

RESEARCH ARTICLE

Noise as an informational cue for decision-making: the sound of rain delays bat emergence

Inga Geipel^{1,2,*}, Marcus J. Smeekes³, Wouter Halfwerk⁴ and Rachel A. Page¹

ABSTRACT

Background noise can have strong negative consequences for animals, reducing individual fitness by masking communication signals, impeding prey detection and increasing predation risk. While the negative impacts of noise across taxa have been well documented, the use of noise as an informational cue, providing animals with reliable information on environmental conditions, has been less well studied. In the tropical rainforest, downpours can be intense and frequent. Strong rainfall may impede efficient orientation and foraging for bats that need echolocation to both navigate and detect prey, and can result in higher flight costs due to increased metabolic rates. Using playback experiments at natural roosts, we tested whether two bat species, differing in their hunting strategies and foraging habitats, use rain noise as a cue to delay emergence from their roosts. We found that both species significantly delayed their emergence time during rain noise playbacks versus silence and ambient noise controls. We conclude that bats can use background noise, here the acoustic component of rainfall, as a reliable informational cue to make informed decisions, in this case about whether to initiate foraging trips or remain in the shelter of their roosts. Our findings suggest that environmental background noise can sometimes be beneficial to animals, in particular in situations where other sensory cues may be absent.

KEY WORDS: Acoustic signals, Environmental conditions, Foraging, Roost emergence, Echolocation, *Micronycteris microtis*, *Molossus molossus*

INTRODUCTION

Throughout the animal world, cues about the environment are critical to fitness and survival (Dall et al., 2005). The ability to rapidly and accurately distinguish stimuli of importance from the background is key to capturing prey, avoiding predation and obtaining a mate (Stevens, 2013). Background noise, however, is ubiquitous and can decrease foraging rates and success (e.g. Villalobos-Jiménez et al., 2017; Siemers and Schaub, 2011; Gomes et al., 2016), heighten predation risk (e.g. Simpson et al., 2016; Morris-Drake et al., 2017) and disrupt interspecific and intraspecific communication (e.g. McIntyre et al., 2014; Halfwerk et al., 2011). While numerous studies have examined the effect of noise on signal transmission (e.g. reviews by Slabbekoorn, 2013; Francis and Barber, 2013) and investigated the mechanisms used by different

taxa to reduce the masking effect of noise (e.g. Roca et al., 2016; Halfwerk and Slabbekoorn, 2015), the use of environmental noise as an informational cue has largely been overlooked.

Animals can use biotic noise as a cue to guide decision-making. Coral larvae, for example, use reef sounds, primarily the noises produced by fish and crustaceans, as a beacon leading them to suitable habitats (Vermeij et al., 2010). Abiotic noise of wind, rain, bodies of moving water and the like can also influence decision-making. Female little torrent frogs (*Amolops torrentis*) prefer male mating calls coupled with high-amplitude stream noise (Zhao et al., 2017). Rocks, vegetation and other aspects of the environment that increase stream turbulence, thereby increasing stream noise levels, may be associated with decreased predation rates and preferred oviposition sites in this species.


Rainfall is a common source of abiotic noise that can interfere with an individual's decision-making (e.g. Halfwerk et al., 2016b). Animals have evolved different behavioural strategies for coping with the acoustic masking effects of rain. Males of the Chiloe Island ground frog (*Eupsophus calcaratus*) increase the rate and duration of their mating calls when confronted with moderate levels of rain noise (Penna et al., 2005). In contrast, tawny owls (*Strix aluco*) reduce vocal activity during nights of heavy rain (Lengagne and Slater, 2002). While the sensory strategies that animals can use to minimise the effect of rain noise have received some attention, the use of rain noise as an informational cue rather than a hindrance has been little investigated.

Bats are acoustic specialists. They use sound as their main sensory modality for orientation and foraging (Griffin et al., 1960). Thus, they commonly face the challenge of filtering acoustic signals and cues of interest from background noise. High levels of noise have been shown to decrease bat echolocation activity (Bunkley et al., 2015). When offered a choice, bats will forage in quiet patches rather than noisy ones (Mackey and Barclay, 1989; Schaub et al., 2008). It is unsurprising that noise can impede bat activity, but to what degree do bats actively use noise as an informational cue to guide their decision-making? In the tropics, heavy rainfall is a common and widespread occurrence, imposing significant metabolic costs on bats (Voigt et al., 2011). Bats with wet fur and wet wings incur higher flight costs than dry bats (Voigt et al., 2011). Sensory costs due to rain are likely to be higher as well. As a result of impedance of their echolocation system (Fenton et al., 1977), bats flying in rain should navigate and forage less efficiently. Indeed, bat activity is often reduced on rainy nights (Audet, 1990; Erickson and West, 2002; Fenton et al., 1977).

Rain noise is generated when raindrops strike a surface, for instance vegetation or the ground. For bats roosting in a shelter, deciding when to leave and forage, rain noise could provide access to information on environmental conditions and their associated costs, e.g. increased metabolic costs associated with getting wet, possible reduced access to prey and impeded navigational ability. Our purpose was to determine whether bats use rain noise as an informational cue to time their roost exits.

¹Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Panama. ²Wissenschaftskolleg zu Berlin, 14193 Berlin, Germany. ³Forest and Nature Management, Van Hall Larenstein, 6882 CT Velp, The Netherlands. ⁴Department of Ecological Science, Vrije Universiteit, 1081 HV Amsterdam, The Netherlands.

*Author for correspondence (inga.geipel@gmail.com)

 I.G., 0000-0003-3118-2460; M.J.S., 0000-0003-0352-5462; W.H., 0000-0002-4111-0930

Further, do bat species with different foraging strategies react differently to rain noise?

We hypothesised that bats hunting in different habitats using different sensory strategies and showing different activity patterns would encounter different challenges from rain. The common big-eared bat, *Micronycteris microtis* (Phyllostomidae), gleans insects (Kalka and Kalko, 2006) and small vertebrates (Santana et al., 2011) from vegetation in the dense understory of tropical forests using echolocation (Geipel et al., 2013a). The Pallas's mastiff bat, *Molossus molossus* (Molossidae), uses echolocation to hunt flying insects in open space (Fenton et al., 1998; Emrich et al., 2014; Willig et al., 1993). *Micronycteris microtis* forage continuously throughout the night, with no strong activity peaks (Kalka and Kalko, 2006), returning to the roost to consume their prey items (Geipel et al., 2013b). In contrast, *M. molossus* forage for a short time period at the beginning of the night, foraging briefly after sunset and again occasionally around sunrise (Chase et al., 1991; Dechmann et al., 2010).

We expected that both species, *M. microtis* and *M. molossus*, would respond to rain noise by delaying roost emergence. We predicted that *M. molossus* would delay longer in the roost because they have the ability to enter torpor, decreasing their metabolic rate to save energy (O'Mara et al., 2017). *Micronycteris microtis*, in contrast, eat throughout the night and thus we predicted they might not have the luxury of remaining in their roosts until the rain stops. To address these questions, we located natural roosts and conducted playback experiments, broadcasting rain and ambient noise shortly before sunset, and quantified bat emergence behaviour.

MATERIALS AND METHODS

Study site and animals

Playback experiments were conducted from April to September 2015 in and around Gamboa, and along Pipeline Road in Soberanía National Park in Panama. Gamboa (9°07'11.5"N, 79°41'55.3"W) is a small town, bordered by Soberanía National Park, which consists both of old growth and mature secondary, semi-evergreen, moist tropical lowland forest along Pipeline Road (Condit et al., 2001; Ibáñez et al., 2002).

We conducted playback experiments at 10 *Micronycteris microtis* Miller 1898 and 10 *Molossus molossus* (Pallas 1766) roosts. The roosts of *M. microtis* were located in large concrete water drainage pipes before and along Pipeline Road and around Gamboa. Molossid roosts were found within the walls of houses in Gamboa. *Molossus bondae* and *Molossus coibensis* occur sympatrically with *M. molossus* in Gamboa (Gager et al., 2016). *Molossus bondae* is locally rare in the Gamboa roosts (Gager et al., 2016); *M. molossus* and *M. coibensis* are only distinguished reliably by genetic analysis (Gager et al., 2016). There is no known difference in foraging and emergence behaviour among these three species. While we were not able to verify the species identity of every individual in each of our molossid roosts, for the roosts for which we do have genetic analyses, we know these bats were primarily *M. molossus* (Gager et al., 2016). Thus, for the sake of simplicity, we refer to individuals in the molossid roosts in this study as *M. molossus*.

For roosts with more than one entrance, all but one entrance was temporally blocked at least 3 days and nights before the experiments started. Large entrances (*M. microtis*) were sealed using insect mesh and small entrances (*M. molossus*) were blocked with soft foam. All blocking materials were removed immediately after the experiment.

We counted the number of bats in each *M. microtis* roost daily for the 3 days before the experiments started and on each day during the experiment. Bats were visually observed and counted for a few

minutes between 09:00 h and noon each day. Counting the *M. molossus* in each of their roosts in this way was impractical, as their roosts are tight cavities within the walls of houses. We monitored each *M. molossus* roost at least once during the 3 days prior to the start of the experiment using a video camera with infrared light (IR) function (DCR-SR45 Handycam, Sony, Tokyo, Japan) and IR lights (HVL-IRM, Sony) to confirm each roost was occupied.

Our playback experiments were licensed and approved by the Government of Panama (Autoridad Nacional del Ambiente permit SE/A-86-14 and Ministerio de Ambiente permit SE/A 69-15) and the Smithsonian Tropical Research Institute (STRI IACUC protocol 2014-0101-2017).

Playback sound files

We prepared 10 audio file pairs containing ambient noise and ambient plus rain noise (henceforth referred to as rain noise). The audio files were drawn from recordings made at 12 different locations along Pipeline Road in 2012 and 2013. At each site, 15 s sounds were recorded at 15 min intervals for 3–10 days continuously throughout both dry and rainy seasons (Halfwerk et al., 2016a). Sounds were recorded with a Song Meter SM2BAT recorder (with a sampling rate of 196 kHz, 16 bit depth resolution and pre-set gain of 60 dB) connected to a US-II microphone (Wildlife Acoustics, Maynard, MA, USA). These audio recordings contained the sonic as well as ultrasonic frequency range (1–88 kHz).

From this dataset, we first sorted for the time of recording to select all files made around sunset local time (~18:30 h), the time our experiments would take place. We listened to each of the subset of files made at sunset and selected 10 recordings that clearly depicted heavy downpours. Each rain sound recording was paired with a recording of ambient sound (in the absence of rain sound), which was recorded around sunset within 3 days of the rain noise recording at the same location. Each original recording had a duration of 15 s. The recordings were looped with the recording and editing software Audacity® version 2.0.6 (<https://audacityteam.org/>) for a total duration of 3 min. All files were amplitude normalised (−3.0 dB). One of these 10 pairs of audio files (ambient and rain noise) was randomly assigned to each of the 10 bat roosts for each species.

Playback experiment

We recorded the emergence behaviour of *M. microtis* and *M. molossus* at their natural roosts under three different treatments: no playback (control, baseline), ambient noise and rain noise. For each roost, the experiment lasted for three consecutive nights. On the first night, we made no playback and quantified baseline emergence behaviour. The following two nights, the two sound stimuli were presented. On one of these two nights we broadcast rain noise and on the other we broadcast ambient noise, randomising the order of the sound treatments. On nights in which it rained before or during a treatment, we aborted the trial and conducted it instead on the next dry night.

For the baseline treatment, a dummy speaker (approximately 14×14×14 cm) resembling the actual speaker was mounted on a tripod positioned 1 m outside the roost entrance. In cases where this positioning was not possible, e.g. because the roost was too high, the dummy speaker was placed as close to the roost entrance as possible and the distance to the roost entrance was noted. For the sound stimuli treatments, a ScanSpeak Ultrasound speaker (frequency range 1–120 kHz, frequency response ±6 dB between 3 and 90 kHz; Avisoft Bioacoustics, Glienicke, Germany) mounted on a tripod was placed in the same position as the dummy speaker during

the baseline treatment, with the front of the speaker directed toward the entrance of the roost. The speaker was connected to an amplifier (UltraSoundGate Player 116, Avisoft Bioacoustics) and the amplifier was connected to a laptop (Thinkpad T420, Lenovo, Beijing, China). The sound files were broadcast at 80 dB SPL (re. 20 μ Pa), measured at 10 cm distance from the entrance outside each roost, using software (RECORDER USGH, Avisoft Bioacoustics) compatible with the amplifier. The sound level was measured with a sound pressure level meter (Digital Sound Level Meter 33-2055, RadioShack, Fort Worth, TX, USA; set to C-weighting, fast and max). The dummy speaker was positioned and the playback initiated approximately 30 min before sunset and was stopped approximately 60 min after sunset.

During all three treatments, the behaviour of the bats at the respective roost entrance was recorded with an infrared video camera (DCR-SR45, Sony) and two infrared lights (HVL-IRM, Sony). The camera and the lights were positioned either over the entrance of the roost facing downwards or below the roost facing upwards, depending on the height of the roost entrance and the surrounding space. We initiated the video recording at the beginning of each treatment, approximately 30 min before sunset. To document the behaviour of the bats after the noise playbacks stopped, we continued video recording for an additional 30 min after the playback ended (ending the video recording approximately 90 min after sunset).

Video and statistical analysis

Videos were analysed with event recording software (version 15.03.15, Solomon Coder, <https://solomoncoder.com/>). Every time a bat emerged from (=out) or entered (=in) the roost, the event and the video time were documented with an accuracy of 1/20 s. For each treatment, we noted the start and stop of the noise playbacks. The video time of the event recordings was converted into actual time, which was further converted into seconds after sunset (sas). We determined the total number of bats in each roost by counting how many bats emerged during the baseline treatment. The median of the total number of bats that flew out of the roost during the baseline treatment was identified (i.e. the middle bat separating the lower from the upper half of the total number of emerging bats). We then quantified the emergence time of this median bat (medianB), derived from the baseline, for each treatment for statistical testing (see Table S1). We took these values for each roost and determined the mean \pm s.d. emergence time for each treatment.

The effect of noise treatment on the median bat (medianB) was compared using linear mixed models in statistical computing software (R, lme4 package, <https://CRAN.R-project.org/package=lme4>). A null model was made with roost ID as random factor. This model was compared with models wherein species ID (*M. microtis* or *M. molossus*), noise treatment and medianB were added as a fixed factor. Models were compared with a likelihood ratio test. A *post hoc* independent contrast was used to follow up on any significant effect of noise treatment or the interactions between noise treatment and species identity.

One *M. microtis* and one *M. molossus* roost were excluded from statistical testing. At the *M. microtis* roost, too few bats (two bats) emerged during the rain noise treatment to be compared with the baseline. The excluded *M. molossus* roost contained only two bats.

RESULTS

Roost emergence behaviour

The bat species differed significantly in their time of emergence in the baseline treatment without sound playback. *Micronycteris microtis* emerged earlier than *M. molossus*. On average, the first

M. microtis individual emerged 386 \pm 494 s before sunset ($n=9$ roosts) and the first *M. molossus* individual emerged 507 \pm 334 sas ($n=9$ roosts). On average, the median *M. microtis* bat emerged 215 \pm 398 sas and the median *M. molossus* emerged 1065 \pm 191 sas.

We observed that after leaving the roost, the *M. microtis* individuals often made small turns to immediately fly back into their roost. During these turns, which we dubbed 'exploration flights', the bats were continuously visible on the video recordings. Sometimes, individuals made several of these exploration flights before they finally left their roost to forage. Exploration flights were observed during all treatments, although they seemed to be more expressed during the baseline treatment (e.g. pattern in Fig. 1). In contrast, *M. molossus* did not show this behaviour; once they emerged from the roost, they immediately left the vicinity for an extended time period. Examples of emergence patterns for a *M. microtis* and a *M. molossus* roost are shown in Fig. 1 (Roost-15 and Mol-03, respectively).

Effect of noise

To determine the effect of rain noise on the emergence behaviour of bats, the time of emergence of the median bat during the baseline condition was calculated and compared with the emergence time of the corresponding median bat of the different noise treatments.

Taking the two bat species together, we found significantly delayed emergence depending on noise treatment (GLMM, $\chi^2=22.91$, d.f.=2, $P<0.0001$, $n=18$). Bats emerged significantly later during the rain noise treatment than during the ambient noise treatment (*post hoc* test, z -score=4.44, $P<0.0001$) and the baseline condition (z -score=5.03, $P<0.0001$). There was no difference in time of emergence between the nights of the ambient playback and baseline condition (z -score=0.60, $P=0.82$).

For *M. microtis*, average emergence time for the median bat during the baseline treatment was 215 \pm 398 sas. There was no significant delay of the emergence time during the ambient treatment compared with the baseline condition, as *M. microtis* only delayed its emergence by 44 \pm 104 s (z -score=-0.30, $P=0.95$). *Micronycteris microtis* delayed its emergence time significantly by 435 \pm 549 s during the rain noise treatment compared with the baseline condition (see Fig. 2A; z -score=2.96, $P=0.0087$). The average emergence time during the baseline condition for *M. molossus* was 1065 \pm 191 sas. There was also no significant delay of the emergence time for the ambient treatment, as *M. molossus* delayed its emergence by 86 \pm 302 s (z -score=-0.54, $P=0.852$). But, like *M. microtis*, *M. molossus* delayed its emergence time significantly during the rain noise treatment (by 663 \pm 560 s; see Fig. 2B; z -score=4.15, $P<0.0001$).

Emergence times of the two bat species differed significantly ($\chi^2=20.14$, d.f.=2, $P<0.0001$), with *M. molossus* on average emerging 15.7 min later than *M. microtis* during all treatments, but they did not react differently to the noise treatments (GLMM, $\chi^2=1.34$, d.f.=2, $P=0.51$).

DISCUSSION

In general, animals face the challenge of extracting signals and cues carrying crucial information from masking background noise (Wiley, 2015). Here, we show that two bat species significantly delay their emergence from the roost when confronted with rain noise. We conclude that noise per se can be used as an informational cue, allowing bats to assess environmental conditions and make informed decisions about when to leave the shelter of their roosts.

Being active during rain is potentially costly for bats. As volant mammals, bats are on a tight energy budget (Speakman and

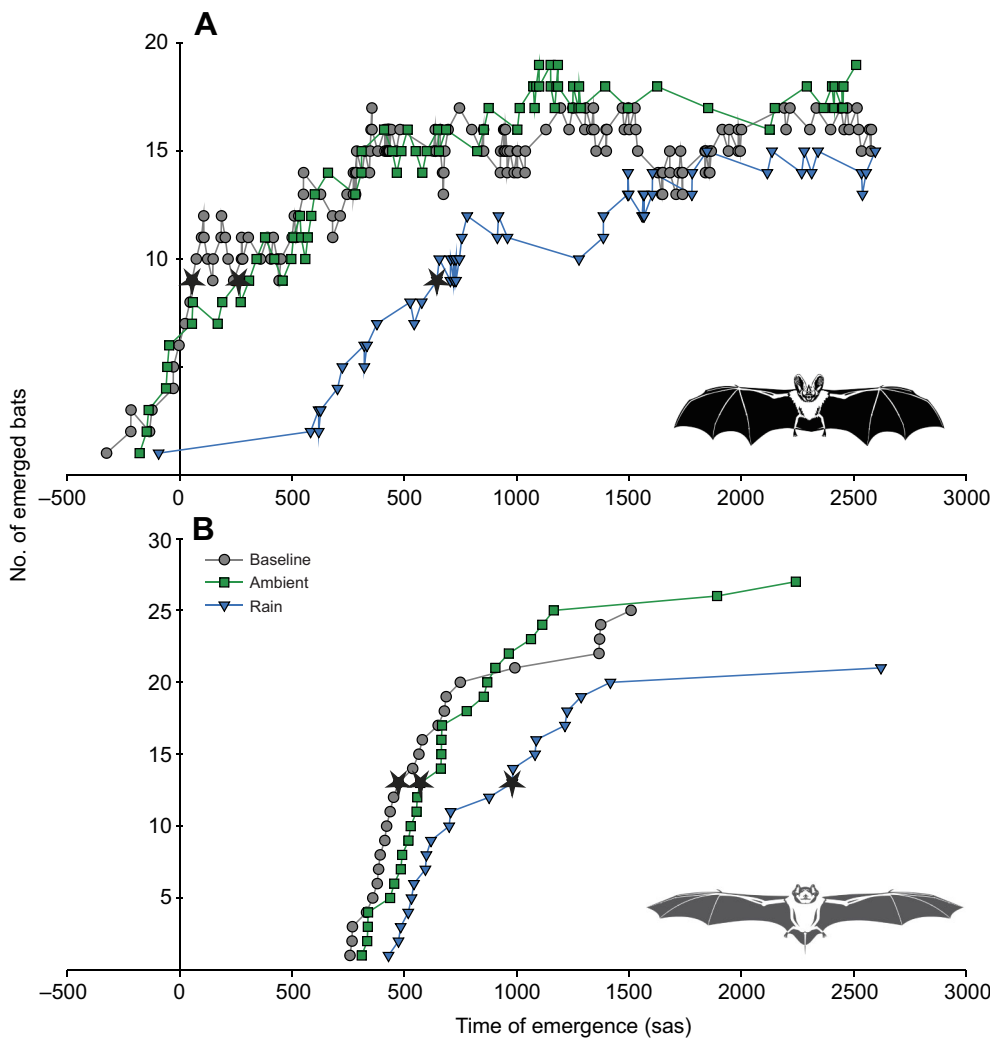


Fig. 1. Example emergence patterns for the two species. Number of bats emerging from the roost during the baseline condition (grey), and ambient noise (green) and rain noise (blue) treatments for *Micronycteris microtis* (A) and *Molossus molossus* (B). Note that *M. microtis* individuals exhibit 'exploration flights', exiting and then returning to the roost within a short period of time. Black stars indicate the median bat. sas, seconds after sunset. Bat illustrations by Diamond Kylo.

Thomas, 2003). Wet bats incur higher metabolic costs than dry bats (Voigt et al., 2011). In addition, during periods of rainfall, bats should experience acoustic costs associated with the rain. Changes in temperature and humidity linked with rainfall impact both atmospheric attenuation and sound speed, altering the transmission and fidelity of bat echolocation calls (Goerlitz, 2018). Recordings suggests that bats flexibly respond to these changes in climatic conditions, altering their calls to improve transmission efficacy (Chaverri and Quirós, 2017). Chaverri and Quirós (2017) show that with an increase in atmospheric attenuation due to shifts in temperature and humidity, bats decrease the frequency and increase the duration of certain call types, which may increase their detection range. In addition to transmission costs induced by changes in temperature and humidity, we argue that the presence of raindrops per se should constitute physical clutter that impedes efficient perception of the returning echoes of echolocation signals. Further, the frequency range of the noise created when rain impacts the ground, vegetation and other surfaces strongly overlaps with the frequency range of the echolocation calls of most bat species (I.G., personal observation), and could thus serve as a potent masker of returning echoes. In sum, while to our knowledge the effect of rain per se on bat sensory systems has not been explicitly tested, we argue that bats are likely to incur three main acoustic costs associated with rainfall: (1) attenuation and degradation of signal transmission due to changes in temperature and humidity, (2)

interference due to the physical clutter of raindrops, and (3) masking due to frequency overlap between echolocation calls and rain noise.

Because of the sensory costs associated with rain described above, we speculate that the two test species should be differentially affected by rain as a result of the disparate ways they use sound for foraging. We argue that *M. microtis*, which uses echolocation calls at close range to detect prey on understory surfaces (Geipel et al., 2013a), would be strongly affected by the noise created by the impact of raindrops on foliage, as well as by interference due to raindrop clutter. In contrast, *M. molossus*, which uses echolocation to detect flying insects in large areas of uncluttered open space (Dechmann et al., 2010) – where there is potentially less masking noise created by raindrops impacting vegetation – might be less affected by rainfall. While the effects of atmospheric attenuation, physical interference and masking rain noise should vary in the open and understory, we argue that both species should be negatively affected in their sensory ability to navigate and detect prey during heavy rainfalls.

Rain noise might also indicate changes in prey availability. In periods of heavy rain, prey abundance can be reduced and insect swarms dispersed (Dechmann et al., 2010). Periods of rainfall can be followed by insect blooms (Chase et al., 1991). As such, depending on the timing and the intensity of the rain, rain noise could serve as an important cue, informing predators about the presence or absence of ephemeral food sources. Observations by

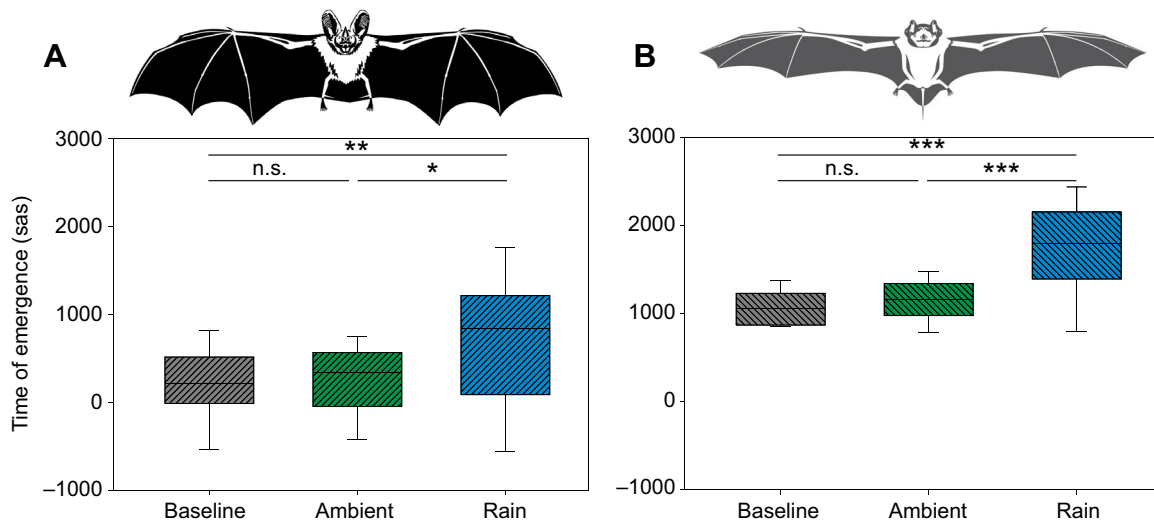


Fig. 2. Time of bat emergence. Time of emergence of the median bat for *M. microtis* (A) and *M. molossus* (B) during the baseline condition (grey), and ambient noise (green) and rain noise (blue) treatments (*** P <0.001, ** P <0.01, * P <0.05; n.s., not significant). Bat illustrations by Damond Kylo.

Chase et al. (1991) support this prediction: *M. molossus* have been reported to leave their roosts for short hunting flights during or immediately after light rain. Thus, in addition to using rain noise to avoid potential metabolic and acoustic costs, we argue that bats could benefit from using rain noise as a source of information about ephemeral food sources.

Molossus molossus has the ability to enter torpor and forage in short concentrated bouts (O'Mara et al., 2017; Dechmann et al., 2010). In contrast, *M. microtis* forages throughout the night (Kalka and Kalko, 2006). We thus hypothesised that *M. molossus* would have the resilience to wait out rainfalls, while *M. microtis* would not have the energy reserves to delay for long periods. Despite differences in their activity patterns and foraging modalities predicting differential costs to foraging in rain, we did not find a difference in delay between the two species. We argue that even though both species may incur different costs associated with rain, they lead to similar emerging behaviour in response to rain noise. Our study suggests that a rain noise-induced delay in roost emergence is a generalised response across a broad range of bats that can vary widely in foraging modalities, strategies and habitats, as well as activity patterns and roost types.

Contrary to expectation, bats did not stay in the roost until rain noise stopped. There are several possibilities why this may be the case. First, our playback did not perfectly mimic the noise of rain. In our experiment, rain noise was broadcast from a single speaker. In nature, rain noise is not a point source, but emanates from every surface raindrops impact. In addition, associated sensory information was missing. In our experiment, we presented only acoustic cues. In nature, rain noise is accompanied by a suite of associated environmental variables: an increase in humidity, a drop in temperature, a decrease in barometric pressure and a change in odour composition (Bear and Thomas, 1964). While each of these factors probably plays a role in bats' decision processes, the results from our experiment suggest that the acoustic component of rainfall has an important influence on whether or not to leave the roost. Decision-making involves a trade-off between speed and accuracy (Stevens, 2013). We argue that of the environmental variables associated with rainfall, sound should be the most immediate and salient source of information to bats, given their sophisticated auditory systems. We suggest that this instantaneous acoustic cue guides bats' initial behaviour, but given time and the

absence of the other variables associated with rain, bats can then reassess their decisions, and emerge prior to the cessation of the experimentally broadcast noise.

Beyond using rain noise to distinguish between the mere presence and absence of rainfall, bats should be able to assess the intensity of a rain event based on differences in the rain noise spectrum and amplitude, and act appropriately, as there is a trade-off: costs associated with being active in rain versus the need to forage. Indeed, rain causes bats to delay their emergence from roosts (Usman et al., 1990; Entwistle et al., 1996). Bat activity ceases during heavy rainfall and is reduced in periods of lighter rain (Audet, 1990; Erickson and West, 2002).

We show that rain noise acts as an informational cue that can have a strong effect on decision-making in bats. We argue that rain noise provides information about costs and benefits for roost emergence and thus for flying in rain. Two of the many predicted trends in the global climate change models are an expansion of the tropical belt (Seidel et al., 2007) and the marked increase in precipitation in tropical regions (Xie et al., 2010). A recent study shows an increase in freshwater accumulation in the wet tropics due to an increase in rainfall (Rodell et al., 2018). This could lead to more rain periods during bat foraging times. In this case, bats must find mechanisms to cope with the increased metabolic and sensory costs associated with increased rainfall events.

Acknowledgements

We thank Asfawossen Asrat for the discussions on climate change, Egbert Leigh for valuable comments on the manuscript, the Wissenschaftskolleg zu Berlin library team for support, and Damond Kylo for the bat illustrations. We thank Brock Fenton and Mark Brigham for their insightful comments which greatly improved this manuscript. We are grateful to the Smithsonian Tropical Research Institute (STRI) for their critical ongoing support.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: I.G., M.J.S., W.H., R.A.P.; Methodology: I.G., M.J.S., W.H.; Validation: I.G.; Formal analysis: M.J.S., W.H.; Investigation: I.G., M.J.S.; Resources: I.G., R.A.P.; Data curation: I.G.; Writing - original draft: I.G., R.A.P.; Writing - review & editing: I.G., R.A.P.; Visualization: I.G.; Supervision: I.G.; Project administration: I.G.; Funding acquisition: I.G., R.A.P.

Funding

I.G. was funded by a Smithsonian Tropical Research Institute Tupper Postdoctoral Fellowship and the Wissenschaftskolleg zu Berlin, Germany. M.J.S. was supported by a Smithsonian Tropical Research Institute internship. R.A.P. and I.G. were funded both by the Smithsonian Tropical Research Institute and by the Human Frontier Science Program (RGP0040/2013).

Data availability

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.192005.supplemental>

References

- Audet, D.** (1990). Foraging behavior and habitat use by a gleaning bat, *Myotis myotis* (Chiroptera: Vespertilionidae). *J. Mammal.* **71**, 420–427.
- Bear, I. J. and Thomas, R. G.** (1964). Nature of argillaceous odour. *Nature* **201**, 993–995.
- Bunkley, J. P., McClure, C. J. W., Kleist, N. J., Francis, C. D. and Barber, J. R.** (2015). Anthropogenic noise alters bat activity levels and echolocation calls. *Glob. Ecol. Conserv.* **3**, 62–71.
- Chase, J., Small, M. Y., Weiss, E. A., Sharma, D. and Sharma, S.** (1991). Crepuscular activity of *Molossus molossus*. *J. Mammal.* **72**, 414–418.
- Chaverri, G. and Quirós, O. E.** (2017). Variation in echolocation call frequencies in two species of free-tailed bats according to temperature and humidity. *J. Acoust. Soc. Am.* **142**, 146–150.
- Condit, R., Robinson, W. D., Ibáñez, R., Aguilar, S., Sanjur, A., Martínez, R., Stallard, R. F., García, T., Angehr, G. R., Petit, L. et al.** (2001). The status of the panama canal watershed and its biodiversity at the beginning of the 21st century. *Bioscience* **51**, 389–398.
- Dall, S. R. X., Giraldeau, L.-A., Olsson, O., Mcnamara, J. M. Stephens, D. W.** (2005). Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.* **20**, 187–193.
- Dechmann, D. K. N., Kranstauber, B., Gibbs, D. and Wikelski, M.** (2010). Group hunting—a reason for sociality in molossid bats? *PLoS ONE* **5**, e9012.
- Emrich, M. A., Clare, E. L., Symondson, W. O. C., Koenig, S. E. and Fenton, M. B.** (2014). Resource partitioning by insectivorous bats in Jamaica. *Mol. Ecol.* **23**, 3648–3656.
- Entwistle, A. C., Racey, P. A. and Speakman, J. R.** (1996). Habitat exploitation by a gleaning bat, *Plecotus auritus*. *Phil. Trans. R. Soc. Lond. B* **351**, 921–931.
- Erickson, J. L. and West, S. D.** (2002). The influence of regional climate and nightly weather conditions on activity patterns of insectivorous bats. *Acta Chiropt.* **4**, 17–24.
- Fenton, M. B., Boyle, N. G. H., Harrison, T. M. and Oxley, D. J.** (1977). Activity patterns, habitat use, and prey selection by some African insectivorous bats. *Biotropica* **9**, 73–85.
- Fenton, M. B., Rautenbach, I. L., Rydell, J., Arita, H. T., Ortega, J., Bouchard, S., Hovorka, M. D., Lim, B., Odgren, E., Portfors, C. V. et al.** (1998). Emergence, echolocation, diet and foraging behavior of *Molossus ater* (Chiroptera: Molossidae). *Biotropica* **30**, 314–320.
- Francis, C. D. and Barber, J. R.** (2013). A framework for understanding noise impacts on wildlife: an urgent conservation priority. *Front. Ecol. Environ.* **11**, 305–313.
- Gager, Y., Tarland, E., Lieckfeldt, D., Ménage, M., Botero-Castro, F., Rossiter, S. J., Kraus, R. H. S., Ludwig, A. and Dechmann, D. K. N.** (2016). The value of molecular vs. morphometric and acoustic information for species identification using sympatric molossid bats. *PLoS ONE* **11**, e0150780.
- Geipel, I., Jung, K. and Kalko, E. K. V.** (2013a). Perception of silent and motionless prey on vegetation by echolocation in the gleaning bat *Micronycteris microtis*. *Proc. R. Soc. B* **280**, 20122830.
- Geipel, I., Kalko, E. K. V., Wallmeyer, K. and Knörnschild, M.** (2013b). Postweaning maternal food provisioning in a bat with a complex hunting strategy. *Anim. Behav.* **85**, 1435–1441.
- Goerlitz, H. R.** (2018). Weather conditions determine attenuation and speed of sound: environmental limitations for monitoring and analyzing bat echolocation. *Ecol. Evol.* **8**, 5090–5100.
- Gomes, D. G. E., Page, R. A., Geipel, I., Taylor, R. C., Ryan, M. J. and Halfwerk, W.** (2016). Bats perceptually weight prey cues across sensory systems when hunting in noise. *Science* **353**, 1277–1280.
- Griffin, D. R., Webster, F. A. and Michael, C. R.** (1960). The echolocation of flying insects by bats. *Anim. Behav.* **8**, 141–154.
- Halfwerk, W. and Slabbekoorn, H.** (2015). Pollution going multimodal: the complex impact of the human-altered sensory environment on animal perception and performance. *Biol. Lett.* **11**, 20141051.
- Halfwerk, W., Bot, S., Buix, J., Van Der Velde, M., Komdeur, J., Ten Cate, C. and Slabbekoorn, H.** (2011). Low-frequency songs lose their potency in noisy urban conditions. *Proc. Natl. Acad. Sci. USA* **108**, 14549–14554.
- Halfwerk, W., Lea, A. M., Guerra, M. A., Page, R. A. and Ryan, M. J.** (2016a). Vocal responses to noise reveal the presence of the Lombard effect in a frog. *Behav. Ecol.* **27**, 669–676.
- Halfwerk, W., Ryan, M. J. and Wilson, P. S.** (2016b). Wind-and rain-induced vibrations impose different selection pressures on multimodal signaling. *Am. Nat.* **188**, 279–288.
- Ibáñez, R., Condit, R., Angehr, G., Aguilar, S., García, T., Martínez, R., Sanjur, A., Stallard, R., Wright, S. J., Rand, A. S. et al.** (2002). An ecosystem report on the Panama canal: monitoring the status of the forest communities and the watershed. *Environ. Monit. Assess.* **80**, 65–95.
- Kalko, M. and Kalko, E. K. V.** (2006). Gleaning bats as underestimated predators of herbivorous insects: diet of *Micronycteris microtis* (Phyllostomidae) in Panama. *J. Trop. Ecol.* **22**, 1–10.
- Lengagne, T. and Slater, P. J. B.** (2002). The effects of rain on acoustic communication: tawny owls have good reason for calling less in wet weather. *Proc. R. Soc. B* **269**, 2121–2125.
- Mackey, R. L. and Barclay, R. M. R.** (1989). The influence of physical clutter and noise on the activity of bats over water. *Can. J. Zool.* **67**, 1167–1170.
- Mcintyre, E., Leonard, M. L. and Horn, A. G.** (2014). Ambient noise and parental communication of predation risk in tree swallows, *Tachycineta bicolor*. *Anim. Behav.* **87**, 85–89.
- Morris-Drake, A., Bracken, A. M., Kern, J. M. and Radford, A. N.** (2017). Anthropogenic noise alters dwarf mongoose responses to heterospecific alarm calls. *Environ. Pollut.* **223**, 476–483.
- O'Mara, M. T., Rikker, S., Wikelski, M., Ter Maat, A., Pollock, H. S. and Dechmann, D. K. N.** (2017). Heart rate reveals torpor at high body temperatures in lowland tropical free-tailed bats. *R. Soc. Open Sci.* **4**, 171359.
- Penna, M., Pottstock, H. and Velasquez, N.** (2005). Effect of natural and synthetic noise on evoked vocal responses in a frog of the temperate austral forest. *Anim. Behav.* **70**, 639–651.
- Roca, I. T., Desrochers, L., Giacomazzo, M., Bertolo, A., Bolduc, P., Deschesnes, R., Martin, C. A., Rainville, V., Rheault, G. and Proulx, R.** (2016). Shifting song frequencies in response to anthropogenic noise: a meta-analysis on birds and anurans. *Behav. Ecol.* **27**, 1269–1274.
- Rodell, M., Famiglietti, J. S., Wiese, D. N., Reager, J. T., Beaudoin, H. K., Landerer, F. W. and Lo, M. H.** (2018). Emerging trends in global freshwater availability. *Nature* **557**, 651–659.
- Santana, S. E., Geipel, I., Dumont, E. R., Kalko, M. B. and Kalko, E. K. V.** (2011). All you can eat: high performance capacity and plasticity in the common big-eared bat, *Micronycteris microtis* (Chiroptera: Phyllostomidae). *PLoS ONE* **6**, e28584.
- Schaub, A., Ostwald, J. and Siemers, B. M.** (2008). Foraging bats avoid noise. *J. Exp. Biol.* **211**, 3174–3180.
- Seidel, D. J., Fu, Q., Randel, W. J. and Reichler, T. J.** (2007). Widening of the tropical belt in a changing climate. *Nat. Geosci.* **1**, 21–24.
- Siemers, B. M. and Schaub, A.** (2011). Hunting at the highway: traffic noise reduces foraging efficiency in acoustic predators. *Proc. R. Soc. B* **278**, 1646–1652.
- Simpson, S. D., Radford, A. N., Nedelec, S. L., Ferrari, M. C. O., Chivers, D. P., McCormick, M. I. and Meekan, M. G.** (2016). Anthropogenic noise increases fish mortality by predation. *Nat. Commun.* **7**, 10544.
- Slabbekoorn, H.** (2013). Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. *Anim. Behav.* **85**, 1089–1099.
- Speakman, J. R. and Thomas, D. M.** (2003). Physiological ecology and energetics of bats. In *Bat Biology* (ed. T. H. Kunz and M. B. Fenton), pp. 430–490. Chicago, IL: University of Chicago Press.
- Stevens, M.** (2013). *Sensory Ecology, Behaviour, And Evolution*. Oxford: Oxford University Press.
- Usman, K., Subbaraj, R. and Subramanian, P.** (1990). Seasonality in the flight activity of the tropical bat *Rhinopoma hardwickei* under natural photoperiod. *Behav. Processes* **21**, 81–94.
- Vermeij, M. J. A., Marhaver, K. L., Huijbers, C. M., Nagelkerken, I. and Simpson, S. D.** (2010). Coral larvae move toward reef sounds. *PLoS ONE* **5**, e10660.
- Villalobos-Jiménez, G., Dunn, A. M. and Hassall, C.** (2017). Environmental noise reduces predation rate in an aquatic invertebrate. *J. Insect. Conserv.* **21**, 839–847.
- Voigt, C. C., Schneeberger, K., Voigt-Heucke, S. L. and Lewanzik, D.** (2011). Rain increases the energy cost of bat flight. *Biol. Lett.* **7**, 793–795.
- Wiley, R. H.** (2015). *Noise Matters: the Evolution of Communication*. Cambridge: Harvard University Press.
- Willig, M. R., Camilo, G. R. and Noble, S. J.** (1993). Dietary overlap in frugivorous and insectivorous bats from edaphic Cerrado habitats of Brazil. *J. Mammal.* **74**, 117–128.
- Xie, S.-P., Deser, C., Vecchi, G. A., Ma, J., Teng, H. and Wittenberg, A. T.** (2010). Global warming pattern formation: sea surface temperature and rainfall. *J. Clim.* **23**, 966–986.
- Zhao, L., Zhu, B., Wang, J., Brauth, S. E., Tang, Y. and Cui, J.** (2017). Sometimes noise is beneficial: stream noise informs vocal communication in the little torrent frog *Amolops torrentis*. *J. Ethol.* **35**, 259–267.