behavior with mixed-effect models in Rstudio (version 1.0.143, *lme4* package, <https://CRAN.R-project.org/package=lme4>; Bates et al. 2015). Model selection was performed by dredging the full model using the *MuMIn* package. The best model was the model with the lowest AICc value. We tested whether treatment had an effect on the emergence time of the median bat with a linear mixed-effect model (LMM). As the response variable, we used the MBE during each treatment. To account for repeated measures, we added roost ID as random slope effect to the model, with slope calculated over trial order (1–3). This is to account for potential order effects within each roost. As fixed factors, the full model included treatment (ambient, traffic, or rain), the MBE of each roost during the baseline condition and roost size, which was the maximum number of bats that emerged during each night. Model diagnostics were successfully checked (version 0.2.0, *DHARMA*-package, <https://CRAN.R-project.org/package=DHARMA>; Hartig 2019). The model that, based on the AICc value, explained most of our data included only treatment and the baseline value as the fixed factors and we therefore removed roost size from our final models (see roost size values in the Supplementary Table S2). Importantly, models with roost size did not yield different statistical results. We compared final models with null models lacking the treatment effect of interest using likelihood ratio tests (LRT).

To test whether treatment had an effect on the number of exploration flights, a similar approach was used. Since the numbers of exploration flights are count data, we used a generalized linear mixed-effect model (GLMM) with a Poisson distribution. The response variable was in this case the number of exploration flights during each treatment. We scaled the continuous predictors whenever needed to achieve convergence (Bates et al. 2015). The model did not suffer from over dispersion, which was successfully tested for using the *DHARMA*-package (version 0.2.0; Hartig 2019). The number of exploration flights was best explained by the model including treatment and the baseline value as fixed factors.

For both, the MBE and the exploration flights, we followed up on significant treatment effects by performing a Tukey HSD test, with Bonferroni correction for multiple comparisons using the *multcomp* package version 1.4-6 (Hothorn et al. 2008). Information on each statistical analysis can be found in the Supplementary Material.

RESULTS

Effect of noise on emergence time

We found a significant effect of playback treatment on the MBE (LRT, $n = 9$, $df = 2$, $\chi^2 = 11.28$, $P < 0.01$; Figure 2a). Post hoc comparisons revealed that bats exposed to rain noise emerged later from their roosts compared to ambient noise (Tukey, $n = 9$, $\beta = 265.39 \pm 82.06$ SE, z -value = 3.234, $P = 0.0035$) and compared to bats exposed to traffic noise (Tukey, $n = 9$, $\beta = 261.58 \pm 84.62$ SE, z -value = 3.091, $P = 0.0056$). Emergence time of the bats during traffic noise did not differ significantly from emergence time during ambient noise (Tukey, $n = 9$, $\beta = 3.81 \pm 85.27$ SE, z -value = 0.045, $P = 0.9989$).

Effect of noise on number of exploration flights

The different noise treatments also affected the number of exploration flights (LRT, $n = 9$, $df = 2$, $\chi^2 = 14.663$, $P < 0.001$; Figure 2b). Treatment with traffic noise differed significantly from rain noise (Tukey, $n = 9$, $\beta = 0.7272 \pm 0.1893$ SE, z -value = 3.841, $P < 0.001$), and nearly significantly from ambient noise (Tukey, $n = 9$, $\beta = 0.5264 \pm 0.2419$ SE, z -value = 2.176, $P = 0.074$). The number of exploration flights did not differ between rain and ambient conditions (Tukey, $n = 9$, $\beta = -0.2008 \pm 0.2028$ SE, z -value = -0.990, $P = 0.579$). Note that the number of exploration flights was highest during playback of traffic noise for all but one roost (see Supplementary Information).

DISCUSSION

Novel, anthropogenic cues can introduce confounding information and consequently lead to negative effects on animals (Schlaepfer et al. 2002; Velilla and Halfwerk 2019). We show that when exposed to different types of noise, bats can successfully discriminate between biologically relevant natural noise, that is, the sound of rainfall, and novel, artificial sounds, that is, human-induced traffic noise. In this context, bats were not misled by acoustic similarities between the noise types. In accordance with previous work, we found that bats delayed emergence from their roosts during rain noise (Geipel, Smeekes, et al. 2019), but not when exposed to traffic noise.

As for other animals, it has been shown that in the foraging context, bats are negatively impacted by anthropogenic noise. Bats prefer to forage in quiet areas over noisy ones (Mackey and Barclay 1989; Bunkley et al. 2015), avoid traffic noise (Schaub et al. 2008), and show reduced foraging activity and efficiency (Siemers and Schaub 2011; Bunkley and Barber 2015). In contrast to those studies, we show that *M. microtis* does not delay its emergence in response to traffic noise. These bats do, however, show an increased number of exploration flights when confronted with traffic noise compared to when exposed to rain noise and a nonsignificant trend to more exploration flights compared to ambient noise. As none of our bat roosts were previously exposed to traffic, this increase in exploration flights could be a result of traffic noise being a novel sound for these colonies, inducing an exploratory behavior that is not seen in response to the rain or ambient noise. If this is the case, we would expect this exploratory behavior to diminish with increased exposure to traffic noise over time, as bats may habituate to the presence of traffic noise. It was found that Brazilian free-tailed bat colonies located in close proximity to traffic noise—that is, those found roosting under urban bridges directly under highways—did not show increased stress levels (blood cortisol levels) in

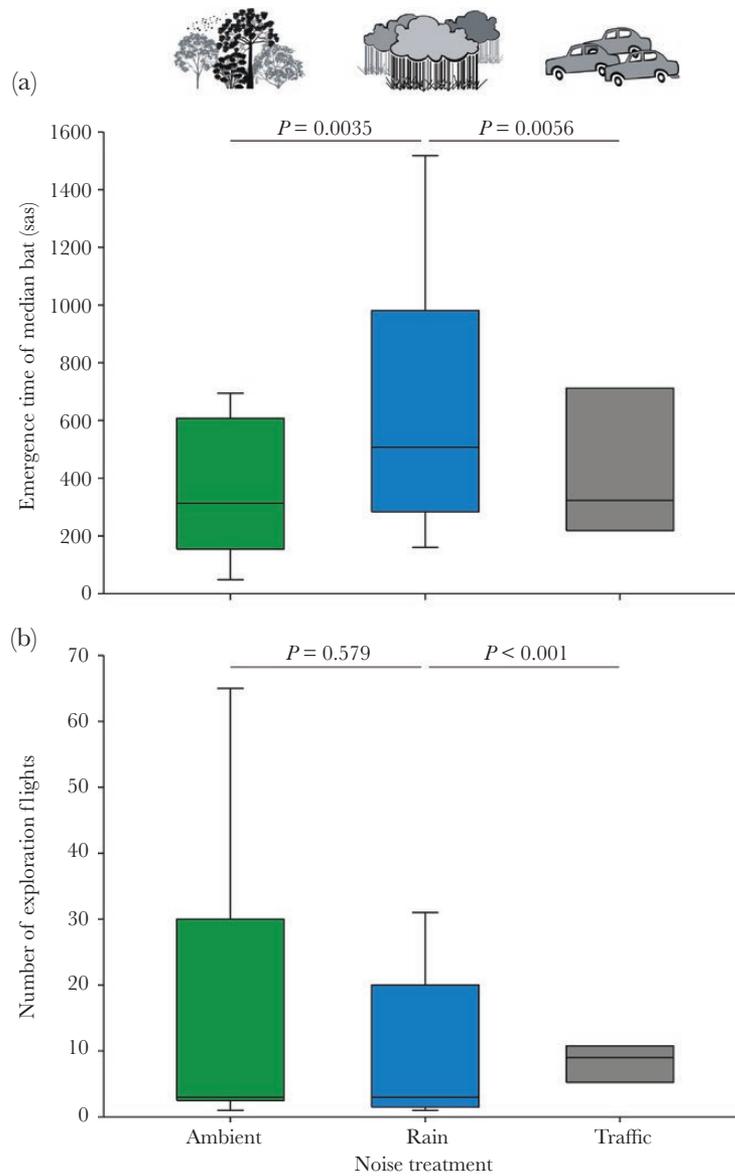


Figure 2

(a) Time of emergence of the median bat in s after sunset (sas) for the different treatments: ambient (green), rain (blue), and traffic noise (gray). (b) Number of exploration flights for three treatments: ambient (green), rain (blue), and traffic noise (gray). The sample size for each treatment was $n = 9$. The box-plots represent the median, 25th and 75th percentiles (lower and upper box boundaries), and 10th and 90th percentiles (whiskers below and above).

comparison to cave-roosting Brazilian free-tailed bats (Allen et al. 2011), suggesting that bats are able to habituate to traffic noise.

As rain noise can inform bats when environmental conditions are favorable to leave the roost to forage (Geipel, Smeekes, et al. 2019) and due to the acoustic similarity between the sounds of traffic and rain, we predicted that traffic noise could mislead bats into making poor decisions, for example, delaying roost emergence when in fact conditions were favorable for foraging. This was not the case in our study, as *M. microtis* were able to discriminate between noise types, and were not misled by acoustic similarities.

It has been suggested that traffic noise acts as a fragmenting agent for gleaning bats, while bats hunting for insects in the open space might be less affected during foraging (Kerth and Melber 2009; Bonsen et al. 2015). In traffic noise, the main energy content is in the low-frequency range. The high, ultrasonic frequencies have generally less energy and are rapidly attenuated over short distances.

Thus, it has been argued that the high-frequency echolocation calls are less affected by traffic noise (Bonsen et al. 2015). Most gleaning bats hunt by eavesdropping on prey-produced sounds (passive listening), such as insect rustling noises and advertising calls of insects and frogs (e.g., Tuttle and Ryan 1981; Belwood and Morris 1987; Kalko 1998; Goerlitz et al. 2008; Page and Ryan 2008). The passive gleaners are sensitive to these low-intensity prey sounds in the lower frequency range (Goerlitz et al. 2008), thus we argue that masking of prey sounds through traffic noise should be quite likely to occur for these bats. Even though some passive gleaning species have the possibility to shift between the two different acoustic sensory modalities and rely more on their echolocation system for prey finding in the presence of noise masking prey-produced sounds (Gomes et al. 2016), we predict that for passive gleaning bat species noise should severely influence hunting success. The active gleaning bat *M. microtis* is not listening for prey-produced sounds, but rather relies only on

its echolocation system to find and catch its prey from leaf surfaces (Geipel, Jung, et al. 2013; Geipel, Steckel, et al. 2019). The difference in foraging strategy might be an explanation for why the bats did not delay their emergence time in the presence of traffic noise. As they were able to differentiate between traffic and rain noise, for this species, traffic noise might not be a hindrance during foraging, and may not be associated with the unfavorable conditions of rain.

Even though we did not find a delay to emerge for foraging, we argue that anthropogenic noise can cause negative effects for the bats in their roost. Long-term exposure to high levels of anthropogenic noise has been shown to have a suite of negative consequences across taxa (Barber et al. 2010). Acoustic masking and reduced attention can hamper the detection of informational sounds (Barber et al. 2010). Thus, we argue that, for example, bats roosting amidst noise may be less able to detect the sounds of an approaching predator. Auditory awareness can be drastically reduced, even through a modest increase in noise exposure, as increased noise levels may reduce the ability to attend to alarm signals or unintended sound cues (Barber et al. 2010). Hermit crabs, for example, are distracted by boat motor noise, which allows predators to approach them more closely (Chan et al. 2010). Increased noise levels also affect social communication in animals. Dolphins, for example, simplify their social whistle calls in response to increased levels of ship noise, with likely consequences of reduced fitness (Fouda et al. 2018). Likewise, birds communicating in urban noise increase the frequencies of their songs to avoid the bandwidths most occupied by anthropogenic noise (Slabbekoorn and Peet 2003; Halfwerk and Slabbekoorn 2009). In response to traffic noise, bats have been found to adjust their echolocation calls, but not their social calls (Song et al. 2018). Thus, we argue that increased noise levels could have strong negative effects for bats communicating in their roosts as well, as vocal learning has been shown to play a significant role in bat social development (Knörnschild et al. 2010).

In our study, we do not find that traffic noise is a misleading cue during the time the active gleaning bat *M. microtis* emerges to start foraging. However, we show that bats reacted to traffic noise through an increase in exploration flights compared to rain noise, and displayed a nonsignificant trend of more exploration flights compared to ambient noise. For future directions, we predict that the impact of traffic noise on foraging passive gleaning bats should be severe, by masking the prey-produced sounds these bats heavily rely on for prey detection. Further, we argue that long-term exposure to traffic noise could have negative effects for bats in the roost: rain noise only occurs for a short time period during rain fall, traffic noise is more constant, sometimes with varying intensities. Bats in their roosts might habituate to traffic noise, but this could be costly in the long run, due to, for example, the impact on social communication in the roost, and strongly reduced detection of predators or actual rain.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

FUNDING

I.G. was funded by a Smithsonian Tropical Research Institute (STRI) Tupper Postdoctoral Fellowship and the Wissenschaftskolleg zu Berlin, Germany. B.A. was supported by a STRI internship, LUF International Study Fund (LISF), and the Holland Scholarship. R.A.P. was funded by STRI. W.H. was funded through the Netherlands Organisation for Scientific Research (NOW) Veni grant (#862.15.006).

We thank Damond Kylo for the drawing of the noise icons and two anonymous reviewers for their insightful comments. We are grateful to the Smithsonian Tropical Research Institute (STRI) for their critical ongoing support. W.H. thanks Neil Carter, Clinton Francis, and Jesse Barber for organizing a workshop on noise and light pollution where the term 'misleading cue hypothesis' was coined.

I.G., B.A., R.A.P., and W.H. conceived the study; I.G. and B.A. conducted the playback experiments; B.A. conducted the data analysis; B.A. and W.H. carried out the statistical analyses; and I.G. and R.A.P. wrote the manuscript. All authors gave final approval for publication.

Conflict of Interest: The authors have no competing interests.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Geipel, Amin, et al. (2019).

Handling editor: Ulrika Candolin

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