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Traffic noise playback reduces the activity and feeding behaviour of free-living bats☆

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ABSTRACT

Increasing levels of road noise are creating new anthropogenic soundscapes that may affect wildlife globally. Bats, which form about a third of all mammal species, are sensitive bioindicators, and may be particularly vulnerable because of their dependency on echolocation. Here we present the first controlled field experiment with free-living bats. Using a Before-After-Control-Impact phantom road experimental design, we examine the impacts of traffic noise on their activity and feeding behaviour. Disentangling the impacts of traffic noise from other co-varying exposures such as habitat quality, the experiment demonstrates a significant negative effect on the activity of each of the five, ecologically different, species (genus for *Myotis* spp.) examined. This suggests that the results are widely applicable. The negative effects are largely attributable to noise in the sonic spectrum, which elicited aversive responses in all bat species tested,whereas responses to ultrasoundwere restricted to a single species. Our findings demonstrate that traffic noise can affect bat activity at least 20m away from the noise source. For *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*, feeding behaviour, as well as overall activity, was negatively affected. Ecological Impact Assessments are therfore needed wherever there are significant increases in traffic flow, and not just when new roads are built. Further research is required to identify effective mitigation strategies, to delineate the zone of influence of road noise, and to assess whether there is any habituation over time.

1. Introduction

The exponential growth of the human population and the rapid increase in global urbanisation has profound implications for wildlife. Networks of roads have been built through the natural environment, posing barriers to the movement of animals through collision risk and habitat loss, as well as causing indirect effects on habitat quality that can compromise foraging and commuting (Fensome and Mathews, 2016; Forman, 2003; Keller and Largiader, 2003). While road densities have only increased by approximately 10% between 1990 and 2011 in OECD countries (Organisation for Economic Co-operation and Development), traffic densities have increased by 55% (OECD Publishing, 2013). This has led to a global growth in anthropogenic noise pollution and the creation of new soundscapes, which can alter how animals use their primary sensory systems to detect or recognise cues to forage, communicate, find mates and avoid predators (Brumm and Slabbekoorn, 2005; Senzaki et al., 2016; Swaddle et al., 2015). Species diversity, occupancy, reproductive success and survival (e.g. Goodwin and Shriver, 2010; Halfwerk et al., 2011; Wiącek et al., 2015), can be affected through the masking of both territorial and predatory alarm calls (Mockford and Marshall, 2009; Nelson et al., 2017; Templeton et al., 2016), and by eliciting avoidance behaviour and stress responses (Hastie et al., 2018; McClure et al., 2013; Troïanowski et al., 2017).

Compared to birds, little research has been undertaken with bats to disentangle the impact of traffic noise from overall effects, which could include a combination of light, sound and air pollution as well as habitat changes (e.g. Berthinussen and Altringham, 2012; Claireau et al., 2019; Medinas et al., 2019; Pourshoushtari et al., 2018). However, recent experimental evidence, based on captive animals, using acoustic playback systems in an enclosed environment suggests that traffic noise can reduce the feeding success of *Myotis myotis*, *Myotis daubentonii* and *Antrozous pallidus* (Bunkley and Barber, 2015; Luo et al., 2015; Schaub et al., 2008; Siemers;

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Schaub, 2011). Both Schaub et al. (2008) and Siemers and Schaub (2011) found that traffic noise may mask echolocation calls, owing to the frequency overlap between *M. myotis* and the traffic noise being played. In contrast, Luo et al. (2015) found no evidence of acoustic masking or reduced feeding attention in *M. daubentonii*. Rather, three out of four of the captive bats in their experiment showed signs of avoiding noise below the frequency at which they echolocate, with this avoidance being responsible for reduced feeding success. It was not possible to distinguish whether the reduced feeding success reported by Bunkley and Barber (2015) was owing to call masking or avoidance behaviour.

Given this experimental evidence from captive animals, we have conducted the first controlled field experiments (i.e. outside the laboratory) to test the impacts of traffic noise on free-living bat assemblages. This is vital, as unlike in laboratory studies free-living individuals have a choice of whether they want to be present in the vacinity of the noise source or not. Our study aims to disentangle the effect of traffic noise from other correlated risk factors seen in operational roads, e.g. habitat fragmentation or lighting, by replaying traffic noise in a roadless environment. We are therefore able to examine the local effects of traffic noise in isolation, on a diverse range of bat species. To understand the general consequences of traffic noise for bats, we recorded activity and feeding behaviour for four species with contrasting flight patterns, echolocation and foraging techniques (Dietz and Kiefer, 2016; Russ, 2012), and also for the genus *Myotis*.

We hypothesised that, at a local scale, the full acoustic spectrum (sonic and ultrasonic spectra combined) of traffic noise would reduce activity for all species recorded. Additionally, we hypothesised that the sonic spectrum (<20 kHz frequency noises) would have a larger negative effect than the ultrasonic spectrum (>20 kHz frequency noises), when played separately, due to bats showing avoidance behaviour rather than their calls being masked. We predicted that the bat assemblage would not become habituated to traffic noise over the period of the experiment, because of the short duration of the exposure, but that feeding activity would also decrease.

2. Material and methods

2.1. Traffic noise surveys

Traffic noise from a dual carriageway (A38, Devon, England, 50.5702555°, −3.6485612°), with a surface cover of asphalt, was recorded at a distance of 3m from the centre of the carriageway closest to the road side verge. Both sonic and ultrasonic frequencies were recorded as wav-files on separate Song Meter SM2BAT + monitors (Wildlife Acoustics Inc., Maynard, Massachusetts), fitted with SMX-II (sonic) and SMX-U1 (ultrasonic) microphones (for details of the spectral response see Wildlife Acoustic (2019)). Microphones were placed horizontally, side by side, at a height of 1.5m off the ground, and were perpendicular to the the centre of the road (i.e. faced the centre). Traffic noise from the vehicles was recorded on a dry, windless day, without a wind guard on the microphones (i.e. under dry asphalt conditions) (Schaub et al., 2008), over a period of approximately 3 h. No low or high pass filters were applied during the recordings. The mean vehicle speed, as assessed over 50m,was 110 km/h.

To calculate the average recorded pass duration of a vehicle, 50 vehicles were studied. We used Adobe Audition CC (Adobe® Systems, Mountain View, CA, USA) to measure the time at which the vehicles were initially detected by the microphones (assessed by change in frequency compared to background noise) to when the frequency returned to background noise levels. The mean duration of the length of sound from the passing vehicles was 1.4s (SE 0.57). We therefore selected a pass of duration of 1.4s— equivalent to a single passing vehicle — to use in our experiment. The recording deployed was chosen at random from those of this length available. To make the experiment represent real field conditions as closely as possible, we counted the volume of traffic on a dual carriageway for an hour starting at dusk in May. We recorded a mean vehicle pass rate of 26 vehicles per minute. Therefore, this repetition rate was used in the experiment, with the 1.4-s-long passes being dispersed equally across the minute. To mimic a natural road, the normal recorded background noise of the road was added to the gaps between the vehicle passes, thus avoiding large sections of the recording being artificially blank. As this is the first time free-living bats have been experimentally exposed to traffic noise, we chose to examine whether there was an effect of a single 1.4-s-long pass and background noise for both the sonic and ultrasonic recordings, rather than testing multiple sounds. This approach allows for easy replication in future research. However, we other study designs, for example using multiple recordings during playback experiments, could also be considered (e.g. Arroyo-Solís et al., 2013). The sonic amplitude of passing vehicles was measured at the roadside over a 2-h period (Precision Gold, NO5CC Sound Level Meter, 30–130 dB(A), fast leq), and was found to have a peak of 86 dB SPL 3m away from the centre of the carriageway closest to the road side, however it did oscillate as the vehicle arrived at, and continued past, the recording point. These oscillations in noise, caused by the vehicles passing a static point, were included in the playback for the field experiment.

Both our sonic and ultrasonic recordings were created and arranged in Adobe Audition CC, and were played simultaneously through Audacity® (version 2.1.3) (Carnegie Mellon University, PA, USA). Our sonic sound files had a high pass filter set at 1 kHz (to avoid damaging the speakers (Schaub et al., 2008)) and a low pass filter set at 20 kHz. Our ultrasonic recording had a high pass filter set at 20 kHz and had a sampling rate of 192 kHz (contained frequencies up to 96k Hz; supporting information Fig. S1) (Adobe Audition; digital FFT filter, 2048 points, Blackman window).

2.2. Field experiment set up

Before-After-Control-Impact (BACI) designs were used for both the first field experiment in 2017, which examined the impact of the full spectrum of traffic noise (including both sonic and ultrasonic spectra) on bat activity, and for the second field experiment in 2018, which examined the sonic and ultrasonic spectra independently.

The first experiment took place at seven sites around four greater horseshoe bat (*Rhinolophus ferrumequinum*) roost sustenance zones (RSZ; area of land within 3 km of a roost) between May and August 2017 in Devon, England. During this first period of data collection, both the sonic and ultrasonic spectra of traffic noises were combined and played back to recreate the full acoustic spectrum of traffic noise. Experimental locations were along linear features (hedgerows/treelines), which were specifically chosen to include different surrounding habitats: grasslands, arable fields, woodland edges and riparian corridors, to enable the results to be generalised as widely as possible. These features had previously had no known disturbance from traffic noise.

Within each of the seven sites, we selected an Experimental location and a Control location. Control locations were at least 500m from any Experimental location to avoid disturbance from noise playback. Each of the Control locations were paired with their respective Experimental locations by choosing locations that had similar habitat features/types surrounding them and were in the same RSZ. For example, if the Experimental location was along a treeline with grass fields on their side, then a Control location along a treeline and by grass fields was chosen.

The protocol at our Experimental locations consisted of two control nights where no traffic noise files were played, followed by three treatment (sound playback) nights. On treatment nights, traffic noise files were played from 30min before sunset for 3.5h. Recordings of bats were made during this time-period on both control and sound treatment nights using four Song Meter SM2BAT + monitors (Wildlife Acoustics Inc., Maynard, Massachusetts). We placed a single bat detector 20m in front of the first speaker and another 20m behind the last speaker, and the final two were placed in the middle between the three speakers (Fig. 1). In addition, one detector was placed at the Control locations and were set to record in the same way and on the same nights as those at Experimental locations. Both traffic noise recordings were played back on a loop from a laptop computer, through an external D/A-converter (MAYA44 eX 4-in/4-out PCIe audio interface, sampling rate 192 kHz, ESI Audio, Germany), broadband amplifiers (WPA-600 Pro, Conrad Electronics, Hirschau, Germany) and through three loud-speakers (Avisoft, Speaker Vifa, frequency range 1–120 kHz, +/− 9 dB) which were set on tripods 1.5m off the ground. Tripods were placed at Experimental locations for both the control and treatment nights. All speakers faced in the same direction (horizontal) and were placed 1.5m out from the linear feature and at 20m intervals along it. Both the ultrasonic and sonic noises were played at the same amplitude on the amplifier to create a peak sonic frequency of 86 dB. The experiment only proceeded on nights when wind speeds were ≤11 km/h, temperatures were above 10 °C at dusk, and in dry conditions. The impact of noise has been shown not to affect the attention available for foraging or the search effort of bats to capture prey in captive settings but a frequency shift has been found in the echolocation call of the greater horseshoe bat (Hage and Metzner, 2013; Luo et al., 2015). It is therefore reasonable to infer that a decline in acoustic activity recorded using bat detectors reflects a true decline in the presence of bats, rather than a reduction in the detectability of the animals due to alteration in their echolocation patterns.

The second experimental period took place between June and August 2018 at six new locations in Sussex and Dorset, England. Because of the generality of the effects observed in the first experiment, the sites were not specifically chosen to be in RSZs (only one was in this category), but all were in locations known to be used regularly by bats. The methods were identical to the first experiment, except that sonic and ultrasonic components of road noise were replayed on separate nights at the Experimental locations: the pattern of playback was one control night, two nights of the sonic components of traffic noise, and two nights of the ultrasonic components of traffic noise. The order in which the noises were played alternated between sites, such that three sites played ultrasonic noise first followed by sonic noise, and three sites did the reverse. This controlled for the effects of treatment order on the findings. All sites were along treelines.

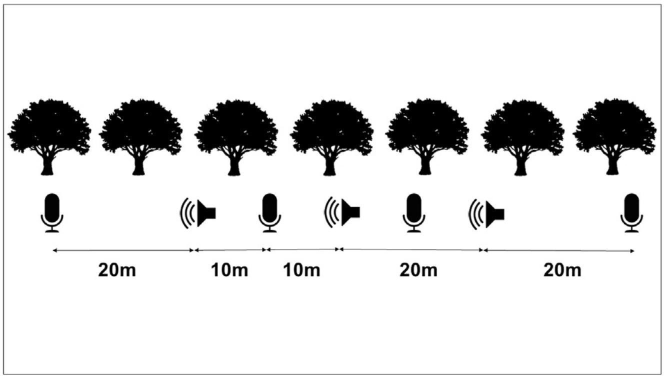

Fig. 1. Depiction of the experimental set up at Experimental locations, with three speakers placed along a linear feature and bat detectors placed between, in front of, and behind them to record bat activity.

2.3. Bat sound analysis

The analyses of bat activity were conducted using Kaleidoscope software (version 3.1.1; Bats of Europe classifier version 3.0.0; Wildlife Acoustics, Maynard, Massachusetts); all files were also checked manually. Relative bat activity was assessed as the number of bat passes per night during the 3.5 hour survey window (e.g. Charbonnier et al., 2014; Jung et al., 2012). Individual bat passes were defined as two or more echolocation calls within 1 s of each other (Fenton, 1970; Walsh and Harris, 1996). Some species of *Myotis* bats can be difficult to distinguish, owing to their similar call structures (Schnitzler and Kalko, 2001), therefore all *Myotis* species were grouped together for analysis at genus level. The five UK species of *Myotis* that were likely to be recorded during this experiment were *Myotis nattereri*, *Myotis bechsteinii*, *Myotis daubentonii*, *Myotis brandtii* and *Myotis mystacinus*. Feeding activity was defined and recorded as the number of times a feeding 'buzz' , the calls emitted while homing in on prey (Kalko and Schnitzler, 1989), occurred per night during the survey window. Detailed characteristics of the evolutionary traits of all species examined in this study, including the call structure and their foraging strategies, can be found in Russ (2012) and Dietz and Kiefer (2016). An example of the call structure of all bats examined in this study is given in the supporting information Fig. S2-6.

2.4. Statistical analysis

Generalised Linear Mixed Models (GLMM), 'lme4' (Bates et al., 2015), with a negative binomial distribution, were used to examine the potential impact of traffic noise on total bat activity (11 species); and then separately for the four species and one genus that represented most calls (97%): *Rhinolophus ferrumequinum*, *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus*, *Nyctalus noctula* and *Myotis* species. Conditional R^2 values were calculated using the 'MuMIn' package where appropriate (Barton and Barton, 2019; Nakagawa and Schielzeth, 2013). All analyses were completed in R (version 3.3.0) (R Core Team, 2016).

We used a BACI approach with the data collected from the first experimental period to assess the impact of playing traffic noise (including both the sonic and ultrasonic spectra) on the number of bat passes per night per detector. This allowed us to ask whether there were differences between Experimental and Control locations that were contingent on time (and hence treatment). The outcome variables were the counts of bat passes per night, and the exposure variables were the temporal variable (control *v.s.* sound treatment nights; fixed factor), the spatial variable (Experimental location *v.s.* Control location; fixed factor) and the interaction between them. The models also included detector position, nested within unique site identities and RSZ identities, as random effects to account for the pairing of the Experimental and Control locations, and the possible non-independence of some of the seven experimental sites that fell within the same RSZ. Using detector position nested within site as a random factor also allowed the models to account for non-independence multiple detectors at each location.

Having established that there were no significant differences at Control locations across time, we then examined whether the amount of recorded activity at the Experimental locations only varied according to the position of the detector relative to the speakers. For this model, the fixed effects were specified as time (control *v.s.* sound treatment nights), detector location (behind the speakers; in the middle of the speakers; or in front of the speakers; Fig. 1) and their interaction. Detector position, site identity, and RSZ identity, were again specified as random effects. For each species, where significant interactions were identified and suitable data were available, three additional models were created using only data from a single detector location (before the speakers; in the middle of the speakers; or in front of the speakers) at a time. This allowed for time (control *v.s.* sound treatment nights; fixed effect) to be compared at each individual detector location individually to determine if traffic noise impacted bat activity at that specific location. Both site and RSZ were used as random effects in these models. We assessed potential short-term habituation by testing for an interaction between time (control *v.s.* sound treatment nights) and night of treatment nested within time (i.e. from night one to night five). Detector position, site identity, and RSZ identity, were again specified as a random effect.

To examine whether feeding activity was affected by traffic noise playback, binomial GLMMs were created using the number of feeding 'buzzes' recorded per night compared with the number of all other calls (excluding social calls) as the outcome variable. The overall model, examining total feeding activity, used the same fixed and random effects as the initial negative binomial models. If any interactions were observed, we then examined if there was an effect at just Experimental locations, using time (control *v.s.* sound treatment nights) as a fixed factor and the same random factors as the original model for both *P. pipistrellus* and *P. pygmaeus*. Models using feeding buzz data could only be created for *P. pipistrellus* and *P. pygmaeus* owing to the lack of data for other taxa. *Myotis* spp. and *N. noctula* were not examined because there was little feeding activity at baseline, as would be expected in these habitats; and feeding calls are difficult to distinguish for *R. ferrumequinum*.

Finally, we used the data from the second experimental period to assess whether the impacts of road noise resulted from exposure to sonic or ultrasonic components of the sound spectrum. Using a negative binomial GLMM we initially assessed whether there were differences in bat activity between Control and Experimental locations that were contingent of time (using a temporal variable (control *v.s.* sonic noise *v.s.* ultrasonic noise treatment nights; fixed factor); a spatial variable (Experimental location *v.s.* Control location; fixed factor) and the interaction between them. Then, isolating data from the Experimental locations, we investigated whether nights playing sonic or ultrasonic traffic noise (fixed effect) had an impact on bat activity relative to control nights. The models also included detector position, nested within unique site identities as random effects. Using a binomial GLMM, we then examined whether total feeding activity was predicted by the interaction of the time and spatial variables, before examining *P. pipistrellus* and *P. pygmaeus* individually at Experimental Locations. Detector position, nested within unique site identities were added to the models as a random factor. If a detector failed to record any bat activity, owing to technically difficulties, the detector position from that site was removed from the analysis. However, similar results were obtained from the BACI analysis when the data were excluded. Given that the data from the Experimental sites were collected under similar environmental conditions, with no significant difference, the data were included in the final analysis. All model residuals were examined to ensure they met the assumptions of the models. Effects were judged as statistically significant when p was less than 0.05.

To test whether environmental conditions, temperature and humidity, significantly influenced nightly bat activity, we included them in our initial analysis when examining treatment night and survey locations (Control and Experimental). For both experiments, we used the same random effects for these negative binomial models, as described above. There was no significant relationship activity and either temperature or humidity and so these variables were not considered further.

3. Results

The playback of traffic noise experiment elicited substantial decreases in overall bat activity (Fig. 2). Using the BACI approach, we determined that the total amount of bat activity recorded at Control relative to Experimental locations differed between noise and control nights (interaction term: $p = 0.008$). Significantly fewer bat passes were recorded at Experimental locations when traffic noise was being played, whereas at Control locations activity did not differ between control and noise treatment nights (Fig. 3). This provides strong evidence that the reduction in activity was caused by the traffic noise playback. Further summary statistics can be found in the supporting information Table S1 and S2.

There was a significant interaction between the amount of bat activity recorded at Control relative to Experimental sites on sound treatment and control nights for *R. ferrumequinum* (interaction term: $p = 0.013$), *P. pipistrellus* (interaction term: $p = 0.032$), *P. pygmaeus* (interaction term: $p = 0.035$) and *Myotis* species (interaction term: $p = 0.046$) but not for *N. noctula* (interaction term: $p = 0.576$). When bat activity was examined at Experimental locations only, the number of bat passes for all species/genus was significantly lower on sound treatment compared with control nights: *R. ferrumequinum* (Odds Ratio (OR): 0.23, CI: 0.12–0.43, $p < 0.001$, R^2: 0.82), *P. pipistrellus* (OR: 0.16, CI: 0.09–0.29, $p < 0.001$, R^2: 0.68), *P. pygmaeus* (OR: 0.08, CI: 0.04–0.17, $p < 0.001$, R^2: 0.85), *N. noctula* (OR: 0.41, CI: 0.24–0.71, $p = 0.001$, R^2: 0.91) and *Myotis* species (OR: 0.14, CI: 0.07–0.28, $p < 0.001$, R^2: 0.85).

Within Experimental locations, significant interactions between detector location and time (treatment *vs.* control nights) were found for, *P. pipistrellus* (interaction term: $p = 0.050$), *P. pygmaeus* (interaction term: $p = 0.037$) and *Myotis* species (interaction term: $p = 0.016$). For *R. ferrumequinum* the interaction term was marginal: $p = 0.072$) and for *N. noctula* the interaction term had $p = 0.336$). Further models examining individual detector locations could only be created for *P. pipistrellus* and *P. pygmaeus* owing to the lack of data for other taxa. For these species, traffic noise had a significant negative impact on activity at detectors placed both at the speakers and 20m in front of the speakers (*P. pipistrellus* OR: 0.08, CI: 0.04–0.17, $p < 0.001$, R^2: 0.67; OR: 0.18, CI: 0.10–0.36, $p < 0.001$, R^2: 0.82, respectively; *P. pygmaeus* OR: 0.03, CI: 0.01–0.13, $p < 0.001$, R^2:

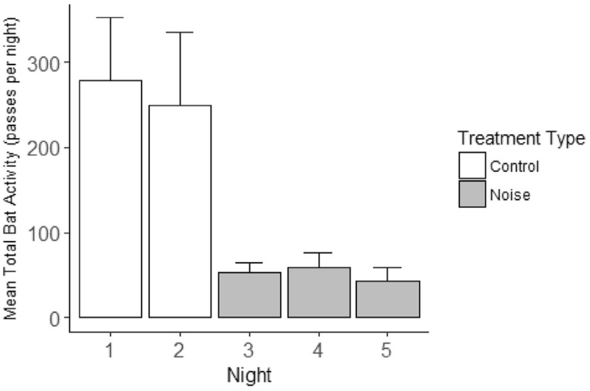

Fig. 2. Mean nightly bat activity (+SE) during control (white) and noise (grey) treatment nights across the seven study sites; graph based on raw activity data. Total number of passes at Experimental locations = 13817 (on control nights: total = 10836, mean = 264, SE = 56; on noise treatment nights: total = 2981, mean = 51, SE = 9).

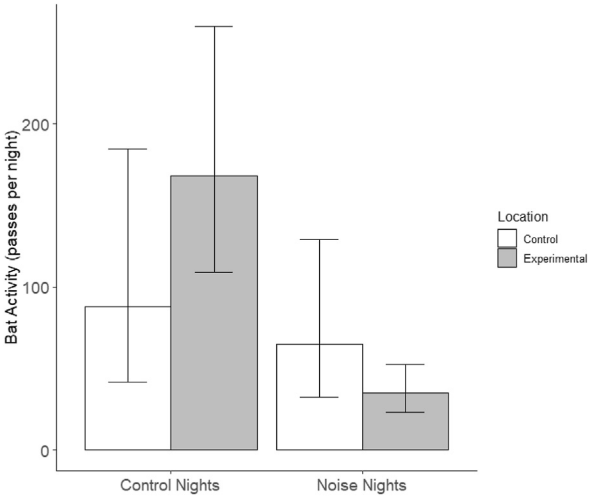

Fig. 3. Predicted bat activity on control and noise treatment nights, at Control (white) and Experimental (grey) locations. Bars show 95% confidence intervals.

0.91; OR: 0.16, CI: 0.01–0.47, $p < 0.001$, R^2: 0.73, respectively). There was also a significant reduction in activity 20m behind the speakers for both *P. pipistrellus* (OR: 0.30, CI: 0.10–0.94, $p = 0.038$, R^2: 0.60) and *P. pygmaeus* (OR: 0.33, CI: 0.12–0.94, $p = 0.038$, R^2: 0.67). We also assessed whether there was evidence of habituation or increased responsiveness at each Experimental location during the noise treatment nights. There was no significant interaction between location and the night on which the noise was played ($p = 0.146$) with activity staying relatively constant over time at Experimental locations.

We examined whether differences between Experimental and Control locations depended on whether it was a noise treatment or control night, and found a significant negative interaction for total feeding activity ($p = 0.025$). At Experimental locations, feeding activity was lower on noise treatment nights compared with control nights for both *P. pipistrellus* (OR: 0.57, CI: 0.47–0.69, $p < 0.001$) and for *P. pygmaeus* (OR: 0.53, CI: 0.35–0.79, $p = 0.002$).

Having established that road noise playback strongly influenced bat activity, we then tested whether the effects were generated by the sound in the ultrasonic or sonic spectrum. As in the previous experiment, there were no significant differences between bat activity recorded at Control locations. Additionally, at Experimental locations, there were significant differences between control and sound treatment nights for total bat activity (interaction term: $p = 0.043$) and *P. pipistrellus* (interaction term: $p = 0.008$), but not *P. pygmaeus* (interaction term: $p = 0.552$) or *Myotis* species (interaction term: $p = 0.368$). Owing to very low pass rates for *N. noctula* and the rare *R. ferrumequinum,* these species were not analysed further. Both sonic and ultrasonic noise playback had significant negative effects on total bat activity at Experimental locations, though the effect sizes were larger for the sonic treatment (sonic: OR: 0.32, CI: 0.22–0.47, $p = 0.001$; ultrasonic: OR: 0.50, CI: 0.35–0.72, $p < 0.001$, R^2: 0.45) and *P. pipistrellus* (sonic: OR: 0.34, CI: 0.23–0.51, $p < 0.001$; ultrasonic: OR: 0.53, CI: 0.36–0.78, $p = 0.001$, R^2: 0.47). For *P. pygmaeus* and *Myotis* species, sonic noise playback reduced bat activity (OR: 0.40, CI: 0.24–0.64, $p < 0.001$, R^2: 0.75; OR: 0.34, CI: 0.21–0.55, $p < 0.001$, R^2: 0.61, respectively) but ultrasonic noise had no effect ($p > 0.05$).

We identified that there were significant negative interactions between Experimental and Control locations and treatment night for total feeding activity ($p < 0.01$), during the second experiment. Feeding activity appeared to be reduced at Experimental locations on nights with sonic and ultrasonic playback compared with control nights for both *P. pipistrellus* (sonic: OR: 0.65, CI: 0.53–0.80, $p < 0.001$; ultrasonic: OR: 0.79, CI: 0.69–0.92, $p = 0.001$) and for *P. pygmaeus* (sonic: OR: 0.61, CI: 0.46–0.82, $p = 0.001$; ultrasonic: OR: 0.49, CI: 0.39–0.62, $p < 0.001$).

4. Discussion

We have established, for the first time, that playback traffic noise alone can reduce the activity of free-living bat assemblages, even in the absence of other features associated with roads such as lighting and habitat loss. Reduced activity in response to playback of traffic noise (sonic and ultrasonic spectra combined) was observed for each species that we examined. This includes those species that have markedly different flight heights, speeds, foraging strategies, and with contrasting echolocation patterns. For example species such as *R. ferrumequinum* can emit high frequency ultrasonic calls (82 kHz), whereas species like *N. noctula* can have low frequency calls within the sonic range (18 kHz), other species emit frequency modulated sweeps (e.g. *Myotis spp.*), constant frequency calls (*R. ferrumquinum*) and calls combining frequency modulation and constant frequency elements (e.g. *Pipistrellus* spp.) (Russ, 2012). The results suggest that the response of bats to traffic noise is a generalised phenomenon that has a negative impact across all functional groups examined. It is notable that sound in the sonic spectrum had a negative impact on the activity of all species, whereas ultrasound produced less marked responses and was absent in some species. This suggests that the mode of action is likely to be through general deterrence and avoidance, rather than through the masking of echolocation calls used for orientation or foraging. These results are similar to the findings of laboratory-based studies (e.g. Luo et al., 2015). Comparable results were also identified from perceived point noise sources, that caused acoustically-mediated distractions for bats (e.g. Bunkley and Barber, 2015). In addition, high frequency sound waves (ultrasound) propagate over smaller distances through air than lower frequency sounds. Therefore, the effective distance over which ultrasound generates an ecological impact — whether derived from experimental playback or from real roads — is likely to be lower than for sonic noise. It is unlikely that our speakers fully replicated the true coverage and extent of real road noise. However, this means that the effects observed in this study are likely to be conservative estimates of the true impact of traffic noise on free living bat species.

The deterrent effects of traffic noise, within the local area of the Experimental locations, were evident at distances of at least 20m from the source in our experiment, and was more severe beside the sources of the noise and in the direction it is coming from. Nevertheless, effects are still observed behind the speakers because noise drifts and bounces off objects, emphasising that consideration must be given to the diffusion of noise through space. Further work is required to establish the spatial scale of the impacts. This is important as many studies have demonstrated a reduction in general animal species diversity and abundance in relation to distances to roads (Benítez-López et al., 2010; Berthinussen and Altringham, 2012; Claireau et al., 2019; Wiącek et al., 2015),: our results suggestthat traffic noise is likely to be an important factor. Nevertheless, other studies do demonstrate that fast flying bats are not as affected by roads and traffic noise compared to slower flying bats though (Bonsen et al., 2015; Myczko et al., 2017). It is unclear however, whether bats would habituate to playback noise over the long-term, but over the relatively short duration of our study, the aversive effects appeared too consistently low over time.

Traffic noise reduced feeding activity (measured as the ratio of feeding calls to orientation calls) for both *P. pipistrellus* and

P. pygmaeus — species with very similar echolocation patterns. When exposed to sonic and ultrasonic noise separately, stronger negative effects were observed for the former. The results of these experiments therefore support the inferences made by previous contrasting studies: ultrasonic noise reduces bat ability to feed, potentially by masking the echolocation calls used by foraging bats (e.g. Schaub et al., 2008; Siemers and Schaub, 2011), but there is also a larger effect from sonic noise which does not overlap with the echolocation calls (Luo et al., 2015). The mechanism for the latter is unclear but it may appear that the foraging bats actively avoid the aversive stimulus of traffic noise.

Now that we have established that the experiments have shown significant negative impact of traffic noise on bat activity and foraging behaviour using a single sound file, future research should focus on examining the effects of multiple target sound files (traffic noise) with similar components recorded over longer periods of time (Kroodsma et al., 2001). Additionally, a ‘cross playback’ (reversing the control and treatment locations after the initial experiment) could be conducted to ensure that all local variation within sites are considered and accounted for within the experimental design.

Many bats are of high conservation concern (e.g. in Europe, all species are protected under the Habitats Directive 92/43/EEC). Environmental Impact Assessments therefore need to consider the potential effects of road noise on habitat quality, landscape connectivity, and population viability. These effects need to be considered in combination to those of street lighting, collision and direct habitat loss and prioritised accordingly (e.g. Azam et al., 2018; Day et al., 2015; Mathews et al., 2015; Pauwels et al., 2019; Stone et al., 2009). Given that road noise increases with the extent of traffic flow, the ecological impacts of greater traffic flow on existing routes — whether generated by transport policies or by specific projects such as a peri-rural housing development — must be considered, not just new road construction schemes. Potential mitigation strategies include noise barriers, substrate alterations and speed limits (Ishizuka and Fujiwara, 2004; Wayson, 1998) but research is needed to test the effectiveness and proportionality of alternative strategies. New mitigation strategies are particularly needed to reduce the impact of sonic noise created by vehicles. Unfortunately, this is more difficult than mitigation for ultrasound that is readily attenuated over a short distance in air. Although the transition to electric vehicles may reduce road noise within urban centres, it is unlikely to have a material impact for most roads because at speeds >75 km/h, sound is generated primarily by the contact between the tyres and road surface rather than by engines (The Highway Agency et al., 2011). Alterations to tyre composition and structures are therefore a more promising route to reducing traffic noise.

Data accessibility

Supporting data for this study have been deposited on Figshare digital repository (10.6084/m9.figshare.11639700).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Domhnall Finch: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Project administration. **Henry Schofield:** Resources, Writing - review & editing, Visualization, Supervision, Funding acquisition. **Fiona Mathews:** Conceptualization, Methodology, Formal analysis, Resources, Writing - review & editing, Visualization, Supervision, Project administration, Funding acquisition.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2020.114405.

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