

Temperate bats may alter calls to partially compensate for weather-induced changes in detection distance

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ABSTRACT:

Echolocation is the use of self-emitted calls to probe the surrounding environment. The atmosphere strongly absorbs sound energy, particularly high frequencies, thereby limiting the sensory range of echolocating animals. Atmospheric attenuation varies with temperature and humidity, which both vary widely in the temperate zone. Since echolocating insectivorous bats rely on ultrasound to capture insects, their foraging success might decrease with seasonal and daily variations in weather. To counteract weather-induced variations in prey detection, we hypothesised that European bats decrease call frequency and increase call energy when atmospheric attenuation increases, thereby maintaining their prey detection distance. Using acoustic localisation and automated call analysis, we measured call frequency and energy in free-flying bats of three common European insectivorous species. One species, *Pipistrellus nathusii/kuhlii*, increased call frequency, but simultaneously decreased call energy, while the two other species (*P. pipistrellus* and *Myotis daubentonii*) did not alter call parameters. We estimated the detection distance for prey based on the recorded call parameters and prey characteristics, using a custom-developed theoretical model. None of the three species maintained prey detection distance (it decreased by 1.7 to 3.4 m) when atmospheric attenuation increased. This study contributes to a better understanding of the sensory challenges faced by animals in fluctuating environments. © 2023 Acoustical Society of America. <https://doi.org/10.1121/10.0019359>

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I. INTRODUCTION

Animals need to acquire information about their surroundings to guide their actions, such as mate choice, foraging decisions, and predator avoidance. Given the influence of these behaviors on survival and fitness, sensory systems are under strong selection pressure to collect sufficient and relevant information (Dall *et al.*, 2005). The sensory drive hypothesis postulates that sensory systems and signals are adapted to environmental characteristics (Cumplings and Endler, 2018; Endler, 1992), including both evolutionary adaptations as well as short-term behavioral plasticity (Basolo and Endler, 1995). For instance, the eyes of marine invertebrates are more sensitive to light of shorter wavelength than terrestrial animals, as longer wavelengths are strongly absorbed underwater (Marshall, 2017). In fluctuating environments, many animals adjust their signals to maintain detectability by targeted receivers, for example, by vocalizing louder in noisy conditions [Lombard effect (Brumm and Zollinger, 2011)]. Active sensing systems, such as bat echolocation, are ideal to understand how animals optimize signaling to maximize information transmission. Echolocating bats emit a sensory probe of energy, namely an ultrasonic call, and analyze the returning echoes to obtain information about their environment (Griffin *et al.*, 1960). Crucially, bats adjust the probe very flexibly to the

current task and situation (Lewanzik and Goerlitz, 2021), for example, while commuting and hunting (Mutavhatsindi, 2018; Obrist, 1995; Schnitzler *et al.*, 2003), to object distance (Brinkløv *et al.*, 2010; Kalko and Schnitzler, 1993; Lewanzik and Goerlitz, 2018), conspecifics, and noise conditions (Luo *et al.*, 2015; Obrist, 1995).

Bat echolocation calls are mostly ultrasonic (approximately 9–200 kHz). The higher their frequency, the stronger the calls are attenuated by the air (Griffin, 1971; Hartley, 1989). For instance, a call at 50 kHz (typical for European bats) is attenuated by about 1.2 dB every meter (Goerlitz, 2018). In foggy conditions, ultrasound attenuation has even been shown to reach values of 35 dB/m due to the resonance of water droplets, and bats avoid the fog patches altogether (Pye, 2021, 1971). To counteract atmospheric attenuation, bats emit echolocation calls at a very high intensity [100–140 dB SPL re 20 μPA at 10 cm (Surlykke and Kalko, 2008), which is close to and above the human pain threshold]. Despite this high intensity, bats can only detect their insect prey over rather short distances of typically just a few meters (Goerlitz *et al.*, 2020; Holderied and von Helversen, 2003; Møhl, 1988; Stiltz and Schnitzler, 2012). In addition to sound frequency, atmospheric attenuation also depends on the air's temperature and relative humidity in a non-linear fashion, causing weather-dependent variations in prey detection distance beyond the bat's control (Goerlitz, 2018). Prey detection distance limits the amount of detectable prey and in turn foraging success (Luo *et al.*, 2014; Safi and Siemers, 2010; Stidsholt *et al.*, 2021). Thus bats have been suggested

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to plastically adjust echolocation call parameters to the ambient atmospheric conditions to counteract this effect (Snell-Rood, 2012).

Bats in temperate areas face a broad range of atmospheric conditions with rather fast daily and seasonal changes, causing large and short-term variations in atmospheric attenuation and prey detection distance (Lawrence and Simmons, 1982). For example, an increase in nightly temperature from 8 °C in March to 20 °C in July increases the atmospheric attenuation of a call at 50 kHz by more than 50% (from 1.1 dB/m to 1.7 dB/m, at 70% relative humidity; Fig. 1), in turn reducing the detection distance of a small moth by 20%, from 7.9 to 6.3 m (given a call source level of 130 dB SPL @ 10 cm). Converted to volume, a loss of 20% sensory range equals a loss of ~50% in perceived space. To date, individual differences in response to changes in atmospheric attenuation was only shown in two tropical free-flying species (Chaverri and Quirós, 2017) and suggested for another tropical, resting hipposiderid species in captivity (Wu *et al.*, 2021). Despite the stronger variation in atmospheric conditions faced by temperate bats, individual call plasticity was not tested in bats outside tropical regions. In addition, previous work focused on changes in call frequency (Chaverri and Quirós, 2017; Jacobs *et al.*, 2017; Mutavhatsindi, 2018; Snell-Rood, 2012), neglecting other call parameters, which also influence detection distance. While reducing call frequency is one means of reducing atmospheric attenuation, increasing call level and call duration directly increase call energy (Heil and Neubauer, 2003) and can be much more relevant to improve sound perception (Luo *et al.*, 2015). Despite the central importance of source level for sensory range (Goerlitz *et al.*, 2020; Stidsholt *et al.*, 2021), there is still a lack in data—likely due to the difficulty of precisely measuring the position of quickly moving animals in three dimensions in the dark.

To address this gap in knowledge, we tracked the spatial position of three species of free-flying European insectivorous bats over two seasons, recorded their echolocation calls and analyzed their call parameters across the natural range of temperature and humidity conditions that these animals faced throughout the year. We hypothesized that bats maintain their prey detection distance by adjusting their echolocation call parameters to counteract weather-induced variation in atmospheric attenuation. We used the collected data to test whether bats (1) decrease call frequency and/or (2) increase call energy with increasing atmospheric attenuation [Fig. 2(B)]. Furthermore, we developed a quantitative model based on the sonar equation (Möhl, 1988), prey size, call parameters, and weather conditions, to test whether (3) bats maintain the detection distance for prey independently of weather conditions.

II. METHODS

A. Field sites, recording setup, and species

We opportunistically recorded the echolocation calls of wild free-flying insectivorous bats at seven different hunting grounds in southern Bavaria near ponds and rivers, which attract insect prey. The sites were more than 5 km apart and visited for 30 nights (10 nights in 2017 and 20 nights in 2019) from sunset until about two hours after sunset. The most common recorded species were the Common pipistrelle (*Pipistrellus pipistrellus*), the Nathusius or Kuhl’s Pipistrelles (*P. nathusii/kuhlii*), which we did not attempt to distinguish, and Daubenton’s bat (*Myotis daubentonii*). We recorded their echolocation calls with an array of four omnidirectional microphones (FG-O; Avisoft Bioacoustics, Germany), an audio interface (USG-416H; Avisoft), and the AVISOFT RECORDER software, as 4-channel .wav files to a

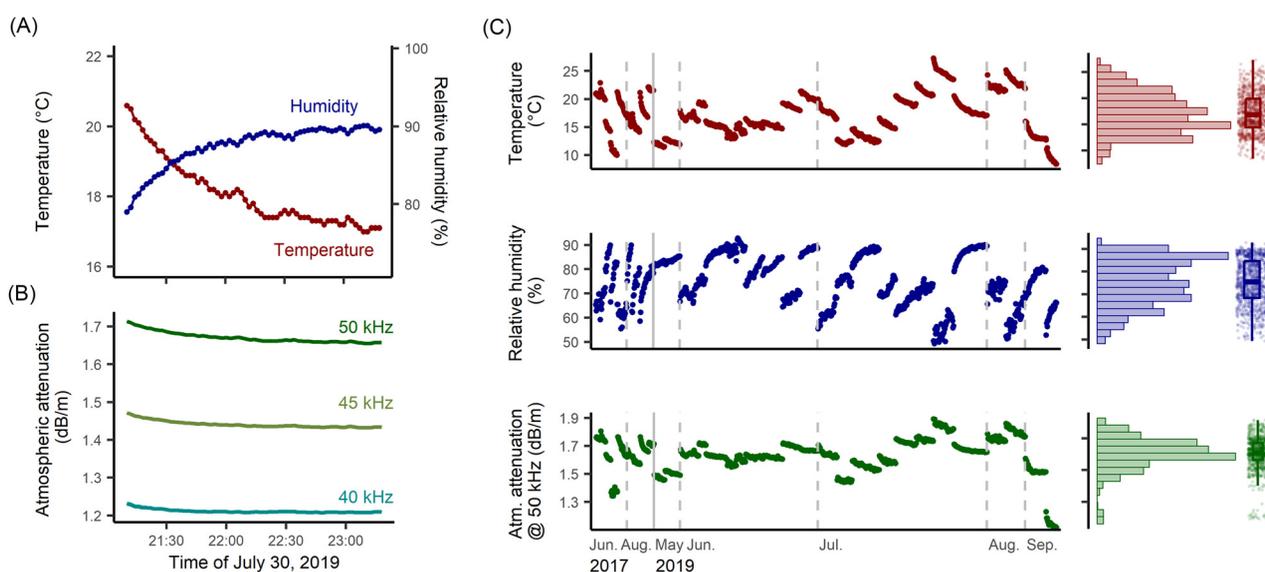


FIG. 1. (Color online) Temperature, humidity and atmospheric attenuation vary across a night [(A), (B)] and the season (C). (A) Temperature and relative humidity for one evening (July 30th, 2019). (B) Atmospheric attenuation at 40 (bottom), 45 (middle), and 50 (top) kHz for one evening, corresponding to the weather conditions in A. (C) Temperature (top), relative humidity (middle), and atmospheric attenuation at 50 kHz (bottom) across all 30 nights in 2017 and 2019. Each comma-shaped group of points corresponds to a different night; histograms and boxplots on the right combine all data points.

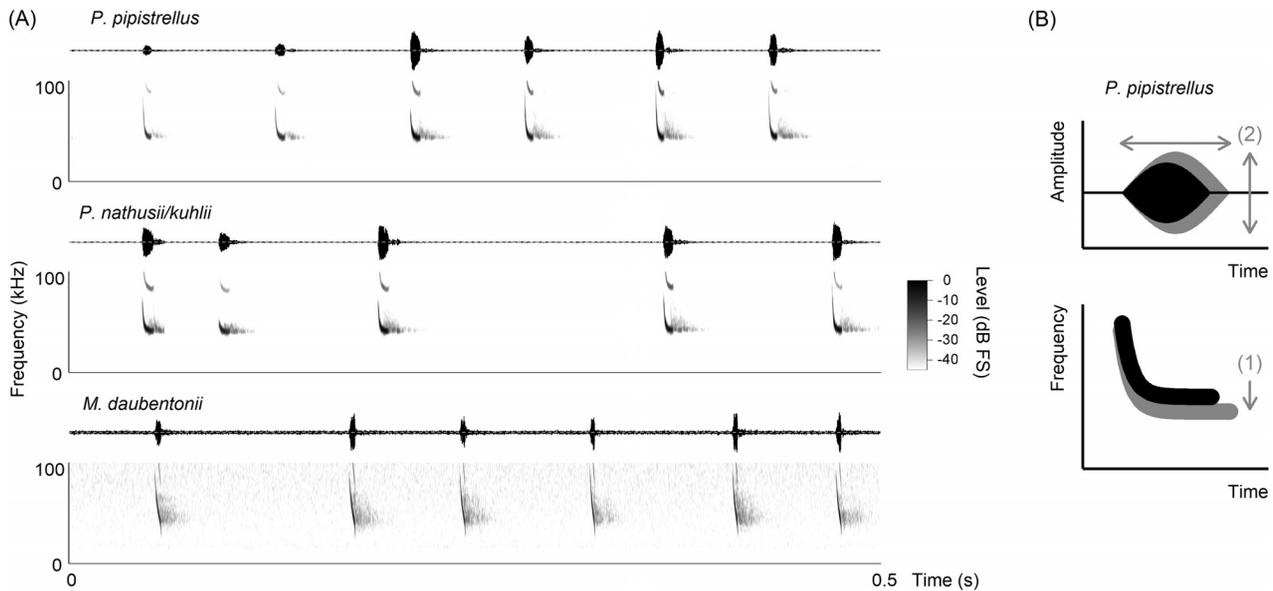


FIG. 2. Typical echolocation call sequences and predictions. (A) Oscillogram (top) and spectrogram (bottom) of a 0.5-s-long sequence of echolocation calls for each of the three studied species (groups). (B) Our two main hypotheses visualised on an oscillogram (top) and spectrogram (bottom). As indicated by the arrows, we predicted that bats emit shorter calls of lower amplitude (= less energy, hypothesis 2) and higher frequency (hypothesis 1) when atmospheric attenuation is low (black) and, vice versa, we predicted that they emit longer calls of larger amplitude and lower frequency when atmospheric attenuation is high (gray).

laptop at 500 kHz sampling rate and 16-bit resolution. The microphones were arranged as a planar star-shaped array, with one central microphone surrounded by three peripheral microphones at 60 cm distance and 120° inter-microphone angle. The array was positioned against a background structure (close to trees or hedgerows) and directed towards the common approach directions of the bats. We measured the array's inclination, height above ground, and distance to surrounding objects and trees (inclinometer and laser range finder GLM 50 C, Bosch, Germany). We maximized the recording gain of the audio interface without clipping the recordings and noted it for further source-level analysis. We manually started recordings when bat calls were visible on the live oscillogram display, including a 5 s pre-buffer, and stopped them after maximally 10 s, to include about 1 to 5 bat passes in each recording. Temperature and relative humidity were continuously logged in 2-min intervals throughout the recording session (Kestrel 4000 Pocket Weather Tracker; Kestrel Meters, USA).

B. Reconstruction of flight trajectories and acoustic call analysis

We analyzed the recordings to obtain the bats' three-dimensional position at call emission and the acoustic call parameters as emitted by each bat. First, we manually screened all recordings in SASLAB Pro (Avisoft) to select high-quality recordings, i.e., which contain multiple calls with peak amplitudes ≥ -20 dB full-scale, few overlapping calls, and minimal interference patterns indicated by variation in the amplitude envelope. Selected call sequences were semi-automatically analyzed with the custom-written software TOADSUITE [Peter Stilz; see Goerlitz (2018) and Lewanzik and Goerlitz (2018)] for MATLAB (version R2007b; The Mathworks, Inc., Natick,

MA). Second, the recordings were bandpass-filtered around each species' echolocation call frequencies. Echolocation calls were detected and extracted from the recordings of the central microphone with an amplitude threshold and a refractory period after each call detection to exclude echoes (settings were adjusted for each recording session, see Table S1 in the supplemental material¹). Third, we calculated the time-of-arrival difference between the detected calls on the central microphone and each peripheral microphone using cross correlation and used them to calculate the bat's three-dimensional position at each emitted call.

We then visualized the bats' 3D positions and their call spectrograms for each recording, and manually combined positions into trajectories, based on spatial and temporal relationships. Species ID per trajectory was determined based on minimum frequency [measured manually in AVISOFT using the procedure in Dietz and Kiefer (2016) and Russ (2012)] and social calls (Middleton *et al.*, 2014), if present. We only included high-quality search calls into the trajectories and excluded approach and buzz calls and low-quality calls (e.g., containing interference patterns, overlapping calls, full-scale amplitude lower than -30 dB). We excluded approach and buzz calls from the moment we saw the typical decrease in call duration, call interval, and change in call shape when bats approach a target (Griffin *et al.*, 1960; Schnitzler *et al.*, 2003). Trajectories were smoothed with cubic-smoothing splines over time (intermediate TOADSUITE smoothing factor of 1) and used to calculate the flight speed, flight angle, and velocity relative to the microphone.

For all detected calls, we automatically calculated multiple acoustic parameters as emitted by the bat. Since atmospheric attenuation and spherical spreading over the distance from the bat's position to the microphone affect call

recordings, we corrected the recordings for distance-dependent atmospheric attenuation and spreading to obtain the call parameters as emitted by the bat (at 10 cm distance from its mouth). We extracted each call from the recordings of the central microphone, calculated its amplitude and phase spectrum with a fast Fourier transformation (FFT), corrected the amplitude spectrum for distance-dependent geometric attenuation (spherical spreading) and distance-, frequency-, and weather-dependent atmospheric attenuation, and reconstructed the call's emitted waveform with an inverse FFT, which we used to calculate the call's duration, lowest frequency apparent source level, and source energy. We first determined each call's start and end time and its duration from the smoothed (moving average across 0.2 ms) Hilbert-envelope at -12 dB relative to the envelope's peak value. The lowest frequency, defined as the lowest frequency with an amplitude at -12 dB relative to the highest amplitude, was calculated from the call's time-averaged spectrogram (window length 2048 samples, overlap 95%) from call start to call end (Fig. S1 in the supplemental material¹). A graphical illustration of the measured parameters is shown in Fig. S1. Apparent source-level aSL (RMS dB re $20 \mu\text{Pa}$ @ 10 cm) was calculated as the root mean square (rms) of the call waveform and expressed relative to $20 \mu\text{Pa}$. Apparent source energy aE (RMS dB re $20 \mu\text{Pa} * 1 \text{ s}$ @ 10 cm) was calculated from the apparent source level and call duration as

$$aE \text{ (dB rms @ 10 cm)} = aSL \text{ (dB rms @ 10 cm)} + 10 \log_{10}(\text{duration (s)}). \quad (1)$$

We corrected the lowest frequency for the Doppler shift induced by the bat's movement relative to the microphone as

$$F_{corr} = F \times \frac{(\text{sound speed} - \text{bat velocity relative to the mic})}{\text{sound speed}}. \quad (2)$$

For the final analyses, we only used those search calls that we manually assigned to trajectories. We furthermore excluded calls with a signal-to-noise-ratio (SNR) < 20 dB, with a peak frequency > 55 kHz (i.e., calls with more energy in the second harmonic or wrongly measured peak frequency), or with a non-realistic flight speed (< 2 or > 10 m/s), and obvious measurement errors (call duration below 2 ms, above 15 ms, call interval < 50 ms, which corresponds to approach and feeding buzz calls). Furthermore, we excluded trajectories with less than five calls. In total, we analyzed 1490 recordings with 33 374 calls, resulting in 2385 reconstructed trajectories, of which we excluded 5158 calls and 61 trajectories (final N: 2324 trajectories, 28 216 calls).

C. Statistical analysis of the effect of weather conditions on call parameters

To maintain detection distance despite increasing atmospheric attenuation, bats could either lower call frequency,

since low frequencies experience less atmospheric attenuation than high frequencies, and/or increase call energy, since the ears of vertebrates are energy integrators [Fig. 2(B); Heil and Neubauer (2003) and Luo *et al.* (2015)]. We thus analysed the effect of weather conditions on call frequency and call energy. We chose to analyse the call's lowest frequency, assuming that bats obtain the maximum detection distance for a target prey with the lowest frequency. We chose to analyse call energy, since it is the sum of the squared amplitude values over the call's duration, i.e., a combination of call duration and source level. Bats may alter source level and call duration independently to increase call energy, and thus to maintain echo detection. Increasing duration at a constant source level increases detection range, as does increasing source level at a constant duration. To address detection with one common variable we chose to study call energy instead of duration and source level independently.

Echolocation calls are directional, having the highest intensity along the call axis (Hartley and Suthers, 1989; Surlykke *et al.*, 2009) and lower energy with increasing off-axis angles. Since bats move their sonar beam to scan their environment (Seibert *et al.*, 2013) and do not necessarily fly directly towards the microphone, the beam axis of their echolocation calls is rarely centred on the microphone. Calculated call source levels thus underestimate the real source level. To counteract this effect, we calculated the so-called apparent energy (aE) per trajectory as the 90th percentile of the energy of all calls in a trajectory. Furthermore, for each trajectory, we calculated the atmospheric attenuation coefficient α (Goerlitz, 2018; International Organization for Standardization, 1993), using the measured ambient temperature, relative humidity, and two frequency measures: (1) the median of the lowest frequency of all calls in the trajectory to obtain the real α for the current trajectory ("responsive bat") and (2) using the median of the lowest frequency medians across all trajectories of each species, to obtain the average α for a hypothetical bat that does not adjust its call parameters to weather-conditions ("non-responsive bat").

We fitted two mixed-effect models in R (version 4.0.4) using the package *lme4* (version 1.1–26) to determine the effect size of atmospheric attenuation on the lowest frequency and apparent call energy, using the median lowest frequency and the apparent call energy per trajectory as response variables. We used the species and the year of recording as fixed effects, to control for species-specific differences and differences introduced by two different experimenters. The interaction between the species and atmospheric attenuation was placed in the model, to get the species-specific response to changes in temperature and humidity. Recording session per night and recording site were added as random effects. Because we could not individually identify the bats, we hypothesized that two trajectories that immediately follow each other have a higher probability to be from the same bat, circling in front of the microphone, than two trajectories randomly sampled in the dataset. To account for this, we added a species-specific trajectory ID as

a random slope nested within the recording session. The quality of model fits was evaluated by inspecting the distribution of residuals and random effects, and confirming the absence of autocorrelation, heteroscedasticity or obvious trends in the residuals (Pinheiro and Bates, 2006). We calculated Bayesian credible intervals (CrI) of model coefficients with flat priors by simulating the models 1000 times and calculating the 2.5% and 97.5% percentile of the posterior estimates using the *arm* package (version 1.11-2).

D. Estimating detection distance

The maximum detection distance depends on call frequency and amplitude, sound transmission (i.e., atmospheric attenuation) as well as insect reflective properties. The target strength describes the echo-acoustic reflective properties of an object, stating how much of the incoming sound is reflected. For example, small insects reflect low frequencies worse than large insects due to the scattering of sound, which potentially changes insect detectability across frequencies (Safi and Siemers, 2010). Previous work has suggested that echolocation call frequency does not influence insect detectability in the range used by bats since the target strength of large insects is stable across frequencies (Surlykke *et al.*, 1999), or the increased attenuation balances the increase in target strength of small insects with higher frequencies (Houston *et al.*, 2004). However, there is to date no general formalized description of the maximum detection distance expressed as a function of call frequency and insect size. Such a model is necessary to understand the implications of call parameter alteration on prey detection, especially when sound transmission characteristics change due to variations in weather conditions. We thus devised a model that calculates target strength as a function of object size and call frequency, and then calculates the detection distance for this object given certain call parameters and weather conditions. We used this model for two purposes: (1) to estimate the theoretical parameter space of target strengths and detection distances for the varying call parameters and weather conditions, and (2) to test whether the empirically measured changes in call parameters enable bats to compensate for weather-induced changes in detection distance (Fig. 5).

The target strength depends on the object’s size, its geometry, and the wavelength of the impinging sound. When an object is smaller than the sound’s wavelength, less energy is reflected. We calculated the target strength (TS) of an insect as a function of its insect-equivalent disk area (surface of a disk that has the same target strength than an insect of a given size [A, in m² (Kerry, 2004)] and the sound wavelength λ (m) (Kerry, 2004),

$$TS = 10 \log_{10} \left(\frac{A^3}{A^2 + \lambda^4} \right). \tag{3}$$

We then used the target strength to calculate prey detection distance, i.e., the maximum distance over which an insect can be detected by a bat, based on the sonar equation

(Møhl, 1988), which calculates the echo level as a function of source level, distance, atmospheric attenuation, and target strength,

$$\begin{aligned} \text{Echo Level} = & \text{Source Level} - 40 * \log_{10} \left(\frac{1}{\text{dist}} \right) \\ & - 2 * \text{Atm. Attenuation} * \text{distance} \\ & - \text{Target strength}. \end{aligned} \tag{4}$$

The detection distance is the largest distance for which the echo level is still above a detection threshold, which we set to 20 dB re 20 μPa SPL (Kick, 1982).

In a first step, we calculated the target strength for insects of six different sizes (insect-equivalent disk area A = 10, 30, 60, 100, and 200 mm²) and for six typical bat call frequencies between 40 and 50 kHz. We then calculated the detection distance for these insects for the atmospheric attenuation of six typical weather conditions (10, 15, or 20 °C and 65% or 85% relative humidity) and by a typical pipistrelle bat calling with a source level of 110 dB re 20 μPa SPL @ 10 cm and with peak frequencies between 40 and 50 kHz.

In a second step, we then used Eq. (4) to calculate the detection distance for the modelled insects of different sizes based on our field data, i.e., using the call source level and lowest frequency measured for each bat species across the range of ambient temperatures and humidities. In this way, we modelled prey detection distances for bats that changed call parameters as a function of changing temperature and humidity. We compared these prey detection distances of a “responsive bat” to the prey detection distance calculated with species-specific average call parameters, thereby modelling a “non-responsive bat.” We analysed the variation of detection distance with increasing atmospheric attenuation, as well as the difference between the detection distance of responsive bats and non-responsive bats with the same statistical mixed effect model described in the preceding paragraph.

III. RESULTS

We recorded bat echolocation calls and atmospheric conditions over 30 nights of two years, covering a broad range of temperature (9.6–26.1 °C) and relative humidity (50.6%–92.8%). This variation in weather conditions resulted in high variation in atmospheric attenuation. For example, for a 50-kHz call, the atmospheric attenuation coefficient ranged from 1.13 to 1.86 dB/m (Fig. 1), i.e., a difference of >60% (~0.7 dB/m) from the lowest to the highest absorption conditions. We analysed 28 216 calls from 2324 trajectories of three different species (groups): two species (groups) of the edge-space aerial-hawking genus *Pipistrellus*, namely, *P. pipistrellus* (1497 trajectories and 18 477 calls) and *P. nathusii/kuhlii* (690 trajectories and 8878 calls), and the trawling species *Myotis daubentonii* (138 trajectories and 861 calls).

A. Weather-correlated changes in echolocation call parameters

Typical echolocation call sequences of all three species are shown in Fig. 2(A). Median lower frequency was 40.1 kHz for *P. pipistrellus* (interquartile range 38.9–41.4 kHz), 34.6 kHz (33.6–35.5) for *P. nathusii/kuhlii*, and 33.9 kHz (32.0–37.2) for *M. daubentonii* (Fig. S2 in supplementary material¹), and generally decreased with increasing call duration (Fig. S3). Median call duration was 5.4 ms for *P. pipistrellus* (interquartile range 4.7–6.1), 6.1 (5.2–6.9) for *P. nathusii/kuhlii*, and 3.6 (3.1–4.5) for *M. daubentonii* (Fig. S2). Median apparent source level, estimated per trajectory as the 90th percentile of all calls, was 116 dB SPL RMS re 20 μPa @ 10 cm distance for both pipistrelle species (interquartile range 113–120) and slightly lower for *M. daubentonii* (median of 112 dB SPL RMS, interquartile range 108–115, Fig. S2).

We found potentially relevant weather-correlated changes in call parameters in only one species group, *Pipistrellus nathusii/kuhlii* (Table I, Fig. 3). As predicted, these bats lowered their lowest call frequency with increasing atmospheric attenuation, with a mean effect size of –5.8 kHz for every increase in atmospheric attenuation by 1 dB/m (95% credible interval (CrI)=[–9.3, –2.3]; Fig. 3(B)). Opposite to our prediction, however, the call energy decreased with increasing atmospheric attenuation [–14.4 [–22.5, –6.2] dB for every increase in AA by 1 dB/m; Fig. 3(A)]. The other two species, *P. pipistrellus* and *M. daubentonii*, showed no clear directional change in call frequency since the credible intervals included Zero for both species (*P. pipistrellus*: –0.5 [–2.9, 1.8] kHz and *M. daubentonii*: –0.9 [–7.5, 5.4] kHz, for an increase in AA by 1 dB/m). For call energy, credible intervals only barely included Zero, indicating some probability that these species also

lowered call energy with increasing atmospheric attenuation (*P. pipistrellus*: mean: –5.1 [–10.6, 0.4] dB; *M. daubentonii*: –14.3 [–28.4, 0.4] dB for an increase in AA by 1 dB/m). As another estimate of the probability that these species lowered their call energy, we calculated the probability that the true mean was lower than a biologically relevant change by –3 dB, which was 0.77 for *P. pipistrellus* and 0.93 for *M. daubentonii*.

B. Interacting effects on prey detection distances

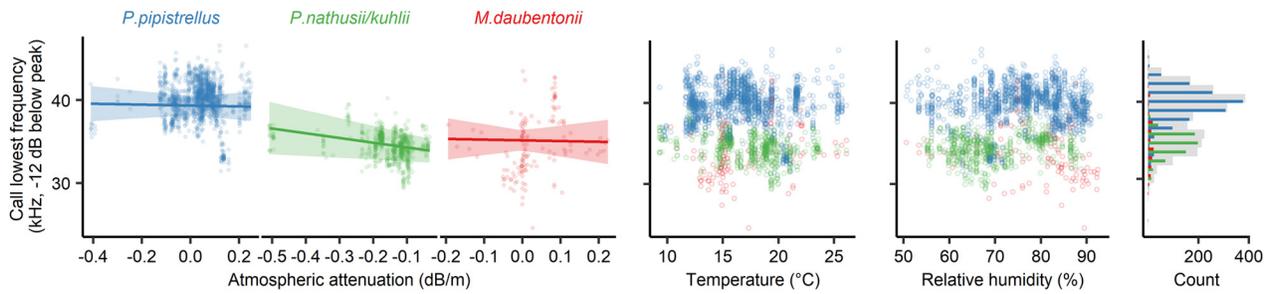
First, we quantified by how much bats could theoretically increase their detection distance by decreasing their call frequency. The maximum detection distance increases with larger target strength (Goerlitz, 2018; Möhl, 1988; Stilz and Schnitzler, 2012) and decreases with atmospheric attenuation [Eq. (4)], which both depend on call frequency. Decreasing call frequency has two effects: it reduces atmospheric attenuation, but may also reduce target strength once the ratio between insect size and sound wavelengths becomes too small, i.e., more so for small than for large insects (Kerry, 2004; Surlykke et al., 1999). For example, decreasing call frequency from 100 kHz to 10 kHz (wavelength increases from 3.6 mm to 36 mm) reduces the target strength of a large insects (area 100 mm²) by only 3 dB, while it reduces target strength of a small insect (area 10 mm²) by 37 dB.

Across the typical frequencies (40–50 kHz) and weather conditions (10, 15, and 20 °C, 65% and 85% relative humidity) tested in our theoretical model, prey size has a predominant effect on detection distance. The mean detection distance for large prey with 200 mm² surface area was 3.7 m (+/– 0.18 m SD), which is 2.4× longer than the detection distance of 1.1 m (+/– 0.06 m SD) for a small prey with 10 mm² surface area [Fig. 4(B)].

TABLE I. Estimate and 95% credible interval (in brackets) of the effect size (slope) of four mixed-effect models describing the species-specific variation of the lowest call frequency, the call energy, the detection distance of a 60 mm² insect, and the difference between the detection distance for a responsive bat and a non-responsive bat that emits calls of average frequency and energy. Example to read the table: The lowest frequency of *P. pipistrellus* changed by –0.5 kHz (credible interval: –2.9, 1.8) when the atmospheric attenuation increased by 1 dB/m.

Species	Predictor	Response variable			
		Lowest frequency (kHz)	Call energy (dB)	Detection distance (m)	Delta detection distance (m)
<i>P. pipistrellus</i>	(intercept)	39.3 (38.3, 40.5)	94.3 (92.8, 95.9)	3.5 (3.4, 3.6)	0.1 (–0.1, 0.3)
	Atmospheric attenuation (1 dB/m)	–0.5 (–2.9, 1.8)	–5.1 (–10.6, 0.4)	–1.7 (–2.4, –1.0)	–0.8 (–1.4, 0.2)
<i>P. nathusii/kuhlii</i>	(intercept)	33.7 (32.5, 35.0)	93.1 (91.0, 95.2)	3.1 (2.9, 3.3)	–0.4 (–0.6, –0.2)
	Atmospheric attenuation (1 dB/m)	–5.8 (–9.3, –2.3)	–14.4 (–22.5, –6.2)	–3.4 (–4.4, –2.4)	–2.4 (–3.3, –1.4)
<i>M. daubentonii</i>	(intercept)	35.1 (33.9, 36.3)	89.1 (87.3, 90.9)	3.0 (2.9, 3.2)	0.2 (0, 0.3)
	Atmospheric attenuation (dB/m)	–0.9 (–7.5, 5.4)	–14.4 (–28.4, 0.6)	–1.9 (–3.7, –0.1)	–1.2 (–3.1, 0.6)
	Year	–0.2	–1.5	–0.1	–0.1
	2017	(–1.8, 1.2)	(–3.7, 0.8)	(–0.3, 0.1)	(–0.3, 0.1)

(A) Call lowest frequency



(B) Call energy

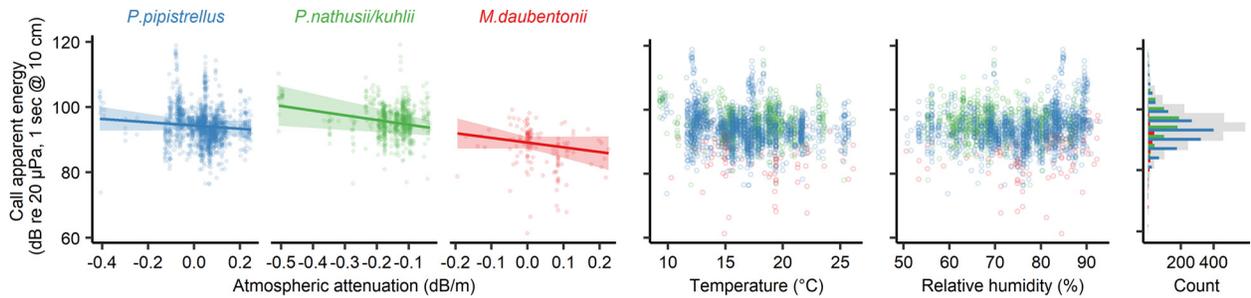


FIG. 3. (Color online) Changes in call energy and frequency with atmospheric conditions. Median lowest call frequency (A) and median call energy (B) per trajectory as a function of atmospheric attenuation (raw data, mean and 95% credible interval from the linear mixed model), as function of the temperature and the relative humidity, then followed by the distribution of the call parameter. Bat species are coded with shades.

The effect of frequency on detection distance depended heavily on prey size. For large prey (200 mm²), lower frequencies always resulted in longer detection distance, due to their lower atmospheric attenuation for all weather conditions [Fig. 4(B), 200 mm²]. For example, reducing call frequency from 50 to 40 kHz, extends the detection distance by 14 cm (~4%) at 10 °C and 65% RH, and by 42 cm (12%) at 20 °C and 85% RH. Therefore, lowering call frequency will always increase the detection distance of large prey at constant weather conditions. However, for changing weather conditions, which decrease detection distance by up to 13% across the range of modelled weather conditions, reducing call frequency from 50 to 40 kHz (the typical range of echolocation calls of *P. pipistrellus*) is barely sufficient to maintain detection distance. In contrast, for small prey (10 mm²), lower frequencies always resulted in shorter detection distances, due to the small prey’s weaker target strength, for all weather conditions [Fig 4(B), 10 mm²]. Finally, the effect of frequency on the detection distance of medium-sized prey (size-to-wavelength-ratio around 1) is harder to predict and additionally depends on the weather conditions [Figs. 4(A) and 4(B)]. For example, in weather conditions with high atmospheric attenuation (e.g., 15 °C, 85% RH), the bats could mitigate a further increase in attenuation (e.g., because of a temperature rise to 20 °C, which would lower the detection distance at 50 kHz by 2%) by decreasing call frequency, which would increase the detection distance by up to 3%, thereby compensating the weather-induced loss. In contrast, the opposite is true in weather conditions with low atmospheric attenuation (e.g., 10 °C, 65%). If weather

conditions increase atmospheric attenuation (e.g., because of a rise in humidity to 85%), lowering call frequency will have the opposite effect and will decrease detection distance even further. In summary, bats always benefit from lowering the call frequency for detecting large prey, never benefit from lowering call frequency for detecting small prey and might be able to compensate some weather-induced shortening of detection distance by lowering call frequency only in some weather conditions.

Finally, we used the measured call parameters of all three species and the corresponding weather conditions and modelled the detection range of responsive bats for an insect with 60 mm² surface (caddis fly). Overall, the prey detection range was between 1.1 and 7.7 m (Table I, Fig. 5). Atmospheric attenuation had a negative effect on detection distance across species, shortening detection distance by 1.7–3.4 m for each increase in atmospheric attenuation by 1 dB/m (mean [95% CrI] for *P. pipistrellus* = -1.7 [-2.4, -1.0] m/(dB/m); *P. nathusii/kuhlii* = -3.4 [-4.4, -2.4] m/(dB/m); *M. daubentonii* = -1.9 [3.7, -0.1] m/(dB/m); Table I, Fig. 5). This indicates that the bats did not fully compensate for the loss in detection distance caused by increasing atmospheric attenuation due to changing weather conditions. We compared the detection distance of the responsive bats to the detection distance of simulated, non-responsive bats that use average call parameters (Fig. 5, dotted line). The differences in detection distance between the responsive bats and a non-responsive bat had either a negative slope in case of *P. nathusii/kuhlii* (mean [95% CrI] = -2.4 [-3.3, -1.4] m/(dB/m)) or a flat slope for the

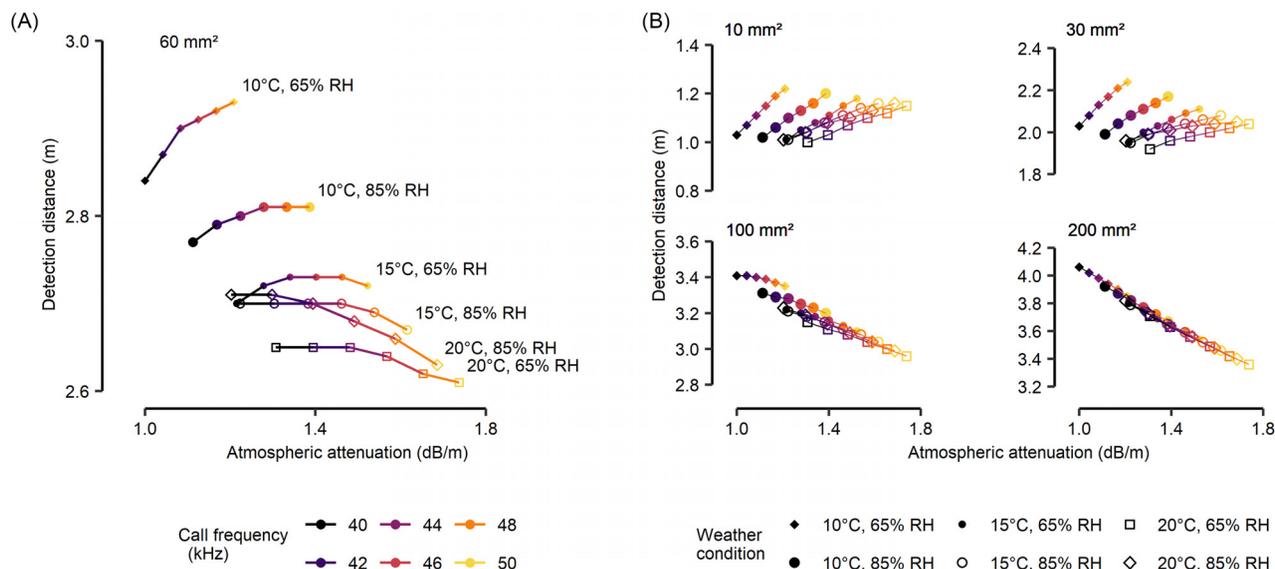


FIG. 4. (Color online) Maximum detection distance for prey depends on prey size, call frequency and weather conditions. (A) The maximum detection distance for prey of 60 mm² surface area (e.g., a small moth with a wingspan of ~15 mm) as a function of atmospheric attenuation, shown for six weather conditions (lines: 10, 15, and 20 °C; 65% and 85% relative humidity) and call frequencies (colors). The detection distance can increase or decrease with increasing atmospheric attenuation, depending on the weather conditions. (B) The maximum detection distance for prey of four different size classes (10, 30, 100, and 200 mm², corresponding to small midges, caddisflies, and two moths) as a function of atmospheric attenuation, weather conditions (lines) and call frequencies (40–50 kHz, colors). For small prey, in any weather condition, lower call frequencies (blue) always have shorter detection distance than higher call frequencies (yellow). In contrast, for large prey (>100 mm²), lower call frequencies always have longer detection distance. Note the different y axes. The model was calculated for six combinations of typical nightly temperatures and relative humidities (T: 10, 15, and 20 °C; RH: 65% and 85%) and for call parameters of a common pipistrelle (frequencies 40 to 50 kHz, source-level 110 dB re 20 μPa @ 10 cm).

other two species (mean [95% CrI] for *P. pipistrellus* = -0.8 [-1.4, 0.2] m, *M. daubentonii* = -1.2 [-3.6, 0.6] m/(1 dB/m)). This indicates that responsive bats experience a constant, or even shorter detection distances with increasing atmospheric attenuation than non-responsive bats.

IV. DISCUSSION

Bats have precise and fast control over their vocalisations and adjust the parameters of their echolocation calls, such as timing, amplitude and frequency, almost

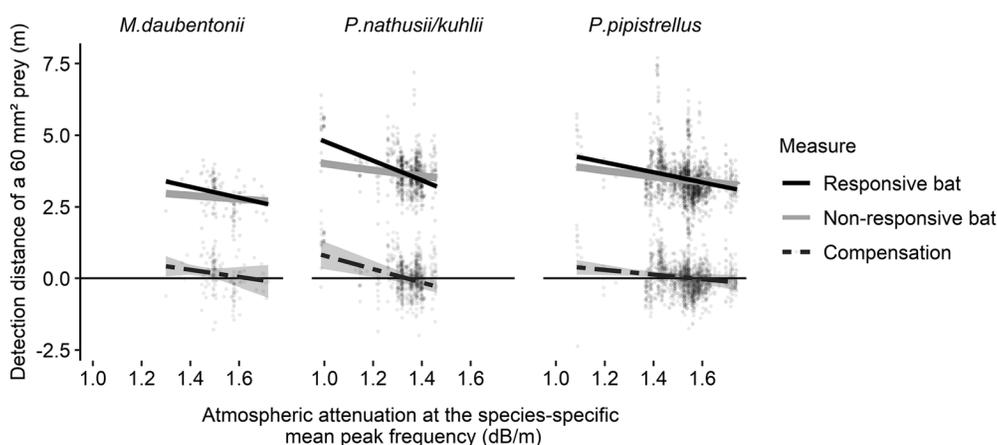


FIG. 5. Bats do not compensate for weather-induced detection distance loss. Instead, the weather-dependent call changes lead to a shorter detection distance at high attenuation than if they used their average call frequency and energy. Maximum prey detection distance for echolocation call parameters as recorded in free flying bats (black), for constant (species-specific average) call parameters, mimicking a non-responsive bat (gray), and the difference of the two distances, estimating the magnitude of vocal adjustments (dashed line = real - average). A flat dotted line (no difference between the detection distance of responsive and of modelled non-responsive bats) indicates that bats do not respond to variations in atmospheric attenuation. A positive slope indicates that bats (fully or partially) compensate for a loss in detection distance caused by increasing atmospheric attenuation. A negative slope shows that real responsive bats have even shorter detection distance under high atmospheric attenuation conditions than when using average call parameters. Plots show raw data (dots) and modelled effect sizes (lines, including 95% credible interval for the compensation). Prey size = 60 mm².

instantaneously to the task and external parameters [e.g., Geberl *et al.* (2015), Kalko and Schnitzler (1993), Lewanzik and Goerlitz (2021), Luo *et al.* (2015), Ratcliffe *et al.* (2013), Schaub and Schnitzler (2007), Schnitzler *et al.* (2003), Übernickel *et al.* (2013)]. Given this remarkable flexibility and the limitations imposed by atmospheric attenuation on insect detection (Luo *et al.*, 2014), we hypothesized that echolocating bats (i) decrease call frequency and increase call energy with increasing atmospheric attenuation [Fig. 2(B)] to (ii) maintain the detection distance across weather conditions (Snell-Rood, 2012). To test these hypotheses, we first measured echolocation call parameters of temperate bats in relation to daily and seasonal variations in atmospheric attenuation induced by changes in temperature and humidity. Second, we modelled the detection distances for prey of different sizes and for different typical ambient temperatures, humidities, and for responsive and non-responsive, average call parameters. Our results do not generally support our hypotheses. Only one species group (*P. nathusii/kuhlii*) decreased call frequency with increasing atmospheric attenuation in line with our predictions, while the other two species showed no weather-correlated changes in call frequency. Opposite to our prediction, none of the bats increased call energy; we even detected a strong decrease in energy with increasing attenuation in *P. nathusii/kuhlii*. This resulted in a lack of compensation and even a decrease in detection distance compared to a hypothetical non-responsive bat.

Across taxa, behavioural plasticity to mitigate the effects of fluctuating sound perception has been mostly gathered in response to noise. Noise-related, instantaneous increase in amplitude, frequency and calling rates, or even noise avoidance have been shown repeatedly in many taxa, such as birds, mammals (Brumm and Zollinger, 2011), and anurans (Halfwerk *et al.*, 2016). In birds, variations in atmospheric attenuation *per se* do not trigger compensation mechanisms in tropical wrens (Grabarczyk and Gill, 2019), but other studies have suggested that atmospheric attenuation has a relevant impact on prey detection for some bat species. First, bats might have adapted their echolocation calls to the average weather condition over evolutionary times: the resting frequency of African horseshoe bats increases from the south towards the equator, along with mean annual temperature (Jacobs *et al.*, 2017; Mutumi *et al.*, 2016). Similarly, the call peak frequency of North American bats decreases with proximity to the tropics, where higher temperature and humidity cause stronger sound attenuation (Snell-Rood, 2012). At the individual level, tropical free-tailed bats increase call duration and decrease call frequency at higher temperature (Chaverri and Quirós, 2017).

Our results here only partly align with these findings in tropical species, although temperate bats face a broader range of weather conditions. Specifically, despite the decrease in call frequency in one of our study species, *P. nathusii/kuhlii*, the concurrent reduction in call energy resulted in shorter detection distances in conditions of higher atmospheric attenuation. A potential explanation

might be a coupling between call frequency and call amplitude. In humans and birds, frequency and amplitude are coupled when vocalising at the physiological limits (very high or very low vocal amplitude): low frequency vocalisations can only be emitted at lower amplitudes and high frequencies are typically of higher amplitudes (Nemeth *et al.*, 2013; Titze, 1992). Echolocation calls are very intense, close to the bats' physiological limits (Currie *et al.*, 2020). Although the frequency-amplitude coupling has not yet been demonstrated in bats, emitting calls at the physiological (amplitude) limit might restrict the vocal flexibility of bats for adjusting the amplitude, frequency, and frequency-time structure of echolocation calls. This might explain the joined decrease in call energy and frequency of *P. nathusii/kuhlii* with increasing atmospheric attenuation yet would require further support.

In the two other species we studied, we could not detect any weather-correlated adjustments of echolocation calls (Table I, Fig. 3). This might be connected to differences in their foraging ecology, the foraging context, or the type and distance of objects that the bats were focusing their attention on. First, atmospheric attenuation mostly affects long-distance detection (Embleton, 1996), therefore, calls designed to detect objects at short distances are less likely to be adjusted to the atmospheric attenuation conditions. This was shown for two tropical Molossid species that emit two types of calls (Chaverri and Quirós, 2017). With increasing atmospheric attenuation, both species only modified their long, constant frequency call type, which is primarily suited for long-range object detection and orientation, but did not modify their short, broad-band call type, which is mainly used for short-range orientation. Prey detection, however, is only one function of echolocation. Orientation and obstacle avoidance is the other key function, for which all echolocating bats analyse the echoes of objects in their environment. Since these objects (e.g., trees, ground, etc.) are much larger than prey, they reflect more intense echoes which are detectable over longer distances (Stülz and Schnitzler, 2012). The detection distances for such large background structures are likely long enough, regardless of changes in atmospheric attenuation, so that bats emit calls at their preferred call frequency and amplitude without adjustments to the weather conditions. Second, *M. daubentonii* is a trawling bat that gleanes its prey from the surface of water bodies while flying at a very low altitude (Denzinger and Schnitzler, 2013), while pipistrelle bats are aerial hawkers. Such different foraging strategies might not be affected by the same environmental variations. The different responses in the two investigated *Pipistrellus* species are harder to explain, since both species hunt aerial prey (Denzinger and Schnitzler, 2013; Schnitzler *et al.*, 2003) and probably share a similar ecological niche in summer (Dietz and Kiefer, 2016). Maybe differences in the ecology and phenology might underlie these differences. As a long-distance migrant, *P. nathusii* might be more flexible in its echolocation and feeding strategies than *P. pipistrellus* as an adaption to a larger diversity of foraging grounds. In addition, the calls of *P.*

nathusii are about 5 kHz lower in frequency than those of *P. pipistrellus*. Since lower frequencies are more suited to the detection of larger prey, this difference in call frequency between two species of the same body size might suggest that the two species target different insect groups of different size. More details on the diet in echolocating bats are needed to support this hypothesis.

We used pre-existing models that determine insect target strength and detection distance to calculate if bats could fully compensate the weather-induced variations in detection distance by changing call frequency. Our model correctly predicted the target strength measurements of Surlykke *et al.* (1999), thus we believe it to be accurate and valid. In contrast to Surlykke *et al.* (1999) and Houston *et al.* (2004), who found no biologically relevant effect of call frequency on target strength and detection distance, respectively, our model predicted a change of about 32 cm (10%) in the detection distance of a medium sized insect (60 mm²) across weather conditions and frequencies. Furthermore, our model indicated that bats could potentially compensate the weather induced variations in detection distance partially by lowering call frequency (Fig. 4). In theory, changing the call frequency has an impact on detection distance, however, we cannot ascertain its biological relevance, and our result that bats did not maintain the detection distance does not support it either. Specifically, we found that a decrease in call frequency is only beneficial for detecting large prey, but not for small prey below the calls' wavelength. Moreover, even decreasing the frequency over the entire species-specific frequency range would not be sufficient to fully maintain the detection distance across the range of atmospheric attenuations bats experience during a year. Overall, this suggests a low effect of weather-induced variability in atmospheric attenuation on prey detectability and/or call parameters.

In conclusion, we hypothesized that bats adjust their echolocation calls to maintain the detection distance for their insect prey when the weather conditions lead to higher sound absorption and thus shorter detection distances. Contrary to our predictions, we found that only one out of three species decreased its call frequency, but simultaneously also decreased its call energy, thereby leading to a shorter detection distance of prey under more challenging conditions. Modelling the effect of call frequency on prey detection across different weather conditions, we argue that behavioural plasticity is not sufficient to counteract increased atmospheric attenuation if the prey is small, but it can benefit the detection of large insects. Our study contributes to understanding behavioural plasticity as a potentially adaptive trait in sensory ecology and how species-specific ecological differences cause different requirements and lead to different adaptive solutions.

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¹See supplementary material at [10.1121/10.0019359](https://doi.org/10.1121/10.0019359) for detail on the call analyses and an overview of raw data.

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1 **Temperate bats may alter calls to partially compensate for weather-induced changes in**
2 **detection distance**

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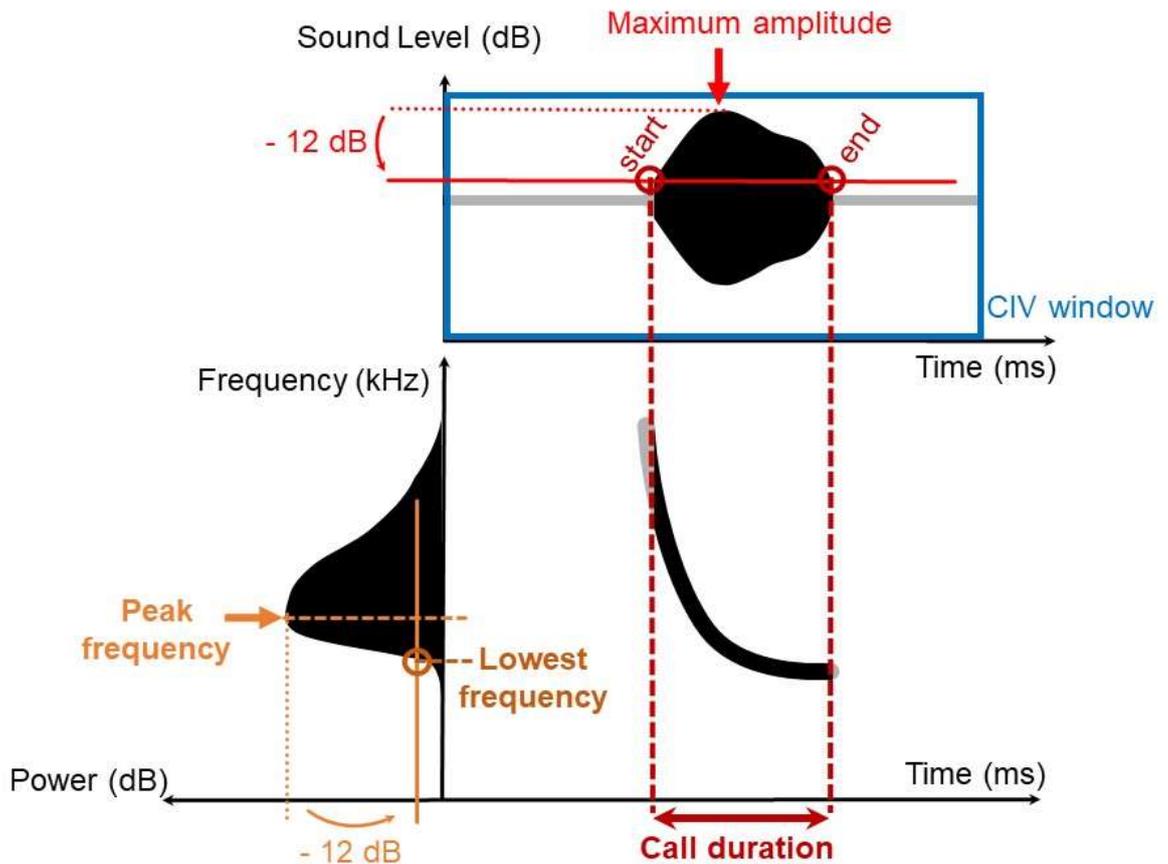
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SUPPLEMENTARY INFORMATION

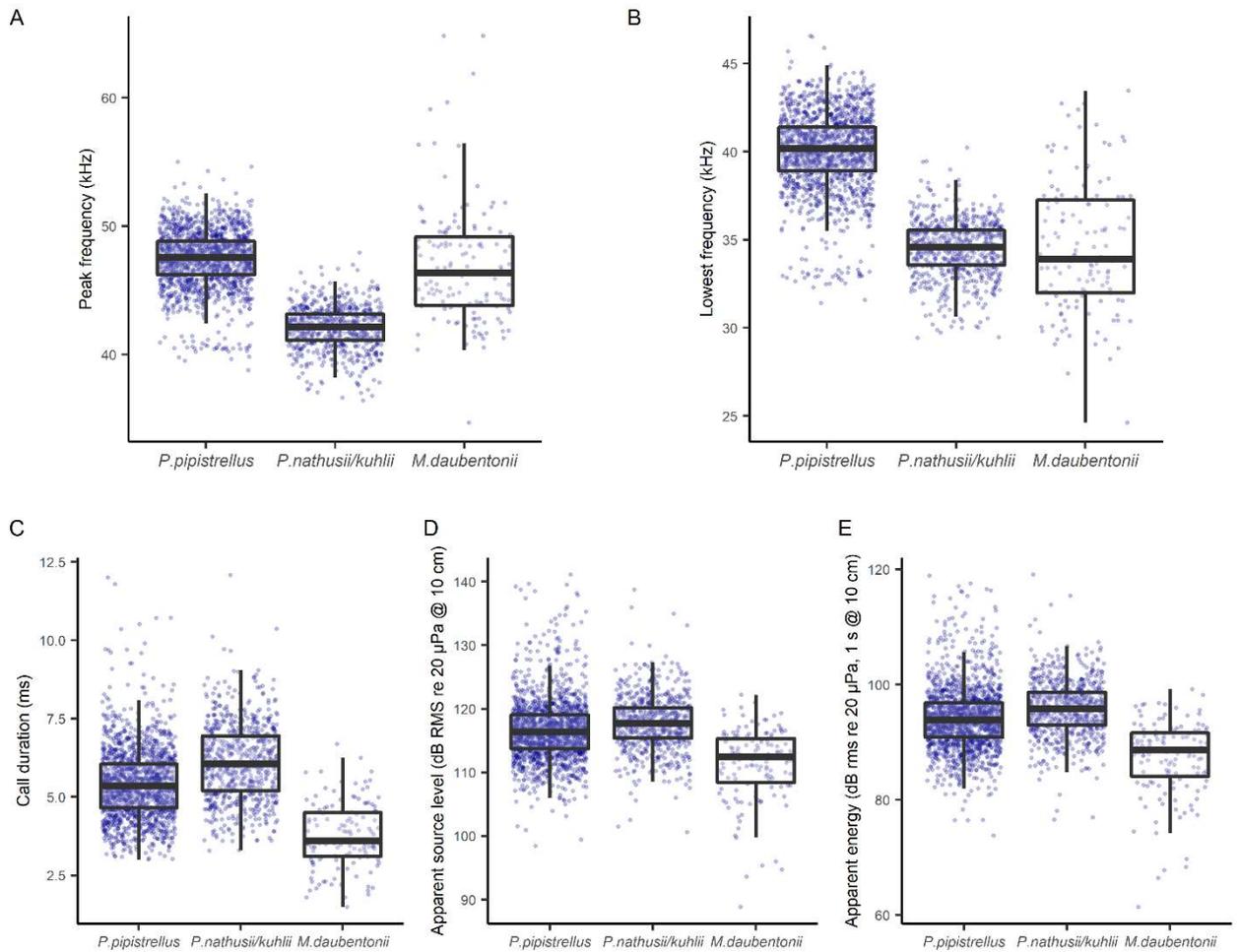
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15 **Fig. S1: Graphical representation of the measured call parameters, showing a**
 16 **spectrogram (centre), oscillogram (top) and spectrum (left) of an echolocation call.** First,
 17 the point of maximum amplitude was determined (red arrow on the top) and a short portion of
 18 the recording is extracted: the CIV window. The start and end time were defined as the time
 19 where the envelope crossed a threshold at 12 dB below the maximum amplitude. The spectrum
 20 of the call (left plot) was then computed based on the call between the start and end time, from
 21 which the peak frequency and the lowest frequency (at a threshold of 12 dB below the peak
 22 frequency) were calculated.

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26 **Fig S2: Call parameters per species.** Boxplots show median, quartiles and 90th percentile of the:

27 A) median peak frequency per trajectory

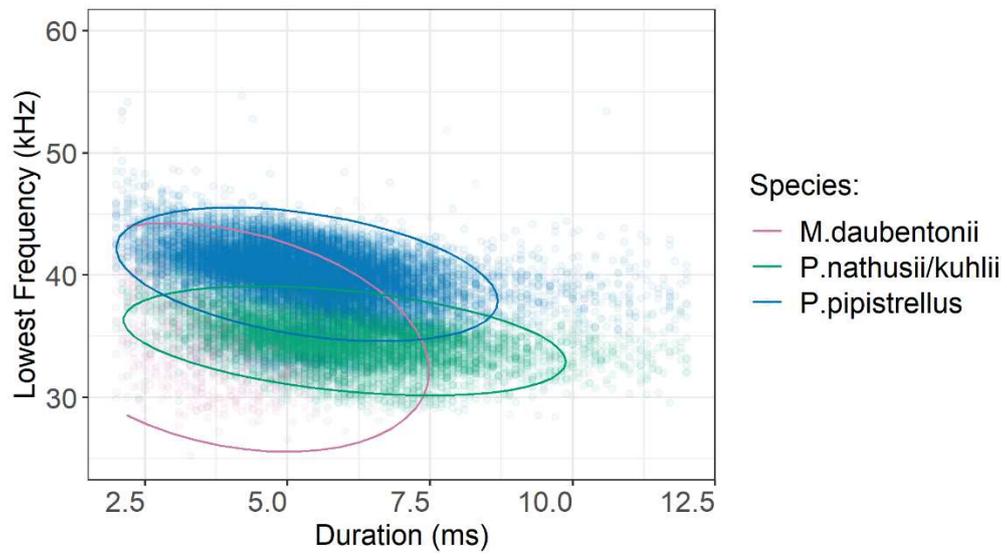
28 B) median lowest frequency per trajectory

29 C) median call duration per trajectory

30 D) 90th percentile of call apparent source level per trajectory

31 E) 90th percentile of call energy (calculated from the call duration and apparent source level)

32



33

34 **Fig. S3: Call frequency becomes lower with increasing call duration.** Shown are the lowest
35 frequency of individual echolocation calls as a function of their call duration, for three bat species
36 (groups).

37

38

39 **Table S1: Parameters used for the call analysis.** N rec: number of recordings analysed in the
 40 session. HP: high pass filter (kHz). LP: Low pass filter (kHz). CIV: duration of the recording that
 41 is extracted at each call detection (ms). ICI: duration of the minimum inter call interval: no new
 42 call will be detected immediately after a call detection and for the duration of the ICI (s). Thr:
 43 detection threshold. Session: number of the recording session per night.

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Year	Month	Day	Session	Location	Genus	N rec	HP	LP	CIV	ICI	Thr
2017	6	1	001	Englischer Garten	Pipistrellus	31	20	90	9	0.02	0.05
2017	6	3	001	Englischer Garten	Myotis	38	28	90	10	0.03	0.02
2017	6	3	002	Englischer Garten	Pipistrellus	27	20	90	9	0.02	0.05
2017	6	3	003	Englischer Garten	Pipistrellus	12	20	90	11	0.02	0.025
2017	6	4	001	Englischer Garten	Pipistrellus	26	25	90	11	0.02	0.02
2017	6	4	002	Englischer Garten	Pipistrellus	31	25	90	13	0.02	0.01
2017	6	7	001	Englischer Garten	Pipistrellus	22	30	90	11	0.02	0.01
2017	6	12	001	Englischer Garten	Pipistrellus	20	30	90	12	0.02	0.007
2017	6	13	001	Englischer Garten	Pipistrellus	20	25	90	13	0.02	0.005
2017	6	13	002	Englischer Garten	Pipistrellus	30	35	90	11	0.02	0.018
2017	8	13	001	Wuertzburg	Pipistrellus	11	35	100	11	0.02	0.06
2017	8	13	002	Wuertzburg	Pipistrellus	24	35	100	11	0.02	0.03
2017	8	22	001	Wuertzburg	Pipistrellus	2	35	90	10	0.02	0.04
2017	8	22	002	Wuertzburg	Pipistrellus	25	30	90	11	0.02	0.013
2017	8	22	003	Wuertzburg	Pipistrellus	41	30	90	11	0.02	0.035
2017	8	23	001	Wuertzburg	Pipistrellus	16	30	90	11	0.02	0.03
2017	8	23	002	Wuertzburg	Pipistrellus	26	35	90	11	0.02	0.03
2017	8	23	003	Wuertzburg	Pipistrellus	66	35	90	11	0.02	0.02
2017	8	23	004	Wuertzburg	Pipistrellus	23	30	80	10	0.02	0.031
2017	8	25	001	Wuertzburg	Pipistrellus	29	35	90	10	0.03	0.02
2017	8	25	002	Wuertzburg	Pipistrellus	31	35	90	11	0.02	0.02

2017	8	25	003	Wuertzburg	Pipistrellus	17	35	90	11	0.02	0.02
2019	5	31	001	Gräfelding	Pipistrellus	63	30	90	10	0.02	0.05
2019	5	31	002	Gräfelding	Myotis	5	30	90	10	0.02	0.05
2019	6	3	001	Zorneding	Pipistrellus	22	30	90	12	0.02	0.025
2019	6	3	002	Zorneding	Pipistrellus	19	18	90	16	0.02	0.025
2019	6	7	002	Lochhausen	Myotis	13	28	120	7	0.02	0.025
2019	6	10	001	Lochhausen	Pipistrellus	39	30	90	8	0.02	0.03
2019	6	10	002	Blutenburg	Pipistrellus	32	30	90	11	0.02	0.03
2019	6	10	003	Blutenburg	Myotis	26	18	100	8	0.02	0.07
2019	6	10	004	Blutenburg	Pipistrellus	26	25	90	16	0.02	0.02
2019	6	13	001	Bernried	Pipistrellus	72	25	90	11	0.02	0.06
2019	6	13	002	Bernried	Myotis	6	25	100	7	0.02	0.015
2019	6	16	001	Blutenburg	Pipistrellus	47	30	90	10	0.01	0.1
2019	6	16	003	Blutenburg	Myotis	28	25	90	9	0.02	0.04
2019	6	17	001	Blutenburg	Pipistrellus	54	30	90	9	0.02	0.05
2019	6	17	002	Blutenburg	Myotis	4	25	125	8	0.02	0.02
2019	6	17	003	Blutenburg	Pipistrellus	20	30	90	12	0.01	0.04
2019	6	25	001	Zorneding	Pipistrellus	22	35	90	10	0.02	0.03
2019	7	3	001	Blutenburg	Pipistrellus	40	30	90	13	0.02	0.03
2019	7	3	002	Blutenburg	Pipistrellus	21	30	90	12	0.01	0.03
2019	7	3	003	Blutenburg	Myotis	12	19	100	8	0.02	0.0185
2019	7	9	001	Lochhausen	Pipistrellus	54	30	90	10	0.02	0.03
2019	7	9	002	Lochhausen	Myotis	5	20	120	6	0.02	0.02
2019	7	15	001	Zorneding	Pipistrellus	51	30	90	12	0.02	0.025
2019	7	15	002	Zorneding	Pipistrellus	38	30	90	12	0.02	0.05
2019	7	15	003	Zorneding	Myotis	1	25	125	6	0.02	0.03
2019	7	16	001	Gräfelding	Pipistrellus	21	30	90	12	0.02	0.04
2019	7	16	002	Gräfelding	Myotis	22	20	100	7	0.02	0.02
2019	7	22	001	Englischer Garten	Pipistrellus	58	28	90	12	0.02	0.04
2019	7	22	002	Englischer Garten	Pipistrellus	31	25	90	12	0.02	0.018
2019	7	22	003	Englischer Garten	Pipistrellus	21	25	90	12	0.02	0.015
2019	7	22	004	Englischer Garten	Myotis	3	25	100	10	0.02	0.018
2019	7	23	001	Gräfelding	Pipistrellus	15	28	90	11	0.02	0.04
2019	7	23	002	Gräfelding	Myotis	25	20	100	7	0.02	0.02
2019	7	25	001	Blutenburg	Pipistrellus	44	30	90	10	0.02	0.04
2019	7	25	002	Blutenburg	Myotis	7	24	125	7	0.02	0.04
2019	7	30	001	Zorneding	Pipistrellus	42	25	90	11	0.02	0.03
2019	7	30	002	Zorneding	Myotis	11	22	125	7	0.018	0.25
2019	7	30	003	Zorneding	Pipistrellus	59	25	90	11	0.02	0.018
2019	8	9	001	Lochhausen	Pipistrellus	12	30	90	9	0.02	0.025

2019	8	9	002	Lochhausen	Myotis	7	20	120	8	0.02	0.03
2019	8	18	001	Blutenburg	Pipistrellus	38	28	90	11	0.02	0.05
2019	9	6	001	Blutenburg	Pipistrellus	43	28	90	10	0.02	0.03
2019	9	19	001	Gräfelfing	Pipistrellus	12	28	90	10	0.02	0.02
2019	9	19	002	Gräfelfing	Pipistrellus	24	28	90	10	0.02	0.03

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