Global warming alters sound transmission: differential impact on the prey detection ability of echolocating bats

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Climate change impacts the biogeography and phenology of plants and animals, yet the underlying mechanisms are little known. Here, we present a functional link between rising temperature and the prey detection ability of echolocating bats. The maximum distance for echo-based prey detection is physically determined by sound attenuation. Attenuation is more pronounced for high-frequency sound, such as echolocation, and is a nonlinear function of both call frequency and ambient temperature. Hence, the prey detection ability, and thus possibly the foraging efficiency, of echolocating bats and susceptible to rising temperatures through climate change. Using present-day climate data and projected temperature rises, we modelled this effect for the entire range of bat call frequencies and climate zones around the globe. We show that depending on call frequency, the prey detection volume of bats will either decrease or increase: species calling above a crossover frequency will lose and species emitting lower frequencies will gain prey detection volume, with crossover frequency and magnitude depending on the local climatic conditions. Within local species assemblages, this may cause a change in community composition. Global warming can thus directly affect the prey detection ability of individual bats and indirectly their interspecific interactions with competitors and prey.

1. Introduction

Depending on the magnitude of CO2 emission, the global surface temperature is predicted to rise by 1.1–6.4 °C during the twenty-first century [1]. Although our planet has only warmed by approximately 0.6 °C during the past century [1], ecological responses are already occurring [2–6]. Direct temperature-related effects on individuals and species have been observed, such as spring advancement of phenology, expansion of species distributions to higher latitudes and altitudes and reduction of body size [2,3,6]. Besides these direct effects, climate change also alters species interactions by differentially affecting interacting species [4,7], leading to complex, nonlinear ecological response patterns. In contrast to the ecological effects of global warming, the direct mechanisms that link global warming to these effects often remain unknown [7–9].

Acoustic signals are widely used by animals for communication, orientation and foraging [10,11]. The active space within which a receiver can detect and recognize a sender’s signal depends both on the sound signal per se and the process of sound transmission [11–13]. Many animal sounds are adapted to the acoustic properties of the animal’s habitat in a way that minimizes sound transmission loss [12–14]. Consequently, changing acoustic properties of habitats can change animals’ fitness. Sound attenuation is a direct function of ambient temperature. Therefore, global warming has the potential to change the acoustic
properties of animal habitats and to directly impact the sensory ecology of sound-mediated behaviours.

Bats (Chiroptera) are the second most species-rich order of mammals and occur from the tropics to the polar circle on all continents except Antarctica. Like other animals, bats are vulnerable to climate change [15], with predicted and observed effects on their biogeographic patterns and reproductive success [8,16–18]. Some of these changes can be attributed to direct effects of rising temperature on temperature-dependent processes, including hibernation and reproduction [19]; other indirect effects might be mediated by habitat degradation, changes in prey abundance and extreme weather events [15,19]. Here, we consider another mechanism based on the physics of sound transmission, which has the potential to directly affect the perception in the roughly 1000 bat species that rely on ultrasonic echolocation for navigation and/or foraging.

Echolocating bats emit ultrasonic calls, which spread through the ambient air and reflect off surrounding objects. Echolocation is limited by the maximum distance over which audible echoes return, which depends on the atmospheric attenuation of sound in air, which, in turn, is a nonlinear function of both call frequency, air temperature and humidity [20–22]. If changing ambient temperature increases atmospheric attenuation, then echolocating bats will be subjected to reduced maximum prey detection distances and reduced prey detection volumes (figure 1a).

Unlike the daily and seasonal fluctuation of temperature, global warming is characterized by an average rise of ambient air temperature [1]. Thus, global warming will shift the present-day temperature distribution to higher values. Here, our aim was to use present-day climate data and the predicted temperature rise of the twenty-first century to examine the effect of the shifted temperature distribution on the prey detection ability of echolocating bats. We first obtained the present-day distribution of weather conditions and predicted the future distribution based on models of global warming. We then operationalized prey detection ability as prey detection volume, a physically clearly defined parameter which describes the maximum volume that a bat can sample when searching for prey and which is a function of the temperature-dependent sound attenuation. We used the weather data to calculate the temperature-dependent change of prey detection volume for the entire range of bat echolocation call frequencies and for climate zones around the globe.

2. Material and methods

2.1. Present-day and future distribution of weather parameters

We retrieved the distribution of present-day air temperature and relative humidity for a typical temperate (Germany) and tropical (Malaysia) biome from Weather Online UK (www.weatheronline.co.uk; figure 1b). Many bat species, especially those foraging in open and edge air space, concentrate their foraging activities in the first hours after sunset to take advantage of the higher prey abundance [23–27]. To represent the weather conditions during the main activity period of bats, we thus only used data within ca 1–2 h after sunset (obtained from www.timeanddate.com, temporal resolution of data: 1 h) and from May to September for Germany. For Germany, weather data originated from 2009 to 2011 (September: 21:00; May and August: 22:00; June and July: 23:00), totalling 85,420 data points (measured by 26–218 weather stations per day, median = 204). For Malaysia, weather data originated from 2000 for all months of 2009–2011, totalling 17,443 data points measured by one to 20 stations per day (median = 16). Air pressure was set to 101,325 Pa.

To obtain the future distribution of weather parameters, we used the present-day distribution and predictions for global warming [1]. Global surface temperature is predicted to rise by 1.1–2.9°C under the lowest CO2 emission scenario (B1, best estimate: 1.8°C) and by 2.4–6.4°C under the highest CO2 emission scenario (A1FI, best estimate: 4°C) during the twenty-first century [1]. To represent both scenarios, we increased each temperature data point in the distribution by 2°C and 4°C (figure 1c). We kept the values for relative humidity and air pressure constant. Relative humidity is believed to be stable in the process of global warming owing to water vapour feedback from intensified water cycles [28,29]. Measured and predicted change of air pressure in response to global warming is at the most in the order of −10 to 7 hPa [30], resulting in negligible change of atmospheric attenuation of at most ±1.5%, yet mostly markedly less than 1%.

2.2. Physical model of maximum prey detection distance

The prey detection ability of bats is limited by the maximum distance d over which they can detect prey echoes (figure 1a). d is determined by the transmission loss of sound in air (loss due to spherical spreading and atmospheric attenuation) and by bat- and prey-specific parameters (hearing threshold, call intensity, target strength), as given by the sonar equation [31]:

\[ DT = SL + TS + TLS + TLA, \]

(2.1)

where DT is bat detection threshold for echoes (dB sound pressure level, SPL), SL is source level (in dB SPL at 1 m in front of the bat), TS is target strength (the sound level reflected off a target measured at 1 m distance, in dB relative to the impinging sound), TLS and TLA are transmission losses owing to spherical spreading and atmospheric attenuation of sound, respectively, both on the way from the bat to the prey and back (dB).

Detection threshold, source level and target strength are independent of weather conditions. We thus combined them into the variable MTL, which is the maximum transmission loss tolerable by the bat at detection threshold:

\[ MTL = DT - SL - TS. \]

(2.2)

Commonly used values of the echo detection threshold DT are 0 dB SPL, which is close to the standard mammalian hearing threshold under quiet conditions, and 20 dB SPL to account for noise [32–35]. Source level (SL) for aerial-hawking bats varies between 110 and 137 dB SPL at 10 cm in front of the bat [33–37], corresponding to ca 90–120 dB SPL at 1 m distance. TS ranges from −70 to −30 dB for smallest to largest prey at 1 m distance [38]. Thus, MTL can assume values between 0 and −90 dB. For our model, we selected two exemplary, conservative values around the median MTL of −20 and −60 dB.

Both TLS and TLA can be computed from the distance that the sound travels, d. TLS, the transmission loss owing to spherical spreading, is defined as:

\[ TLS = 40 \log_{10} \frac{d_{ref}}{d}, \]

(2.3)

where \( d_{ref} \) is the reference distance to the sound source. \( d_{ref} \) is required, because sound pressure cannot be measured at the source itself. Commonly used values are 10 cm or 1 m, yet
the actual value does not affect our calculations as long as it is kept constant.

TLA, the transmission loss owing to atmospheric attenuation, additionally depends on the atmospheric attenuation coefficient $\alpha$ and is defined as:

$$\text{TLA} = 2\alpha(d_{\text{ref}} - d).$$

(2.4)

The atmospheric attenuation coefficient $\alpha$ is a nonlinear function of call frequency, air pressure, temperature and relative humidity [20]. Changing weather conditions will thus change the atmospheric attenuation of emitted call and reflected echo, and thus also the maximum distance over which bats can detect echoes. $\alpha$ functionally couples the maximum prey detection distance to bat species (call frequency), climate zone (weather conditions) and global warming. We estimated $\alpha$ based on the international standard ISO 9613 [39], which has an error of less than 10% for almost the entire range of tested environmental conditions (see electronic supplementary material, figure S1). Because we estimated prey detection volumes before and after global warming of $+2^\circ\text{C}$ and $+4^\circ\text{C}$, i.e. for two very similar climatic conditions, the error of the change in prey detection volume studied here (equation (2.5)) will be much smaller than the similar errors of the absolute prey detection volumes, which almost cancel each other out.

Because the sonar equation cannot be solved analytically for $d$, we used the iterative Newton method to compute $d$ for all frequency, temperature and relative humidity values.

2.3. Physical model of the change of maximum prey detection volume

We operationalized ‘prey detection ability’ of bats as the prey detection volume, the total air space from within which a bat can hear the echo of a prey item (figure 1a). The change in prey detection volume ($\Delta V$) is the difference between the detection volume before and after global warming ($V - V_0$), normalized to the initial detection volume ($V_0$):

$$\Delta V = \frac{V - V_0}{V_0} \times 100\%.$$  

(2.5)

We modelled the change of prey detection volume $\Delta V$ separately for perch-hunting (stationary) and aerial-hawking (flying)
bats (figure 1a). Perch-hunting bats are stationary and cannot detect prey beyond the maximum detection distance of a single call. We approximated their prey detection volume by a spherical sector with the bat at the sphere’s centre and the sector’s opening angle defined by the width of the sonar beam [40]:

\[ V = \frac{2\pi d^3}{3} \left(1 - \cos\frac{\theta}{2}\right) \]

(2.6)

where \( d \) is maximum prey detection distance of bats (=radius of the sphere), \( \theta \) is full width of sonar beam (=sector’s opening angle). The change in detection volume (\( \Delta V \); equation (2.5)) is independent of the sonar beam width and can be directly calculated from the detection distance:

\[ \Delta V = \frac{V - V_0}{V_0} \times 100\% = \frac{d^3 - d_0^3}{d_0^3} \times 100\%. \]

(2.7)

In contrast to stationary bats, flying bats might detect prey beyond the detection distance of one call with the next call emitted closer to the prey. We thus estimated the volume covered by one given call, without the volume covered by the following call (\( V \), yellow dotted line, figure 1a). We defined this volume \( V \) as the volume of a spherical sector \((V_{\text{sector}}\), equation (2.6)) added a cylindrical detection volume owing to the forward displacement of the bat during call emission \((V_{\text{cylinder}})\) and subtracted that part of \( V_{\text{sector}} \) which will also be covered by the next call \((V_{\text{overlap}}):\)

\[ V = V_{\text{sector}} + V_{\text{cylinder}} - V_{\text{overlap}}. \]

(2.8)

As before, we then used equation (2.5) to calculate \( \Delta V \), which depends on flight speed, call interval, call duration and sonar beam width. Across the natural range of these parameters, the variation of \( \Delta V \) is small (differences \(-0.5\) to 2.1 percentage points) for changes of flight speed, call interval and call duration, and almost non-existent for changes of beam angle (differences \(< \pm 0.01 \) percentage point). We thus used common values for an aerial-hawking bat in search flight of 6 m s\(^{-1}\) flight speed, 100 ms call interval, 10 ms call duration and 45° full sonar beam width.

A typical bat community is composed of species with different and species-specific call frequencies, which together cover a broad frequency range [33,41]. We calculated \( \Delta V \) for the typical range of call frequencies of insectivorous bats from 10 to 150 kHz, for maximally tolerable sound transmission losses (MTL) of \(-20\) and \(-60\) dB, and for every data point of the present-day and future \((+2\) C and \(+4\) C) weather conditions of the temperate (Germany) and tropical (Malaysia) biome. Per call frequency, MTL, temperature rise and biome, we then averaged the \( \Delta V \)-values calculated for all single weather data points to obtain the mean \( \Delta V \), i.e. the average change in prey detection ability of echolocating bats after an increase of the present-day temperature distribution by \(+2\) C and \(+4\) C. Our model is based on more than 100000 weather data points describing the distribution of weather conditions in temperate and tropical climate zones. This approach maintains the daily and seasonal fluctuation of temperature, which persists in the temperature distribution shifted by \(+2\) C and \(+4\) C. As this detailed data, however, will not always be available, we also calculated a model based only on mean values of temperature and humidity and compared it with our full model (see the electronic supplementary material, figure S2).

2.4. Potential vocal compensation for reduced prey detection volume

Changing temperature alters the atmospheric attenuation coefficient \( \alpha \), thus changing the atmospheric attenuation of call and echo and consequently prey detection distance and volume. If prey detection volume is reduced, then bats might compensate for this effect by changing call parameters that influence the atmospheric attenuation (equation (2.3)) or the sonar equation (equation (2.1)). Specifically, bats could (i) decrease call frequency to counterbalance the effect of rising temperature on \( \alpha \), thus keeping \( \alpha \) overall constant, or (ii) increase source level to compensate for the increased atmospheric attenuation of sound after global warming. Calculations were performed using the mean weather conditions of both climate zones before (temper- ate: 14.7°C, 78%; tropical: 27.1°C, 85%) and after (+2°C and +4°C) global warming and only for those call frequencies at which bats would suffer a reduced prey detection volume. For every call frequency, we used the estimate of \( \alpha \) [39] and the iterative Newton method to calculate the post-warming call frequency at which \( \alpha \) resumed its pre-warming value despite the increased temperature. The required change in call frequency, \( \Delta f \), is the difference between the original and the post-warming call frequency. The required change in source level, \( \Delta \text{SL} \), was calculated for every call frequency from equation (2.2), combined with the equations of TLS and TLA (equations (2.3) and (2.4)). Inserting the post-warming \( \alpha \) and the desired unchanged pre-warming detection distance into the equations yields the required post-warming MTL. \( \Delta \text{SL} \) is the difference between pre- and post-warming MTL, because no other components of MTL have changed.

2.5. Change of prey detection volume in climate zones around the globe

We used the same physical model of prey detection volume to calculate the potential impact of global warming on bat communities from any climatic condition around the globe. For all combinations of temperature \((0–35°C)\), relative humidity \((0–100%)\) and bat call frequencies \((10–150\) kHz), we calculated \( \Delta V \) for global warming of +2°C and +4°C (see electronic supplementary material, figure S3 for exemplary results). To summarize these data and to describe the severity of the effect of global warming on bat communities in different climatic conditions, we extracted four parameters for each temperature–humidity condition (cf. inset in the electronic supplementary material, figure S4). (i) Crossover frequency \( f_c \): the frequency at which the prey detection volume will not change. (ii) Overall magnitude: the difference between the maximum and minimum change in prey detection volume as a measure of the overall effect size across the full range of call frequencies. It describes the overall effect between the most advantaged and disadvantaged bat species, i.e. the magnitude of change within a community of potentially interacting species. Finally, we calculated the derivative of the change in prey detection volume with respect to frequency. This yields the slope of the curves depicted in figure 2 at each frequency and is a measure of how much the effect of global warming differs between close-by call frequencies (in contrast to the previously calculated overall effect size). We computed the (iii) maximum, and (iv) the mean of these absolute slopes and expressed them as percentage point difference in detection volume per 10 kHz call frequency. The maximum absolute slope describes the most extreme effect on two bats differing in call frequency by 10 kHz, whereas the mean absolute slope describes the average effect across the whole frequency range on any two bats differing in call frequency by 10 kHz.

Note that these different measures did not qualitatively disagree on the relative impact of global warming on bat communities in different climates (see electronic supplementary material, figure S4) and only slightly differed in the exact climatic values for which the minimum and maximum impact on bat communities will occur.
3. Results

3.1. Change of maximum prey detection volume in temperate and tropical bats

All models showed that global warming will alter the maximum prey detection volume of echolocating bats in a species- and climate-dependent manner (figure 2). We found a consistent pattern that across bat species with different call frequencies, rising temperature will lead to increased detection volume at lower frequencies and reduced detection volume at higher frequencies. At medium frequencies, a crossover frequency \( f_0 \) exists at which the maximum detection volume will stay constant. Depending on call frequency, global warming will thus directly enhance the prey detection ability of some species, whereas others will have a reduced prey detection volume. The effect of rising temperature on prey detection volume will be larger for the \(+4^\circ C\) than for the \(+2^\circ C\) temperature rise (figure 2, red and blue lines), for situations with higher tolerable transmission losses (MTL), which are determined by the temperature-independent bat hearing threshold, call intensity and echo intensity. (a,b) Perch-hunting bats. (c,d) Flying bats; the mean change of detection volume for flying bats is 60–85% of the effect on perch-hunting bats.

Furthermore, species-specific effects, which are determined by the sound frequency-dependence of atmospheric attenuation, will be mediated in a biome-specific way depending on the local climatic conditions (figure 2a,c versus b,d). In particular, the models predict that both the crossover frequency \( f_0 \) between detection volume gain at lower call frequencies and detection volume loss at higher call frequencies, and the overall impact of rising temperature will be affected by the local climate. The crossover frequency will be around 35 kHz for temperate and around 95 kHz for tropical bat communities. The impact of rising temperature will be stronger on temperate bat communities than on tropical ones. In temperate climate, prey detection volume will increase by up to 14% or decrease by up to 21% (perch-hunting bats, \(+4^\circ C\), MTL = –20 dB). In tropical climates, prey detection volume will increase and decrease by up to 16% and 10%, respectively.

We used the difference in prey detection volume change as a simplified measure for the differential impact on sympatric species in a given climate. We found an overall magnitude of 35 percentage points difference between the most benefiting and the most disadvantaged bat species in the temperate bat community, and a smaller overall magnitude of 18 percentage points in the tropical bat community (see §3.3 and the electronic supplementary material, figure S3 for additional measures comparing community effects).

3.2. Potential vocal compensation for reduced prey detection volume

Echolocating bats might be able to compensate for a reduced detection volume either by lowering call frequency...
(i.e. lowering atmospheric attenuation; figure 3a) or increasing call intensity (i.e. counteracting the increased atmospheric attenuation; figure 3b), thus keeping the detection volume constant at present-day values. For a 4°C temperature rise and an MTL of −60 dB, temperate bat species would be required to reduce call frequency by up to 14 kHz or increase call intensity by up to 4.9 dB (almost a doubling of amplitude), compared with 7 kHz and 2.4 dB for tropical bats (figure 3).

3.3. Change of prey detection volume in climate zones around the globe

To go beyond our two exemplary bat communities from temperate and tropical climates, we quantified the effects of rising temperature on the prey detection volume of echolocating bats for the entire range of climatic conditions found in bat habitats around the globe. We found a consistent pattern along the gradients of temperature (0–35°C) and relative humidity (0–100%; figure 4 and the electronic supplementary material, figures S3 and S4). The crossover call frequency f0, i.e. the frequency with no change in prey detection volume, is predicted to increase from 10 to 150 kHz with warmer and more humid climates, with little difference between the two emission scenarios of +2°C and +4°C global warming (figure 4a,b). By contrast, the overall magnitude, i.e. the difference in the change of prey detection volume between the most benefiting and the most disadvantaged sympatric species will increase with the amount of global warming to up to 20 and 40 percentage points for the two scenarios, respectively (perch-hunting bats, MTL = −60 dB; figure 4c,d). Likewise, the differential effect on sympatric species reaches up to 16 and 30 percentage point differences in change of prey detection volume for species differing by 10 kHz in call frequency (electronic supplementary material, figure S4e,f). The differential effect on bat species (figure 4 and electronic supplementary material, figure S4) is smallest in tropical regions and is strongest for biomes along a gradient of climatic conditions from low-temperature–high-humidity (cold to temperate regions) to high-temperature–low-humidity (arid regions).

4. Discussion

4.1. Direct impact of climate change on individuals and species

Rising temperature can impact animals via multiple mechanisms, e.g. directly as an abiotic effect on temperature-dependent physiological processes and indirectly through changes in the biotic environment, caused by the differential effects on participants in interspecific interactions [15]. Using present-day climate data, predicted temperature rises and a physical model of sound transmission, we show that global warming will lead to both positive and negative changes in the prey detection volume of echolocating bats. Furthermore, we quantitatively show how these changes depend on the species’ call frequency and the local climatic conditions. Thereby, we found that global warming will directly act on the prey detection of echolocating bats. This is the first example of a mechanism by which global warming can directly act on the sensory perception of animals.

Generally, bats using lower call frequencies will have enlarged prey detection volumes, whereas the detection volumes of species calling above a crossover frequency will decrease. Even without competitive interactions between species (we discuss potential competitive interactions in §4.3), this can alter community structure. Bats with calls below the crossover frequency will benefit from climate change, whereas individuals using higher call frequencies will experience foraging costs, leading to differential changes in foraging and reproductive success.

On a global scale, we found the strongest differential effect of global warming on prey detection volume for sympatric bats living along a gradient from cold-and-wet to hot-and-dry regions. Besides the larger effect magnitude under these climatic conditions than in the tropics, also the crossover frequency is lower and splits the range of call frequencies of aerial-hawking bats in two (figure 2). Therefore, our model predicts that bat communities in cold to temperate and arid regions will experience the largest effects on community composition, whereas communities in tropical climates will be less affected. In the natural world, most bat species that search for prey in open and edge airspace—and
for these, detection volume likely matters the most—use low call frequencies well below 100 kHz \[41,42\]. Most tropical species of this group are predicted to gain prey detection volume (figure 2); however, the differences in gain may still alter community composition. By contrast, in temperate and arid climates, this shift is predicted to be stronger, because the crossover frequency falls within the frequency range of aerial-hawking bats. In Europe, for example, four to five aerial-hawking species call above the crossover frequency \[41\] and are predicted to lose prey detection ability, whereas about nine species call around and below \( f_0 \) \[41\] and will have constant or increased detection ability. Even if the disadvantaged species were fully able to compensate for the reduced detection volume, then the enlarged detection volume of the benefiting species might give them an advantage over the sympatric species.

The accuracy of our quantitative estimates of the change in prey detection volume is dependent on the assumption that bats use their complete detection volume while foraging. This assumption is strongly supported by the fact that aerial-hawking bats use calls of high intensity \[33,34\] to maximize detection range, and between-call intervals that are long enough that echoes from the edge of the detection volume return before the next call is emitted \[33\]. Thus, bats listen for echoes from the entire prey detection volume.

Increased prey detection volume will lead to increased foraging efficiency under the assumption that prey density stays the same. Currently, there is no clear evidence whether insect abundance will increase or decrease \[43\], because different insect taxa will respond differently to climate change \[43,44\]. For example, climate change can cause extinction, range shifts and declining abundance of many insects, including beetles, butterflies and moths \[45–48\], whereas the abundance of herbivorous insect pests is predicted to increase \[49\]. Therefore, future insect prey availability may differ for different predators depending on the specific response of their prey species to climate change. Our model thus only describes the physical limits of bats’ prey detection ability; their future foraging efficiency will be influenced by the combination of their reduced or increased detection ability and the specifically changed prey availability. However, even if prey density does not stay constant, but changes in the same direction for several species, then the differential change in prey detection volume will cause differences in foraging success between species.

Figure 4. Effect of global warming on bat communities in different climatic zones. (a,b) Crossover call frequency \( f_0 \) (kHz; see inset in a) as a function of ambient temperature and relative humidity. \( f_0 \) is independent of MTL. Grey area next to the axes origin: no \( f_0 \) exists between 10 and 150 kHz and detection volume will decrease for all these sound frequencies. Pink area: a second \( f_0 \) exists between 10 and 14 kHz (cf. electronic supplementary material, figure S3). (c,d) Magnitude of detection volume change (percentage points) between the most benefiting and the most disadvantaged bat species (see inset in a). See the electronic supplementary material, figure S4 for additional measures comparing community effects. Calculated for \(+2^\circ\)C (left) and \(+4^\circ\)C (right) temperature rise and for a perch-hunting bat and MTL = \(-60\) dB. Present-day weather distributions of temperate (GER), tropical (MAL) and an arid desert biome (NEG: Negev, Israel; May–September) are shown as grey-scaled histograms (80%, 60%, 40% and 20% relative frequency).
4.2. Potential compensation for reduced prey detection volume

While sensory systems are capable of adapting to short- and long-term changes [50], and bats adjust call frequency and intensity on a short-term basis to the present task and habitat [37,42], it is unknown whether and to what extent they are able to behaviourally compensate for long-term changes of sound transmission loss. Caused by the existing variation in temperature, bats might already have mechanisms to adapt their (vocal) behaviour to variable atmospheric attenuation, or to manage the costs of variable prey detection ability. However, global warming acts in addition to the existing natural variation. Although the shift in temperature caused by global warming is smaller than the natural daily, seasonal and spatial variation (figure 1c), it will exert extra pressure on any already existing mechanism to deal with varying prey detection abilities, likely causing additional costs. By contrast, species with constant or increased detection volume will not experience these additional costs.

Ecological, morphological and energetic constraints may limit the potential for vocal compensation. Because echolocation calls are adapted to the echo-acoustic requirements of a species’ ecological niche at both broad (e.g. open versus cluttered foraging space) [42] and fine scale (e.g. niche differentiation within the same habitat type) [51], foraging ecology may prevent any changes in call parameters. For example, lowering call frequency is a two-sided sword. It increases detection volume, but at the same time reduces echo intensity of small prey and thus their detection distance and perceived availability [41]. For constant-frequency bat species (Rhinolophidae, Hipposideridae, Pteronotus parnellii), the auditory processing is morphologically and neuronally precisely tuned to a narrow frequency range [52], rendering behavioural plasticity in call frequency futile. Even though echolocation is normally not energetically expensive during flight [53], the around twofold increase in call amplitude required for the compensation (figure 3) might cause substantial energetic costs [54] or fatigue of the vocal apparatus [55], and even more so for stationary bats [56–58]. Over longer timescales, by contrast, bat species might adapt to the local climatic conditions. Both in different species of the genus Rhinolophus [59] and in some geographically disjunctive populations of a single species [60,61], call frequency was correlated to local precipitation levels, suggesting an evolutionary adaptation of call frequency to average local sound attenuation. Despite daily and seasonal fluctuation of ambient temperature, it is thus conjecturable that reduced average prey detection ability caused by global warming will shift call frequency and intensity in the directions predicted by figure 3. However, because the current climate change is very rapid due to its anthropogenic causes and bats reproduce slowly and have long generation times, the time available might not suffice for an evolutionary change.

Bats might use further behavioural strategies, in addition to vocal compensation, to compensate for reduced foraging efficiency. Individuals could extend periods of foraging or actively select areas with higher perceived prey density [62] or cooler climate (e.g. higher latitudes and altitudes). In the latter case, the temperature-dependence of atmospheric sound attenuation could be one of several mechanisms underlying the observed shift of bat distribution ranges [15]. On the other hand, these behavioural strategies might incur additional costs, as for the vocal compensation. Increasing periods of foraging will require additional energy and time spent on foraging, whereas areas with higher prey density or cooler climate might be limited or less suitable for other reasons. The ability to compensate will likely vary with the species, its biotic and abiotic interactions and how global warming will influence these interactions.

To summarize, bats may compensate for the reduced foraging efficiency caused by global warming, but this compensation will likely incur costs. By contrast, species with constant or increased detection volume will not experience these additional costs and thus again have an advantage over the negatively affected species.

4.3. Indirect effect of global warming through changed interspecific interactions

So far, we have discussed the direct impact of global warming on the prey detection ability of individuals and have shown that it will affect sympatric species differentially (the difference reaching up to 40% in some exemplary cases; figure 4c,d) and will thereby potentially shift community balance. These effects can be further potentiated by changes in interspecific interactions, particularly competition among sympatric bat species and interactions between bats and their eared insect prey.

If species, whose foraging efficiency will be reduced by climate change, are competing for the same food resources with species whose prey detection volume will increase, then the latter species may outcompete the former. The benefiting species will dwell and may potentially spread to new habitats, whereas the disadvantaged species may be excluded from these habitats. Competition for food among sympatric species is hard to prove in nature; however, in bats, there is indirect evidence that competition affects community composition [51,63]. Changes in competitive ability of sympatric species owing to anthropogenically altered habitats destabilizes present-day communities and alters relative species abundances, as suggested for European bat species [63] and many other animal and plant species [64].

Temperature-dependent changes in atmospheric attenuation can also influence the predator–prey interactions between bats and insects with bat-detecting ears [65]. Given constant bat call intensity and frequency, global warming will change detection distances for calls (by insects) and echoes (by bats). The maximum detection distance is shortened more severely for bats than for eared insects [35], because bat calls have suffered only a one-way transmission loss, while they reach the insect, whereas echoes reaching the bat have suffered a two-way transmission loss. As a result, the ecological and evolutionary balance between predators and prey can change.

Biotic interactions are thus an important mechanism underlying the ecological responses of species to climate change [7], including changes in the structure and biodiversity of present-day communities.

5. Conclusion

Global warming affects the energetics [8] and biogeography [15] of bats and also the abundance of their insect prey [49], often via unknown mechanisms [7–9]. Because echolocating bats largely perceive their surroundings by
ultrasound travelling through air, the temperature-dependence of atmospheric attenuation is a mechanism that functionally links global warming to their sensory capabilities. This mechanism will likely also influence the acoustic behaviour of species other than bats. For example, the height of songbird posts has increased in recent years as an adaptation to altered local climatic conditions [66]. In summary, global warming can affect the prey detection ability of the diverse predator community of echolocating bats, with potential consequences for their foraging efficiency and interspecific interactions. Ultimately, this mechanism may contribute to the observed and predicted effects of global warming on bats and may affect their community structure, distribution and biodiversity as well as those of their insect prey [67,68].

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