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# Evaluating methods to deter bats

Lia Rose Vincent Gilmour

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of PhD in the Faculty of Life Sciences.

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# Abstract

Bat deterrents, such as radar and acoustic methods have been suggested as potential mitigation for when bats are at risk of harm from human activities and/or structures. To date, no study has compared bat responses to these methods, for use in a European context. In this thesis, I aimed to (i) test acoustic and radar as potential deterrent devices, at foraging sites in the UK, (ii) determine the effect of an acoustic deterrent device with increasing distance and (iii) explore bat responses to an acoustic deterrent device and potential mechanisms for deterrence. I found that acoustic but not radar deterrents were effective at reducing bat activity at foraging sites and therefore I focussed on acoustic deterrents for the rest of the thesis. I developed a 2-dimensional (2D) thermal bat tracking system and used it in combination with acoustic and visual bat pass counting methods to examine bat responses to an acoustic deterrent with increasing distance. Results from a fine-scale study indicated an 80% reduction in bat activity at 15 m from the acoustic deterrent, reducing to 25% reduction at 30 m, but a larger scale experiment found no deterrent effect beyond 40 m. I then developed the thermal tracking method further and examined bat responses in 3D to deterrent broadcast and also examined the deterrent's effect on echolocation call parameters. Bats increased their flight speed, decreased the tortuosity of their flight paths and focussed the signal of their echolocation calls into a reduced bandwidth, in line with a decrease in foraging behaviour and in support of the hypothesis that a masking effect of the deterrent sound affects echolocation behaviour. I conclude that acoustic deterrence shows great promise in the management and conservation of bat populations but warn that these methods should always be used with careful consideration and on a case-by-case basis.

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# Author's declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's *Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

Lia Rose Vincent Gilmour

SIGNED: DATE:

# Table of Contents

# List of Tables

# List of Figures

# CHAPTER 1

## General Introduction

## 1.1 Deterrence systems for bats

In this thesis, I test and evaluate methods to deter bats from areas where they may be at risk from structures built by and/or activities performed by humans. Where animals exist near to humans, human-wildlife conflicts and impacts can arise (Madden 2004; Redpath et al. 2013) and deterrence is often used as mitigation measure to ameliorate impacts on wildlife and/or human resources (Arnett et al. 2013; Schakner & Blumstein 2013; Mahjoub et al. 2015). In this section, I introduce animal deterrence methods as mitigation for human-wildlife conflict and discuss bat deterrent literature published to date.

### 1.1.1 Human-wildlife conflict and mitigation

An expanding human population inevitably places demands on resources, such as food, water and energy, and this often leads to degradation of the environment and impacts on biodiversity (McGill et al. 2015; Johnson et al. 2017). Human-wildlife conflict is therefore a major conservation issue (Madden 2004; Hedges & Gunaryadi 2010; King et al. 2011; Meijaard et al. 2011; Redpath et al. 2013; Redpath et al. 2015; Aziz et al. 2016; King et al. 2017) that can arise when stakeholders with different interests clash over conservation of wildlife, human welfare and/or resources (such as livestock, crops, fish) (Nyhus 2016). Often quoted examples involve large charismatic species, such as crop-raiding elephants (*Elephas maximus* and *Loxodonta africana africana*) (Hedges & Gunaryadi 2010; King et al. 2011; King et al. 2017) or orangutans (*Pongo* spp.) being killed and displaced to make way for palm oil plantations (Meijaard et al. 2011). However, it is important to define what we mean when we use the term ‘human-wildlife conflict’, which can be misleading, as it encourages an antagonistic narrative between humans and wildlife, by implying they are in direct conflict (Redpath et al. 2015). More useful phrases are therefore ‘human-wildlife impacts’ and/or ‘conservation conflicts’, which more carefully describe the conflicts among humans that arise from human impacts on wildlife, or vice versa (Redpath et al. 2013; Redpath et al. 2015).

In this thesis, I explore methods to deter bats which are at risk from human structures and/or activities. Wind turbines pose a direct threat of mortality to bats, which forage around these structures and can get hit by the turbine blades or killed by pressure changes (barotrauma) from entering the rotor-swept area (Baerwald et al. 2008; Rydell et al. 2010a; Rydell et al. 2010b; Rollins et al. 2012; Rydell & Wickman 2015; Arnett et al. 2016; Rydell et al. 2016).

Roads and other transportation networks can also affect bats in a variety of ways, including via collision or through indirect effects such as noise pollution and habitat loss (Bennett & Zurcher 2013; Altringham & Kerth 2016; Fensome & Mathews 2016). Therefore, rather than being a human-bat conflict, the conflict that arises is between groups wishing to conserve bat species from human impacts and those with more commercial or anthropocentric interests. Bat deterrents have also been used to alleviate conflict between stakeholders such as bat conservation charities, government bodies and those who wish to conserve historical buildings that bats roost in and cause damage with their urine and faeces (Packman et al. 2015; Zeale et al. 2016). Conservation conflicts and human-wildlife impacts are also an important global issue in marine ecosystems (Schakner & Blumstein 2013), with depredation of fish stocks and entanglement of marine mammals causing significant socio-economic and conservation concerns (Read et al. 2006; Gazo et al. 2008; Read 2008; Hamer et al. 2012; Dawson et al. 2013; Guinet et al. 2015).

Mitigation methods to alleviate human-wildlife impacts and conservation conflicts are often therefore focused on removing animals from an area where they may come to harm, where their presence is causing conflict, or where they are regarded as a nuisance (Schakner & Blumstein 2013). Many non-lethal mitigation strategies include ways of keeping animals out of an area that contain crops, livestock or other resources (Marker et al. 2005), or reducing animal interactions with human-built structures, i.e. deterrence (Hedges & Gunaryadi 2010; King et al. 2011; Arnett et al. 2013; Schakner & Blumstein 2013; Mahjoub et al. 2015; King et al. 2017). Methods for animal deterrence that have received attention in the literature include chemical, acoustic, visual, electrical and even hydrological approaches (Mooney et al. 2009; Hedges & Gunaryadi 2010; King et al. 2011; Noatch & Suski 2012; Dawson et al. 2013; Schakner & Blumstein 2013; Dieter et al. 2014; Mahjoub et al. 2015; Hansen et al. 2016; Swaddle et al. 2016; Zeale et al. 2016; King et al. 2017). Below I discuss some of these methods and then focus on deterrence methods specifically for bats.

### 1.1.2 Animal deterrence methods

The aim of a deterrent is to remove an animal from an area using a stimulus that an animal finds uncomfortable, aversive or distracting, or one that masks the ability to sense other salient stimuli, for example from predators and/or conspecifics (Nicholls & Racey 2007, 2009; Hedges & Gunaryadi 2010; King et al. 2011; Arnett et al. 2013; Schakner & Blumstein 2013; King et al. 2017). For example, chilli pepper and beehive fences deterred elephants from raiding crops in Indonesia and Africa (Hedges & Gunaryadi 2010; King et al. 2011) and chemical deterrents reduced crop raiding by geese and rodents (Dieter et al. 2014; Hansen et al. 2016). Air bubbles and light have been used as deterrence methods in fisheries management, as well as chemical, acoustic and electrical techniques (Patrick et al. 1985; Noatch & Suski 2012). Bird deterrents such as air crackers and birds of prey and their silhouettes have been used at airports, where bird strikes are a problem (Burger 1983).

Acoustic deterrents have shown potential for use with birds (Burger 1983; Marques et al. 2014; Mahjoub et al. 2015; Swaddle et al. 2016; Schlichting et al. 2017), bats (Arnett et al. 2013; Packman et al. 2015; Zeale et al. 2016) and some marine mammals (Dawson et al. 2013; Schakner & Blumstein 2013). For example, bycatches of small cetaceans were reduced when sound emitting devices called ‘pingers’ were used with gill nets (Dawson et al. 2013). However, similar devices failed to cause aversive responses in other species that depredate from nets, probably due to habituation (Gazo et al. 2008; Carretta & Barlow 2011; Schakner & Blumstein 2013). Acoustic bird deterrents have also been explored for use at wind turbines (Marques et al. 2014), airfields (Swaddle et al. 2016; Schlichting et al. 2017) and in reduction of crop damage (Mahjoub et al. 2015; Swaddle et al. 2016). For example, European starlings (*Sturnus vulgaris*) were deterred from an airfield (Swaddle et al. 2016) and from inflicting crop damage when an acoustic deterrent disrupted their communication and vigilance behaviour (Mahjoub et al. 2015; Swaddle et al. 2016). Acoustic devices that have a narrow beam width and high enough sound levels to cause physical discomfort at large distances were also effective at deterring vultures (*Coragyps atratus* and *Cathartes aura*) and gulls (Laridae), but not blackbirds (Icteridae), or water species in avian dispersal trials (Schlichting et al. 2017). Ultrasound can also be used to deter bats (Arnett et al. 2013; Zeale et al. 2016) and in the next section, I explore the potential use of acoustic deterrents on bats, along with other methods described in the scientific literature.

### 1.1.3 Methods for deterring bats

Bat deterrence devices have recently received attention as possible mitigation for reducing bat collisions with wind turbines (Nicholls & Racey 2007, 2009; Arnett et al. 2013; Gorresen et al. 2015) and for when bats roost in historic buildings (Packman et al. 2015; Zeale et al. 2016). Deterrent stimuli that show potential for investigation include the use of light, radar and ultrasound to deter bats from using an area (Nicholls & Racey 2007, 2009; Arnett et al. 2013; Zeale et al. 2014; Gorresen et al. 2015; Packman et al. 2015; Zeale et al. 2016).

#### 1.1.3.1 Light

Some bat species are deterred by certain types of lighting, for example streetlights or flood-lights (Stone et al. 2012; Stone et al. 2015; Rowse et al. 2016; Rydell et al. 2017). Lighting has recently been tested as a potential bat deterrent for use in churches where urine and faeces can cause damage and a cleaning burden (Packman et al. 2015; Zeale et al. 2016). Illumination of ‘no-fly zones’ within churches limited bats use of those areas, but bats became entombed in roosts that were directly lit, causing the authors to caution against using this method without careful consideration and further investigation (Zeale et al. 2016). Indeed, lighting in churches can be problematic and even detrimental for bat species that roost there. For example, roosting colonies of *Plecotus* species were significantly reduced in churches in Sweden, where flood-lights had been installed, when compared to non-lit churches over the same 25+ years (Rydell et al. 2017).

Ultraviolet (UV) light has also shown potential as a deterrent for Hawaiian hoary bats (*Lasiurus cinereus semotus*) at wind turbines, where they are at risk of collision (Gorresen et al. 2015). However, light has the potential to be attractive to some bat species, rather than deterrent (Stone et al. 2015; Rowse et al. 2016), probably due to its attractive effect to insects, which often aggregate around street lights, especially those that emit UV (Rydell 1992; Rydell 2006; Wakefield et al. 2018). Therefore, due to the attractive effect of light to some bat species and the potential for adverse effects of light deterrents outweighing the potential benefits for others, I decided not to include them in experiments for my thesis. Instead, I focus on radar and acoustic deterrents in Chapter 2 and acoustic methods only in Chapters 3 and 4.

#### 1.1.3.2 Radar

Radar is a detection system that uses pulses of high intensity electromagnetic fields (radio or microwaves) and has military, aviation, meteorological and wildlife detection applications (Chapman et al. 2002; Chapman et al. 2004; Zaugg et al. 2008; Smith et al. 2016; Olsen & Asen 2017; Bauer et al. 2019). Lower radio frequencies (below 10 GHz) can penetrate tissues and exposure in humans and other animals can cause behavioural and physiological changes in both fully grown individuals and developing young, such as oxidative changes and histopathology due to heating of internal organs (D'Andrea et al. 2003; Chauhan et al. 2017; Sharma et al. 2017). An auditory response to pulsed radar has also been documented for humans and other animals, which rather than being related to the radar frequencies, is a function of brain size (Sienkiewicz 1998; Elder & Chou 2003).

Nicholls & Racey (2007) found that bats in Scotland avoided air traffic control stations where radar was being deployed and suggested its potential as a deterrent for use at wind turbines. A follow-on study recorded reduced bat activity and foraging when an X-band (8-12 GHz) marine radar unit was used at riparian foraging sites, also in Scotland (Nicholls & Racey 2009). The experiment was repeated with three different radar operations, including a fixed antenna (no rotation) emitting a short pulse length/lower duty cycle program, a fixed antenna emitting a medium pulse length/higher duty cycle program (which both affected bat activity and feeding), and a rotating antenna emitting the short pulse program, that had no effect on bat activity or feeding. The deterrent mechanism was likely due to an auditory microwave effect, rather than a thermal burden produced by induction (Nicholls & Racey 2009). Due to thermoelastic expansion of their brain tissue, it is possible that bats hear a high frequency sound of around 40 kHz, that is a function of their brain size, which may interfere with their ability to respond to their echolocation echoes from insects and the surrounding environment, or may simply be stressful (Sienkiewicz 1998; Elder & Chou 2003; Nicholls & Racey 2007, 2009). Therefore, I aim to test radar as a deterrent at riparian foraging sites, using a similar method to Nicholls & Racey (2009) and compare it to acoustic deterrence, which I introduce in the next section.

#### 1.1.3.3 Acoustic bat deterrents

In this section, I outline current literature to date exploring acoustic bat deterrents and briefly outline the reasoning for the use of ultrasound for bat deterrence. For a detailed exploration of the potential mechanisms for acoustic deterrence, see Introduction section 1.2 below.

The potential for using ultrasound to deter bats from approaching wind turbines has been demonstrated by researchers in North America in lab and field-based experiments and is regarded as a mitigation measure that requires further attention and exploration (Szewczak & Arnett 2007; Horn et al. 2008a; Arnett et al. 2013). Foraging bats tend to avoid ultrasonic noise, whether from natural causes (e.g. turbulent water or rain) (Mackey & Barclay 1989; Geipel et al. 2019) or anthropogenic noise pollution (e.g. traffic noise) (Schaub et al. 2008; Bunkley et al. 2015; Luo et al. 2015). Ultrasound may deter bats as it has a masking effect on echolocation, which bats use for prey detection or orientation, or simply because it produces a disturbing airspace (see Introduction 1.2 below) (Schaub et al. 2008; Bunkley et al. 2015; Luo et al. 2015). Sources of ultrasound may also affect a bat's ability to communicate with conspecifics or indeed the ability to eavesdrop on echolocation calls of other bats (which can be beneficial for finding foraging sources and mates) (Dechmann et al. 2009; Voigt-Heucke et al. 2016). Bats are also affected by high frequency ultrasonic clicks produced by some noxious moths (and their mimics) and this is thought to be due, in part to some 'jamming' mechanism that leaves the bats echolocation system unusable (Hristov & Conner 2005; Corcoran et al. 2009; Corcoran et al. 2011; Corcoran & Conner 2012). Therefore, bat deterrent systems are usually designed with the aim to mask or jam the echolocation calls of bats (Szewczak & Arnett 2006; Szewczak & Arnett 2007; Arnett et al. 2013).

Early work with rodent deterrents that emitted ultrasound were ineffective at deterring little brown bats (*Myotis lucifugus*), but this may have been due to the deterrents' low amplitude emissions (Hurley & Fenton 1980). Bats were deterred from ponds by an ultrasonic pest deterrent (26-70 kHz) in a small study carried out in the US (Johnson et al. 2012). Laboratory and field experiments carried out in North America have shown the potential of ultrasound deterrents for reducing bat fatalities at wind turbines (Spanjer 2006; Szewczak & Arnett 2006; Szewczak & Arnett 2007; Horn et al. 2008a; Arnett et al. 2013). Feeding and non-feeding trials were first conducted on the big brown bat (*Eptesicus fuscus*) in the laboratory (Spanjer 2006) and a prototype speaker was then tested in field trials at water bodies in the US (Szewczak & Arnett 2006; Szewczak & Arnett 2007). In the laboratory, bats were significantly less likely to land in an area and take a tethered mealworm from an area when ultrasonic noise was broadcast (compared to a control) (Spanjer 2006). The field trials also reported a significant decrease in number of bats passing across the near infrared camera field of view when ultrasonic speakers were deployed (broadband continuous ultrasound, 20-80 kHz) (Szewczak & Arnett 2006; Szewczak & Arnett 2007). Similar deterrents were then tested at turbines that were monitored using thermal imaging cameras, at a wind farm in New York State, USA, with varying success (Horn et al. 2008a). The same researchers then developed a 16-transducer speaker unit, capable of emitting broadband ultrasound (20-100 kHz), with maximum transmission at 50 kHz, the same as used in this thesis (see Chapter 2 Methods for power spectrum and spectrogram of deterrent output). These speakers were tested *in situ* at a wind energy facility in Pennsylvania in the USA, with encouraging results (Arnett et al. 2013). Fatality searches for dead bats, corrected for field biases in searcher efficiency and carcass removal rates were conducted daily, under 10 treatment and 15 control turbines, during the summer and autumn of the two-year study. In 2009, 21-51% fewer bats were killed at treatment turbines. However, after accounting for inherent differences between control and treatment turbines in 2010, between 2% more and 64% fewer bats were killed at deterrent treatment turbines. Species deterred by the speakers included hoary bats (*Lasiurus cinereus*) in both years of the experiment and silver haired bats (*Lasionycteris noctivagans*) in 2010. A likely limitation of the study was due to the treated airspace not extending beyond the rotor-swept area of turbines and that the distance the sound travelled would have been limited by the high humidity at the wind farm.

Acoustic bat deterrents also have the potential to be implemented in historic buildings such as churches where bats roost and cause problems with their urine and faeces (Packman et al. 2015; Zeale et al. 2016). The same speakers that were tested at wind farms and in this thesis, were effective at moving roosting Natterer's bats (*Myotis nattereri*) to new roosts inside churches in Norfolk, UK, so that damage to church artefacts could potentially be reduced. A follow-on study showed the potential for deterrents to be used as a viable long-term mitigation method in churches for *M. nattereri*, however some habituation to broadcast ultrasound was reported in soprano pipistrelles (*Pipistrellus pipistrellus*) (Packman et al. 2015). Therefore, acoustic bat deterrence clearly shows potential and warrants further investigation.

## 1.2 Mechanisms for acoustic deterrence in bats

When evaluating the use of a deterrent, it is important to understand the mechanism by which it works, not only in evaluating its efficacy, but also to safeguard from any unwanted negative effects on target and also non-target animals (Schakner & Blumstein 2013). Acoustic deterrence can be thought of as akin to a novel noise in an animal’s environment, for example from a natural source such as rain or turbulent water (Mackey & Barclay 1989; Geipel et al. 2019), or indeed anthropogenic noise from e.g. transport, construction or other human activities (Schaub et al. 2008; Bunkley & Barber 2015; Bunkley et al. 2015; Luo et al. 2015). Therefore, it is important to explore animal responses to noise and how this might be relevant to acoustic deterrence.

### 1.2.1 Animal responses to noise

Animals encounter a wide range of noise in their natural environment, which combine to form the ambient or background noise level (Moore 2013). Natural ambient noise can be made up of sounds emitted by other animals or natural processes and is increasingly added to in many areas by anthropogenic noise (e.g. noise pollution from transportation, construction or other human activities), often elevating it above the normal ambient level (Barber et al. 2010; Francis & Barber 2013). Anthropogenic noise also often has a relatively high amplitude low frequency component but can also extend into the ultrasound (> 20 kHz) and so has the possibility of affecting a wide range of animals (Barber et al. 2010; Chan & Blumstein 2011; Bennett & Zurcher 2013; Bunkley et al. 2015).

An animal’s response to noise is dependent on how the animal has evolved in a specific auditory environment and therefore unnatural noises (e.g. from anthropogenic sources) can induce changes at the behavioural (Barber et al. 2010) and physiological level (Kight & Swaddle 2011). Literature has focused on the impacts of noise (mainly anthropogenic) on foraging (Purser & Radford 2011; Wale et al. 2013; Luo et al. 2015; Gomes et al. 2016; Mason et al. 2016), courtship (de Jong et al. 2018a; de Jong et al. 2018b; Senzaki et al. 2018), migration (McClure et al. 2013; Ware et al. 2015; McClure et al. 2017) and predator avoidance behaviour (Chan et al. 2010). Impacts of noise on the immune, cardiovascular and reproductive systems, metabolism and even an animal's genetics (e.g. levels of gene expression) could also contribute to an effect on fitness (Kight & Swaddle 2011). Noise also has potential to affect behaviour at the social level (Tidau & Briffa 2019) and species distributions and assemblages may also be altered by the spread of noise pollution as urban environments continue to grow (Francis et al. 2009, 2011). Animal hearing organs and structures are often highly specialised for specific auditory tasks important for survival and reproduction (Pena & Gutfreund 2014; Mooney et al. 2015; Scherberich et al. 2017; Yin & Muller 2019). For example, some bat and cetacean species have convergently evolved a sophisticated system of echolocation, which they use to orientate and find prey (Shen et al. 2012; Teeling et al. 2016).

As well as being aware of a species' sensory ecology and physiology when assessing potential impacts of a noise, it is also important to understand the mechanism(s) underpinning an animal's response to that noise (Luo et al. 2015; Zhou et al. 2019), in order to evaluate and mitigate for potential effects. Mechanisms fit broadly under three hypotheses: auditory masking, noise avoidance or aversion, and the distraction or reduced attention hypothesis (Chan et al. 2010; Luo et al. 2015; Zhou et al. 2019). In the next three sections, I therefore outline each hypothesis and any literature relating specifically to mechanisms of noise response in bats.

#### 1.2.1.1 Auditory masking

Auditory masking is a term from the field of psychoacoustics which describes a situation where the perception of one sound is affected by another 'masking sound' (Moore 2013). Masking in humans can occur in the time domain (temporal masking) and/or the frequency domain (spectral masking). Temporal masking occurs when a sound is made less audible by the sudden onset of another sound either before or after the first (masked) sound. Spectral masking occurs when the threshold for the ability to hear one sound is increased by the presence of another sound. The masking sound is usually at a similar frequency to the masked sound, although upward (a lower frequency sound masking a higher one) and downward masking (a usually intense level of high frequency sound masking a lower one) are possible (Zwicker & Fastl 1990). However, the amount of masking that occurs depends not only on the characteristics of the original sound and the masker, but also on the hearing system of the individual listener (Moore 2013).

Masking sounds can affect an animal's ability to find food (Schaub et al. 2008; Bunkley & Barber 2015; Bunkley et al. 2015; Luo et al. 2015; Mahjoub et al. 2015) and avoid predators (Mahjoub et al. 2015; Morris-Drake et al. 2017; Zhou et al. 2019). For example, masking may affect an animal's ability to relay or glean important information to or from conspecifics about the presence of predators (Mahjoub et al. 2015; Morris-Drake et al. 2017; Zhou et al. 2019). Superb fairy wrens (*Malurus cyaneus*) and European starlings (*Sturnus vulgaris*) were less likely to react to conspecific alarm calls (Mahjoub et al. 2015; Zhou et al. 2019) and dwarf mongooses (*Helogale parvula*) to heterospecific alarm calls (Morris-Drake et al. 2017), when a masking noise was broadcast. Foraging in starlings was also reduced by sound broadcast by about a half, in food patch choice experiments, due to masking of contact calls that the birds rely on to communicate when foraging (Mahjoub et al. 2015). Foraging in the mouse-eared bat (*Myotis myotis*) was also reduced by broadcast traffic noise, which overlapped in frequency with prey-generated sounds (Schaub et al. 2008).

Acoustic masking from anthropogenic noise may also reduce the acoustic space available for animal communication, for example in fish (Radford et al. 2014), marine mammals (Clark et al. 2009), and some birds (Francis et al. 2011). For example, auditory sensitivity was reduced in three species of fish by boat noise recorded in a marine protected reserve (Codarin et al. 2009). Response latency to conspecific intruders' songs in the spotted towhee (*Pipilo maculatus*) and the chipping sparrow (*Spizella passerina*) was increased during playbacks of songs with low frequency masking noise added (Kleist et al. 2016). However, some animals seem to be able to adapt to sounds masking their communication, either by increasing the amplitude (i.e. the Lombard effect), or by changing temporal or frequency components of their calls (Foote et al. 2004; Lowry et al. 2012; Roca et al. 2016; Bittencourt et al. 2017; Dorado-Correa et al. 2018; Song et al. 2019). For example, noisy miners (*Manorina melanocephala*) increased the amplitude of their calls in noisy urban environments (Lowry et al. 2012). Mallard ducks also increased the amplitude of their calls during broadband noise playback at 0-12 kHz (Dorado-Correa et al. 2018) and orca (*Orcinus orca*) increased the duration of their calls in the presence of boats (Foote et al. 2004). Some bat species also alter their echolocation call characteristics in response to a masking sound, which I discuss further in the following section.

##### *1.2.1.1.1 Auditory masking in bats*

Bats have evolved a sophisticated system of echolocation which relies on active hearing (Metzner & Müller 2016). Therefore, being able to echolocate, bats are susceptible to a type of masking specific to sonar signals, often called 'jamming' (Griffin et al. 1963). Masking/jamming of echolocation calls can occur when a sound interferes with a bat's ability to discern relatively quiet echoes of echolocation calls returning from objects in the environment (Bates et al. 2008; Tressler & Smotherman 2009; Corcoran et al. 2011; Corcoran & Conner 2012; Hase et al. 2018). Sources of masking noise include conspecific calls (Jarvis et al. 2013; Amichai et al. 2015; Fawcett & Ratcliffe 2015), noises from other animals such as insects (Gillam & McCracken 2007; Corcoran et al. 2011; Corcoran & Conner 2012), other natural sources of sound (Mackey & Barclay 1989; Geipel et al. 2019) and anthropogenic noise (Tressler & Smotherman 2009; Bunkley et al. 2015).

Bats can also exhibit a jamming avoidance response (JAR), in which they alter the spectral or temporal components of their calls in the presence of a masking sound

(Gillam et al. 2006; Bates et al. 2008; Tressler & Smotherman 2009; Takahashi et al. 2014; Amichai et al. 2015; Fawcett & Ratcliffe 2015; Hase et al. 2018). For example, pairs of *Myotis daubentonii* flying together emitted echolocation calls with greater spectral differences than those flying alone (Fawcett & Ratcliffe 2015). Big brown bats (*Eptesicus fuscus*) also shifted the narrowband components of their calls away from a jamming stimulus of similar frequency in forced choice detection tasks in the laboratory (Bates et al. 2008). However, bats do not always alter the spectral components of their signals in order to reduce interference by a masking sound. For example, *Pipistrellus kuhlii* emitted calls of higher intensity, longer duration and more often in response to playbacks of conspecific echolocation calls from multiple speakers (Amichai et al. 2015). However, as *P. kuhlii* did not alter the spectral component of its calls, this response was more likely to increase the signal-to-noise ratio, rather than an avoidance of spectral overlap. Brazilian free-tailed bats (*Tadarida brasiliensis*) also increased duration and decreased bandwidth of their calls to increase signal-to-noise ratio (Bunkley et al. 2015). However, the changes to call characteristics documented in bats flying together may also be due to conspecifics flying nearby representing acoustic clutter, which can induce similar spectral and temporal effects on calls to JARs (Gotze et al. 2016).

Masking can also occur when bats are unable to hear prey-generated sounds (Schaub et al. 2008; Bunkley & Barber 2015). Anthropogenic noise pollution such as traffic noise often overlaps with the frequencies produced by for example arthropods walking along the ground (Schaub et al. 2008). For example, playbacks of anthropogenic noise increased the search time of two types of bats that hunt by passive listening, the mouse-eared bat (*Myotis myotis*) (Schaub et al. 2008) and the pallid bat (*Antrozous pallidus*) (Bunkley & Barber 2015). Natural sounds may also affect bats’ ability to locate their prey due to the masking of glints caused by insect bodies in echoes returning from echolocation calls (Mackey & Barclay 1989; Geipel et al. 2019). For example, two species of rainforest bats (*Micronycteris microtis* and *Molossus molossus*) delayed emergence in response to playbacks of rainfall noise (Geipel et al. 2019) and big and little brown bats (*Eptesicus fuscus* and *Myotis lucifugus*) avoided areas of water over which playbacks of turbulent water noise were broadcast (Mackey & Barclay 1989).

However, animals can also exhibit noise responses even when the sound in question does not overlap in range with a signal they are trying to detect (Luo et al. 2015; Senzaki et al. 2018). Indeed, noise can also affect the processing of information from other sensory cues, such as from olfactory and visual stimuli and lead to reduction in attention or predator vigilance (Chan et al. 2010; Purser & Radford 2011; Morris-Drake et al. 2016), discussed in the next sections.

#### 1.2.1.2 Reduced attention hypothesis

Animals contend with a wide range of sensory inputs, that they also rely on to carry out tasks important to survival and reproduction (Dukas & Kamil 2000; Persons et al. 2001; Barber et al. 2003; Amichai et al. 2015; Dell'Aglio et al. 2016; Gomes et al. 2016). Performance in one task can be limited by attention to another and this has implications in, for example predator avoidance (Dukas & Kamil 2000; Chan et al. 2010; Morris-Drake et al. 2016), intraspecific communication (Senzaki et al. 2018) and finding or catching prey (Barber et al. 2003; Purser & Radford 2011). Noise, especially from anthropogenic sources, can therefore act as a distractive stimulus, resulting in reduced attention given to important cues (Chan & Blumstein 2011). For example, noise can disrupt courtship communication, by distracting receivers so they fail to react to mating signals (Senzaki et al. 2018). Phonotaxis of female anurans towards male advertisement was affected by both overlapping and non-overlapping noise, suggesting a reduced attention or aversive effect, rather than a masking one (Senzaki et al. 2018). Foraging efficiency can also be affected by a distracting noise in an animal’s environment (Purser & Radford 2011). For example, three-spined sticklebacks (*Gasterosteus aculeatus*) reduced foraging efficiency in response to playbacks of noise (Purser & Radford 2011). Noise may also interfere with an animal’s ability to react to predator cues or conspecific communication and this can even occur across sensory modalities

(Chan et al. 2010; Kunc et al. 2014; Morris-Drake et al. 2016). For example, distraction by boat noise reduced predator vigilance in Caribbean hermit crabs (*Coenobita clypeatus*) (Chan et al. 2010) and dwarf mongooses took longer to detect predator faeces and were less likely to increase their vigilance in response to these cues, during traffic noise playbacks (Morris-Drake et al. 2016). Common cuttlefish (*Sepia officinalis*) also changed colour more frequently in visual communication displays during playback of anthropogenic noise (Kunc et al. 2014). Responses to noise are not always due to masking or distraction, however. Noise aversion or avoidance can also be due to a simple stress response (Kight & Swaddle 2011) or due to the inability to carry out important behaviours such as finding food, mates or communicating with conspecifics (Mackey & Barclay 1989; Luo et al. 2015; Geipel et al. 2019).

#### 1.2.1.3 Noise avoidance hypothesis

Noise can have wide reaching behavioural and physiological effects, as previously discussed in this chapter. Although some of these effects may be due to masking or distraction, noise may also just represent potentially stressful, aversive or uncomfortable stimuli (Wright et al. 2007; Luo et al. 2015). Novel noises, especially those from anthropogenic sources can therefore cause animals to exhibit an aversive response or in some cases outright avoidance of an area where the sound is present (Schaub et al. 2008; Bunkley et al. 2015; Luo et al. 2015; Geipel et al. 2019). Animals might avoid an area as they are unable to carry out their normal behaviour due to the presence of a sound and therefore find that noise aversive. For example, *Micronycteris microtis* and *Molossus molossus* delayed emergence from roosts in response to rainfall noise (Geipel et al. 2019) and *Eptesicus fuscus* and *Myotis lucifugus* avoided turbulent water noise when foraging (Mackey & Barclay 1989). However, it is often difficult tell whether an aversive response to a noise is simply due to stress or whether masking or distraction also play a part (Luo et al. 2015). Luo et al. (2015) devised a framework to test the mechanism of response to traffic noise in Daubenton's bats (*Myotis daubentonii*). The authors recorded reduced foraging efficiency, but no effect of noise on search effort, ruling out the reduced attention hypothesis. Bats also responded to both noise that did and did not overlap in frequency with the species' echolocation calls and therefore their responses were unlikely to be affected solely by a masking effect. The most likely mechanism was therefore simply avoidance of the noise as it represented an aversive stimulus.

### 1.2.1.4 Impacts of bat deterrence

Acoustic deterrence systems usually work by removing an animal from an area where it may come to harm or where conflict is caused by its presence or interaction with humans (Arnett et al. 2013; Schakner & Blumstein 2013; Zeale et al. 2016). Evaluation of whether the sound is acting as a stressor and its potential impacts on a species is crucial in the development of any deterrence system (Schakner & Blumstein 2013). This is especially relevant when exploring the use of acoustic deterrence systems in bats, which are likely to utilise masking or aversive effects to remove animals from an areas and potentially away from important resources (Schaub et al. 2008; Bunkley & Barber 2015; Bunkley et al. 2015; Luo et al. 2015). However, it is important to remember that many animals, including bats have evolved in acoustically complex soundscapes and therefore have the ability to adapt dynamically to a changing acoustic environment (Griffin et al. 1963; Takahashi et al. 2014; Amichai et al. 2015; Bunkley et al. 2015; Corcoran & Moss 2017; Hase et al. 2018). Many human activities also pose a relatively higher risk than the use of noise for deterrence (Baerwald et al. 2014; Lehnert et al. 2014; Altringham & Kerth 2016; Arnett et al. 2016; Rowse et al. 2016; Voigt & Kingston 2016). Therefore, it is necessary to carefully weigh up the impacts of using deterrence systems on any given animal compared to the human activity or structure that they may need protection from.

## 1.3 Thermal imaging methods for tracking bats

In this thesis, I develop a thermal tracking system for bats, which I use to examine both 2-dimensional (2D) and 3-dimensional (3D) responses to an acoustic deterrent. Acoustic and image-based flight path tracking methods (Grodzinski et al. 2009; Polak et al. 2011) and stereo photogrammetry (Jones & Rayner 1988, 1991; Jones 1995) and videogrammetry (Holderied et al. 2005) have all been used to study bat behaviour in flight, and thermal imaging is proving a useful tool in studying bat populations and their behaviour (Hristov et al. 2008). However, to date, only a handful of studies have used stereo- thermal videogrammetry and flight path tracking to study bats (Betke et al. 2008; Yang et al. 2013). In this section, I introduce these methods and discuss their application to bat ecology and biology.

### 1.3.1 Thermal imaging of wildlife

Thermal imaging involves the detection of infrared radiation or heat, emitted by all objects on Earth that are above absolute zero (0°K or -273.15°C) (Cilulko et al. 2013; McCafferty 2013). Thermal imaging cameras usually detect wavelengths of radiation in the range of 8-15 µm, not to be confused with near infrared (NIR) cameras, which record near infrared light, which has a wavelength (1 µm) much nearer the visible region of the electromagnetic spectrum (and usually requiring extra illumination). All the pixels in a thermal image contain an individual temperature or radiometric reading, which can be used in for example, the study of animal thermoregulation (Hristov et al. 2008; Kuhn & Meyer 2009), physiology (Evangelista et al. 2010) and welfare (Yahav et al. 2005). However, radiometric data are not usually relevant for detection, counting or tracking applications, like those needed in this thesis (McCafferty 2013; Dell et al. 2014). Thermal imaging is therefore a non-invasive method that allows animal behaviour to be recorded over relatively long distances, and is especially helpful in imaging animals that fly at night, when incidentally the thermal contrast happens to be greatest (McCafferty 2013). It is also a method that is becoming increasingly more affordable and portable and therefore has been useful in the study of bats in recent decades. For example, thermal imaging has allowed more accurate counting and study of emergence behaviour in bats that roost in caves in large colonies (Betke et al. 2008; Hristov et al. 2008; Hristov et al. 2010). Bat behaviour at wind turbines has also been studied using thermal imaging (Horn et al. 2008b;

Cryan et al. 2014). Along with flight path tracking methods (discussed in the next section), thermal footage has also been used to study flight (Yang et al. 2013) and foraging behaviour in bats (Hristov et al. 2008). Thermal imaging tracking methods have also shown potential in the detection and classification of birds and bats at offshore wind farm sites, where they may be at risk of collision (Cullinan et al. 2015; Matzner et al. 2015). Therefore, in the next section, I discuss the use of tracking methods in the study of animal movements and finish by introducing the potential of using stereo thermal videogrammetry to study bats.

### 1.3.2 Image-based tracking methods and stereo-videogrammetry

Until relatively recently, the study of animal movements and interactions has been limited to bio-logging techniques such as telemetry and/or direct observation of animal behaviour on previously recorded footage (Dell et al. 2014). Recent developments in recording equipment and computer vision systems have allowed researchers access to sophisticated image-based tracking systems that have been used for example, in studying animal behaviour, welfare, physiology and neurobiology (for a review see Dell et al. 2014).

Tracking usually includes three main steps: image acquisition, tracking and analysis of tracking data (Dell et al. 2014). Image acquisition includes the recording of data in the form of a sequence of image stills, with a defined spatial (pixel dimensions) and temporal (number of frames per second) resolution. Tracking normally relies on a process called background subtraction, where movement is detected between frames by subtracting one frame from the proceeding frame and the plotting of a localisation coordinate. Successive localisations are linked up to plot trajectories of an individual object’s movement over time. Trajectory characteristics and interaction between individuals can then be analysed in post or real-time processing (Dell et al. 2014). Accuracy in tracking and the quality of the subsequent analysis is dependent on the type of tracking attempted (2D, 3D, thermal tracking etc.), the number of individuals to be tracked and the data collection environment (Dell et al. 2014; Betke et al. 2017). Much literature has focussed on image-based tracking systems designed for laboratory use, in for example, the study of animal neurobiology (Straw et al. 2011; Gomez-Marin et al. 2012), welfare (Matthews et al. 2017) and behaviour (Straw et al. 2011; Matsumoto et al. 2013). Collecting tracking data in a relatively complex environment, such as a natural habitat, outside the laboratory, is much more difficult, and the challenges increase with the number of individuals and the use of 3D techniques (Betke et al. 2017). Out of the laboratory, 2D tracking has been used in the automatic classification of birds and bats at offshore windfarms (Cullinan et al. 2015; Matzner et al. 2015) and in monitoring large colonies of bats that roost in caves (Betke et al. 2008; Hristov et al. 2010). Stereo-tracking or stereo-videogrammetry requires the use of multiple synchronised cameras and calibration of those cameras in 3D space, in order to obtain accurate triangulation and localisation (Dell et al. 2014; Betke et al. 2017). Accuracy of resulting 3D trajectories can be affected by the camera properties and placements and also calibration procedures (Betke et al. 2017). However, once the challenges of 3D calibration and accurate triangulation have been overcome, stereo-tracking methods can allow detailed information about animal distributions and behaviour to be collected (Ballerini et al. 2008; Hristov et al. 2008; Yang et al. 2013; Attanasi et al. 2014). For example, 3D tracking systems have proved a useful tool in the study of collective movements in midge swarms (Attanasi et al. 2014), fish schools (Viscido et al. 2004) and European starling murmurations (Ballerini et al. 2008). Stereo-videogrammetry was also used to measure flight speeds and echolocation source levels in the bat *Eptesicus bottae* (Holderied et al. 2005) and in studying how individual bats localise each other in tandem flights (Giuggioli et al. 2015).

Combining 3D tracking methods with thermal imaging allows animals that fly in the dark, such as bats to be studied in more detail than has been previously possible and without extra illumination. However, to date only a handful of studies have used stereo thermal videogrammetry to study bats. Hristov et al. (2008) used thermal 3D tracking to study foraging behaviour and predator-prey interactions, in bats' pursuit of moths around street lights. Yang et al. (2013) combined stereo thermal videogrammetry with LiDAR to reconstruct bat flight paths through a forest.

Therefore, for this thesis, I developed both 2D and 3D thermal flight path tracking methods in order to study bat responses to an acoustic deterrent.

## 1.4 Thesis aims and outline

Human-bat conservation conflicts and impacts are an increasingly important concern for many bat species globally (Arnett & Baerwald 2013; Altringham & Kerth 2016; Arnett et al. 2016; Aziz et al. 2016; Fensome & Mathews 2016; Rowse et al. 2016; Voigt & Kingston 2016). Threats to populations include direct mortality from wind turbines (Arnett & Baerwald 2013; Arnett et al. 2016) and human transportation networks (Bennett & Zurcher 2013; Altringham & Kerth 2016; Fensome & Mathews 2016) and indirect impacts from noise (Bennett & Zurcher 2013; Hage & Metzner 2013; Bunkley & Barber 2015; Bunkley et al. 2015; Luo et al. 2015) and light pollution (Stone et al. 2009, 2012; Stone et al. 2015; Rowse et al. 2016), or from conservation conflicts, when bats are regarded nuisance animals, for example in historical buildings (Zeale et al. 2016) or fruit orchards (Aziz et al. 2016). Bat deterrence devices may therefore ameliorate some human impacts and have potential to be used as mitigation in a variety of scenarios (Arnett et al. 2013; Altringham & Kerth 2016; Zeale et al. 2016).

Acoustic deterrents have been tested for use on birds and marine mammals with some success (Schakner & Blumstein 2013; Mahjoub et al. 2015; Swaddle et al. 2016; Schlichting et al. 2017). However, to date there have been only a small number of papers published evaluating the efficacy of bat deterrence devices (Arnett et al. 2013; Zeale et al. 2016). Thermal imaging and image-based tracking methods allow night flying animals such as bats to be visualised and their flight path trajectories analysed and quantified (Hristov et al. 2008; Dell et al. 2014; Betke et al. 2017). Therefore, in this thesis, I investigate bat deterrence methods (radar and ultrasound) that have shown potential in reducing bat activity and foraging behaviour in previous studies. I also use thermal imaging and tracking methods to evaluate bat responses to an acoustic deterrent and explore potential mechanisms for deterrence. The specific objectives of this thesis are therefore as follows:

- To test whether radar and acoustic deterrents reduce the activity and foraging behaviour of bats at riparian foraging sites in the UK.
- To quantify bat activity with increasing distance from an acoustic deterrent and model how the deterrent sound is likely to propagate in the riparian environment.
- To evaluate bat flight trajectory and echolocation call characteristics recorded during acoustic deterrent broadcast compared to a silent control and investigate mechanisms for deterrence.
- To develop a 2-dimensional thermal bat tracking and 3-dimensional stereo thermal videogrammetry method to test bat responses to an acoustic deterrent *in situ* at natural riparian foraging sites in the UK.

In Chapter 2 of this thesis, I compare the effectiveness of radar and acoustic bat deterrence in reducing bat activity and foraging at riparian sites on the border of England and Wales. Results indicate that acoustic, but not radar deterrents are effective at reducing bat activity and foraging and therefore I focus on acoustic deterrence only for the rest of the thesis.

In Chapter 3, I develop and use thermal bat tracking methods along with traditional bat pass counting methods (acoustic and visual) to investigate the effect of an acoustic deterrent on bat activity at distances of 15-30 m in a fine-scale experiment and over 0-120 m in a larger scale study. I also use sound modelling to predict the propagation of the deterrent speaker output in a riparian habitat and evaluate whether bats are likely to be able to hear it at different frequencies and distances.

In Chapter 4, I develop a thermal stereo videogrammetry method and examine echolocation call characteristics to test the predictions that i) bats avoid acoustic deterrent treated airspace due to a masking effect on their echolocation calls and

ii) this masking effect results in a reduction of foraging activity, which is associated with an increase of flight speed and a decrease in tortuosity (curvature) of flight paths.

In Chapter 5, I discuss the wider potential and applications of deterrence for use in mitigation for human impacts on bats and some of the potential limitations and welfare implications of these methods. I also caution against the broadscale use of deterrents and highlight the importance of evaluation of their use in a case-by-case basis. Finally, I outline potential research directions and further development of tracking methods for studying bat activity and behaviour.

# CHAPTER 2

## Comparing radar and acoustic bat deterrents at foraging sites in the UK

**Chapter contributions**

All experimental method development, data collection, statistical analysis, calculations and writing were carried out by L.R.V. Gilmour.

Supervisory role and chapter proof reading carried out by G. Jones, M.W. Holderied and S.P.C. Pickering.

## 2.1 Abstract

Where humans and wildlife co-exist, mitigation is often needed to alleviate potential conflicts and impacts. Deterrence methods can be used to reduce impacts of human structures or activities on wildlife, or to resolve conservation conflicts in areas where animals may be regarded as a nuisance or pose a health hazard. In this chapter, I test two methods (acoustic and radar) that have shown potential for deterring bats away from areas where they forage and/or roost. Using both infrared video and acoustic methods for counting bat passes, I show that ultrasonic speakers were effective as bat deterrents at foraging sites, but radar was not. Ultrasonic deterrents decreased overall bat activity (filmed on infrared cameras) by ~80% when deployed alone and in combination with radar. However, radar alone had no effect on bat activity when video or acoustic data were analysed using generalised linear mixed effect models. Feeding buzzes of all species were reduced by 79% and 69% in the ultrasound only treatment when compared to the control and radar treatments, but only the ultrasound treatment was significant in post-hoc tests. Species responded differently to the ultrasound treatments and I recorded a deterrent effect on both *Pipistrellus pipistrellus* (~40-80% reduction in activity) and *P. pygmaeus* (~30-60% reduction), but not on *Myotis* species. However, only the ultrasound and radar treatment was significant (when compared to control and radar) in post-hoc tests for *P. pipistrellus*. Deterrent treatment was marginally non-significant for *P. pygmaeus*, but the ultrasound only treatment was significant when compared to radar in post-hoc tests. In conclusion, I suggest that acoustic methods, but not radar are explored further as deterrence methods for bats, and therefore focus on acoustic only for subsequent chapters of this thesis.

## 2.2 Introduction

In this chapter, my aim was to explore the effectiveness of different bat deterrent devices that have shown potential in the literature for reducing human-bat impacts and conservation conflicts. With an ever-expanding world population, increased incidences of human-wildlife conflicts and interactions are inevitable. These interactions can lead to detrimental impacts on wildlife, ranging from habitat loss to direct mortality and in some cases can also have significant impacts on human lives (Nyhus 2016).

In areas where humans and wildlife coexist, conflict often arises between stakeholders wishing to conserve species and those who have other more anthropocentric interests (Redpath et al. 2015). Although often used to describe situations where humans and wildlife come into contact, the phrase 'human-wildlife conflict' can be misleading, as it pitches humans and animals against each other (Redpath et al. 2015). Therefore, the phrases 'human-wildlife impacts' and 'conservation conflicts' more adequately sum up human-wildlife interactions (Redpath et al. 2013; Redpath et al. 2015).

Human-wildlife impacts and conservation conflicts are often key conservation concerns for a wide range of taxa (Redpath et al. 2013). Many human structures and activities put species at risk, for example by inducing changes in behaviour, degrading habitats or by producing a direct mortality risk (Loss et al. 2015; Leopold & Hutchins 2016; Shannon et al. 2016). Conservation research has therefore focussed on mitigation strategies that exclude animals from areas where they may come to harm, or where they may impact or cause damage to human activities/structures, for example using deterrence (Hedges & Gunaryadi 2010; Wang et al. 2010; King et al. 2011; Noatch & Suski 2012; Dieter et al. 2014; Mahjoub et al. 2015; Swaddle et al. 2016; Zeale et al. 2016; King et al. 2017).

Bats are one group for which deterrence has been suggested as a potential mitigation method for reducing human impacts and conservation conflicts (Nicholls & Racey 2007, 2009; Arnett & Baerwald 2013; Arnett et al. 2013; Zeale et al. 2016). Protecting bat species is a key conservation concern for many European countries and many species have legal protection and/or are listed as 'Endangered' (Voigt & Kingston 2016). Being slow to reproduce, long-lived and subject to the high energy requirements of flight, bats are regarded as vulnerable to threats such as habitat loss, climate change and emerging diseases (Voigt & Kingston 2016). Human structures and activities can also put bat populations at risk and are therefore present potential applications for deterrence. For example, wind energy development and construction pose significant threats to bat populations, with large numbers of fatalities documented in North America in recent decades (Arnett et al. 2008; Arnett et al. 2016). Fatalities in Europe are not documented on such a large scale, but still have the potential to cause deleterious effects to resident and migratory bat populations (Amorim et al. 2012; Camina 2012; Santos et al. 2013; Lehnert et al. 2014; Mathews et al. 2016). Deterrence may therefore provide a way to keep bats away from the rotor-swept zone of wind turbines, reducing fatalities (Arnett et al. 2013).

Roads and other transport infrastructures are also likely to have significant negative impacts on bat populations, due to habitat loss, noise pollution and mortality due to collision, yet mitigation is at present mostly insufficient (Altringham & Kerth 2016). Deterrence could therefore be used alongside existing mitigation such as green bridges or overpasses, diverting bats away from flight lines over roads where they may be at risk from collision, towards safer routes.

Bats can also cause damage and a cleaning burden in historic buildings where they roost (Zeale et al. 2016) and in some cases pose a human health hazard in workplaces, schools and places of worship (Mgode et al. 2014; Voigt et al. 2016). Conservation conflicts can therefore arise between those wishing to conserve bat populations and people using a building where bats are roosting and causing problems (usually with their urine and faeces) (Mgode et al. 2014; Zeale et al. 2016). In some cases, this leads to exclusion of bats from buildings, which if carried out unlawfully or without careful consideration, can be detrimental to a colony's survival (Voigt et al. 2016).

Therefore, reducing the impact of human structures, activities and conservation conflicts on bat populations, is crucial for bat conservation, and should be a priority. However, before a deterrence method is implemented, exploration of alternatives should be undertaken, following the mitigation hierarchy, first seeking to avoid or minimise any impacts before moving to reduce or compensate (Peste et al. 2015). Indeed, using deterrence to move bats out of an area may cause unintended effects, such as habitat loss, barrier effects and/or stress, which need to be weighed up against alternative mitigation (Kight & Swaddle 2011). However, where more benign alternatives fail, deterrence is a method that should be considered, especially in situations where bats are at risk of serious harm or direct mortality.

Potential deterrence methods for bats include light, radar and sound (Nicholls & Racey 2009; Stone et al. 2009; Arnett et al. 2013; Gorresen et al. 2015; Rowse et al. 2016; Zeale et al. 2016). Some bat species are deterred by certain types of lighting, for example streetlights or flood-lights (Stone et al. 2012; Stone et al. 2015; Rowse et al. 2016; Rydell et al. 2017). Lighting has recently been tested as a potential bat deterrent for use in churches where urine and faeces can cause damage and a cleaning burden (Packman et al. 2015; Zeale et al. 2016). Illumination of 'no-fly zones' within churches limited use of those areas, but bats became entombed in roosts that were directly lit, causing the authors to caution against using this method without careful consideration and further investigation (Zeale et al. 2016). Indeed, lighting in buildings where bats roost can be problematic and even detrimental for species that roost there, causing delays in emergence, roost abandonment, habitat fragmentation, effects on commuting, foraging and hibernation, and in some cases death (Stone 2013; Rowse et al. 2016). One striking example was the report of a 40watt light bulb causing the sudden deaths of over 1000 *Myotis myotis* bats in Germany, when it was left on inside a roost for two days (Stone 2013). Roosting colonies of *Plecotus* species were also significantly reduced in churches in Sweden, where flood-lights had been installed, when compared to non-lit churches over the same 25+ years

(Rydell et al. 2017). Ultraviolet (UV) light has also shown potential as a deterrent for Hawaiian hoary bats (*Lasiurus cinereus semotus*) at wind turbines, where they are at risk of collision (Gorresen et al. 2015). However, light has the potential to be attractive to some bat species, rather than a deterrent (Stone et al. 2015; Rowse et al. 2016), probably due to its attractive effect on insects, which often aggregate around street lights, especially those that emit UV (Rydell 1992; Rydell 2006; Wakefield et al. 2018). Therefore, due to the potential for adverse effects of light deterrents for bats outweighing the potential benefits, I decided not to include these methods in this chapter and focussed instead on radar and acoustic deterrents.

Radar has been proposed as a bat deterrent, specifically for use at wind turbines (Nicholls & Racey 2007, 2009). Suggested mechanisms of deterrence include a thermal burden effect of the electromagnetic radiation, or a jamming effect on echolocation, by high frequency sound produced during thermoelastic expansion of brain tissue (Nicholls & Racey 2009). Bat activity and foraging effort were lower at air traffic control regions in Scotland where radar was deployed (Nicholls & Racey 2009). A follow-on study, also in Scotland, recorded reduced bat echolocation call activity and foraging when an X-band (8-12 GHz) marine radar unit was used at riparian foraging sites (Nicholls & Racey 2009).

The potential for using ultrasound (high frequency sound above 20 kHz) to deter bats has also received attention (Arnett et al. 2013; Zeale et al. 2016). Foraging bats tend to avoid noise, whether from natural sources (e.g. high frequency sounds emitted by insects and/or produced by turbulent water) (Mackey & Barclay 1989; Gillam & McCracken 2007) or anthropogenic noise pollution (e.g. traffic noise) (Schaub et al. 2008; Bunkley & Barber 2015; Bunkley et al. 2015; Luo et al. 2015). Ambient noise may deter bats, as it precludes the use of echolocation for prey detection or orientation, masks sounds made by insect prey, or simply because it produces a disturbing airspace (Mackey & Barclay 1989; Gillam & McCracken 2007; Schaub et al. 2008; Bunkley et al. 2015; Luo et al. 2015). Sources of ultrasound may also affect a bat’s ability to communicate with conspecifics or indeed the ability to eavesdrop on echolocation calls of other bats (which can be beneficial for finding foraging sources and mates) (Dechmann et al. 2009; Voigt-Heucke et al. 2016). Bats are also affected by high frequency ultrasonic clicks produced by some noxious moths (and their mimics) and this is due, in part to a 'jamming' mechanism that leaves the bats echolocation system unusable (Hristov & Conner 2005; Corcoran et al. 2009; Corcoran et al. 2011; Corcoran & Conner 2012). Therefore, bat deterrent systems are usually designed with the aim to mask or jam the echolocation calls of bats (Arnett et al. 2013). Field trials of acoustic deterrents at wind farm sites in North America were successful in reducing the numbers of bat fatalities (Arnett et al. 2013). The same speakers also showed potential in reducing conservation conflicts in historic buildings, where bat droppings and urine can potentially damage valuable historic artefacts (Packman et al. 2015; Zeale et al. 2016).

Deterrence is therefore a method that has potential in cases where other measures have failed, to reduce impacts of human structures and activities on bats and alleviate conservation conflicts in areas where bats roost and come into contact with humans. Therefore, in this chapter, I aim to compare the effectiveness of radar and acoustic bat deterrents at foraging sites in the UK and predict that as previously demonstrated, both methods will significantly reduce bat activity and foraging in the treated airspace.

## 2.3 Methods

### 2.3.1 Site selection and experimental procedure

I carried out experiments during June-September 2015 at 14 riparian sites (> 1 km apart to minimise the chances of recording the same individuals) that contained a stretch of river or canal with an area of still water and a bridge, chosen as they were likely to have relatively high concentrations of foraging bats (Warren et al. 2000) (Figure 2.1). River sites were located on the border of England and Wales (Herefordshire/Shropshire and Powys) and canal sites in Gloucestershire and Somerset. I deployed ultrasonic speakers (Deaton engineering Inc., Texas, USA) and radar (X-band Marine Radar FR-8062, Furuno Electric Co., Ltd, Tokyo, Japan), together and in isolation, alternately with a silent control (no sound/radar) for 10 mins per treatment, over 4 treatment blocks (with a 5-minute recovery period between treatments where no sound/radar was deployed).

Experiments lasted 1 hour, starting 30-45 mins after sunset (depending on ambient light levels), when bat activity was likely to be at its highest. I alternated the order of treatment (ultrasound, radar, ultrasound and radar and control) in the four time blocks over the fourteen sites in a counterbalanced design. Sixteen sites were initially chosen to follow a temporal Latin square design of treatment order, but two sites could not be used in the analysis due to equipment failure. However, statistical analysis using generalized linear mixed effect models controls for unbalanced order in experimental design (see Methods 2.3.4 below). I also included time block as a fixed effect in statistical analysis, to control for temporal changes in bat activity during the experiment.

**Figure 2.1** Example of riparian canal site in Frampton-on-Severn, Gloucestershire, UK. Including a tree line along one side of the canal and still water. Photo taken by L.R.V. Gilmour from bridge across the canal in 2015.

### 2.3.2 Experimental set-up

I placed the radar unit on a table, with the antenna at 1 m height, in the fixed position (rather than rotating) and set it to emit a pulse length of 0.3 µs (repetition rate 1200 Hz, peak power 6 kW; beam width: horizontal = 1.9°, vertical = 22.0°), as this was the most likely set-up and duty cycle to affect bat activity found by Nicholls & Racey (2009). I placed two ultrasonic speakers on chairs at ~0.5 m height and angled them in the same direction as the radar beam towards the middle of the treatment area. Speakers were the same units as used at a wind energy facility in North America (Arnett et al. 2013) and in churches in the UK (Zeale et al. 2014; Packman et al. 2015; Zeale et al. 2016) and had 16 transducers capable of emitting continuous broadband ultrasound at 20-100 kHz, with a frequency of most energy of 50 kHz (Senscomp, Michigan, USA; source level at 1 m 110 dB SPL min at 50 kHz; 85 dB SPL at 20 meters, 20°C, 10% relative humidity and 101.33 kPa (Arnett et al. 2013); beam angle 15° at -6 dB) (Figure 2.2). The speakers were chosen for testing as their frequency of most energy overlapped with the echolocation call frequencies of British bat species likely to be present during experiments, including *Pipistrellus pipistrellus* (frequency of most energy 45 kHz), *P. pygmaeus* (55 kHz) and *Myotis* species (30-50 kHz) (Figure 2.2).

I used a near-infrared (NIR) security camera (Y-cam HD, Y-cam Inc., Twickenham, UK), with NIR illumination (2 LED lamps, Shantou Scene, Shenzhen, China) and a laptop computer, placed behind the deterrents to film the 'treated airspace' for 1 hour (Figure 2.3). I recorded bat activity acoustically using an SM2BAT+ bat detector with an SMX-US omnidirectional ultrasonic microphone (Wildlife Acoustics Inc., Massachusetts, USA; continuous .wav recording; 384 kHz sampling rate; SNR 10), placed at the edge of the treatment zone at ~20 m (covering a range of ~30 m).

I recorded temperature every 15 mins using a Watson W-8681-SOLAR weather station (Watson Inc., Beijing, China). Experiments were carried out on low wind nights (wind speeds < 5 m/s) when there was no rainfall forecast, as wind and rain can reduce bat activity. I powered the camera and acoustic deterrents using a low-noise generator (Honda EU10i, Honda, Tokyo, Japan), placed > 10 m from the treatment area, and the radar unit by a Bosch 12 V battery (Robert Bosch Ltd., Uxbridge, UK). The generator was running during both control and treatment periods. A study with a similar portable generator found no effect of generator noise on bat activity when controls with and without noise were compared (Stone et al. 2009).

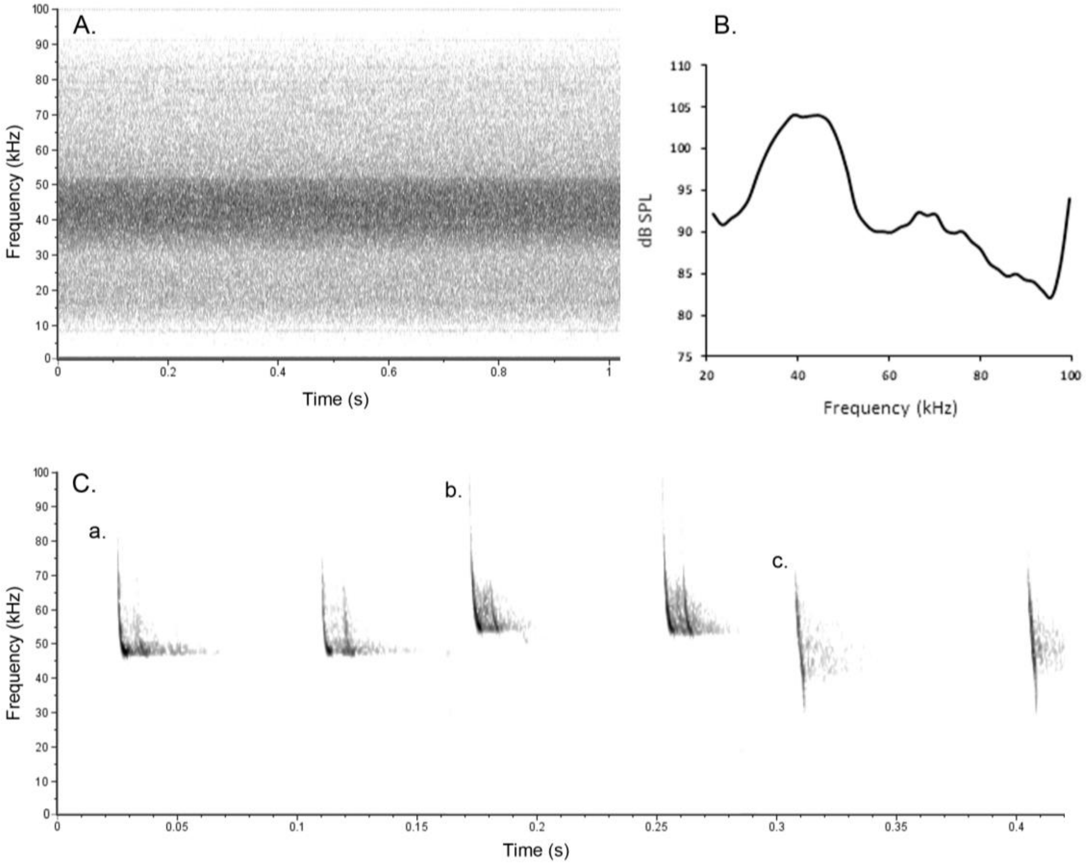


**Figure 2.2** Acoustic deterrent speaker unit output plotted as (A.) a spectrogram and (B.) a power spectrum, and (C.) spectrogram of bat echolocation calls of three species likely to be present at experimental sites. Speaker plots calculated from on-axis anechoic chamber recordings using a Sanken CO-100K Super Wide Range Microphone and calibrated using a type 4231 Brüel & Kjær calibrator (114 dB SPL at 1 kHz). Power spectrum dB SPL measurements calculated at 1 m and adjusted for spectral sensitivity of microphone and distance (original distance 2.2 m, FFT 128, Hamming window, calculated in Avisoft SASLab Pro). Spectrograms of bat echolocation calls include two calls from a sequence identified as (a.) *Pipistrellus pipistrellus*, (b.) *P. pygmaeus* and (c.) *Myotis* species. Both spectrograms were created using Raven Lite 2.0.0 with the same settings (spectrogram window Hann, size 512, brightness 69, contrast 71).

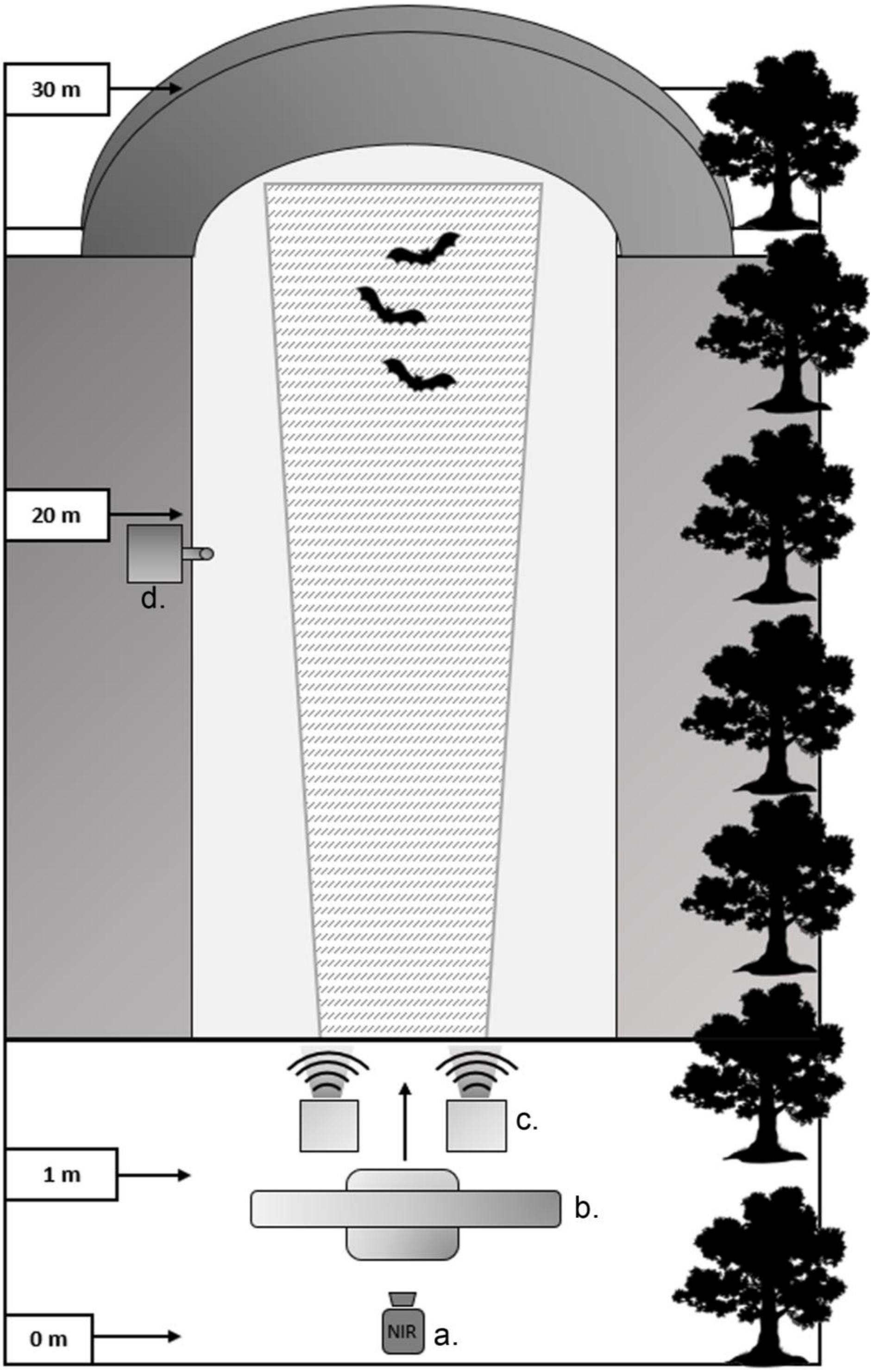


**Figure 2.3** Schematic of experiment set-up at riparian sites in an area of river/canal with a bridge, flanked by a tree line or hedge on one side. Treated airspace is represented by textured area and equipment set-up included (a.) near infrared (NIR) video camera and laptop at 0 m, (b.) radar unit on a table at 0.5 m from the camera, (c.) acoustic deterrent speaker units on chairs at 1 m and (d.) SM2 BAT+ bat detector at ~20 m.

### 2.3.3 Video and acoustic analysis

I calculated bat activity from NIR footage for each treatment (number of bats moving in and out of frame) using Quick Time Player (v7.7.8, Apple Inc, Cupertino, USA). I carried out video analysis blind to treatment. Counts of passes were similar (< 5% difference) when an independent observer carried out the same analysis for five randomly selected sites.

I identified bat passes manually in Bat Sound (v4.1.4, Pettersson, Uppsala, Sweden; FFT size: 1024; FFT window: Hanning) to genus or species level where possible using echolocation call characteristics (Russ 2012). *Myotis* species were grouped due to the similar nature of their broadband echolocation calls, but *Pipistrellus* passes (*P. pipistrellus* and *P. pygmaeus*) are usually discernible to species level (Russ 2012). I also grouped *Nyctalus* and *Eptesicus* species passes, due to their similar long-range echolocation calls (Jones 1995; Russ 2012). I counted the number of passes for each species in a 10 s file and then calculated counts for each 10-minute treatment time block (as a sum of all the 10 s file counts). I also calculated counts of feeding buzzes for each treatment block. A new pass was identified as a sequence of calls > 1 s from the last and feeding buzzes are discernible due to their high repetition rate (Fenton 1970; Russ 2012).

Bat calls at eight sites were more difficult to score due to masking by speaker noise (peak frequency threshold of > 40 kHz). For the remaining six sites, calls were discernible during ultrasound treatment files, but still less so than in radar and control files. I therefore added files containing only the deterrent (recorded at 20 m from the deterrent) to files recorded during non-ultrasound treatments (radar and control treatments) using MATLAB 2016a *sum wave files* function (Mathworks, Natick, USA), to avoid any bias introduced by some files being easier to score. I then analysed these composite files along with files from the ultrasound treatments.

### 2.3.4 Statistical analysis

I analysed bat pass count data with generalized linear mixed effect models (GLMMs), with a negative binomial family and log link function in R (v3.2.2), using the lme4 package (v.1.1-13) (Bates et al. 2015). I followed the backwards step-wise model selection method to find the most parsimonious, yet best-fit model for the data (final model) (Crawley 2007; Bolker et al. 2009). I removed terms sequentially from a more complicated model when likelihood ratio tests (LRT) were non-significant and the difference in second order Akaike information criterion (AICc) for the models was < 2. I obtained significant term statistics (presented as $\chi^2$, df and *p* value) from LRTs between a model containing a term, and a nested model without that term (or the null model).

I validated final models and checked for overdispersion, zero inflation and heteroscedasticity by simulation and reference to residual plots, using the R package DHARMa v.0.2.0 (Hartig 2018). I present effect sizes and standard errors for final models in a table and post-hoc Tukey contrast test results in the text as *z*-statistics and *p* values obtained using the multcomp package (v1.4-1)(Hothorn et al. 2015). Non-significant effect statistics were obtained from an LRT between a model containing only that term with the null model. For model selection statistics see Supplementary Material Table S2.1.

### 2.3.5 Variables and model specification

I analysed the following response variables using GLMMs: visual bat activity (NIR video), acoustic bat activity (including *Pipistrellus pipistrellus*, *P. pygmaeus* and *Myotis* species) and bat feeding buzzes for all species. I included the fixed effects *deterrent treatment* (with levels: *radar*, *ultrasound*, *radar and ultrasound*, *control*), *treatment block order* (levels: *A-D*) and *temperature* (°C) in full models for the video data. However, temperature data were missing at one site, due to equipment failure and were substituted for the mean of all sites (< 10% of data). Full models for acoustic data were the same but did not contain temperature data, due to missing data representing > 10%.

I retained the random effects of site (*N* = 14 for NIR data, *N* = 6 for acoustic data) and treatment block (nested in site, *N* = 4) in final models to control for the repeated measures design and to prevent pseudoreplication.

## 2.4 Results

### 2.4.1 Near-infrared video passes

I recorded a total of 3,668 bat passes from 14 hours of near infrared (NIR) video footage and a mean (± SD) bat pass count of 489.07 ± 253.04 per site. Bat activity (NIR video passes) was significantly reduced when an ultrasonic deterrent was deployed, but radar had no significant effect (Table 2.1; Figure 2.4a; Table S2.1). Post-hoc Tukey contrast tests showed there was a significant reduction in bat activity, per unit time, when the ultrasonic deterrent was deployed compared to the control period and to radar alone (81% and 84% reduction respectively) (ultrasound-control: $z = -4.63$, $p < 0.001$; ultrasound-radar: $z = -4.89$, $p < 0.001$).

Counts of bat passes were also significantly reduced (by 78% and 82%) when ultrasound and radar were deployed together, compared to the control, and to radar respectively (Tukey contrasts: ultrasound & radar-control: $z = -4.30$, $p < 0.001$; ultrasound & radar-radar: $z = -4.56$, $p < 0.001$). Tukey contrasts showed there was no difference between ultrasound treatments and there was no reduction in bat activity when radar was compared to the control (ultrasound & radar-ultrasound: $z = -1.46$, $p = 0.46$; radar-control $z = 0.28$, $p = 0.99$).

### 2.4.2 Acoustic passes

A total of 3,073 acoustic bat passes were identified at six sites and a mean of 512.17 (±287.79) per site. Passes included 1,518 *Pipistrellus pygmaeus*, 618 *P. pipsitrellus* and 388 *Myotis* species passes and 514 feeding buzzes from all species (representing 49, 20, 13 and 17% of passes). *Rhinolophus hipposideros*, unknown *Pipistrellus* species, *Eptesicus serotinus* and *Nyctalus* species made up the remaining passes (1%).

*P. pipistrellus* passes were significantly reduced by 52% and 79% respectively during ultrasound treatments (compared to *control*) and deterrent treatment was significant when data were analysed with a GLMM (but there was no effect of time block order) (Figure 2.4; Table 2.1; Table S2.1). There was also a 39% and 72% reduction in *P. pipistrellus* passes during the *ultrasound* only, and *ultrasound and radar* treatments respectively, when compared to the *radar* only treatment. However, only *ultrasound and radar* treatments were significantly different in Tukey tests (Table 2.1; Figure 2.4; Tukey contrasts: ultrasound & radar-control: $z = -3.75$, $p < 0.01$; ultrasound & radar-radar: $z = -2.61$, $p < 0.05$; ultrasound-control: $z = -2.34$, $p = 0.09$; ultrasound-radar: $z = -1.17$, $p = 0.65$; radar-control: $z = -1.18$, $p = 0.64$, ultrasound & radar-ultrasound: $z = -1.46$, $p = 0.46$).

I recorded a 61% and 40% reduction in *P. pygmaeus* activity compared to the *control*, and a 56% and 33% reduction compared to *radar*, when *ultrasound* was deployed alone and combined with *radar* (Figure 2.4c). However, the null model was the most parsimonious when *P. pygmaeus* data were analysed using a GLMM and deterrent treatment was marginally non-significant in LRT tests (Table 2.1; Table S2.1). Despite this, *ultrasound* and *radar* were significantly different in Tukey contrast tests (ultrasound-radar: $z = -2.63$, $p < 0.05$; ultrasound-control: $z = -2.01$, $p = 0.93$; ultrasound & radar-control: $z = -1.44$, $p = 0.47$; ultrasound & radar-radar: $z = -2.05$, $p = 0.17$; radar-control: $z = 0.61$, $p = 0.93$; ultrasound & radar-ultrasound: $z = 0.56$, $p = 0.94$).

*Myotis* species activity was not significantly affected by any of the deterrent treatments, with similar numbers of passes recorded for all treatments (Figure 2.4d; Table 2.1; Table S2.1). Bat feeding activity was significantly reduced (by 79% and 69%) during the *ultrasound* treatment, compared to the *control* and *radar* treatments and by 48% during *ultrasound and radar* treatment when compared to the control (Figure 2.4e; Table 2.1; Table S2.1). However, bat activity was higher (25% increase) in *ultrasound and radar* treatments when compared to *radar*, although no significant effect of the *ultrasound and radar* treatment, or *radar* was observed in Tukey contrast tests (ultrasound-control: $z = -3.57$, $p < 0.01$;

ultrasound-radar: $z = -2.65$, $p < 0.05$; ultrasound & radar-control: $z = -1.87$, $p = 0.24$; ultrasound & radar-radar: $z = -0.92$, $p = 0.79$; radar-control: $z = -0.96$, $p = 0.77$; ultrasound & radar-ultrasound: $z = 1.75$, $p = 0.30$).

**Table 2.1** Final model estimates and SE from negative binomial GLMMs (log link), for counts of passes from near infrared (NIR) video, echolocation calls from *Pipistrellus pipistrellus*, *P. pygmaeus* and *Myotis* species passes and feeding buzzes of all species. Likelihood ratio test (LRT) statistics (including *p* values) are presented for significant and non-significant terms. Variance, standard deviation and percentage of total variance presented for random effects. Model selection statistics are presented in Table S2.1.

| **Model** | **Model terms** | **Estimates** | **SE** | **$\chi^2$** | **df** | ***p*** |
|---|---|---|---|---|---|---|
| **NIR video** | (Intercept) | 3.32 | 0.28 | | | |
| | **Deterrent treatment** | | | **29.92** | **3** | **< 0.001** |
| | Radar | 0.09 | 0.31 | | | |
| | Ultrasound | -1.51 | 0.33 | | | |
| | Ultrasound & radar | -1.39 | 0.32 | | | |
| | Time block | | | 0.69 | 3 | 0.88 |
| | Temperature | | | 1.53 | 1 | 0.22 |
| | Deterrent treatment * temperature | | | 3.63 | 3 | 0.3 |
| | **Random effects** | **Variance** | **SD** | **% total** | | |
| | Block (within site) (*N* = 4) | 0.62 | 0.79 | 59.12 | | |
| | Site (*N* = 14) | 0.43 | 0.65 | 40.88 | | |
| ***P. pipistrellus*** | (Intercept) | 3.62 | 0.36 | | | |
| | **Deterrent treatment** | | | **11.72** | **3** | **< 0.01** |
| | Radar | -0.52 | 0.44 | | | |
| | Ultrasound | -1.06 | 0.45 | | | |
| | Ultrasound & radar | -1.76 | 0.47 | | | |
| | Time block | | | 0.04 | 1 | 0.84 |
| | **Random effects** | **Variance** | **SD** | **% total** | | |
| | Block (nested within site) (*N* = 4) | 0.55 | 0.74 | 74.45 | | |
| | Site (*N* = 6) | 0.19 | 0.43 | 25.55 | | |
| **Feeding buzzes** | (Intercept) | 3.04 | 0.46 | | | |
| | **Deterrent treatment** | | | **10.8** | **3** | **< 0.01** |
| | Radar | -0.36 | 0.38 | | | |
| | Ultrasound | -1.45 | 0.41 | | | |
| | Ultrasound & radar | -0.72 | 0.39 | | | |
| | Time block | | | 2.05 | 3 | 0.56 |
| | **Random effects** | **Variance** | **SD** | **% total** | | |
| | Block (nested within site) (*N* = 4) | 0.35 | 0.59 | 29.2 | | |
| | Site (*N* = 6) | 0.84 | 0.92 | 70.8 | | |
| ***P. pygmaeus*** | Deterrent treatment | | | 7.36 | 3 | 0.06 |
| | Time block | | | <0.01 | 1 | 0.95 |
| | **Random effects** | **Variance** | **SD** | **% total** | | |
| | Block (nested within site) (*N* = 4) | 0.84 | 0.92 | 64.12 | | |
| | Site (*N* = 6) | 0.47 | 0.69 | 35.88 | | |
| ***Myotis* spp.** | Deterrent treatment | | | 2.68 | 3 | 0.44 |
| | Time block | | | 3.78 | 3 | 0.29 |
| | **Random effects** | **Variance** | **SD** | **% total** | | |
| | Block (nested within site) (*N* = 4) | 1.22 | 1.1 | 59.22 | | |
| | Site (*N* = 6) | 0.84 | 0.92 | 40.78 | | |

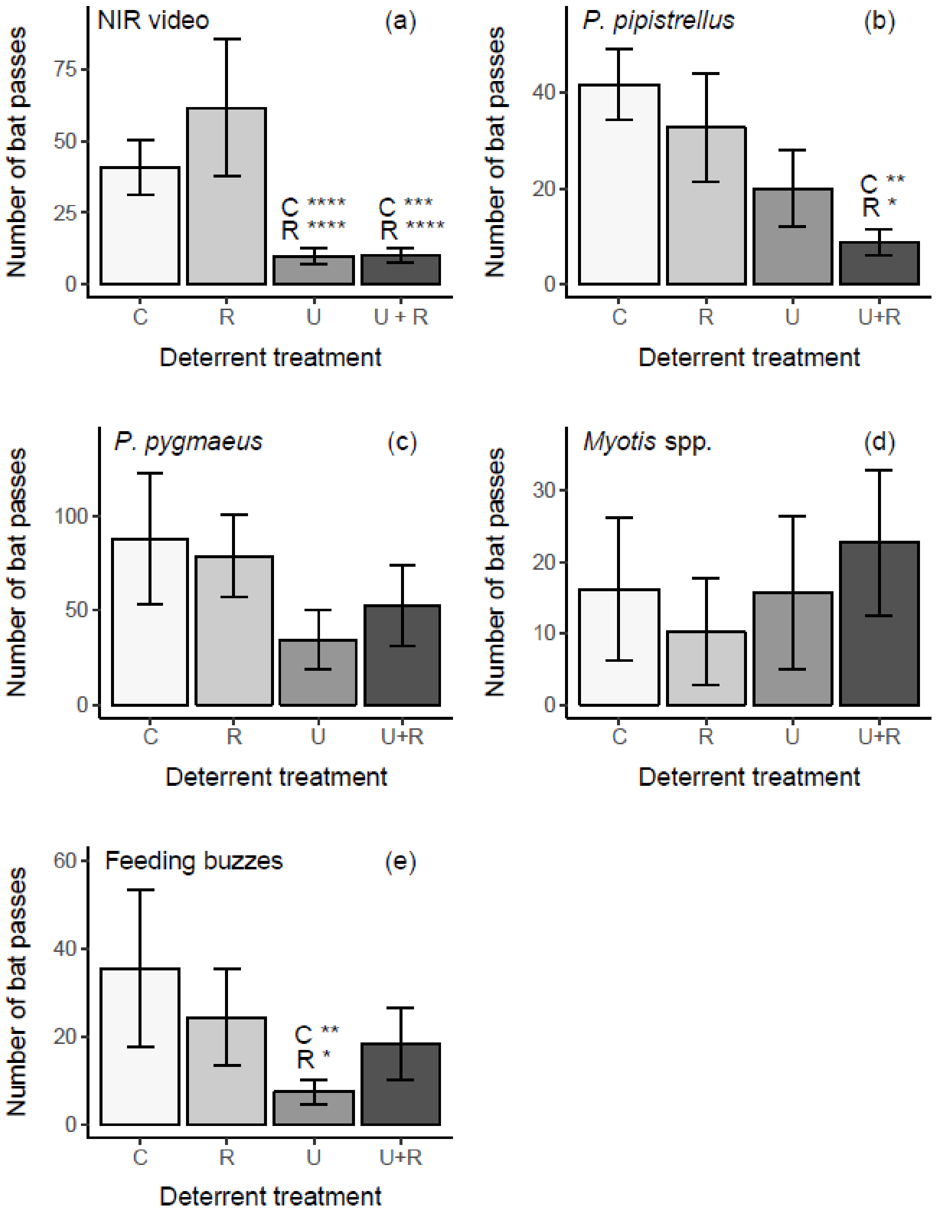


**Figure 2.4** Bat activity (mean number of passes) during four treatments of ultrasound (U), radar (R), ultrasound and radar (U+R) and a control (C), including (a) counts of bat passes recorded on near-infrared (NIR) video footage and acoustic bat passes identified as (b) *Pipistrellus pipistrellus*, (c) *P. pygmaeus*, (d) *Myotis* spp. and (e) feeding buzzes of all species. Including SE error bars and *p* values from post-hoc Tukey comparisons, presented as significance stars and associated label of treatment comparison (* = p < 0.05, ** = p < 0.01, *** = p < 0.001, **** = p < 0.0001). NIR video *N* = 14, acoustic data *N* = 6.

## 2.5 Discussion

In this chapter, I have shown that contrary to my predictions and to previous research, radar was ineffective as a deterrent for bats at foraging sites, but acoustic methods showed promise. Previous work suggested that bat activity was reduced by radar deployment over 10-30 m (Nicholls & Racey 2009). However, I could not confirm this deterrent effect, using video or acoustic data, despite recording over the same range of up to 30 m. The radar beam area projected by the unit used in both my study and the previous work in Scotland was highly directional. The horizontal and vertical beam angle of 1.9° and 22°, respectively, would result in a treated airspace of ~0.7-1 m wide and 8-12 m tall (at ~20-30 m from the deterrents). In comparison, the 15° beam angle of the speakers would have resulted in a ~5-8 m treated airspace both horizontally and vertically. Therefore, bats may have only encountered the radar beam briefly at the centre of treatment area, when flying through it, possibly limiting any potential for deterrence, if any exists. However, the speakers were positioned with the same line of site of the radar beam, with one speaker either side of the centre of the antenna (Figure 2.3) and so were likely to have covered the same treatment area vertically. Despite this and the fact that the radar unit and methodology were very similar, it is unclear why the results of this chapter did not corroborate the findings from the Scottish study (Nicholls & Racey 2009).

Bats are known to avoid ambient and broadcast noise and this chapter supports previous research in this area (Mackey & Barclay 1989; Schaub et al. 2008; Arnett et al. 2013; Bunkley et al. 2015; Zeale et al. 2016). However, this study is the first to show a reduction in bat activity at foraging sites in the UK using broadcast ultrasound. I recorded a clear effect of ultrasound on bat activity with an ~80% reduction seen in the video footage data (when compared to control and radar treatments). However, the acoustic data do not show such a clear trend, possibly due to unavoidable noise in the data from bat echolocation calls being recorded outside the range of the deterrent and small sample sizes. It was also not possible to discern bat feeding buzzes to species level due to high levels of overall activity and often more than one species in each file. Despite this, ultrasound treatments had the lowest mean number of bat passes recorded for all datasets, excluding *Myotis* species (Figure 2.4). I also found an effect of the ultrasound and radar treatment (when compared to control and radar only) and the ultrasound only treatment (when compared to radar) on *Pipistrellus pipistrellus* and *P. pygmaeus* activity respectively. There was also an effect of ultrasound only on feeding activity of all species.

*Myotis* species were not significantly affected by any deterrent treatment. Due to the nature of the riparian sites, the *Myotis* species bats recorded were likely to be *Myotis daubentonii*, which feed directing their ultrasound towards the water (Siemers et al. 2001). As high frequency sounds can be highly directional, it is likely that there was a stronger effect of the deterrent above the water, compared to at the water's surface where *M. daubentonii* was feeding. The *Myotis* bats may have also been moved along the water during ultrasound treatments, away from the speakers, to nearer where I had placed the bat detector at the edge of the treated airspace, resulting in more passes recorded during ultrasound treatments. As *Pipistrellus* species are not limited to feeding over water, they may have dispersed in different directions when the sound was broadcast, rather than in the direction of the microphone. A previous study using the same deterrent speakers found that *Myotis nattereri* were deterred from specific roosting areas in churches in Norfolk, UK, with no habituation effect found after 15 days (Zeale et al. 2016). I also found a significant effect of the acoustic deterrent on *Myotis* species (likely *M. daubentonii*) in Chapter 4 of this thesis. Therefore, a deterrent effect of ultrasound can not be ruled out for *Myotis daubentonii*, without a follow-up exploration of acoustic deterrents focussed on this species (e.g. with speakers pointing at the water's surface).

My findings demonstrate that ultrasonic speakers show promise for use as bat deterrents at foraging sites in the UK and Europe. I therefore recommend that these methods be considered as a way of reducing bat activity, as part of mitigation aiming to alleviate the impacts of human-built structures and activities on bat populations. For example, these methods could be used at wind turbines to reduce bat fatalities, similar to what has been done in North America (Arnett et al. 2013); for diversion of bats away from roads, which are a direct threat to bats from collision (Altringham & Kerth 2016); or as mitigation for conservation conflicts arising from bats roosting in buildings. In the rest of this thesis, I therefore focus on the mechanisms underpinning acoustic deterrence and the distance over which the speakers are effective.

# Supplementary material

**Table S2.1** Model selection statistics for near infrared (NIR) video pass count and bat pass and feeding buzz count data.

**Table S2.1** Model selection statistics for final models for bat pass data, including models with negative binomial and Poisson error structure. Including near-infrared (NIR) video and acoustic activity of *Pipistrellus pipistrellus*, *P. pygmaeus*, *Myotis* spp. and feeding buzzes. Models arranged by AICc weight (AICc Wt) and include number of model parameters (K). Final model in bold.

| Response variable | Model | K | AICc | ΔAICc | AICc Wt | Cum. Wt |
|---|---|---|---|---|---|---|
| **NIR video** | Deterrent treatment | 7 | 466.95 | 0.00 | 0.68 | 0.68 |
| | Deterrent treatment + temperature | 8 | 469.03 | 2.10 | 0.24 | 0.92 |
| | Deterrent treatment + block | 10 | 471.86 | 4.90 | 0.06 | 0.98 |
| | Deterrent treatment + temperature + block | 11 | 474.37 | 7.40 | 0.02 | 1.00 |
| | Deterrent treatment * temperature + block | 14 | 480.99 | 14.00 | 0.00 | 1.00 |
| | Null model | 4 | 489.32 | 22.40 | 0.00 | 1.00 |
| | Temperature | 5 | 490.21 | 23.30 | 0.00 | 1.00 |
| | Time block | 7 | 496.18 | 29.20 | 0.00 | 1.00 |
| ***P. pipistrellus*** | Deterrent treatment | 7 | 217.47 | 0.00 | 0.53 | 0.53 |
| | null | 4 | 218.30 | 0.80 | 0.35 | 0.88 |
| | Time block | 5 | 221.48 | 4.00 | 0.07 | 0.95 |
| | Deterrent treatment + block | 8 | 222.04 | 4.60 | 0.05 | 1.00 |
| ***P. pygmaeus*** | null | 4 | 256.20 | 0.00 | 0.84 | 0.84 |
| | Deterrent treatment | 7 | 259.74 | 3.50 | 0.14 | 0.98 |
| | Time block | 7 | 263.62 | 7.40 | 0.02 | 1.00 |
| | Deterrent treatment + block | 10 | 274.30 | 18.10 | 0.00 | 1.00 |
| ***Myotis* spp.** | null | 4 | 183.44 | 0.00 | 0.96 | 0.96 |
| | Time block | 7 | 190.56 | 7.10 | 0.03 | 0.99 |
| | Deterrent treatment | 7 | 191.66 | 8.20 | 0.02 | 1.01 |
| | Deterrent treatment + block | 10 | 202.70 | 19.30 | 0.00 | 1.01 |
| **Feeding buzzes** | null | 4 | 200.80 | 0.00 | 0.51 | 0.51 |
| | Deterrent treatment | 7 | 200.90 | 0.10 | 0.48 | 0.99 |
| | Block | 7 | 209.64 | 8.80 | 0.01 | 1.00 |
| | Deterrent treatment + block | 10 | 214.54 | 13.70 | 0.00 | 1.00 |

# CHAPTER 3

## Distance-dependent responses to an acoustic deterrent by bats, studied using thermal bat tracking and acoustic methods

**Chapter contributions**

All writing, data collection, method development, statistical analysis and calculations were carried out by L.R.V Gilmour, with additional contributions outlined below:

All original MATLAB scripts were written by M.W. Holderied and developed further and finalised by L.R.V Gilmour with help from M.W. Holderied.

L.R.V Gilmour and G. Jones provided a supervisory role in experimental design and data collection for the larger scale distance study. Data were collected by C. Wevill (The Ecology Consultancy) and P. Shepherd (BSG), along with a team of subcontractors from their respective companies. All statistics on data collected for this study were carried out by L.R.V. Gilmour.

Anechoic chamber recordings of deterrent output were made by L.R.V. Gilmour and M.R.K. Zeale. All predictions and figures made using recorded files were made using calculations by L.R.V. Gilmour.

G. Jones and M.W. Holderied provided a supervisory role for the work in this chapter, including providing comments and feedback on experimental design, data collection and writing.

## 3.1 Abstract

Acoustic deterrents have shown potential as a mitigation measure for bats in the other chapters of this thesis, at wind farms in North America and in churches in the UK. However, it is important to understand the range over which these deterrent speakers work and quantify how effective they are at reducing bat activity at different distances. To do this, it is important to understand two factors affecting deterrence at different distances: how the deterrent sound is likely to propagate *in situ* at foraging sites and if bats are able to hear and respond to the broadcast sound. I therefore compared bat responses to an acoustic deterrent at different distances in two studies, carried out at different scales. In the fine-scale riparian study (15-30 m from the deterrent), I used thermal bat tracking methods developed especially for this thesis and collected acoustic data to gain species information. For the larger scale (0-120 m) distance study, I analysed data collected using thermal imaging and acoustic methods along linear features (non-riparian). I also modelled how the deterrent sound was likely to propagate up to 100 m, using recordings made in an anechoic chamber and in the field. Bats were deterred up to ~30-40 m, but after 40 m there was no deterrent effect. Bat activity was reduced by 50-60% at up to 20 m in both studies. The deterrent effect was stronger nearer the speakers, with an 80% reduction in bat activity at 15 m, where sound pressure levels were likely to be relatively high (~50 dB at 50 kHz). Species present were unlikely to hear the deterrent beyond 40 m as frequencies of around 50 kHz were likely to be below bat hearing threshold levels of 20-30 dB. The most abundant species present and deterred at up ~20-30 m in the larger scale study were *Pipistrellus pipistrellus* and *Myotis* species, and *P. pygmaeus* in the fine-scale experiment. *P. pygmaeus* passes and feeding buzzes were reduced by 23 and 35% respectively, in the fine-scale experiment. In conclusion, I recommend that acoustic deterrents are evaluated for use on a case-by-case basis, taking into consideration site-specific and weather effects and species likely to be deterred.

## 3.2 Introduction

In Chapter 2 of this thesis, I conclude that acoustic deterrence shows potential as a mitigation measure for use in areas where bats forage but may be at risk from human development and activities. For any mitigation to be successful, it is important to understand firstly whether it works, but also the range over which it is effective and if the target animal is likely to respond within a given distance. Arnett et al. (2013) suggested that ultrasound broadcast by acoustic deterrents at a North American wind facility (using the same speakers as used in this thesis) was unlikely to be at a high enough amplitude to deter bats all the way from the nacelle to the edge of the rotor-swept zone (~40 m). However, acoustic deterrence still reduced bat fatalities of some species by up to 50-60% at wind farm sites, when corrected for field biases and inherent turbine differences (Arnett et al. 2013). How effective an acoustic bat deterrent is likely to be in the field is dependent on two factors: how the deterrent sound propagates through the specific environment it is placed in, and how the bat species present experience that sound and respond to it.

High frequency sound (ultrasound, frequencies > 20 kHz) is subject to relatively rapid attenuation in air and can be increasingly directional, depending on the frequency of the sound and the specification of the sound-emitting device (Griffin 1971; Lawrence & Simmons 1982). Ultrasound is also affected by frequency-dependent atmospheric absorption (Bazley 1976) and weather conditions such as temperature and humidity can significantly affect how far it spreads through the environment (Goerlitz 2018). Atmospheric attenuation of sound in air is dependent on four factors which all interact in a non-linear way on the resultant sound, including the frequency of the sound and the ambient temperature, humidity and air pressure, with higher frequency sounds affected relatively more than lower frequencies (Goerlitz 2018).

How sound propagates in the environment is also affected by the topography of the surrounding site. Landscape features such as vegetation, reflective surfaces (e.g. water) and movement in the air (i.e. wind) can all influence the soundscape. For example, echoes from ripples in water (Rydell et al. 1999) and vegetation such as trees and shrubs can increase acoustic clutter (Schnitzler et al. 2003) and attenuation of high frequency sound is likely to be greater in higher wind speeds (Wiley & Richards 1978; Gillam et al. 2009).

Bats have evolved in acoustically intense and complex environments to be able to discern relatively quiet echoes from their own calls, amongst high amplitude calls of conspecifics and other sources of ultrasound such as noise made for example by insects or turbulent water (Griffin et al. 1963; Mackey & Barclay 1989; Gillam & McCracken 2007; Gillam et al. 2010; Bunkley et al. 2015; Corcoran & Moss 2017). Bats are therefore dynamic in their use of sound and will alter the spectral and temporal characteristics of their echolocation calls in response to topography of a site, the presence of other bats and to weather conditions such as temperature and humidity (Fawcett & Ratcliffe 2015; Chaverri & Quiros 2017; Corcoran & Moss 2017).

How a bat responds to a deterrent sound over distance may be in part due to its hearing threshold. Hearing thresholds are measured on the dB scale and the human threshold for hearing is usually given as 0 dB (Zwicker & Fastl 1990). However, bats tend to have more sensitive hearing than humans and therefore can have negative hearing thresholds at some frequencies. Typically, thresholds of bats range from about 20-30 dB SPL, but may be 0 dB SPL or below and this also might depend on frequency (Simmons et al. 2016; Goerlitz 2018; Lewanzik & Goerlitz 2018). Thresholds are also unlikely to be fixed and can range not only between species, but also between individuals and from day-to-day for an individual bat by up to 6 dB SPL (Simmons et al. 2016). Bats avoid areas of ambient ultrasound when foraging (Mackey & Barclay 1989; Bunkley & Barber 2015; Bunkley et al. 2015) and this may be due to masking of their echolocation calls or just avoidance of an aversive stimulus (Griffin et al. 1963; Schaub et al. 2008; Bunkley & Barber 2015; Bunkley et al. 2015; Luo et al. 2015; Gomes et al. 2016). However, big brown bats (*Eptesicus fuscus*) did not alter their hearing thresholds in response to short periods of broadband high frequency noise (Simmons et al. 2016). Therefore, to determine the range a device such as an acoustic deterrent is likely to work over, it is important to understand both how the sound emitted might propagate in the environment, but also how foraging bats respond *in situ* at different distances.

Recent developments in computer vision systems and tracking algorithms have allowed researchers to gain detailed insights into animal movement and behaviour, not previously attainable with standard counting and monitoring methods (Dell et al. 2014). Based on methods of background subtraction (where one frame is subtracted from the previous frame), algorithms have been developed that can pick up movement between frames and track an object in real time, or in pre-recorded footage. Tracking is even possible with multiple individuals moving in the same space and has been used to study collective animal movement, behaviour and interactions (Viscido et al. 2004; Betke et al. 2008; Attanasi et al. 2014; Betke et al. 2017).

To date, most literature has focussed on tracking animals during the day with conventional filming techniques or in lit up areas (Viscido et al. 2004; Holderied et al. 2005; Polak et al. 2011; Dell et al. 2014). Spending most of their time flying in darker conditions, bats are harder to film and track using these methods. Recent development of thermal imagining technology has allowed it to be more affordable and therefore accessible for bat research (Hristov et al. 2008; Betke et al. 2017). Tracking bats using thermal imaging footage therefore allows us to gain a unique insight into how bats behave, interact and respond to certain stimuli whilst flying in their natural environment (Betke et al. 2008; Hristov et al. 2008; Yang et al. 2013; Betke et al. 2017).

For this chapter, I have developed a thermal tracking system for bats that can be used on footage recorded in areas where bats forage and carry out their normal behaviour. Therefore, in this Chapter, I aim to use thermal bat tracking and acoustic methods in a fine-scale study and thermal and acoustic bat pass data collected at a larger scale to determine how bat activity changes at different distances from an acoustic deterrent in riparian foraging sites. I predict i) that bat activity will decrease as distance from the deterrent increases and ii) that whether the deterrent is effective or not, will be dependent on whether bats are likely to hear the deterrent sound at different distances.

## 3.3 Methods

For this chapter, I compare bat responses to an acoustic deterrent at two different scales. I carried out a fine-scale distance study at 15-30 m, with a 1 m distance band resolution, using a thermal bat tracking method developed especially for this thesis. I also extracted and analysed data collected for a larger scale study (see beginning of chapter for contributions) carried out at 0-120 m, with 20 m distance band resolution and used bat pass data collected using thermal imaging and acoustic methods. To determine whether bats were likely to hear the acoustic deterrent at different distances, I also modelled sound propagation of the speaker output covering most of the range of the two studies (0-100 m).

### 3.3.1 Fine-scale distance study

In this chapter, I explain the development of a 2-dimensional (2D) thermal tracking system for bats. This system forms the basis for Chapter 4, where I develop these methods further into a stereo thermal videogrammetry system for 3D tracking of bat flight paths in response to an acoustic deterrent.

#### 3.3.1.1 Camera synchronisation and recording

Accurate two-camera synchronisation is an essential pre-requisite for multi-camera 2D imaging and stereo imaging, as significant frame delays by either camera can cause discrepancies in combined field of view (FOV) and/or triangulation errors (Betke et al. 2017). I therefore performed synchronisation trials with two Optris PI640 thermal imaging cameras (640x480 pixel resolution, 33° lenses; Optris GmbH, Germany), prior to purchase and established that cameras were synchronized to within 1 frame at 32 Hz. To achieve accurate synchronization throughout the experiment period, I set the cameras to be re-synchronised every 30 s using a process interface (PIF) cable that supplied a digital input from one camera acting as a 'master' to the 'slave' camera. During this re-synchronization period, frames on both cameras would freeze for 3 s. I therefore made sure cameras were synchronized in the same way for both control and treatment periods. Although some data were lost (6 s per min), this freeze was unavoidable to ensure adequate synchronisation between cameras was maintained throughout the experiments.

Software demands on the processing system of the computer, large file sizes of uncompressed video (up to 133 GB) and high demand on data transfer rates through USB all affected synchronisation and overall performance of the system. Normally, the multiple camera system supplied by the manufacturers is used in an indoor industry scenario (such as car manufacture), with high-spec desktop computers with multiple external hard drives, designed to cope with the high demands and large file sizes produced when recording uncompressed video. Therefore, in using this software for this task, I was pushing the boundaries of the system and it was important to carry out field and lab-based trials to refine the set-up. After trialling several laptop/camera systems, I bought a high specification Dell XPS 15 laptop, with a separate graphics card and solid-state drive (6th Gen. Intel Core i7-6700HQ, 32GB RAM, 1 TB SSD, NVIDIA® GeForce® GTX 960M graphics card, Dell, Texas, USA). The laptop was used in conjunction with specialist camera software Optris PI Connect (Optris GmbH, Germany), offline and with antivirus software disabled. I recorded a merged FOV of both cameras in .avi uncompressed video format (with radiometric functionality turned off), at the maximum frame rate available, 32 Hz (Figure 3.1).

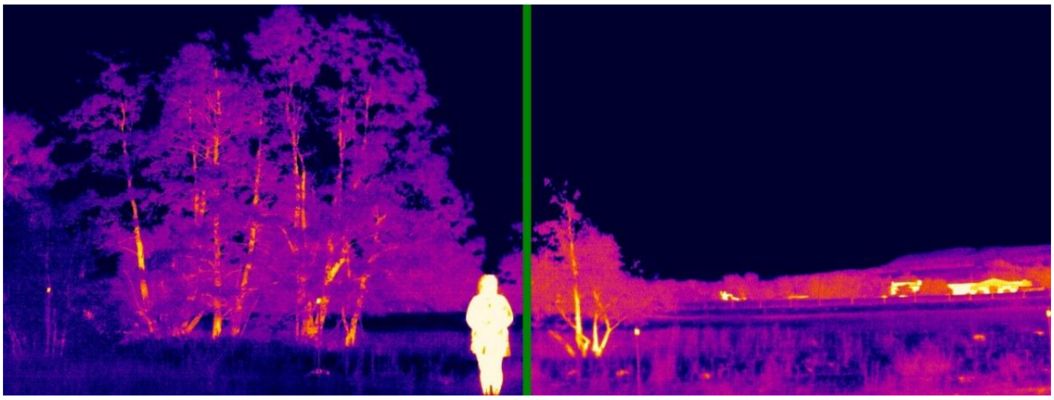


**Figure 3.1** Thermal image example of a merged field of view from two thermal imaging cameras at a riparian site in Herefordshire, UK. Image includes the thermal signature of a person at a river bank flanked by trees on one side and a field on the other.

### 3.3.1.2 Site selection and experimental procedure

I collected data in 2017 at three linear riparian sites all situated along the Teme valley (> 1 km apart, to reduce the likelihood of recording the same individual bats), around the border of England (Herefordshire/Shropshire) and mid-Wales (Powys), over three repeat nights, totalling nine experiment hours. Sites were selected from those previously visited in Chapter 2, due to high levels of bat activity and specific topography, including a river, flanked by a grassy bank on one side and by a hedge or tree line on the other (Figure 3.2).

I attached two acoustic deterrent speakers (Deaton engineering Inc., Texas, USA; see section 3.3.3 below for further speaker info) to stepladders at a height of ~1.6 m, and placed them 15 m from the edge of the treatment zone (Figure 3.3). The treatment zone included 15 m of riparian habitat, an area 15-30 m from the deterrents. I attached thermal markers (re-usable hand warmers) to stakes placed at 15, 20, 25 and 30 m locations and visualised the treatment area with the two synchronised thermal imaging cameras (placed along the same plane, 1 m apart and 15 m from the treatment area).

I used a low-noise generator (Honda EU10i, Honda, Tokyo, Japan), to power all equipment, which I placed at least 10 m away from the treatment area. Generator noise was unlikely to have an effect on bat activity, as a study that used a similar model found no difference between silent controls and those with the generator running (Stone et al. 2009). I started filming at about half an hour to 1 hour after sunset (depending on ambient light levels and bat activity). A silent control period of 10 mins where no sound was played (but the generator was running), was followed by 10 mins of deterrent playback and this was repeated totalling 1 hour of filming time per night. Bat activity at these sites tended to peak around an hour to 2 hours after sunset and to capture this window of activity, I monitored bat activity and started the experiment when activity was increasing, and bats started to forage (about 2-3 passes a minute). In order to monitor levels of activity, I kept treatment block order the same each night, starting with a silent control period. Therefore, to control for the effect of time of night on bat activity, I included time block order as a fixed effect in statistical analysis (see Statistical Methods 3.3.1.6).

I recorded acoustic bat activity using an SM2BAT+ detector and SMX-US microphone (Wildlife Acoustics Inc., Massachusetts, USA; continuous .wav recording; 384 kHz sampling rate; SNR 10) placed by the bridge at each site (~30-40 m from the deterrent), angled towards the treatment area. I recorded temperature and humidity over the experiment hour using a Watson W-8681-SOLAR weather station (Watson Inc., Beijing, China).

**Figure 3.2** Photographs of three riparian sites used in experiments, located on the border of mid-Wales and England. All sites included a stretch of still water and a bridge, flanked by hedges and/or tree lines. Photo credits L.R.V Gilmour.

**Figure 3.3** Photographs of experiment set-up at a riparian site: (a.) dual camera set-up, including red arrow indicating positioning of 15 m thermal marker at beginning of FOV and treatment area, (b.) example of speaker positioning *in situ*, (c) speakers positioned on ladders and (c) close-up of hand warmer used as thermal marker attached to stake on site. Photo credits L.R.V. Gilmour and S.R. Vincent.

### 3.3.1.3 Development of the thermal tracking system

I extracted bat trajectory data from recorded .avi files using a bespoke MATLAB script, written by M.W. Holderied (developed further by M.W. Holderied and L.R.V. Gilmour). The script was developed to allow plotting of individual bat localisations that are then sorted into trajectories using defined temporal and spatial parameters. The process involved reading in the video, converting frames to grey scale and defining a pixel threshold (threshold of pixel colour scale value) and maximum area of localisation points (in pixels). Bat localisations in each frame were then plotted using background subtraction, a method often used to detect movement in computer vision systems (Dell et al. 2014). The method works by comparing one frame to its preceding frame and any frame-to-frame differences (within the maximum area) are plotted. Localisations were then sorted into trajectories using the following specified parameters: maximum change in localisation area in pixels per frame, maximum gap in number of frames between localisation points making up a trajectory, maximum distance between localisations (in pixels) and the minimum number of localisations to count as a trajectory. A spreadsheet in Microsoft Excel containing *x* and *y* coordinates, pixel area, frame number and trajectory allocation for each bat localisation was then produced for all frames. A plot of all trajectories was also produced by the script which allows detection of any errors in data extraction and refinement of parameters (Figure 3.4).

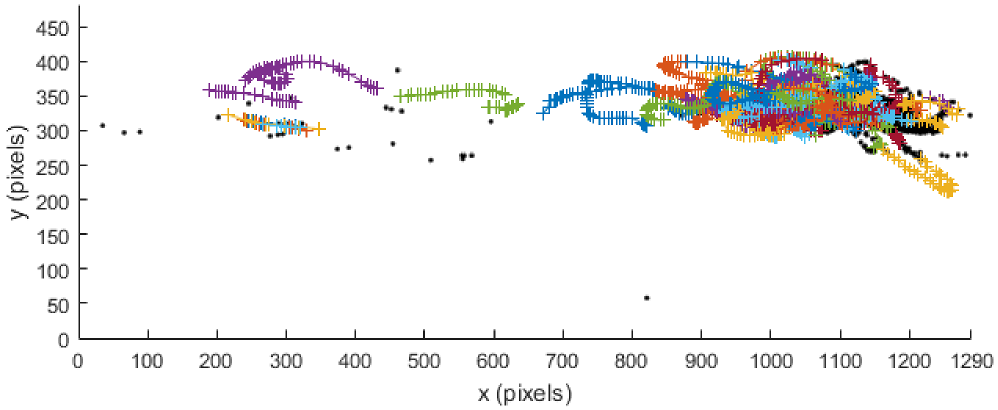


**Figure 3.4** Example MATLAB figure of all trajectories plotted from all localisations identified in 30 s of thermal video footage, recorded during a silent control period. Two camera frames were merged to produce one combined FOV of 1290 x 480. Localisations bigger than a max area of 30 pixels and shorter than 6 localisations in length are plotted as black dots and are not incorporated into any trajectory.

### 3.3.1.4 Bat trajectory data extraction

I cut up uncompressed .avi files recorded on site into shorter 5 min sequences using VirtualDub (v. 1.10.4, Free Software Foundation, Inc, Cambridge, MA, USA). Due to uncompressed video sizes and the high levels of bat activity at the sites, longer files took a much longer time to read in and integrate and would often cause MATLAB to crash. Extracted trajectory files for videos any longer than 5 mins were also often too busy (in terms of bat activity) to carry out quality checks and refine parameters.

I carried out trials with short sections of video to select a pixel threshold for each night and used that same value for data extraction from all 5-min time blocks from that night. Setting the pixel threshold too high could mean some bat localisations are missed and too low a threshold may introduce noise into the data as well as potentially picking up large insects such as moths, which have a cooler thermal signature than bats. I set a max cut-off area of 30 pixels per bat localisation, based on the biggest UK bats' wingspan being ~400 mm and the minimum pixel length in the treatment area 15 m from cameras being 13.6 mm (calculated using Optris calculator: www.optris.global/optics-calculator). I set a max change in localisation area of 15 pixels per frame, a max gap of 15 frames between localisations in a trajectory, a maximum distance between localisations as 30 pixels and the minimum length of a trajectory as containing 6 localisations.

I extracted trajectory coordinate data from the second 5 mins of each 10 min time block (e.g. from 5 to 10 mins in the first block, 15 to 20 mins in the second etc.). Using alternate 5 min periods for each 10 mins of treatment or control, reduced the possibility of overspill effects from the deterrent in subsequent blocks, which could bias the trajectory distance data extracted. I then allocated each trajectory to a 1 m distance band (15-30 m), by filtering using defined pixel coordinates calculated by dividing the length of $x$ in pixels (1290) by the distance in m (15 m) (each 1 m contained 86 pixels). I then calculated a count of the number of trajectories per distance for each 5 min time block and used this for statistical analysis.

### 3.3.1.5 Acoustic data extraction

I extracted 10 s files from SM2 BAT+ recordings for each 10-minute treatment period. I analysed the second 5 mins of acoustic bat call data (30 10 s files) from each 10 min time block (in the same way as the video footage data). In each 10 s file, I identified bat passes/feeding buzzes to genus or species level where possible using the same method as in Chapter 2.3.3. I then summed counts of passes/feeding buzzes/social calls for each 10 s file to get an overall count for each

10-minute time block. I used a MATLAB script to add the deterrent noise at the level recorded during noise playback to silent control files (using the same method as in Chapter 2.3.3), to avoid bias introduced by control files being easier to analyse. On one night, there was a microphone malfunction and acoustic data for some time blocks were not recorded or only partially recorded. Therefore, I only included data for 25-30 and 35-40 mins for that night to keep the number of treatment and control blocks equal.

#### 3.3.1.6 Statistical analysis

I analysed trajectory count data using the lme4 package in R (Bates et al. 2015). I used Akaike second order information criterion (AICc) and likelihood ratio tests (LRTs) to compare generalised linear mixed effect models (GLMMs) with a negative binomial or Poisson distribution to find the most parsimonious yet best fit model for the data. Full models included the fixed effects of *deterrent treatment* (levels: deterrent/control)*, time block order* (A-D), *distance* (to the nearest m) and an interaction term between *deterrent treatment* and *distance*. I included the random effects of *site*, *night* and *time block* in all models (nesting structure site/night/time block). Data are presented in tables and include estimates and SE for final models and LRT statistics for significant and non-significant fixed effect terms.

I analysed acoustic data using the same methods as above, but without the fixed effects of distance and the interaction term. Response variables included *Pipistrellus pygmaeus, P. pipistrellus*, *Myotis* species pass counts and *P. pygmaeus* and *Myotis* species feeding buzzes and *P. pygmaeus* social calls. There were not enough data to model for any other species' pass, feeding buzz or social call counts (< 20 calls recorded per night).

## 3.3.2 Larger-scale distance study

### 3.3.2.1 Site selection and experimental design

I provided an advisory role (along with G. Jones) in experimental design and data collection at four sites in 2016 and three sites in 2017 for this study. Sites were selected that contained linear features (tree lines and/or hedges) next to an arable field and were situated in the Radstone area of Northamptonshire.

Two acoustic deterrent speakers were placed at the top of stepladders adjacent to one another at 2 m above the ground and 2 m from the linear feature (Figure 3.5). Near infrared (NIR) cameras (Canon HD XA10, Canon, Japan) were placed behind the deterrents (at -10 m) and in front of the deterrents (at 10 m, 50 m and 100 m), with their fields of view (FOVs) parallel to the linear feature and along 'line of sight' of the deterrent speakers (Figure 3.6). A FLIR T650 thermal imaging camera (640x480 pixel resolution; 30 Hz frame rate; FLIR Systems, Wilsonville, Oregon, USA) was also set to record at -10 m in the same way as the NIR cameras, with the ability to visualise up to 100 m, depending on conditions and topography of the site. Two field assistants were located with each NIR camera (apart from at -10 m where one was situated with the thermal imaging camera and one with the NIR camera) and Batlogger M bat detectors (Elekon, Luzern, Switzerland) were also set to record bat calls automatically at each of these locations (full spectrum .wav recording at sampling rate of 384 kHz). Bat passes and distance from the deterrent were noted by field assistants when viewed on camera screens and data were checked later by comparing timings with acoustic data recorded on bat detectors and thermal imaging footage.

Bat passes were identified to species level or genus level where possible from acoustic data, with *Myotis* species being grouped due to the similar nature of their echolocation calls (Russ 2012). Experiment nights included two hours per night where the acoustic deterrent speakers were deployed for 20 mins, alternated with a silent control also of 20 mins. Sites were repeated for four-six nights, depending on the year and site.

To control for time of night effects on bat activity, control and treatment blocks were alternated as the first block on different repeat nights and time was included as a fixed effect in models (see Statistical analysis below).

**Figure 3.5** Example of experiment set-up at one site in Northamptonshire, UK, including photos of (a.) the habitat and speaker location, (b.) speaker angles and view along the tree line from behind the cameras to ~100 m and (c.) ladders at 2 m height with speakers attached. Photo credits L.R.V. Gilmour.

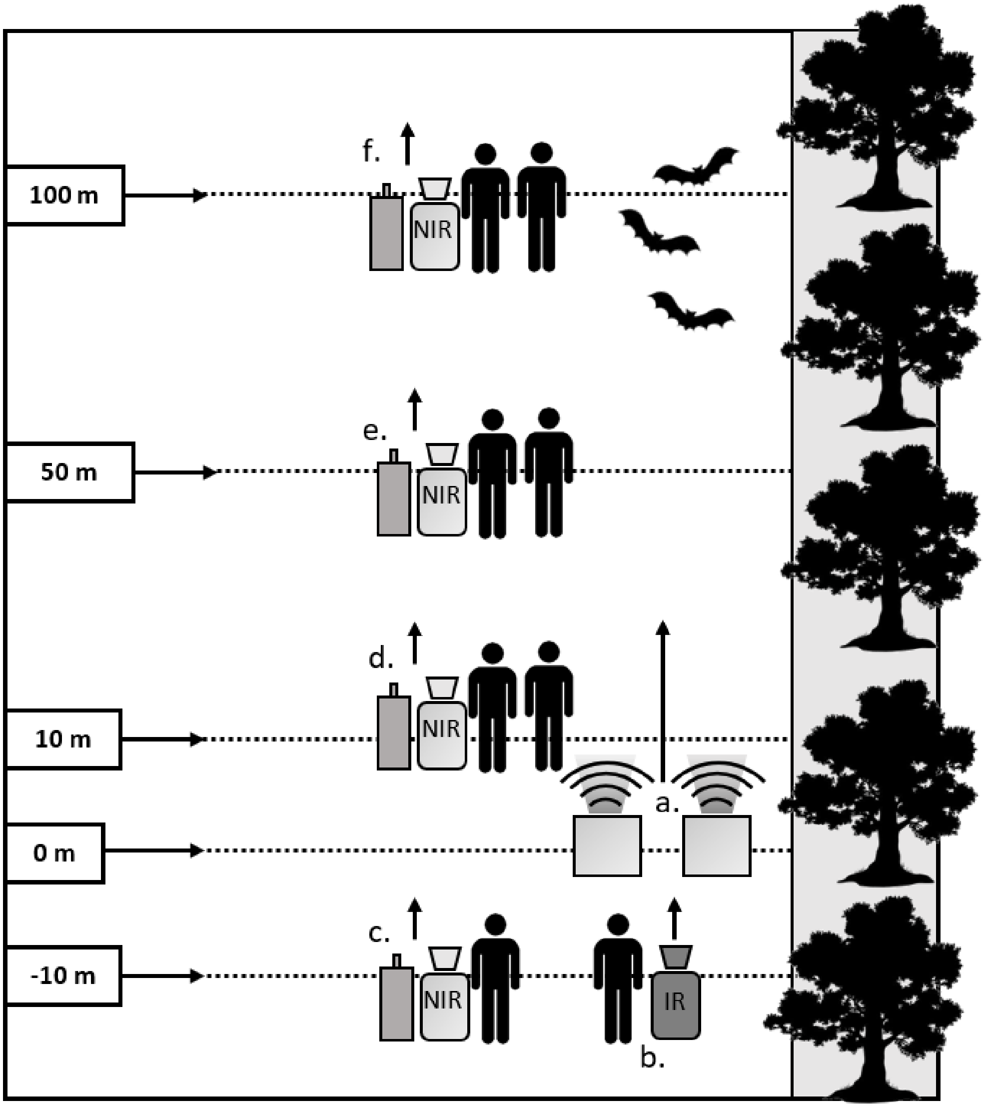


**Figure 3.6** Schematic of large-scale experimental set-up, at a site with a linear feature (hedge/tree line) next to a field: (a.) two deterrent speakers at 0 m, (b.) field assistant with thermal imaging camera at -10 m, (c. to f.) stations at -10 m, 10 m, 50 m and 100 m with field assistant(s), near infrared (NIR) cameras and Bat Logger M bat detectors. Arrows indicate the direction of the speakers, bat detector microphones and fields of view cameras.

### 3.3.2.2 Statistical analysis

I analysed bat pass data using the same method as in the fine-scale distance experiments, but specified models for each 20 m distance band (-20 to 120 m) for each species group. I also modelled for all distances combined per species group. I analysed distance bands of 20 m individually due to low counts of bat passes at some distances on some nights. Therefore, splitting the data up and doing individual analysis meant I could include nights where enough data were available to model. Distances that had insufficient data were not modelled (< 60 passes in total over all 28 nights). Data for individual distance bands were not repeated between bands, i.e. data were unique to each band and did not overlap, to minimise pseudoreplication.

Response variables included pass counts for all species combined and counts of *Pipistrellus* species and *Myotis* species passes. *Pipistrellus* species were grouped for statistical analysis, although due to low numbers of *P. pygmaeus* and *P. nathusii* passes at these sites, data are likely more representative of *P. pipistrellus*. I included the fixed effects *deterrent treatment* (levels: deterrent/control) and *time block order* (A-F) and random effects of *site repeat* (*N* = 3), *site* (*N* = 4)*, night* (*N* = 8), *time block* (*N* = 6). Random effects had the nested structure of site repeat/site/night/time block.

### 3.3.3 Deterrent sound modelling

I used recorded .wav files of deterrent speaker outputs to model how the emitted sound was likely to be transmitted in the field environment. Recordings were made by M.R. Zeale and L.R.V Gilmour in an anechoic chamber at the University of Bristol in 2014 for a mitigation study on bats roosting in churches (Zeale et al. 2016). Each speaker was recorded individually, on-axis, at 2.2 m, using a Sanken CO-100K Super Wide Range Microphone (Sanken Microphone Co. Ltd., Tokyo, Japan; for frequency response see Figure S3.1). I also recorded the same speakers in the field simultaneously, on seven nights in 2018, during experiments for Chapter 4, using a Pettersson D1000X full spectrum bat detector (Pettersson Elektronik, Uppsala, Sweden; recorded by hand in .wav at 384 kHz sampling rate; Frequency response in Figure S3.2). Due to speakers being positioned at ~1.6 m, I could not make on-axis field recordings. Recordings were therefore made off-axis with the D1000X on a stool at 0.4 m and with speaker units on ladders at 1.6-2.0 m, depending on the topography of the site and at 6-8 m from the bat detector microphone, depending on gain settings required on each night to avoid overload.

I calibrated field recordings in Avisoft SASLab Pro using the calibrate function with recordings of an Avisoft Ultrasound Gate calibrator (Avisoft Bioacoustics, Glienicke, Germany; 40 kHz pure tone; 70 dB at 0.25 m). I calibrated anechoic chamber recordings in the same way but using a recorded Brüel & Kjær calibrator (Brüel & Kjær, Nærum, Denmark; Acoustical calibrator type 4231, 114 dB at 1 kHz directly on-axis).

I calculated amplitude (dB SPL) in Avisoft SASLab Pro after calibration, using the average power spectrum function (RMS amplitude; FFT size 128, window Hamming) (see Figure 2.2 in Chapter 2 for spectrogram and power spectrum). I adjusted dB SPL measurements for differing spectral sensitivity of the microphones using spectral sensitivity plots obtained from the microphone manufacturers (Figure S3.1; Figure S3.2). I calculated source level (SL) for each speaker at 1 m from anechoic chamber recordings and both speakers on experiment nights at field sites, using adapted spreading loss equations (one way) and frequency dependent atmospheric absorption values (dB/m) (Bazley 1976; Møhl 1988; Holderied & von Helversen 2003). I used mean temperature and humidity data recorded on each night in the field in 2018 for field dB SPL calculations at 1 m (values for each night ranged from 13-21°C, 70-95% relative humidity at 101.33 kPa) and a mean of all nights' weather data recorded at field sites in 2017 during the fine-scale distance experiments, for anechoic recordings (14°C and 90% humidity at 101.33 kPa).

I used anechoic chamber recordings to calculate predicted frequency-dependent attenuation of the speaker output and created a heat map of root mean square (RMS) amplitude (dB SPL) of frequencies from 20-100 kHz at 1-100 m (assuming 14°C and 90% humidity at 101.33 kPa). I used trigonometry to calculate the angle from the speaker units to the D1000X microphone on each experiment night and the typical beam pattern for each angle from the deterrent speaker specification (Figure S3.3), to calculate the dB SPL drop off at those angles for 50 kHz (the frequency of maximum energy of the speakers). I added the corresponding dB SPL value to off-axis calculations, to obtain an estimated on-axis dB SPL at 1 m for each experiment night.

Although anechoic chamber recordings were generally greater in accuracy and detail than field recordings, it was important to also record the speakers in the field to account for any site-specific effects and/or effects of temperature and humidity on electrical equipment. I also recorded both speakers individually and together powered by both the mains and the same generator used in field experiments (see above) to see if there were any significant effects of power source on speaker output.

## 3.4 Results

### 3.4.1 Fine scale distance study (15-30 m)

#### 3.4.1.1 Bat trajectories

I extracted 23,364 bat trajectories on nine nights at three sites from nine hours of thermal footage, including 7,433 when the deterrent was broadcast and 15,931 during silent control periods. Trajectories were recorded at all distances from the deterrent speaker (15-30 m), with a mean (± SD) trajectory distance of 21.85 ± 4.37 m.

There was a 48.62% reduction in bat activity over the whole 15 m when the deterrent was broadcast compared to the silent control. There was an increased reduction in bat activity between control and treatment periods with decreased distance from the deterrent (Figure 3.7). I also recorded a significant interaction effect between deterrent treatment and distance when trajectory count data were analysed with a GLMM (

Table **3.1**; see Table S3.1 for model selection statistics). At 15-16 m there was an 82.13% reduction in bat activity, compared to a 55.76% reduction at 20-21 m, 27.64% at 25-26 m and 25.47% at 29-30 m, when mean number of trajectories were calculated for control and treatment periods. Time block order was also significant when included as a fixed effect in the model.

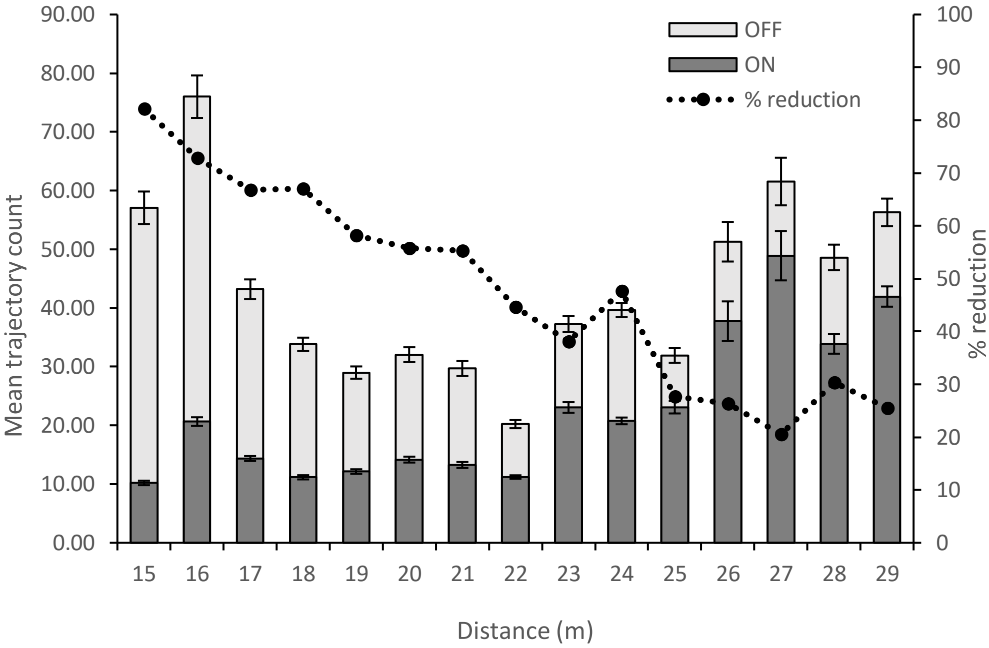


**Figure 3.7** Mean of all bat trajectory counts at each distance over all nights and time blocks, when the deterrent was broadcast (dark grey bars) and during silent controls (light grey bars), including SE error bars and % reduction from the control to deterrent calculated from mean trajectory counts.

**Table 3.1** Final model statistics from significant model of mean trajectory distance data. Likelihood ratio test (LRT) statistics (including *p* values) are presented for significant and non-significant terms. Variance, standard deviation and percentage of total variance presented for random effects. Model selection statistics are presented in Table S3.1.

| **Model** | **Model terms** | **Estimates** | **SE** | **χ2** | **df** | ***p*** |
|---|---|---|---|---|---|---|
| **Distance** | (Intercept) | 4.13 | 0.45 | | | |
| | Deterrent | -1.95 | 0.39 | | | |
| | Distance | -0.02 | 0.01 | | | |
| | **Time block order** | **-0.13** | **0.06** | **5.08** | **1** | **< 0.05** |
| | **Deterrent * Distance** | **0.07** | **0.02** | **17.78** | **1** | **< 0.001** |
| | **Random effects** | **Variance** | **SD** | **% total** | | |
| | Time block (within night) (*N* = 12) | 0.38 | 0.61 | 51.88 | | |
| | Night (within site) (*N* = 3) | 0.05 | 0.23 | 7.23 | | |
| | Site (*N* = 3) | 0.30 | 0.54 | 40.89 | | |

### 3.4.1.2 Acoustic bat passes

I recorded 6,956 passes, 6,218 feeding buzzes and 517 social calls from nine hours of recording from nine nights at three sites (three repeat nights per site). Species present at the sites during experiments included mainly *Pipistrellus pygmaeus* and *Myotis* species (likely *Myotis daubentonii*) (64.49% and 23.49% of acoustic passes respectively). The remaining 12.02% of passes were identified as *P. pipistrellus* and *Nyctalus* and *Eptesicus* species made up the final 0.1%.

*P. pygmaeus* activity was reduced by 22.83% and feeding activity by 34.77% during deterrent treatment and deterrent was significant when included as a fixed effect in GLMMs (Figure 3.8; Table 3.2; see Table S3.2 for model selection statistics). There was no effect of deterrent treatment for *Myotis* species activity or counts of feeding buzzes, or *P. pipistrellus* activity. There were not enough data to model *P. pipistrellus* feeding buzz or social calls counts, *Myotis* species social call counts or *Nyctalus* and *Eptesicus* species activity, feeding buzz or social call counts (< 20 calls recorded in total in one night).

*P. pygmaeus* activity was highest at the beginning of the experiment at 5-10 mins and decreased over the experiment hour and time was significant when included as a fixed effect in a GLMM (Figure 3.9; Table 3.2; Table S3.2). *Myotis* species activity significantly increased over the experiment hour, with a peak in activity at 25 to 30 mins. *P. pipistrellus* activity remained the same over the experiment hour and there was no effect of time when data were analysed with a GLMM.

Feeding buzzes and social calls were identified as being mainly from *P. pygmaeus* (84.82 and 94.00% respectively), with the remaining 15% of feeding buzzes and 6% of social calls identified as *Myotis* species. *P. pygmaeus* feeding activity declined over the experiment hour and time block was significant when analysed with a GLMM (Figure 3.9; Table 3.2; Table S3.2). *Myotis* species feeding activity remained constant over the experiment hour and there was no effect of time when data were analysed with a GLMM. Counts of *P. pygmaeus* social calls decreased over the experiment hour in line with activity until a peak in calls in the last 5 mins and there was no significant effect of time block.

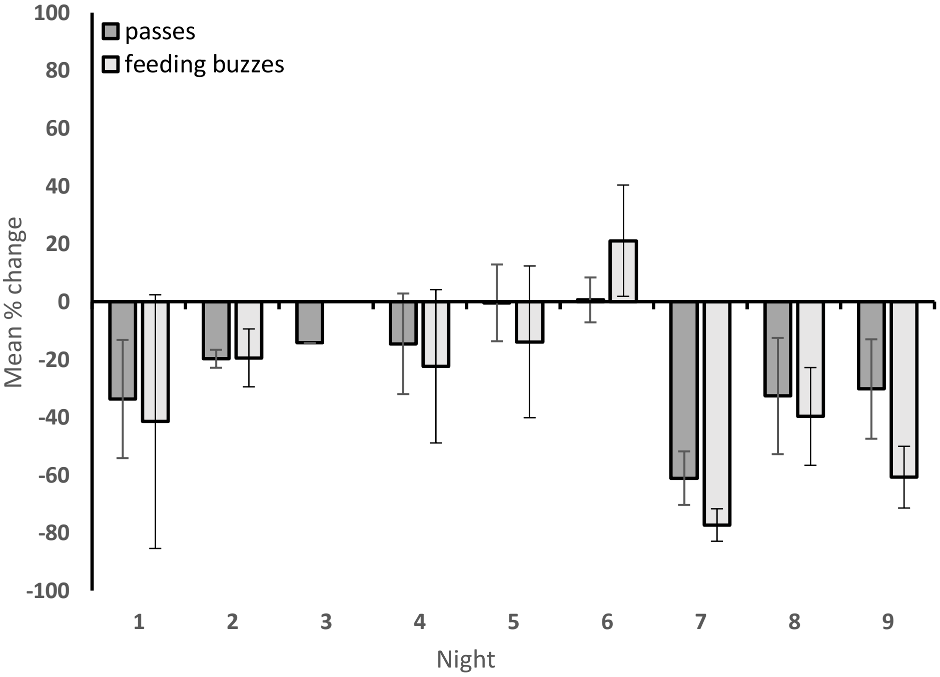


**Figure 3.8** Mean % change in counts of *Pipistrellus pygmaeus* passes (dark grey bars) and feeding buzzes (light grey bars) from control to deterrent treatments (± SE error bars), calculated as the mean of the % difference between counts for control and deterrent treatment for each time block on each night (including three 20 min blocks per night, nine nights and three nights per site). A negative % value, below zero on the vertical (*y*) axis represents a reduction in bat activity and a positive, an increase in bat activity.

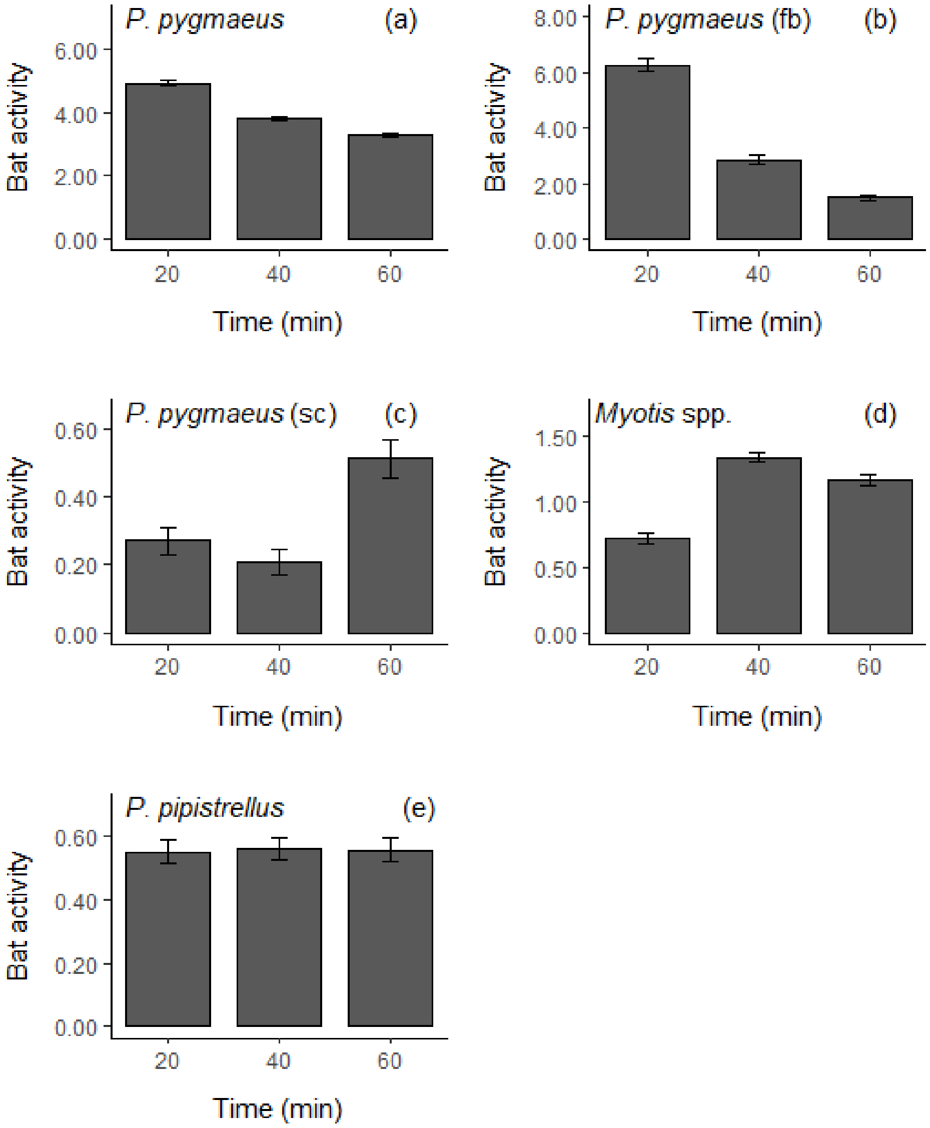


**Figure 3.9** Temporal activity over experiment hour (mean number of passes, including SE error bats, per 10 s file), including *Pipistrellus pygmaeus* passes (a), feeding buzzes (b) and social calls (c), and *Myotis* species (d), and *P. pipistrellus* (e) passes.

**Table 3.2** Final model estimates, SE and *z* statistics from significant GLMMs and likelihood ratio test (LRT) statistics (including *p* values) for significant and non-significant terms, analysing count data of *Pipistrellus pygmaeus*, *P. pipistrellus* and *Myotis* spp. passes and *P. pygmaeus* and *Myotis* spp. feeding buzzes (fb) and *P. pygmaeus* social calls (sc). Variance, standard deviation and percentage of total variance presented for random effects. Model selection statistics are presented in Table S3.2.

| **Model** | **Model terms** | **Estimates** | **SE** | ***z*** | **χ2** | **df** | ***p*** |
|---|---|---|---|---|---|---|---|
| ***P. pygmaeus*** | (Intercept) | 1.83 | 0.16 | 11.37 | | | |
| | **Deterrent treatment** | **-0.20** | **0.07** | **-3.05** | **8.37** | **1** | **< 0.01** |
| | **Time block order** | **-0.01** | **0.00** | **-5.33** | **21.55** | **1** | **< 0.0001** |
| | **Random effects** | **Variance** | **SD** | **% total** | | | |
| | Time block (in site) (*N* = 12) | 0.04 | 0.21 | 37.54 | | | |
| | Night (in site) (*N* = 3) | 0.03 | 0.18 | 28.27 | | | |
| | Site (*N* = 3) | 0.04 | 0.20 | 34.19 | | | |
| ***Myotis* spp.** | (Intercept) | -1.22 | 0.51 | -2.41 | | | |
| | **Time block order** | **0.02** | **0.01** | **2.42** | **5.63** | **1** | **< 0.05** |
| | Deterrent treatment | | | | 0.02 | 1 | 0.89 |
| | **Random effects** | **Variance** | **SD** | **% total** | | | |
| | Time block (in site) (*N* = 12) | 0.85 | 0.92 | 70.73 | | | |
| | Night (in site) (*N* = 3) | 0.03 | 0.17 | 2.26 | | | |
| | Site (*N* = 3) | 0.33 | 0.57 | 27.01 | | | |
| ***P. pygmaeus* (fb)** | (Intercept) | 2.36 | 0.88 | 2.67 | | | |
| | **Deterrent treatment** | **-0.52** | **0.24** | **-2.16** | **1.00** | **1** | **< 0.05** |
| | **Time block order** | **-0.05** | **0.01** | **-7.08** | **33.50** | **1** | **< 0.0001** |
| | **Random effects** | **Variance** | **SD** | **% total** | | | |
| | Time block (in site) (*N* = 12) | 0.64 | 0.80 | 20.65 | | | |
| | Night (in site) (*N* = 3) | 0.72 | 0.85 | 23.34 | | | |
| | Site (*N* = 3) | 1.74 | 1.32 | 56.01 | | | |
| ***P. pipistrellus*** | Deterrent treatment | | | | 0.63 | 2 | 0.73 |
| | Time block | | | | 0.18 | 1 | 0.67 |
| ***P. pygmaeus* (sc)** | Deterrent treatment | | | | 0.71 | 1 | 0.40 |
| | Time block | | | | 0.04 | 1 | 0.84 |
| ***Myotis* spp. (fb)** | Deterrent treatment | | | | 0.34 | 1 | 0.56 |
| | Time block | | | | 1.30 | 1 | 0.25 |

### 3.4.2 Larger scale distance study (0-120 m)

A total of 4,504 bat passes were recorded on 38 nights, at four sites. Most passes were identified as *Pipistrellus pipistrellus* (57%), followed by unknown passes (23%), *Myotis* species (7%) and *Nyctalus* and *Eptesicus* species (7%) (Table 3.3). *P. pygmaeus*, *Plecotus* species (likely *Plecotus auritus*) and *P. nathusii* made up the remaining 6%.

Overall, there was a 32% reduction in bat activity when the acoustic deterrent was broadcast compared to the silent control and this was significant when data for all distances were analysed using a GLMM (Figure 3.10; Table 3.4-3.5; see Table S3.3 for model selection statistics). When *Pipistrellus* species passes were analysed, activity was also significantly reduced by 27% (Table S3.4), whereas although *Myotis* species activity was reduced by 23% overall, this was not significant when the data were analysed with a GLMM (Table S3.5).

When data were analysed as separate 20 m distance bands, there was a significant effect of the deterrent on overall bat activity (all species), at up to 20 m behind, up to 20 m in front and 20 to 40 m in front of the deterrent set-up, with a 45, 61 and 57% reduction in bat activity respectively (Table 3.4; Table S3.3). *Pipistrellus* species activity was also reduced by 36, 61 and 62% at up to 20 m behind, up to 20 m in front and 20 to 40 m respectively, but only data collected at 0-20 and 20-40 m distance bands were significant when analysed with a GLMM (Table 3.4; Table S3.4). *Myotis* species activity was reduced by 49% at 0 to 20 m and there was a significant effect of the deterrent when the data were analysed with a GLMM (Table 3.5; Table S3.5). However, there were not enough data to model for the other 20 m distance bands individually for *Myotis* bats. Bat activity was not significantly reduced by the deterrent for any of the other distance bands for any of the species (40-120 m) (Table 3.4; Table S3.3-3.5).

**Table 3.3** Counts of bat passes of different species groups at seven distance bands and where no distance was recorded (NA), including *Pipistrellus* spp. (*P. pipistrellus*, *P. pygmaeus* and *P. nathusii*), *Nyctalus* spp. (*N. noctula* and *N. leisleri*), *Plecotus auritus*, *Eptesicus serotinus*, *Myotis* spp. and 'unknown' passes.

| | **Distance bands (m)** | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **-20-0** | **0-20** | **20-40** | **40-60** | **60-80** | **80-100** | **100-120** | **NA** | **Total** | **% of total** |
| ***P. pipistrellus*** | 119 | 337 | 57 | 339 | 55 | 107 | 219 | 1333 | 2567 | 56.99 |
| **Unknown** | 14 | 483 | 184 | 146 | 19 | 19 | 12 | 138 | 1015 | 22.54 |
| ***Myotis spp.*** | 13 | 89 | 13 | 31 | 10 | 12 | 15 | 152 | 335 | 7.44 |
| ***Nyctalus noctula*** | 1 | 3 | 6 | 12 | 6 | 4 | 5 | 258 | 295 | 6.55 |
| ***Plecotus auritus*** | 6 | 16 | 3 | 14 | 5 | 1 | 9 | 54 | 108 | 2.40 |
| ***P. pygmaeus*** | 2 | 8 | 1 | 7 | 3 | 3 | 5 | 66 | 95 | 2.11 |
| ***Eptesicus serotinus*** | 0 | 4 | 2 | 2 | 0 | 0 | 0 | 48 | 56 | 1.24 |
| ***N. leisleri*** | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 25 | 27 | 0.60 |
| ***P. nathusii*** | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 5 | 6 | 0.13 |
| **Total** | 155 | 942 | 266 | 552 | 98 | 146 | 265 | 2079 | 4504 | 100 |

**Table 3.4** Counts of bat passes when an acoustic deterrent was broadcast and during control periods, at -20 m behind to 120 m in front of acoustic deterrents. *p* values from likelihood ratio tests and % change in bat passes when the deterrent was broadcast compared to control also presented. Where there were insufficient data, *p* values presented as 'not modelled'.

| Species group | Distance (m) | Control | Deterrent | Total | % change | *p* |
|---|---|---|---|---|---|---|
| **All species groups** | -20-0 | 100 | 55 | 155 | -45.00 | **< 0.01** |
| | 0-20 | 677 | 265 | 942 | -60.86 | **< 0.001** |
| | 20-40 | 186 | 80 | 266 | -56.99 | **< 0.01** |
| | 40-60 | 273 | 279 | 552 | 2.34 | 0.87 |
| | 60-80 | 58 | 40 | 98 | -18.75 | 0.09 |
| | 80-100 | 83 | 63 | 146 | 3.70 | 0.22 |
| | 100-120 | 135 | 130 | 265 | -5.22 | 0.51 |
| | Total | 2676 | 1829 | 4505 | -31.65 | **< 0.001** |
| ***Pipistrellus* spp.** | -20-0 | 74 | 47 | 121 | -36.49 | 0.13 |
| | 0-20 | 248 | 97 | 345 | -60.89 | **< 0.001** |
| | 20-40 | 42 | 16 | 58 | -61.90 | **< 0.01** |
| | 40-60 | 171 | 175 | 346 | 2.34 | 0.91 |
| | 60-80 | 32 | 26 | 58 | -18.75 | 0.43 |
| | 80-100 | 54 | 56 | 110 | 3.70 | 0.58 |
| | 100-120 | 115 | 109 | 224 | -5.22 | 0.69 |
| | Total | 1535 | 1127 | 2662 | -26.58 | **< 0.01** |
| ***Myotis* spp.** | -20-0 | 9 | 4 | 13 | -55.56 | not modelled |
| | 0-20 | 59 | 30 | 89 | -49.15 | **< 0.05** |
| | 20-40 | 9 | 4 | 13 | -55.56 | not modelled |
| | 40-60 | 12 | 19 | 31 | 58.33 | not modelled |
| | 60-80 | 5 | 5 | 10 | 0.00 | not modelled |
| | 80-100 | 10 | 2 | 12 | -80.00 | not modelled |
| | 100-120 | 5 | 10 | 15 | 100.00 | not modelled |
| | Total | 190 | 145 | 335 | -23.68 | 0.1924 |

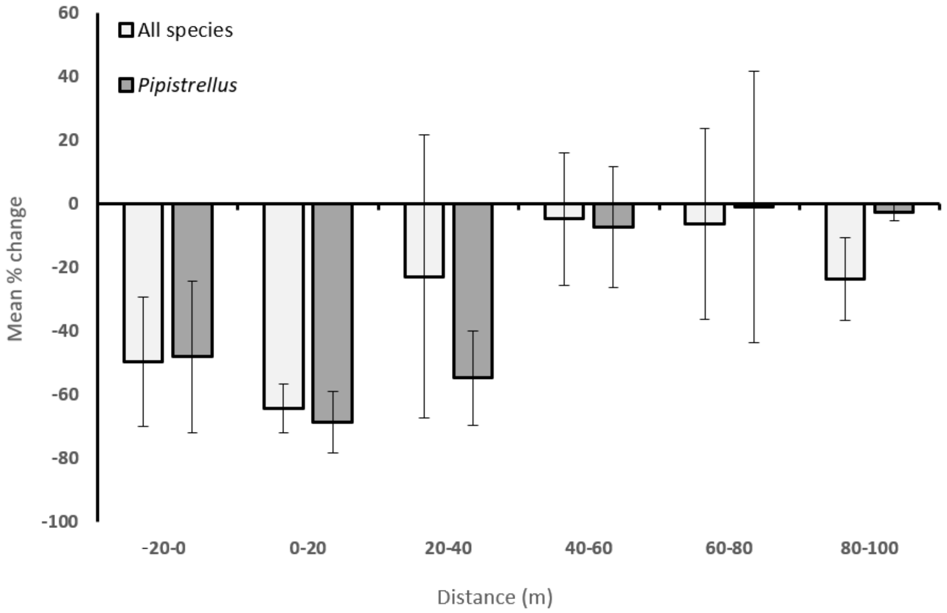


**Figure 3.10** Mean % change (± SE error bars) in passes from -20 to 100 m, of *Pipistrellus* species (grey bars), and passes of all species recorded together (light grey bars), calculated as % difference between mean numbers of bat passes at each site during control and treatment periods. Data for *Myotis* species passes are not presented as only one distance band was modelled due to low numbers of passes.

**Table 3.5** Final model output and likelihood ratio test (LRT) results for GLMMs analysing bat pass count data at different distances (negative binomial distribution and log link). Including effect sizes (± SE) for significant terms and variance (± SD), nesting structure, number of observations for each random effect term and total number of observations. Likelihood ratio test statistics also presented (significant terms in bold). Model selection statistics are presented in Table S3.3-3.5.

| Model | Model terms | Estimate | SE | χ2 | df | *p* |
|---|---|---|---|---|---|---|
| **All species 0 to 20 m** | (Intercept) | 1.52 | 0.26 | | | |
| | **Deterrent** | **-0.84** | **0.17** | **23.45** | **1** | **< 0.0001** |
| | Time block | | | 9.37 | 4 | 0.05 |
| | **Random effects** | **Variance** | **SD** | | | |
| | Time block (in night, 97) | 0.00 | 0.00 | | | |
| | Night (in site, 34) | 0.00 | 0.06 | | | |
| | Site (in repeat, 8) | 0.41 | 0.64 | | | |
| | Repeat (3) | 0.00 | 0.00 | | | |
| | Total observations = 194 | | | | | |
| **All species 20 to 40 m** | (Intercept) | 0.67 | 0.25 | | | |
| | **Deterrent** | **-0.72** | **0.24** | **9.02** | **1** | **< 0.01** |
| | Time block order | | | 1.76 | 4 | 0.78 |
| | **Random effects** | **Variance** | **SD** | | | |
| | Time block (in night, 69) | 0.00 | 0.00 | | | |
| | Night (in site, 31) | 0.08 | 0.29 | | | |
| | Site (in repeat, 8) | 0.17 | 0.41 | | | |
| | Site repeat (3) | 0.00 | 0.00 | | | |
| | Total observations = 131 | | | | | |
| ***Pipistrellus* spp. all** | (Intercept) | 2.40 | 0.22 | | | |
| | **Deterrent** | **-0.48** | **0.15** | **9.58** | **1** | **< 0.01** |
| | Time block order | | | 8.52 | 5 | 0.13 |
| | **Random effects** | **Variance** | **SD** | | | |
| | Time block (in night, 121) | 0.00 | 0.00 | | | |
| | Night (in site, 35) | 0.45 | 0.67 | | | |
| | Site (in repeat, 8) | 0.16 | 0.41 | | | |
| | Site repeat (3) | 0.00 | 0.00 | | | |
| | Total observations = 224 | | | | | |
| ***Pipistrellus* spp. 0 to 20 m** | (Intercept) | 1.19 | 0.01 | | | |
| | **Deterrent** | **-0.97** | **0.01** | **19.78** | **1** | **< 0.0001** |
| | Time block order | | | 2.69 | 3 | 0.44 |
| | **Random effects** | **Variance** | **SD** | | | |
| | Time block (in night, 78) | 0.00 | 0.00 | | | |
| | Night (in site, 32) | 0.11 | 0.33 | | | |
| | Site (in repeat, 8) | 0.11 | 0.34 | | | |
| | Site repeat (3) | 0.00 | 0.00 | | | |
| | Total observations = 156 | | | | | |

**Table 3.5** cont.

| Model | Model terms | Estimate | SE | χ2 | df | *p* |
|---|---|---|---|---|---|---|
| ***Pipistrellus* spp. 20 to 40 m** | (Intercept) | 0.27 | 0.17 | | | |
| | **Deterrent** | **-0.97** | **0.31** | **10.15** | **1** | **< 0.01** |
| | Time block order | | | 1.5 | 4 | 0.83 |
| | **Random effects** | **Variance** | **SD** | | | |
| | Time block (in night, 32) | 0.00 | 0.00 | | | |
| | Night (in site, 20) | 0.00 | 0.00 | | | |
| | Site (in repeat, 8) | 0.00 | 0.00 | | | |
| | Site repeat (3) | 0.00 | 0.00 | | | |
| | Total observations = 64 | | | | | |
| ***Myotis* spp. 0 to 20 m** | (Intercept) | 0.59 | 0.24 | | | |
| | **Deterrent** | **-0.72** | **0.35** | **4.6488** | **1** | **< 0.05** |
| | Time block order | | | 3.2593 | 3 | 0.35 |
| | **Random effects** | **Variance** | **SD** | | | |
| | Time block (in night, 31) | 0.09 | 0.31 | | | |
| | Night (in site, 22) | 0.00 | 0.00 | | | |
| | Site (in repeat, 6) | 0.00 | 0.00 | | | |
| | Site repeat (2) | 0.00 | 0.00 | | | |
| | Total observations = 62 | | | | | |

### 3.4.3 Deterrent sound modelling

I recorded a mean frequency of maximum energy (FmaxE) of 45 kHz for both anechoic chamber and field measurements of the speaker units (calculated respectively from the mean of two speakers recorded on-axis and the mean of two speakers playing simultaneously off-axis in the field on seven nights at three sites). However, the FmaxE stipulated in the speaker specifications was 50 kHz (Figure S3.3), which had a sound output in 2 dB SPL of 45 kHz at 1 m and so I have used 50 kHz for the following dB SPL calculations. Recordings made from the speaker units were also on average 2 dB SPL higher at 1 m when powered by the mains than battery or generator.

I calculated the mean source level (SL) of the two speakers recorded individually on-axis in the anechoic chamber (at 1 m and 50 kHz) as 98 dB SPL (assuming 14°C, 90% relative humidity and 101.325 kPa) (Figure 3.11; Table 3.6). Mean field recordings on seven nights at three sites were similar, ranging from 91-108 dB SPL at the same frequency and distance, with a mean and standard deviation of 99 ± 6.60 dB SPL (when off-axis speaker to microphone angles of 9-15° and dB SPL reductions (ranging from 10-30 dB SPL) were calculated from speaker set-up and specification (see Methods 3.3.3).

Assuming the same atmospheric conditions (14°C, 90% relative humidity and 101.325 kPa), I predict that at a distance of 1 m, the speakers likely exceeded 83 dB SPL at all frequencies (20-100 kHz), reaching over 90 dB SPL at 20-70 kHz (Figure 3.11; Table 3.6). At the maximum distance calculated (100 m), all frequencies were predicted to have sound pressure levels below 0 dB SPL, apart from 20 kHz, which was predicted to be ~2 dB SPL.

Most bats recorded during distance experiments were *Pipistrellus pygmaeus*, *P. pipistrellus* and *Myotis* species, which have echolocation calls with a FmaxE of ~50 kHz (Russ 2012). The calculated sound pressure level was predicted to be 52 dB SPL at 15 m and 21 dB SPL at 30 m at 50 kHz (assuming the same atmospheric conditions as above) (Table 3.6). Beyond 40 m the sound pressure level was calculated as below 3 dB SPL for 50 kHz. The lowest speaker frequency of ~20 kHz was calculated to be 61 dB SPL at 15 m and 48 dB SPL at 30 m and < 40 dB SPL at 40 m and beyond.

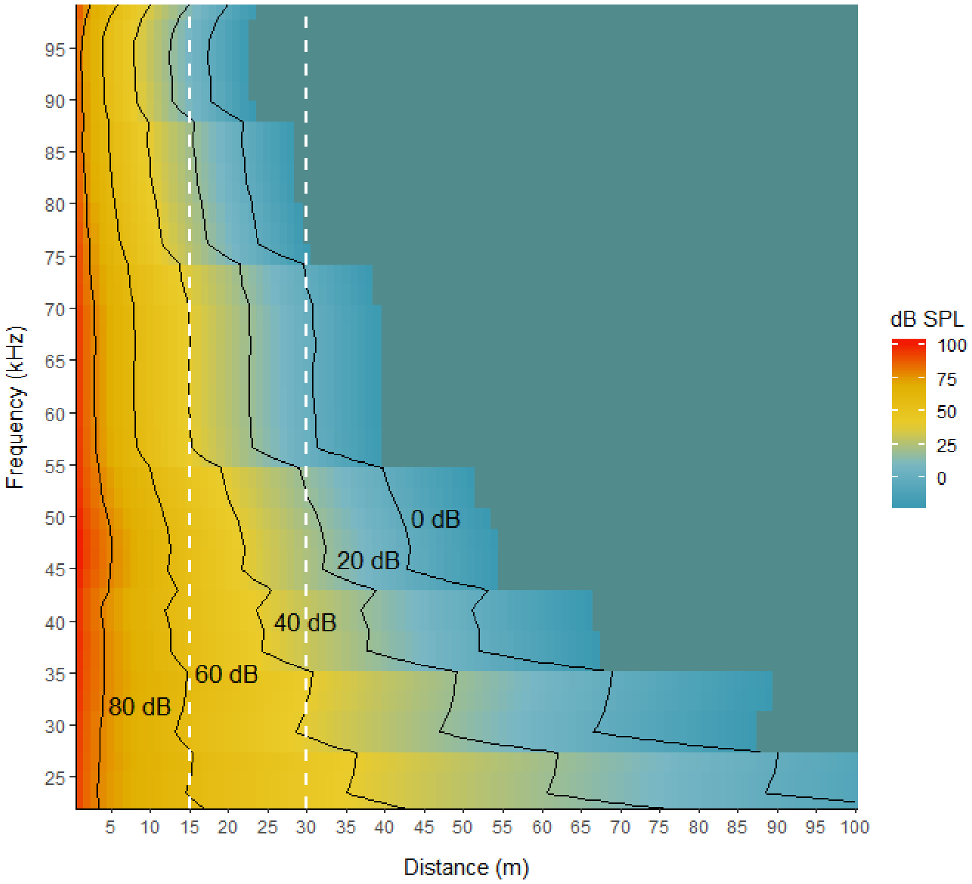


**Figure 3.11** Heat map of predicted dB SPL (RMS amplitude) for 20-100 kHz broadcast by the deterrent speaker unit over distances of 1-100 m, including contours at 0, 20, 40, 60, 80 dB SPL. White dashed lines indicate fine-scale distance experiment treatment area of 15-30 m. Calculated using calibrated anechoic chamber recordings, taking into account atmospheric attenuation and frequency-dependent absorption at 14°C, 90% relative humidity and 101.325 kPa. Teal grey background represents no data (-20 dB SPL and below). Stepped levels due to rounded values for atmospheric attenuation used in calculations.

**Table 3.6** Predicted sound pressure levels (dB SPL) at distance for different frequencies emitted by Deaton acoustic deterrent. Calculated as a mean dB SPL from anechoic chamber recordings of two deterrent speaker units on-axis at 2.2 m, corrected for distance and atmospheric attenuation and frequency-dependent absorption at 14°C, 90% relative humidity and 101.325 kPa. Mean dB SPL values also calculated for frequencies rounded to nearest 10 kHz for each distance value. dB SPL values below 0 are in grey.

| | **Frequency (kHz)** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Distance (m)** | **20** | **30** | **40** | **50** | **60** | **70** | **80** | **90** | **100** |
| **1** | 91.68 | 93.24 | 96.63 | 97.68 | 92.89 | 91.69 | 86.84 | 83.06 | 87.33 |
| **5** | 75.68 | 76.24 | 77.77 | 77.25 | 70.48 | 69.28 | 61.93 | 56.34 | 59.40 |
| **10** | 67.14 | 66.45 | 65.65 | 63.17 | 53.92 | 52.71 | 42.24 | 34.39 | 35.95 |
| **15** | 61.10 | 59.15 | 56.04 | 51.59 | 39.86 | 38.65 | 25.05 | 14.94 | 14.99 |
| **20** | 56.08 | 52.87 | 47.44 | 41.03 | 26.82 | 25.61 | 8.88 | -3.49 | -4.94 |
| **25** | 51.62 | 47.16 | 39.40 | 31.03 | 14.34 | 13.14 | -6.73 | -21.35 | -24.32 |
| **30** | 47.52 | 41.80 | 31.72 | 21.39 | 2.22 | 1.01 | -21.98 | -38.87 | -43.34 |
| **35** | 43.66 | 36.69 | 24.29 | 11.99 | -9.66 | -10.87 | -36.99 | -56.13 | -62.11 |
| **40** | 39.98 | 31.75 | 17.03 | 2.77 | -21.36 | -22.57 | -51.82 | -73.22 | -80.71 |
| **45** | 36.44 | 26.95 | 9.91 | -6.31 | -32.92 | -34.13 | -66.52 | -90.18 | -99.16 |
| **50** | 33.00 | 22.26 | 2.90 | -15.29 | -44.38 | -45.58 | -81.10 | -107.02 | -117.51 |
| **55** | 29.65 | 17.66 | -4.02 | -24.18 | -55.75 | -56.95 | -95.60 | -123.78 | -135.78 |
| **60** | 26.38 | 13.12 | -10.88 | -32.99 | -67.04 | -68.25 | -110.03 | -140.46 | -153.97 |
| **65** | 23.16 | 8.65 | -17.67 | -41.75 | -78.28 | -79.48 | -124.39 | -157.09 | -172.10 |
| **70** | 20.00 | 4.23 | -24.41 | -50.45 | -89.46 | -90.67 | -138.70 | -173.66 | -190.18 |
| **75** | 16.88 | -0.14 | -31.10 | -59.11 | -100.60 | -101.81 | -152.97 | -190.19 | -208.21 |
| **80** | 13.80 | -4.48 | -37.76 | -67.73 | -111.70 | -112.91 | -167.20 | -206.68 | -226.21 |
| **85** | 10.75 | -8.78 | -44.38 | -76.32 | -122.77 | -123.97 | -181.40 | -223.13 | -244.17 |
| **90** | 7.73 | -13.05 | -50.98 | -84.87 | -133.80 | -135.01 | -195.57 | -239.56 | -262.10 |
| **95** | 4.74 | -17.30 | -57.54 | -93.40 | -144.81 | -146.02 | -209.71 | -255.96 | -280.00 |
| **100** | 1.78 | -21.52 | -64.09 | -101.91 | -155.80 | -157.01 | -223.82 | -272.33 | -297.88 |

## 3.5 Discussion

In this study, I have used thermal bat tracking and acoustic methods to show that bats are deterred by an acoustic deterrent at distances up to ~30-40 m, but that after 40 m, there is a significant drop off in the effectiveness of the deterrent, beyond which bats are unlikely to hear the deterrent (Figure 3.7; Figure 3.10; Figure 3.11). In both the fine and larger scale experiments, bat activity was reduced by 50-60% during deterrent treatment periods at around 20 m from the deterrent. This reduction in bat activity is similar to the 50-60% reduction in bat fatalities recorded at wind farm sites in North America when the same acoustic deterrent speaker units were used (Arnett et al. 2013). However, the species most recorded as carcasses under turbines included the hoary bat (*Lasiurus cinereus*) and the silver haired bat (*Lasionycteris noctivagans*), which both have echolocation calls with a frequency of maximum energy (FmaxE) < 30 kHz. Species deterred in this study however, had an echolocation call FmaxE of around 50 kHz and included *Pipistrellus* species (mainly *P. pipistrellus* in the larger scale study and *P. pygmaeus* in the fine-scale riparian experiments) (Figure 3.8; Figure 3.10). *Myotis* species were deterred up to 20 m in front of the deterrent in the larger scale experiment and were likely to include *M. nattereri*, *M. bechsteinii*, *M. brandtii* and/or *M. mystacinus* based on local distribution patterns. However, due to the similarity of *Myotis* species calls (Russ 2012), it was not possible to discern which species were present.

No deterrent effect was found for *Myotis* species in the fine-scale experiments, despite a reduction in activity found in Chapter 4 (Results 4.4.2). Due to the riparian habitat and the bat behaviour at the fine-scale experimental sites, it is likely that the *Myotis* bats recorded were *M. daubentonii*, which feed by trawling and aerial hawking, directing their echolocation calls over the water to detect their insect prey against a smooth surface (Jones & Rayner 1988; Rydell et al. 1999; Warren et al. 2000). In this study the SM2BAT+ bat detector was placed further away from the deterrent speakers than in Chapter 4. Therefore, it is likely that the *Myotis* bats were pushed towards the bridge during deterrent broadcast, but still over the water and not completely out of the treatment area, decreasing the ability to find an effect of the deterrent on this species. *Pipistrellus* species bats generally perform aerial hawking flight higher above the ground or water and are not so limited by flying directly over water, therefore more likely spread out in any direction when the sound was broadcast in the treatment area.

In the fine-scale experiments, bat activity was reduced at 30 m by only 25% (Figure 3.7;

Table **3.1**). Closer to the deterrent there was a stronger deterrent effect, with mean bat activity reduced by 80%. In the larger scale experiments, no significant effect of the deterrent was found beyond 40 m (Table 3.4; Table 3.5). A deterrent effect was also found up to 20 m behind the deterrent when all species were combined in the larger scale study, though there was no effect on *Pipistrellus* species, despite the group making up most passes at that distance band. All other species pass counts were too low to model individually and it is possible that with more data, an effect behind the deterrent may have been found for other species recorded (e.g. *Myotis* and *Plecotus auritus*) (Table 3.3).

Anechoic chamber predictions of sound pressure levels at 40 m were below bat hearing thresholds of 20-30 dB, at < 3 dB SPL at ~50 kHz (the FmaxE of the deterrent speaker and echolocation calls of species present) (Figure 3.11) (Simmons et al. 2016; Goerlitz 2018; Lewanzik & Goerlitz 2018). Bats were more likely to hear the deterrent at 30 m, as the sound pressure level was predicted to be around 20-30 dB SPL at 40-50 kHz, just at or above the threshold level for bat hearing, which can range from 20-30 dB SPL and in some cases be as low as 0 dB SPL (Simmons et al. 2016; Goerlitz 2018; Lewanzik & Goerlitz 2018). However, lower frequencies may have had more of a deterrent effect, despite not overlapping with the FmaxE of species calls. For example, foraging efficiency in *Myotis daubentonii* was more likely reduced due to noise avoidance rather than a masking effect of traffic noise (Luo et al. 2015). Indeed, the 20 kHz component of the deterrent was relatively higher in amplitude than higher frequencies, at ~50 dB SPL at 30 m and closer to 60 dB SPL at 20 m. There may have also been some upward masking of bat echolocation calls by lower and relatively louder frequency components of the deterrent output. These sound levels were also modelled on on-axis recordings, for specific temperature and humidity values and so some caution should be taken in interpretation of the predictions, as in general, operation of the deterrent will depend on site and night-specific variables (Goerlitz 2018). However, the speakers were positioned at a height where most bats were flying and therefore likely to come in contact with sound levels predicted at some point during each experiment hour.

Acoustic bat call data from the fine-scale experiments, which was mainly identified as being from *Pipistrellus pygmaeus* was consistent with the corresponding trajectory data for 30 m (where the bat detectors were placed) and there were similar percentage reductions in activity (23%) and feeding activity (35%) to those recorded in Chapter 4 for this species (26 and 38% respectively). However, unlike the results of Chapter 4, there was no effect of the deterrent on counts of social calls, which peaked in number at the end of the experiment hour (Figure 3.9; Table 3.2). Social calls of *P. pygmaeus* can have a territorial function and this is dependent on insect abundance (Barlow & Jones 1997), which is in turn dependent on temperature conditions (Taylor 1963). More *P. pygmaeus* and *P. pipistrellus* social calls were recorded when insect density was low and playback experiments using the same calls reduced the activity of the conspecifics (Barlow & Jones 1997). The abundance of insect prey also generally peaks just after sunset and declines over the next hour or so with decreasing temperatures and *Pipistrellus* species activity usually follows this pattern (Ciechanowski et al. 2007). As this study was carried out in the relatively cool summer of 2017, cooler experiment nights (ranging from 11-17°C, compared to 13-21°C in 2018) and a resultant increase in territorial behaviour later, when it was cooler, could explain the trend in social calls seen for *P. pygmaeus* in this chapter, compared to Chapter 4.

Using a novel thermal bat tracking method and acoustic techniques, I have shown that an acoustic deterrent is effective at a range of up to about 30-40 m, and by extrapolation, is likely to approach 100% reduction in bat activity in 5-10 m, where sound pressure levels are likely to be in the range of 60-80 dB at 50 kHz (Figure 3.7). I have also shown that bats are unlikely to respond the deterrent beyond 40 m as the sound pressure level is likely to be just at or below the known hearing thresholds of bats at 20-30 dB SPL (Table 3.6; Figure 3.11). However, site-specific effects and weather variations are likely to play a role in how far the deterrent propagates in a real-world scenario. I therefore recommend that evaluation of deterrent use as a mitigation measure should be made on a case-by-case basis, considering site topography, weather conditions and species likely to be present.

# Supplementary material

**Table S3.1** Model selection statistics for bat trajectory data (fine-scale study).

**Table S3.2** Model selection statistics for acoustic bat pass data (fine-scale study).

**Table S3.3** Model selection statistics for all species models (larger-scale study).

**Table S3.4** Model selection statistics for *Pipistrellus* spp. models (larger-scale study).

**Table S3.5** Model selection statistics for *Myotis* spp. models (larger-scale study).

**Figure S3.1** Typical frequency response of Sanken CO-100K Super Wide Range Microphone.

**Figure S3.2** Typical frequency response of D1000X bat detector capacitor microphone.

**Figure S3.3** Typical beam pattern at 50 kHz of SensComp 600 series transducers.

**Table S3.1** Model selection statistics for final models for bat trajectory data, including models with negative binomial and Poisson error structure. Models arranged by AICc weight (AICc Wt) and include number of model parameters (K), cumulative AICc weight (Cum. Wt).

| **Model** | **Distribution** | **link** | **K** | **AICc** | **ΔAICc** | **AICc Wt** | **Cum. Wt** |
|---|---|---|---|---|---|---|---|
| Deterrent * distance + time block | negative binomial | log | 9 | 5916.17 | 0.00 | 0.82 | 0.82 |
| Deterrent * distance | negative binomial | log | 8 | 5919.20 | 3.00 | 0.18 | 1.00 |
| Deterrent + distance + time block | negative binomial | log | 8 | 5931.90 | 15.70 | 0.00 | 1.00 |
| Deterrent * distance + time block | Poisson | log | 8 | 17584.05 | 11667.90 | 0.00 | 1.00 |

**Table S3.2** Model selection statistics for final models for acoustic bat pass data, including models with negative binomial and Poisson error structure. Including *Pipistrellus pygmaeus*, *P. pipistrellus* and *Myotis* spp. passes, feeding buzzes (fb) and social calls (sc). Models arranged by AICc weight (AICc Wt) and include number of model parameters (K), cumulative AICc weight (Cum. Wt).

| **Species** | **Model** | **link** | **Distribution** | **K** | **AICc** | **ΔAICc** | **AICc Wt** | **Cum. Wt** |
|---|---|---|---|---|---|---|---|---|
| ***P. pygmaeus*** | Deterrent + time block | log | Poisson | 6 | 5144.64 | 0.00 | 0.71 | 0.71 |
| | Deterrent + time block | log | negative binomial | 7 | 5146.66 | 2.00 | 0.26 | 0.97 |
| | Time block | log | Poisson | 5 | 5150.99 | 6.40 | 0.03 | 1.00 |
| | Deterrent | log | Poisson | 5 | 5164.17 | 19.50 | 0.00 | 1.00 |
| ***Myotis* spp.** | Time block | log | Poisson | 5 | 3292.64 | 0.00 | 0.64 | 1.00 |
| | Deterrent + time block | log | Poisson | 6 | 3293.92 | 2.00 | 0.24 | 1.24 |
| | Deterrent + time block | log | negative binomial | 7 | 3295.95 | 4.00 | 0.09 | 1.32 |
| | Deterrent | log | Poisson | 5 | 3297.52 | 5.60 | 0.04 | 1.36 |
| ***Myotis* spp. (fb)** | null | log | negative binomial | 5 | 2630.78 | 0.00 | 0.58 | 1.00 |
| | Deterrent | log | negative binomial | 6 | 2632.46 | 1.70 | 0.25 | 1.25 |
| | Deterrent + time block | log | negative binomial | 7 | 2633.17 | 2.40 | 0.17 | 1.42 |
| | Deterrent + time block | log | Poisson | 6 | 2691.00 | 60.20 | 0.00 | 1.42 |
| ***P. pipistrellus*** | null | log | Poisson | 4 | 2031.34 | 0.00 | 0.59 | 0.59 |
| | Deterrent | log | Poisson | 5 | 2032.91 | 1.60 | 0.27 | 0.86 |
| | Deterrent + time block | log | Poisson | 6 | 2034.74 | 3.40 | 0.11 | 0.96 |
| | Deterrent + time block | log | negative binomial | 7 | 2036.79 | 5.40 | 0.04 | 1.00 |
| ***P. pygmaeus* (fb)** | Deterrent + time block | log | negative binomial | 7 | 5027.17 | 0.00 | 0.77 | 1.00 |
| | Time block | log | negative binomial | 6 | 5029.61 | 2.40 | 0.23 | 1.30 |
| | Deterrent + time block | log | Poisson | 6 | 5050.50 | 23.30 | 0.00 | 1.41 |
| | Deterrent | log | negative binomial | 6 | 5058.65 | 31.50 | 0.00 | 1.41 |
| ***P. pygmaeus* (sc)** | null | log | Poisson | 5 | 1718.71 | 0.00 | 0.58 | 1.00 |
| | Deterrent | log | Poisson | 6 | 1720.02 | 1.30 | 0.30 | 1.30 |
| | Deterrent + time block | log | negative binomial | 7 | 1721.99 | 3.30 | 0.11 | 1.41 |
| | Deterrent + time block | log | Poisson | 6 | 1978.87 | 260.20 | 0.00 | 1.41 |

**Table S3.3** Model selection statistics for final models for acoustic bat pass data of all species combined for all distances and -20-120 m, including models with negative binomial and Poisson error structure. Models arranged by AICc weight (AICc Wt) and include number of model parameters (K), cumulative AICc weight (Cum. Wt).

| Response variable | Model | Distribution | K | AICc | ΔAICc | AICc Wt | Cum. Wt |
|---|---|---|---|---|---|---|---|
| **All spp. all distances** | Time block + Acoustic deterrent | negative binomial | 11 | 1863.69 | 0.00 | 0.68 | 1.00 |
| | Time block * Acoustic deterrent | negative binomial | 15 | 1865.26 | 1.60 | 0.31 | 0.32 |
| | Acoustic deterrent | negative binomial | 7 | 1872.88 | 9.20 | 0.01 | 0.01 |
| | Time block | negative binomial | 10 | 1879.95 | 16.30 | 0.00 | 0.00 |
| | Null | negative binomial | 6 | 1886.26 | 22.60 | 0.00 | 0.00 |
| | Time block * Acoustic deterrent | Poisson | 14 | 2611.79 | 748.10 | 0.00 | 0.00 |
| **All spp. -20 to 0 m** | Acoustic deterrent | negative binomial | 7 | 278.13 | 0.00 | 0.86 | 1.00 |
| | Null | negative binomial | 6 | 282.43 | 4.30 | 0.10 | 0.14 |
| | Time block + Acoustic deterrent | negative binomial | 10 | 284.55 | 6.40 | 0.03 | 0.04 |
| | Time block | negative binomial | 9 | 288.12 | 10.00 | 0.01 | 0.01 |
| | Time block * Acoustic deterrent | negative binomial | 13 | 292.87 | 14.70 | 0.00 | 0.00 |
| | Time block * Acoustic deterrent | Poisson | 12 | 318.49 | 40.40 | 0.00 | 0.00 |
| **All spp. 0 to 20 m** | Time block + Acoustic deterrent | negative binomial | 11 | 989.55 | 0.00 | 0.42 | 1.00 |
| | Acoustic deterrent | negative binomial | 7 | 990.08 | 0.50 | 0.32 | 0.58 |
| | Time block * Acoustic deterrent | negative binomial | 15 | 990.47 | 0.90 | 0.26 | 0.26 |
| | Null | negative binomial | 6 | 1011.37 | 21.80 | 0.00 | 0.00 |
| | Time block | negative binomial | 10 | 1011.70 | 22.10 | 0.00 | 0.00 |
| | Time block * Acoustic deterrent | Poisson | 14 | 1180.20 | 190.70 | 0.00 | 0.00 |
| **All spp. 20 to 40 m** | Acoustic deterrent | negative binomial | 7 | 496.49 | 0.00 | 0.94 | 1.00 |
| | null | negative binomial | 6 | 503.28 | 6.80 | 0.03 | 0.06 |
| | Time block + Acoustic deterrent | negative binomial | 11 | 504.03 | 7.50 | 0.02 | 0.03 |
| | Time block * Acoustic deterrent | negative binomial | 15 | 506.58 | 10.10 | 0.01 | 0.01 |
| | Time block | negative binomial | 10 | 510.18 | 13.70 | 0.00 | 0.00 |
| | Time block * Acoustic deterrent | Poisson | 14 | 553.11 | 56.60 | 0.00 | 0.00 |

**Table S3.3** cont.

| Response variable | Model | Distribution | K | AICc | ΔAICc | AICc Wt | Cum. Wt |
|---|---|---|---|---|---|---|---|
| **All spp. 40 to 60 m** | null | negative binomial | 6 | 647.78 | 0.00 | 0.70 | 1.00 |
| | Acoustic deterrent | negative binomial | 7 | 649.99 | 2.20 | 0.23 | 0.30 |
| | Time block | negative binomial | 10 | 653.05 | 5.30 | 0.05 | 0.07 |
| | Time block + Acoustic deterrent | negative binomial | 11 | 655.44 | 7.70 | 0.02 | 0.02 |
| | Time block * Acoustic deterrent | negative binomial | 15 | 658.03 | 10.20 | 0.00 | 0.00 |
| | Time block * Acoustic deterrent | Poisson | 14 | 711.80 | 64.00 | 0.00 | 0.00 |
| **All spp. 60 to 80 m** | Acoustic deterrent | negative binomial | 7 | 233.73 | 0.00 | 0.45 | 0.98 |
| | null | negative binomial | 6 | 234.08 | 0.40 | 0.38 | 0.53 |
| | Time block * Acoustic deterrent | Poisson | 12 | 236.74 | 3.00 | 0.10 | 0.15 |
| | Time block + Acoustic deterrent | negative binomial | 10 | 239.48 | 5.70 | 0.03 | 0.05 |
| | Time block * Acoustic deterrent | negative binomial | 13 | 239.77 | 6.00 | 0.02 | 0.02 |
| | Time block | negative binomial | 9 | 239.98 | 6.30 | 0.02 | 0.00 |
| **All spp. 80 to 100 m** | null | negative binomial | 6 | 240.83 | 0.00 | 0.61 | 1.00 |
| | Acoustic deterrent | negative binomial | 7 | 241.93 | 1.10 | 0.35 | 0.39 |
| | Time block | negative binomial | 9 | 247.35 | 6.50 | 0.02 | 0.04 |
| | Time block + Acoustic deterrent | negative binomial | 10 | 248.79 | 8.00 | 0.01 | 0.01 |
| | Time block * Acoustic deterrent | Poisson | 12 | 251.12 | 10.30 | 0.00 | 0.00 |
| | Time block * Acoustic deterrent | negative binomial | 13 | 254.52 | 13.70 | 0.00 | 0.00 |
| **All spp. 100 to 120 m** | null | negative binomial | 6 | 366.66 | 0.00 | 0.72 | 1.00 |
| | Acoustic deterrent | negative binomial | 7 | 368.87 | 2.20 | 0.24 | 0.28 |
| | Time block | negative binomial | 9 | 372.92 | 6.30 | 0.03 | 0.04 |
| | Time block + Acoustic deterrent | negative binomial | 10 | 375.33 | 8.70 | 0.01 | 0.01 |
| | Time block * Acoustic deterrent | negative binomial | 13 | 380.04 | 13.40 | 0.00 | 0.00 |
| | Time block * Acoustic deterrent | Poisson | 12 | 396.25 | 29.60 | 0.00 | 0.00 |

**Table S3.4** Model selection statistics for final models for *Pipistrellus* spp. passes at all distances and -20-120 m, including models with negative binomial and Poisson error structure. Models arranged by AICc weight (AICc Wt) and include number of model parameters (K), cumulative AICc weight (Cum. Wt).

| **Response variable** | **Model** | **Distribution** | **K** | **AICc** | **ΔAICc** | **AICc Wt** | **Cum. Wt** |
|---|---|---|---|---|---|---|---|
| ***Pipistrellus* spp. all distances** | Acoustic deterrent | negative binomial | 7 | 1525.61 | 0.00 | 0.64 | 1.00 |
| | Time block + Acoustic deterrent | negative binomial | 12 | 1528.05 | 2.40 | 0.19 | 0.36 |
| | Time block * Acoustic deterrent | negative binomial | 17 | 1528.48 | 2.90 | 0.15 | 0.17 |
| | null | negative binomial | 6 | 1533.06 | 7.40 | 0.02 | 0.02 |
| | Time block | negative binomial | 11 | 1535.61 | 10.00 | 0.00 | 0.00 |
| | Time block * Acoustic deterrent | Poisson | 16 | 1972.12 | 446.50 | 0.00 | 0.00 |
| ***Pipistrellus* spp. -20 to 0 m** | null | negative binomial | 6 | 217.94 | 0.00 | 0.51 | 1.00 |
| | Acoustic deterrent | negative binomial | 7 | 218.41 | 0.50 | 0.40 | 0.49 |
| | Time block | negative binomial | 9 | 222.31 | 4.40 | 0.06 | 0.09 |
| | Time block + Acoustic deterrent | negative binomial | 10 | 223.76 | 5.80 | 0.03 | 0.03 |
| | Time block * Acoustic deterrent | negative binomial | 13 | 232.73 | 14.80 | 0.00 | 0.00 |
| | Time block * Acoustic deterrent | Poisson | 12 | 249.08 | 31.10 | 0.00 | 0.00 |
| ***Pipistrellus* spp. 0 to 20 m** | Time block * Acoustic deterrent | negative binomial | 13 | 595.28 | 0.00 | 0.80 | 1.00 |
| | Acoustic deterrent | negative binomial | 7 | 598.38 | 3.10 | 0.17 | 0.20 |
| | Time block + Acoustic deterrent | negative binomial | 10 | 601.99 | 6.70 | 0.03 | 0.03 |
| | null | negative binomial | 6 | 615.96 | 20.70 | 0.00 | 0.00 |
| | Time block | negative binomial | 9 | 619.94 | 24.70 | 0.00 | 0.00 |
| | Time block * Acoustic deterrent | Poisson | 12 | 666.26 | 71.00 | 0.00 | 0.00 |
| ***Pipistrellus* spp. 20 to 40 m** | Acoustic deterrent | negative binomial | 7 | 170.89 | 0.00 | 0.97 | 1.00 |
| | null | negative binomial | 6 | 178.51 | 7.60 | 0.02 | 0.03 |
| | Time block + Acoustic deterrent | negative binomial | 11 | 180.33 | 9.40 | 0.01 | 0.01 |
| | Time block * Acoustic deterrent | Poisson | 14 | 183.81 | 12.90 | 0.00 | 0.00 |
| | Time block * Acoustic deterrent | negative binomial | 15 | 187.18 | 16.30 | 0.00 | 0.00 |
| | Time block | negative binomial | 10 | 187.69 | 16.80 | 0.00 | 0.00 |

**Table S3.4** cont.

| Response variable | **Model** | **Distribution** | **K** | **AICc** | **ΔAICc** | **AICc Wt** | **Cum. Wt** |
|---|---|---|---|---|---|---|---|
| *Pipistrellus* spp. 40 to 60 m | null | negative binomial | 6 | 487.04 | 0.00 | 0.72 | 1.00 |
| | Acoustic deterrent | negative binomial | 7 | 489.32 | 2.30 | 0.23 | 0.28 |
| | Time block | negative binomial | 9 | 493.13 | 6.10 | 0.03 | 0.05 |
| | Time block + Acoustic deterrent | negative binomial | 10 | 495.53 | 8.50 | 0.01 | 0.01 |
| | Time block * Acoustic deterrent | negative binomial | 13 | 497.72 | 10.70 | 0.00 | 0.00 |
| | Time block * Acoustic deterrent | Poisson | 12 | 524.36 | 37.30 | 0.00 | 0.00 |
| *Pipistrellus* spp. 60 to 80 m | null | negative binomial | 6 | 143.14 | 0.00 | 0.74 | 1.00 |
| | Acoustic deterrent | negative binomial | 7 | 145.47 | 2.30 | 0.23 | 0.25 |
| | Time block * Acoustic deterrent | Poisson | 12 | 151.34 | 8.20 | 0.01 | 0.02 |
| | Time block | negative binomial | 9 | 152.46 | 9.30 | 0.01 | 0.01 |
| | Time block + Acoustic deterrent | negative binomial | 10 | 155.31 | 12.20 | 0.00 | 0.00 |
| | Time block * Acoustic deterrent | negative binomial | 13 | 155.79 | 12.60 | 0.00 | 0.00 |
| *Pipistrellus* spp. 80 to 100 m | null | negative binomial | 6 | 199.66 | 0.00 | 0.75 | 1.00 |
| | Acoustic deterrent | negative binomial | 7 | 202.14 | 2.50 | 0.22 | 0.24 |
| | Time block | negative binomial | 9 | 206.82 | 7.20 | 0.02 | 0.03 |
| | Time block + Acoustic deterrent | negative binomial | 10 | 209.54 | 9.90 | 0.01 | 0.01 |
| | Time block * Acoustic deterrent | Poisson | 12 | 212.28 | 12.60 | 0.00 | 0.00 |
| | Time block * Acoustic deterrent | negative binomial | 13 | 216.15 | 16.50 | 0.00 | 0.00 |
| *Pipistrellus* spp. 100 to 120 m | null | negative binomial | 6 | 366.66 | 0.00 | 0.72 | 1.00 |
| | Acoustic deterrent | negative binomial | 7 | 368.87 | 2.20 | 0.24 | 0.28 |
| | Time block | negative binomial | 9 | 372.92 | 6.30 | 0.03 | 0.04 |
| | Time block + Acoustic deterrent | negative binomial | 10 | 375.33 | 8.70 | 0.01 | 0.01 |
| | Time block * Acoustic deterrent | negative binomial | 13 | 380.04 | 13.40 | 0.00 | 0.00 |
| | Time block * Acoustic deterrent | Poisson | 12 | 396.25 | 29.60 | 0.00 | 0.00 |

**Table S3.5** Model selection statistics for final models for *Myotis* spp. pass data at all distances and 0 to 20 m, including models with negative binomial and Poisson error structure. Models arranged by AICc weight (AICc Wt) and include number of model parameters (K), cumulative AICc weight (Cum. Wt).

| **Response variable** | **Model** | **Distribution** | **K** | **AICc** | **ΔAICc** | **AICc Wt** | **Cum. Wt** |
|---|---|---|---|---|---|---|---|
| ***Myotis* spp. all distances** | null | negative binomial | 6 | 555.15 | 0.00 | 0.46 | 1.00 |
| | Acoustic deterrent | negative binomial | 7 | 555.68 | 0.50 | 0.35 | 0.54 |
| | Time block | negative binomial | 9 | 558.60 | 3.50 | 0.08 | 0.18 |
| | Time block + Acoustic deterrent | negative binomial | 10 | 559.15 | 4.00 | 0.06 | 0.10 |
| | Time block * Acoustic deterrent | negative binomial | 13 | 560.18 | 5.00 | 0.04 | 0.04 |
| | Time block * Acoustic deterrent | Poisson | 12 | 655.34 | 100.20 | 0.00 | 0.00 |
| ***Myotis* spp. 0 to 20 m** | Acoustic deterrent | negative binomial | 7 | 216.26 | 0.00 | 0.55 | 1.00 |
| | null | negative binomial | 6 | 217.65 | 1.40 | 0.28 | 0.45 |
| | Time block + Acoustic deterrent | negative binomial | 9 | 219.63 | 3.40 | 0.10 | 0.17 |
| | Time block | negative binomial | 8 | 220.79 | 4.50 | 0.06 | 0.07 |
| | Time block * Acoustic deterrent | negative binomial | 11 | 224.64 | 8.40 | 0.01 | 0.01 |
| | Time block * Acoustic deterrent | Poisson | 10 | 238.86 | 22.60 | 0.00 | 0.00 |

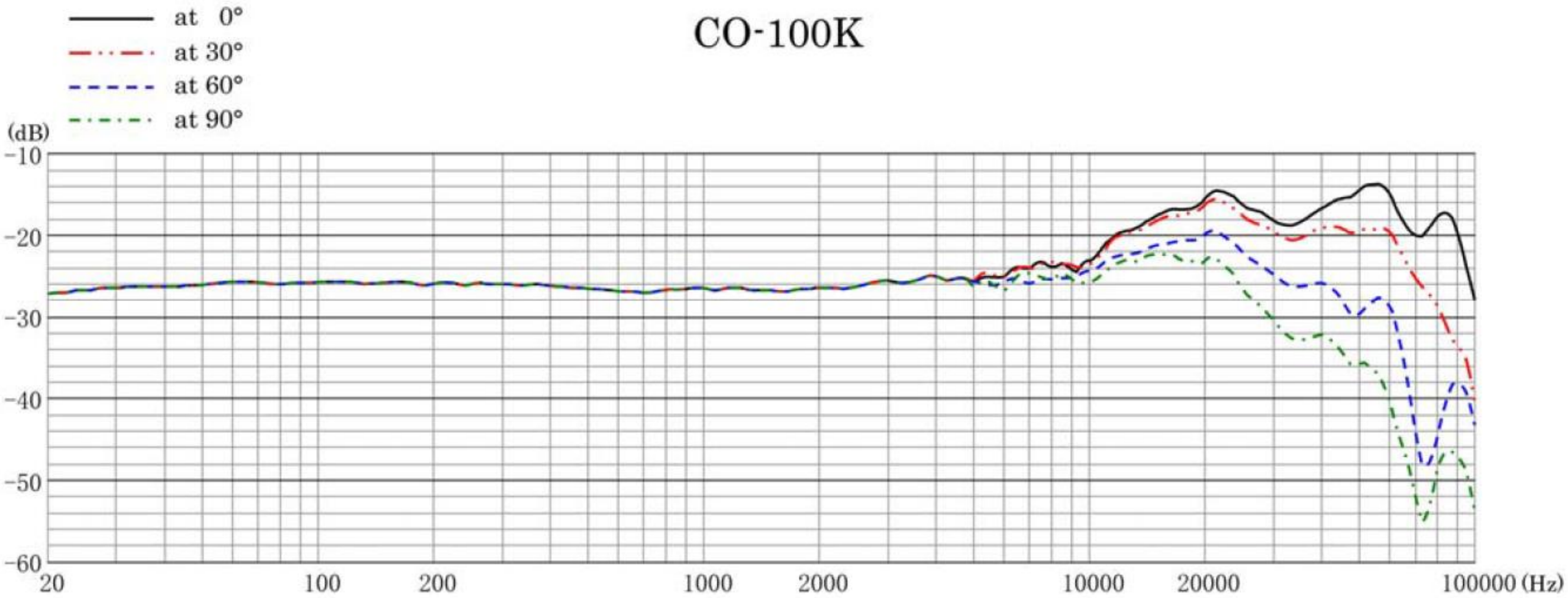


**Figure S3.1** Typical frequency response of Sanken CO-100K Super Wide Range Microphone from specification manual provided by Sanken Microphone Co. Ltd., Tokyo, Japan. Including a maximum frequency response of ± 12 dB at 20 to 100000 Hz (0.02 to 100 kHz). Frequency response of the microphone also included for on-axis recordings and 30°, 60° and 90°.

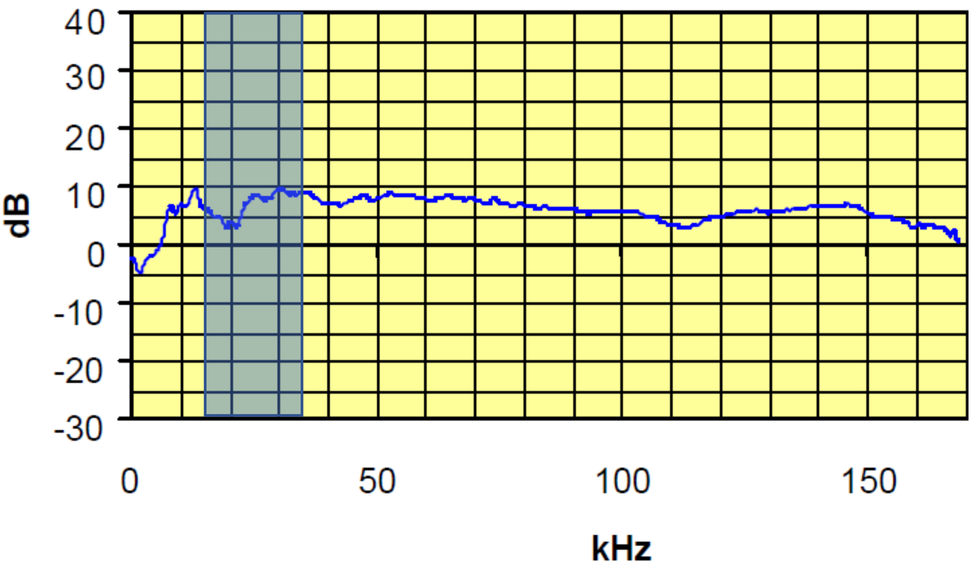
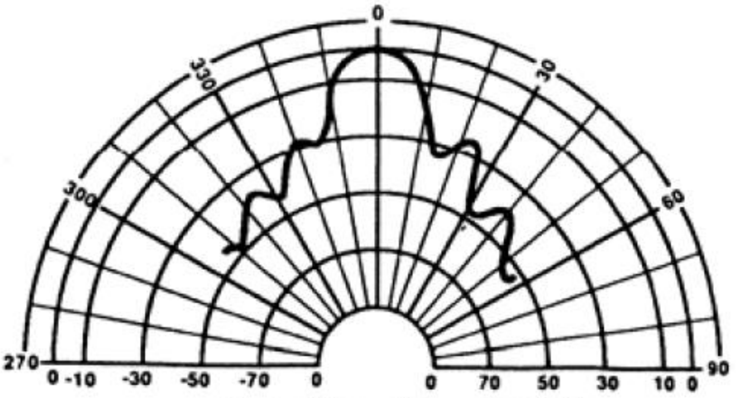


**Figure S3.2** Typical frequency response of D1000X full spectrum bat detector capacitor microphone, provided with permission from Pettersson Elektronik, Uppsala, Sweden. Including a maximum frequency response of ± 10 dB at 0 to 200 kHz. As the measuring system was not accurate below 20 kHz, responses below this frequency (shaded blue area) should be disregarded.



Typical Beam Pattern At 50 kHz

Note: dB normalized to on-axis response.

Note: Curves are representative only. Individual responses may differ.

**Figure S3.3** Typical beam pattern at 50 kHz of SensComp 600 series environmental electrostatic transducers used in the acoustic deterrent speaker unit (which included 12 transducers), from SensComp specification document (www.senscomp.com, Michigan, USA).

# CHAPTER 4

## 3-dimensional bat responses to an acoustic deterrent, studied using stereo thermal videogrammetry and acoustic methods

**Chapter contributions**

All experimental design, data collection, method development, calculation, statistical analysis and writing for this chapter were carried out by L.R.V Gilmour, with the additional contributions below:

All MATLAB scripts were originally written by M.W. Holderied and then developed ready for use by L.R.V. Gilmour with help from M.W. Holderied. Match Point 1.0 software was created by M. W. Holderied especially for the application in this thesis.

G. Jones and M.W. Holderied provided supervision for all experimental work carried out for this chapter and provided comments and feedback on the written document.

## 4.1 Abstract

Acoustic deterrents have shown potential for diverting bats away from areas where they forage and roost such as wind turbines and historic buildings. However, the mechanisms underpinning acoustic deterrence of bats have not yet been explored. Bats avoid areas of ambient ultrasound in their environment and alter their echolocation calls in response to masking noise. Using stereo thermal videogrammetry and acoustic methods, I tested predictions that i) bats would avoid an airspace exposed to high-intensity ultrasound, likely due to a masking effect of the deterrent noise negatively affecting the use of their echolocation for orientation and prey capture and ii) bats would reduce their local foraging activity in response to the deterrent, which would consequently increase their flight speed and reduce the tortuosity of their flight paths. As predicted, bat activity and foraging behaviour were significantly reduced, and bats increased their flight speed in response to the deterrent. There also was a small (1%) reduction in tortuosity at 25-30 m, probably due to bats flying more directly during deterrent playback around and under the bridge at each site. *Pipistrellus pygmaeus*, *Myotis* species (probably *M. daubentonii*) and *Nyctalus* and *Eptesicus* species pass counts were all significantly reduced during deterrent broadcast and returned to normal after playback. *P. pipistrellus* pass counts were not different during deterrent playback and control periods, but a deterrent effect on this species can not be ruled out due to the small sample size (only 6% of total passes). *P. pygmaeus* reduced the bandwidth and start frequency of their echolocation calls in response to the deterrent, probably in a response to the masking effect of the deterrent and their passes and feeding buzzes were also reduced by 28 and 38% respectively. There was less of, but still a significant reduction in *P. pygmaeus* social calls (23% reduction), possibly due to the unavoidable recording of the relatively low frequency calls emitted outside of the treated airspace. Deterrence could therefore be used to remove bats from areas where they forage, for example where they may be under threat from human-built structures or anthropogenic activities.

## 4.2 Introduction

In Chapters 2 and 3 of this thesis, I demonstrated that acoustic deterrents are effective at reducing bat activity at foraging sites in the UK, up to a range of ~40 m. The same ultrasonic speakers reduced bat mortality at wind farms in North America (Arnett et al. 2013) and were successfully used to move bats from roosting in certain problem areas of churches in the UK (Packman et al. 2015; Zeale et al. 2016). However, the mechanism for deterrence by this broadband ultrasonic speaker system has not yet been explored. Understanding how acoustic deterrence works and its impact on bats is therefore important for its safe and appropriate use.

Acoustic deterrence systems can be thought of as analogous to a noise disturbance encountered in an animal's environment, for example from natural sources and/or anthropogenic sources (Mackey & Barclay 1989; Schaub et al. 2008; Bunkley & Barber 2015; Bunkley et al. 2015; Luo et al. 2015; Mahjoub et al. 2015; Simpson et al. 2016). Potential mechanisms for the effect of noise on animals include noise avoidance, a reduction in attention due to the noise and auditory masking (Chan et al. 2010; Purser & Radford 2011; Francis & Barber 2013; Moore 2013; Luo et al. 2015). Noise avoidance usually occurs when a sound in an animal's environment represents an uncomfortable or aversive stimulus or potential stressor (Francis & Barber 2013; Luo et al. 2015). For example, foraging was reduced in Daubenton's bats (*Myotis daubentonii*) by traffic noise playbacks that did not overlap in frequency with returning echolocation echoes and therefore represented an aversive stimulus, rather than a masking one (Luo et al. 2015).

Reduced attention due to noise occurs when an animal's ability to focus on important tasks such as foraging, or predator avoidance are impaired by another sound source (Barber et al. 2003; Chan et al. 2010; Purser & Radford 2011; Luo et al. 2015). Three-spined sticklebacks (*Gasterosteus aculeatus*) made more food handling errors, resulting in a reduction in foraging efficiency in response to noise, and Caribbean hermit crabs (*Coenobita clypeatus*) were more vulnerable to predation in response to boat noise (Chan et al. 2010; Purser & Radford 2011). Auditory masking is where the perception of a sound is affected by another masking sound and the threshold level for hearing the original sound is increased by the presence of the second sound (Moore 2013). For example, wild superb fairy-wrens (*Malurus cyaneus*) were less likely to flee alarm calls in the presence of overlapping high amplitude noise, but not in response to non-overlapping noise (Zhou et al. 2019).

Ambient sound can therefore have a range of impacts on an animal's ability to carry out important behaviours, such as communicating with conspecifics, social behaviour, courtship, foraging and avoiding predators (Schaub et al. 2008; Chan et al. 2010; Radford et al. 2014; Bunkley et al. 2015; Mahjoub et al. 2015; Morris-Drake et al. 2017; de Jong et al. 2018a; de Jong et al. 2018b; Jiang et al. 2019; Tidau & Briffa 2019; Zhou et al. 2019). All three mechanisms are not mutually exclusive, however, and teasing apart underlying reasons for noise effects can be difficult (Luo et al. 2015).

Previous research on deterrence has alluded to a specific masking effect of the acoustic deterrent stimulus on the echolocation system of bats, precluding their ability to hunt and find prey (Arnett et al. 2013). Along with the passive hearing system of most other vertebrates, bats possess an active hearing system and rely on echolocation to orientate and hunt their insect prey at night (Metzner & Müller 2016). Bats are therefore susceptible to another level of auditory masking, often called "jamming", in which sounds from echolocating conspecifics or other ambient sources interfere with returning echoes from their own signals (Griffin et al. 1963). Indeed, bats will often alter their spectral and/or temporal echolocation characteristics in response to jamming by conspecifics, in what is often called a jamming avoidance response (JAR) (Gillam et al. 2006; Bates et al. 2008; Chiu et al. 2010; Jarvis et al. 2013; Takahashi et al. 2014; Amichai et al. 2015; Fawcett & Ratcliffe 2015; Hase et al. 2018). Bats will also alter their echolocation calls in response to ambient noise, from natural sources such as insect sounds and anthropogenic sources such as traffic noise or gas compressor stations (Gillam & McCracken 2007; Tressler & Smotherman 2009; Hage & Metzner 2013; Bunkley et al. 2015; Song et al. 2019).

Not all responses to noise in bats are due to jamming of echolocation calls. Masking can also occur when prey-generated sounds are obscured by noise (Schaub et al. 2008; Bunkley & Barber 2015; Gomes et al. 2016). Bats may also avoid noise if it represents an uncomfortable or stressful stimulus (Luo et al. 2015). Bat communication can also be affected by masking, although this has been studied less (Jiang et al. 2019; Song et al. 2019).

Flying vertebrates such as bats are constrained by the energetic costs of flight and therefore adjust their flight pattern in order to minimise energy expenditure where possible (Pennycuick 1975; Rayner 1999; Grodzinski et al. 2009). Foraging bats therefore tend to fly at reduced speeds and with more tortuous flight paths (taking a longer and more twisted or convoluted route to reach the same point), compared to when commuting, where their flight paths are faster and more direct (Jones & Rayner 1988, 1991; Jones 1995; Holderied & Jones 2009). Commuting bats aim to reach their foraging territories quickly, avoiding predation and therefore fly at higher speeds, using more energy. Once foraging and searching for insects, which represent a patchy resource, bats will forage with slower and more tortuous flight, which is also more energy efficient. Flight speeds and other flight path characteristics can therefore be used to investigate the effect of specific environmental conditions such as light or noise, on bat behaviour (Polak et al. 2011). For example, flight speeds of *Pipistrellus kuhlii* and *Eptesicus bottae* were significantly increased in floodlit areas compared to natural darkness (Polak et al. 2011). *E. bottae* also did not forage in the light and flew closer to commuting speed when passing through the beam.

Animal flight speed, tortuosity and other trajectory characteristics are often measured using 3-dimensional flight path tracking methods (Dell et al. 2014; Betke et al. 2017). Flight paths of bats have been reconstructed using for example stereo photogrammetery, stereo videogrammetry, GPS tracking systems and acoustic tracking systems (Jones & Rayner 1988, 1991; Jones 1995; Holderied et al. 2005; Holderied et al. 2008; Hristov et al. 2008; Grodzinski et al. 2009; Polak et al. 2011; Yang et al. 2013; Sapir et al. 2014; Giuggioli et al. 2015). As bats generally fly at night, visual methods of flight path tracking have often been limited to using a relatively small lit-up area or flash photography (Jones & Rayner 1988, 1991; Jones 1995; Polak et al. 2011; Giuggioli et al. 2015). Thermal imaging methods allow the visualisation of animals in dark environments potentially over larger scales (Hristov et al. 2008; Betke et al. 2017). Some studies have utilised thermal imaging for 2-dimensional flight path tracking, in for example studying emergence patterns of bats from caves and at offshore wind turbine sites (Hristov et al. 2008; Cullinan et al. 2015; Matzner et al. 2015; Betke et al. 2017). However only a handful of studies have utilised both stereo videogrammetry and thermal imaging methods to study bats to date (Hristov et al. 2008; Yang et al. 2013).

Therefore, in this study I aimed to explore the potential mechanisms underpinning acoustic deterrence and its impact on bats, by using a combination of stereo thermal videogrammetry and acoustic recording techniques. I aimed to test the predictions that, i) bats will avoid areas subjected to intense broadband ultrasound, resulting in a decrease in activity (similar to previous chapters), and ii) this is due to the masking effect of the deterrent noise precluding the use of their echolocation. I also predict that iii) mean trajectory flight speed will increase and tortuosity will decrease in response to the deterrent, in line with a decrease in foraging behaviour, iv) bats will alter their echolocation calls in response to the deterrent to avoid auditory masking and v) there will be a significant reduction is feeding buzzes and social calls recorded during deterrent treatments.

## 4.3 Methods

### 4.3.1 Site selection and experimental procedure

I carried out experiments in July and August 2018 at three riparian locations (> 1 km apart, to reduce the possibility of recording the same bat more than once), selected due to high levels of bat activity recorded in previous chapters. Each site had an area of still water next to a bridge and was flanked by hedges along one side, either along the river or perpendicular to the bridge. I filmed bats flying over the river using two thermal imaging cameras (Optris PI640 thermal imaging cameras, 640x480 pixel resolution, 33° lenses; Optris GmbH, Germany), Optris PI Connect software (Optris GmbH, Germany) and a laptop computer (see Chapter 3.3.1.1 Methods), recording in .avi uncompressed video format at 32 fps for one hour per night, for three nights at each site (nine hours of footage in total), starting at ~half an hour to 1 hour after sunset. I alternated 5-minute silent control periods and 5 mins of ultrasonic speaker playback, totalling 12 x 5 min time blocks over the experiment hour. I started each experiment night with a control period, in order to monitor bat activity levels and decide when to start filming (see Chapter 3.3.1.2 Methods).

I placed the two ultrasonic speakers (Deaton engineering Inc., Texas, USA, see Figure 2.2 in Chapter 2 for specification) on ladders at ~2 m high and 10-15 m behind the cameras, so that the sound field covered ~15-30 m in the $z$ plane of the cameras' field of view (FOV). From Chapter 3, I predicted that there would be approximately a 60% reduction on average in bat activity over the treatment area. I therefore chose this distance range to increase the likelihood of recording an effect, but also making sure there were bats to respond to the deterrent present in the treatment area. A treatment area closer to the deterrent could have resulted in a reduced ability to see an effect due to most bats being deterred by the deterrent noise. I positioned the two cameras at the same height (1 m), 4 m apart, parallel to the ground (using a sprit level) and so that the inner edge of their FOV overlapped at 3.2 m and the side edges of their FOV were parallel, so that the combined FOV covered the maximum amount of the treatment area (4-5 m wide, depending on distance) (Figure 4.1).

All equipment was powered by a low-noise generator (Honda EU10i, Honda, Tokyo, Japan) that was unlikely to affect bat activity (Stone et al. 2009). The generator was placed at least 10 m away from the treatment area and ran during both control and treatment periods. I also placed a SM2BAT+ detector and SMX-US microphone (Wildlife Acoustics Inc., Massachusetts, USA; continuous .wav recording; 384 kHz sampling rate; SNR 10) next to the bridge at ~30 m from the deterrent, angled towards the water at each site, to record bat calls in the treatment zone during the experiment hour, but also far enough away to avoid masking effects of the deterrent on recordings.

### 4.3.2 Calibration

I carried out calibration of the treatment area (extrinsics) and the camera lens parameters (intrinsics) using a bespoke commissioned calibration target, comprised of an aluminium cross with 30 11 mm diameter tungsten bulbs (1.5 V, 300 mA) wired in parallel on four arms, powered by four D cell batteries (Figure 4.2). Three of the arms were identical with eight bulbs and one arm had six bulbs arranged in three pairs, to allow its identification in the thermal footage. I thermally insulated the target using heating insulation board and a cardboard panel, so the heat signature from the person carrying the target was obscured as much as possible.

I calculated bulb coordinates and filmed the calibration target in eight different orientations and at three angles (24 positions) on each repeat night and extracted image stills using VirtualDub (v. 1.10.4, Free Software Foundation, Inc, Cambridge, MA, USA). I prepared images using Photoshop CS5 Extended (v.12, Adobe Systems Inc., San Jose, California, United States) threshold, curves and paint brush functions, ready for extraction of *in situ* bulb coordinates from each camera using MatchPoint 1.0 (software developed using original target bulb coordinates and MATLAB by M.W. Holderied especially for this application). I then used specially developed calibration code, based on the stereo vision toolbox in MATLAB (v.R2017a, 9.2.0.556344, Mathworks Inc., Natick, MA, United States) to extract camera intrinsics and extrinsics of each nightly set-up, which were then used to plot bat trajectory data.

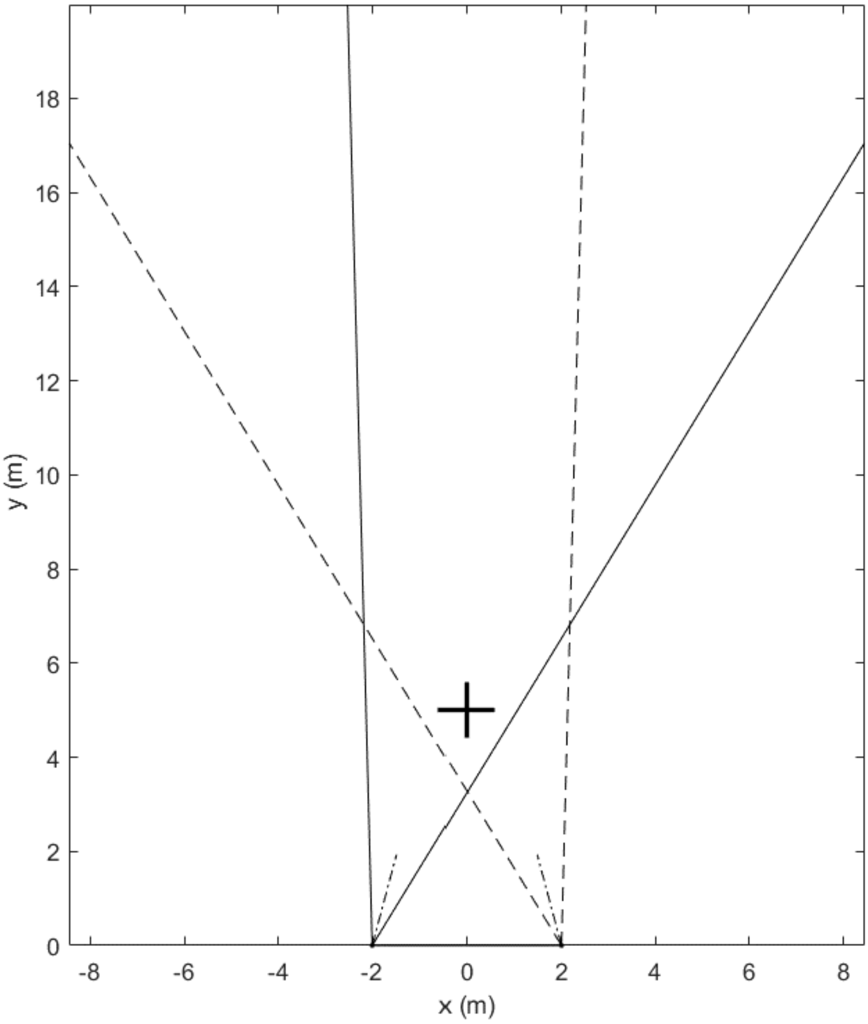


**Figure 4.1** Calibration set-up, with two thermal imaging cameras with 33° opening angles, positioned at 4 m apart. Camera positioning created a ~4 m wide overlapped field of view (FOV) at 0-20 m. Calibration target represented as a cross plotted at 5 m. Diagram created in MATLAB, to scale.

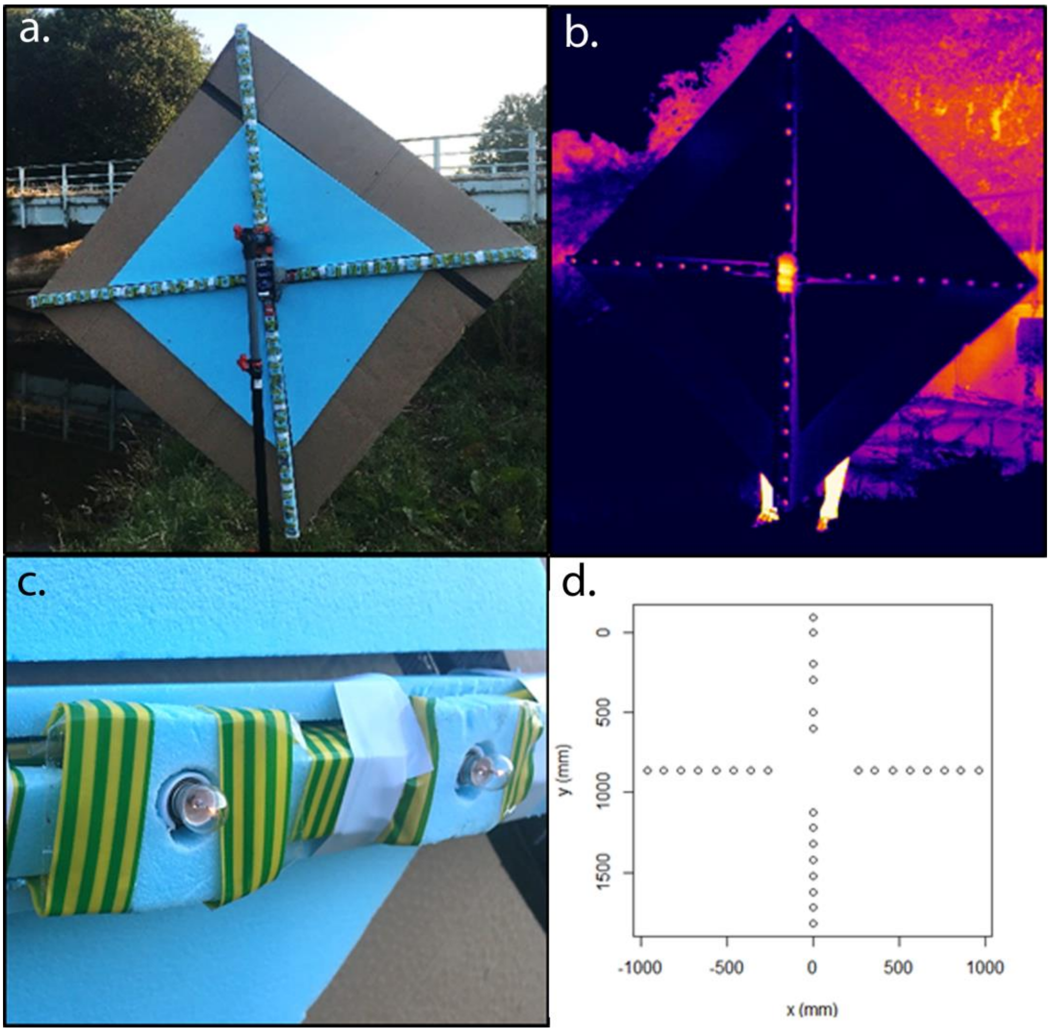


**Figure 4.2** Images of bespoke calibration target: (a) target in situ at a riparian site, (b) thermal image still of target, (c) close-up of one arm, showing bulbs and insulation and (d) scatter plot showing bulb coordinates used to develop MatchPoint 1.0 software. Photo/image credits L.R.V. Gilmour.

### 4.3.3 Reconstructing trajectories

I used another bespoke MATLAB script (written by M.W. Holderied and developed from the script used in Chapter 3) to extract individual bat localisation coordinates for the two cameras using background subtraction between individual frames of 32 fps .avi recordings. All possible localisations were then paired and sorted into potential trajectories using defined parameter values, including a maximum speed of 15 m/s, a maximum frame gap (number of frames in between localisations) of 15, a maximum distance between localisations of 1000 mm and minimum trajectory length (number of localisations making up a trajectory) of six (Figure 4.3).

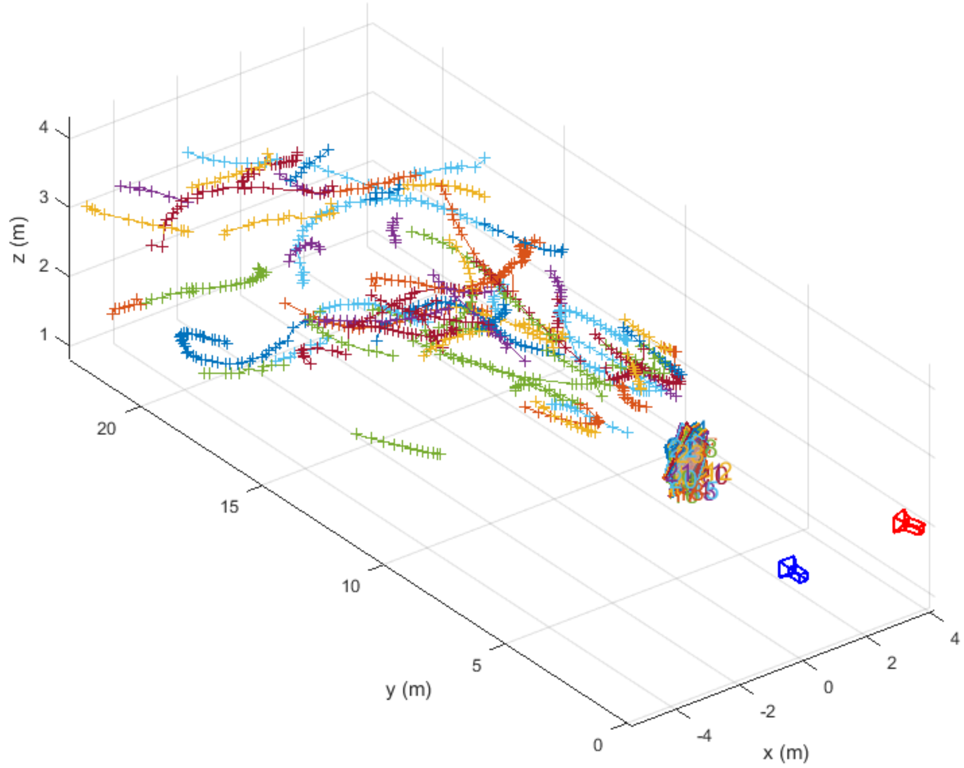


**Figure 4.3** Stereo reconstruction of all possible trajectories in an example 30 s of footage during a silent control period. Cameras are plotted in blue and red. Calibration target positions are also plotted in front of the cameras as 24 separate calibration target coordinates from intrinsic/extrinsic parameter calculations. Figure created in MATLAB.

Before trajectory coordinates were extracted for each night, I determined the best pixel threshold that allowed the maximum number of trajectories to be determined with the minimum amount of noise. A pixel threshold that was too low could result in insect trajectories or erroneous localisations being plotted and a threshold that was too high would reduce the ability to detect bats, especially further away from the cameras.

I selected trajectories that were likely to be true pairings and included those that did not share > 3 localisation points with other trajectories. I discarded trajectories that were likely to be erroneous pairings (by comparing *x* and *y* coordinates from both cameras), those that had inconsistent speeds (a difference of > 3 m/s between subsequent localisations) and/or distorted trajectories that did not appear to follow a smooth pathway and had < 10% erroneous localisations. With the trajectories I included, some replication and distortion of individual localisations in a trajectory was still possible. I therefore took a conservative approach to minimize the likelihood of false positives, which would introduce noise and possibly bias into the dataset. I removed individual distorted and replicated localisations from trajectories that were likely to be true pairings by comparing the trajectory plot and speed calculations. However, this smoothing method was only applied to trajectories where it was obvious there was an erroneous point amongst enough other true localisations (< 10% of all localisations). Removing too many potentially erroneous points from a trajectory could bias the data extracted and it would be better to exclude the whole trajectory than risk including one where more localisations were removed than preserved.

### 4.3.4 Calculating trajectory variables

I calculated flight speed in m/s as the mean of all speeds for each subsequent localisation pair (calculated as the distance between two localisations in three dimensions, divided by the time between frames when each frame was 0.032 s, at a frame rate of 32 fps). I calculated distance from the cameras, as the mean distance (m) from the beginning of the camera field of view (FOV) to each localisation, i.e. the mean of the *y* coordinate (Figure 4.4). I calculated height (m) above or below the cameras in the same way using the mean of the *z* coordinate for each localisation. I calculated trajectory length as the total travelled distance (the sum of all the distance segments (m) travelled between localisations) and tortuosity value as the ratio of the total travelled distance and net displacement (the distance (m) from the first to the last localization coordinate), divided by 10 (to make it bound between 0-1).

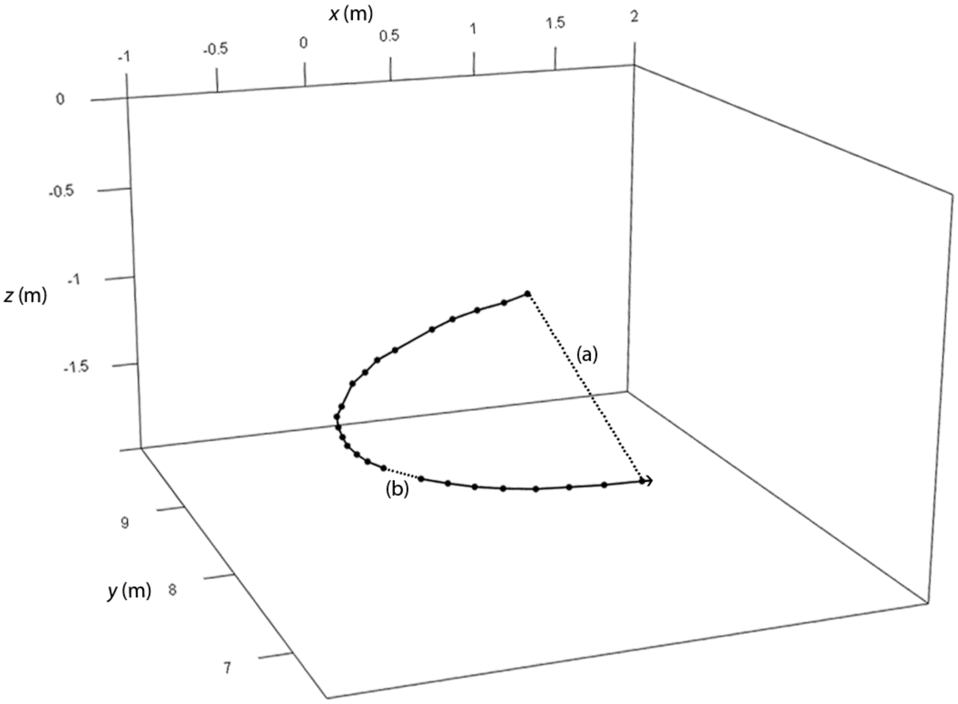


**Figure 4.4** Example of a flight trajectory from a single bat, illustrating calculation of trajectory variables from 3-dimensional localization points. Including (a) net displacement, calculated as the distance from the first to last localisation; (b) distance segment, used to calculate the total distance, as the sum of all segments. Distance (m) and height (m) from the cameras were also calculated as the mean of *y* and *z* localisation coordinates respectively.

### 4.3.5 Acoustic data collection

I split bat calls recorded for each experiment hour (for nine nights at three sites) into 10 s files and for each file manually identified bat echolocation, feeding buzz and social call data to species or genus level in BatSound 4 (v4.1.4, Pettersson, Uppsala, Sweden; FFT size: 1024; FFT window: Hanning) using the same method as in Chapter 2.3.3. *Myotis* species echolocation calls were identified to genus level, due to the similar nature of their broadband frequency modulated calls, however in this habitat most *Myotis* species present were likely to be *Myotis daubentonii*, which generally feeds over water (Jones & Rayner 1988; Russ 2012). *Nyctalus* and *Eptesicus* species were also grouped due to their similar long-range echolocation calls and flight behaviour (Jones 1995; Russ 2012). I identified a new bat pass as a sequence of echolocation calls > 1 s from the last pass and feeding buzzes as a short sequence of calls, characterized by a sudden transition to a high repetition rate (Russ 2012). Social calls are discernible due to their characteristic shape and lower frequency and can also be identified to species or genus level in most cases (Pfalzer & Kusch 2003; Middleton et al. 2014). I took the sum of counts from 10 s files to get an overall pass/feeding buzz/social call count for each 5-minute time block. I added the deterrent noise level recorded during noise playback to control files using a MATLAB script (see Chapter 2 method) before analysis, so not to introduce bias from control files being easier to score.

### 4.3.6 Call parameter measurements

I selected 300 passes from five time block pairs of control and treatment periods (spanning the experiment hour), from nine nights of recording at three sites and extracted call measurements for three calls per pass and one pass per 10 s file using BatSound 4 (v4.1.4, Pettersson, Uppsala, Sweden). I ensured 5-min time block pairs were always balanced in number of passes for control and treatment, totalling 150 passes (450 calls) measured for both control and treatment (300 passes in total). I extracted measurements from search phase passes only, as approach phase calls have a more broadband structure, a higher frequency of maximum energy and an increasingly shorter pulse interval, as the bat approaches the prey. Single bat passes were rare, so I included passes where one or two bats were present simultaneously but controlled for number of bats present in the model specification (see statistical analysis below).

For each call, I manually measured frequency of maximum energy (kHz) using the power spectrum function and end and start frequency (kHz) using the spectrogram and measurement cursor in Bat Sound 4. To avoid the effect of attenuation of high frequencies on calls recorded at distance, I used a cut-off in amplitude of a call of > 15% (using the oscillogram window in Bat Sound 4). I also used the same spectrogram settings for every file, (threshold 0; amplitude contrast 0; frequency resolution 525 Hz; FFT size 1024 samples; FFT window: Hanning; time between FFTs 2.7 ms). I calculated bandwidth (kHz) as the difference between start and end frequency. I also measured call duration as the time (ms) from the beginning to end of the call and pulse interval as the time (ms) from the beginning of one call in a pass to the start of the next.

## 4.3.7 Statistical analysis

### 4.3.7.1 Trajectory measurement data

I analysed trajectory measurement data using linear mixed effect models (LMMs) using the R (v3.5.2) package lme4 (v.1.1-19) (Bates et al. 2015) and generalized linear mixed effect models using glmmTMB (v.0.2.3) (Brooks et al. 2017), depending on the distribution of the response variable. *Flight speed* and *distance* followed a Gaussian distribution and were therefore analysed using an LMM, whereas *height* and *length* required a transformation to be able to carry out an LMM (Boxcox and log transformations, respectively). *Tortuosity value* followed a continuous proportional distribution between 0-1 and therefore I carried out a beta binomial GLMM with a cloglog link function.

Full models all contained the fixed effects *deterrent treatment* (levels: deterrent/control), *time block order* (A-L), *flight distance* (m) and an interaction term between *deterrent treatment* and *distance* (apart from the distance model, which only contained *deterrent treatment* and *time block number*). I retained the random effect structure of *time block* ($N$ = 12) nested in *night* ($N$ = 9), nested in *site* ($N$ = 3) in all models. I selected final models based on second order Akaike information criterion (AICc), where a difference in AICc of > 2 between a model and a nested model indicated a better fit. Estimates, SE and *t/z* values were obtained from model summaries, and $\chi^2$, df and $p$ values were calculated from likelihood ratio tests (LRTs) between a model containing a term, and a nested model without that term (or the null model). Model selection statistics are presented in Supplementary Material Table S4.1-4.4.

#### 4.3.7.2 Acoustic data

I analysed acoustic bat call data in R using the same method as above, with Poisson or negative binomial GLMMs using the lme4 package (Bates et al. 2015), depending on the distribution of the response variable. Response variables included counts of passes, feeding buzzes and social calls of *Pipistrellus pygmaeus*, and passes of *Myotis* species, *P. pipistrellus* and a group containing *Eptesicus serotinus* and *Nyctalus* species. There were not enough data to analyse passes, feeding buzzes or social calls from any other species (< 20 passes per night for majority of nights for a site). I excluded the first minute of each block in my analysis, to minimize spillover effects from previous blocks and make sure each block had the same number of files analysed. I therefore included 24 10 s files (4 mins) from each 5-min time block in the analysis.

#### 4.3.7.3 Call parameter data

I analysed call parameter data using the same methods as the acoustic data analysis, but instead using linear mixed effect models (LMMs) in lme4 (Bates et al. 2015), due to the Gaussian distribution of all response variables. Response variables included *bandwidth*, *start*, *end* and *frequency of maximum energy* (all in kHz) and *duration* and *pulse interval* (ms). I included the fixed effects *deterrent treatment*, *time block order* and *number of bats* (number of bats present simultaneously in a pass). I included the random effects of *site*, *night*, *block pair*, *time block* and *call sequence number* (arranged in a nested design). *Block pair* was included due to the differing numbers of passes analysed for different time block pairs (a block pair consisted of two 5-min time blocks, one control and one treatment). *Call sequence number* was included to identify the pass number, from each time block, for each call. A Bonferroni correction was applied to *p* values obtained from LRTs for each parameter, to control for multiple testing on the same call data. Both adjusted and non-adjusted *p* values are presented in the results below.

## 4.4 Results

### 4.4.1 Bat flight trajectory measurements

I extracted measurements from 1,167 viable flight trajectories from a total of nine hours of footage, recorded on nine nights at three sites (one hour per night, three nights per site), including 284 recorded when the deterrent speakers were on and 883 from control periods. Trajectories ranged from 0.38 to 11.23 m in length, with a mean length (± SD) of 2.56 ± 1.63 m and contained 6-65 trajectory segments (14.65 ± 8.00). Bat trajectories were recorded from the beginning of the stereo field of view at 5.47 m, up to the edge at 26.82 m, at a mean distance of 14.24 ± 3.98 m, equating to a range of ~15-37 m from the deterrent speakers. Bat flight height ranged from 2.59 m below the camera line of site to 5.77 m above, 0.46 ± 1.56 m on average.

Bat flight speed per trajectory ranged from 1.76 to 7.99 $ms^{-1}$ (a mean of 4.62 ± 0.98) and tortuosity value range of 0.03 to 0.95 (0.12 ± 0.05). Bat trajectory speeds were significantly higher (4.86 ± 0.92 $ms^{-1}$ vs 4.54 ± 0.99 $ms^{-1}$) and at greater distances from the deterrent during playback compared with when no sound was played (15.49 ± 4.39 m vs 13.84 ± 3.76 m respectively) (Table 4.1; Figure 4.5; see Table S3.1 for model selection statistics). Bat speed also significantly decreased over the experiment hour. There was no effect of the deterrent on flight height (boxLMM: $\chi2 = 0.036$, df = 1, p = 0.85), or trajectory length (logLMM: $\chi2 = 0.80$, df = 1, p = 0.37) (Table S3.1).

Bat trajectories were less tortuous at greater distances, when the deterrent was deployed and there was a significant interaction between deterrent treatment and distance (Table 4.1; Figure 4.5; Table S3.1). However, despite being significant, the main effects in isolation were not meaningful, due to similar tortuosity values between the treatment and control at shorter distances.

**Table 4.1** Final model estimates, SE and *t*/*z* statistics from significant trajectory measurement models. Likelihood ratio test (LRT) statistics (including *p* values) are presented for significant and non-significant terms. Variance, standard deviation and percentage of total variance presented for random effects. Model selection statistics are presented in Supplementary Material Table S4.1-1.2.

| Model | Model terms | Estimates | SE | *t* or *z* | $\chi^2$ | df | *p* |
|---|---|---|---|---|---|---|---|
| **Speed** | (Intercept) | 5.14 | 0.21473 | 23.92 | | | |
| | **Deterrent treatment** | **0.57** | **0.10556** | **5.42** | **25.84** | **1** | **< 0.001** |
| | **Time block order** | **-0.10** | **0.01544** | **-6.19** | **32.34** | **1** | **< 0.001** |
| | Distance | | | | 0.02 | 1 | 0.88 |
| | Deterrent * distance | | | | 1.56 | 3 | 0.67 |
| | **Random effects** | **Variance** | **SD** | **% total** | | | |
| | Time block (in night) (*N* = 12) | 0.14 | 0.37 | 48.93 | | | |
| | Night (in site) (*N* = 9) | 0.07 | 0.26 | 24.34 | | | |
| | Site (*N* = 3) | 0.08 | 0.28 | 26.74 | | | |
| | No of obs. | 1172 | | | | | |
| **Tortuosity** | (Intercept) | -2.18 | 0.02 | -124.41 | | | |
| | **Deterrent treatment*distance** | **-0.01** | **0.00** | **-65.77** | **4343.30** | **1** | **< 0.001** |
| | Deterrent treatment | 0.10 | 0.02 | 4.87 | | | |
| | Distance | 0.01 | 0.00 | 97.77 | | | |
| | Time block order | | | | 0.50 | 1 | 0.48 |
| | **Random effects** | **Variance** | **SD** | **% total** | | | |
| | Time block (in night) (*N* = 12) | 0.01 | 0.09 | 91.20 | | | |
| | Night (in site) (*N* = 9) | 0.00 | 0.03 | 7.48 | | | |
| | Site (*N* = 3) | 0.00 | 0.01 | 1.32 | | | |
| | No of obs. | 1167 | | | | | |
| **Distance** | (Intercept) | 13.85 | 0.71 | 19.45 | | | |
| | **Deterrent treatment** | **1.91** | **0.55** | **3.44** | **25.84** | **1** | **< 0.001** |
| | Time block order | | | | 0.91 | 1 | 0.34 |
| | **Random effects** | **Variance** | **SD** | **% total** | | | |
| | Time block (in night) (*N* = 12) | 5.14 | 2.27 | 71.55 | | | |
| | Night (in site) (*N* = 9) | 1.36 | 1.17 | 18.95 | | | |
| | Site (*N* = 3) | 0.68 | 0.83 | 9.51 | | | |
| | No of obs. | 1167 | | | | | |

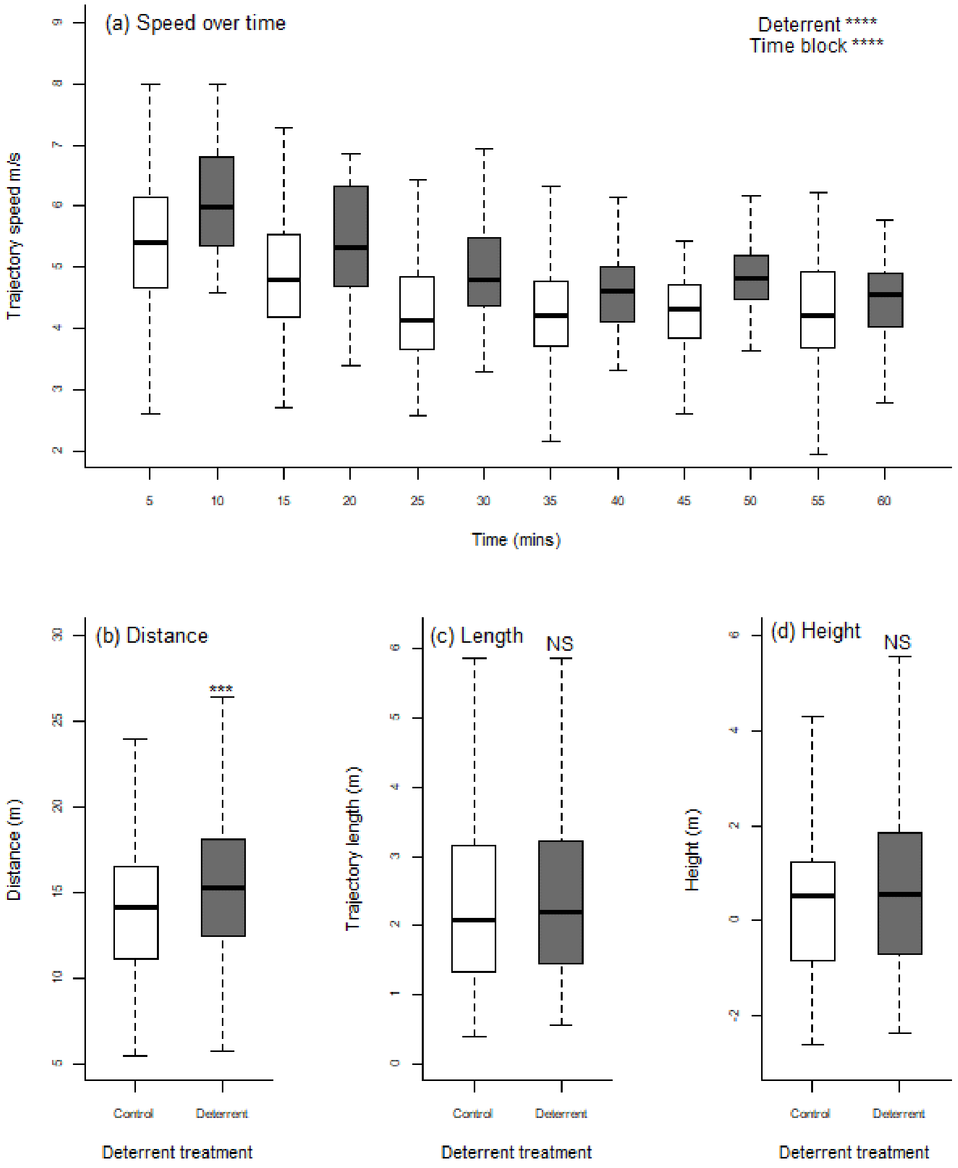


**Figure 4.5** Boxplots of flight trajectory measurements, during control (white) and deterrent (shaded) periods: (a) mean flight speed per trajectory over the experiment hour, (b) mean distance per trajectory from thermal cameras, (c) length of flight trajectories and (d) mean flight height per trajectory. Boxes include 25th percentile, median and 75th percentiles, with 95% confidence interval depicted as 'whiskers'. *p* values from likelihood ratio tests comparing LMM/GLMMs with and without deterrent treatment (all plots) and/or Time block (a) only) (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$), **** = $p < 0.0001$).

### 4.4.2 Acoustic bat call data

I identified 5,440 bat passes, 1,343 feeding buzzes and 718 social calls from a total of nine hours of ultrasonic recording, on nine nights at three sites (one hour per night, three nights per site), a mean (± SD) of 604.44 ± 141.00 passes, 149.22 ± 97.24 feeding buzzes and 79.78 ± 56.94 social calls per night. Most passes were identified as *Pipistrellus pygmaeus* (4304, 79.12%), followed by *Myotis* species (727, 13.36%) and *P. pipistrellus* (323, 5.94%). The remaining 1.58% of passes were made up of *Eptesicus serotinus* and *Nyctalus* species, *Barbastella barbastellus*, *Plecotus auritus* and *Pipistrellus nathusii*. Most feeding buzzes and social calls were from *P. pygmaeus* (1,243, 92.55% and 703, 97.91% respectively), with the remaining feeding buzzes coming from mainly *Myotis* species (78, 5.81%) and social calls from *Myotis* species, *P. pipistrellus* and the *Eptesicus serotinus* and *Nyctalus* species group (2.09%).

All bat passes, feeding buzzes and social calls were reduced by 28.39% by the deterrent, when combined. Acoustic deterrent deployment significantly reduced the number of passes of *P. pygmaeus* and *Myotis* species compared to the control, both by a 26% reduction (Figure 4.6; Table 4.2-4.3; see Table S4.3 for model selection statistics). The deterrent also significantly reduced the number of *P. pygmaeus* feeding buzzes and social calls (38.15% and 22.92% reduction, respectively). *Nyctalus* and *Eptesicus* species passes were also significantly reduced by the deterrent, with a reduction of 68%, however, there was no effect of the deterrent on *P. pipistrellus*. There were not enough data to model for any other species passes, feeding buzzes or social calls (< 20 passes per night for majority of nights).

*P. pygmaeus* passes, feeding buzzes and social calls were similar in number throughout the experiment hour and time block was not significant when data were analysed with GLMMs (Figure 4.7a-c; Table 4.2; Table S4.3). There were more *Myotis* species and *P. pipistrellus* passes in the latter half an hour and time block was significant as a fixed effect when data were analysed with a GLMM (Figure

4.7d-e; Table 4.3; Table S4.3). There were also significantly more *Nyctalus* and *Eptesicus* passes in earlier time blocks and time block order was significant when included as a fixed effect in a GLMM (Figure 4.7f; Table 4.3; Table S3.2).

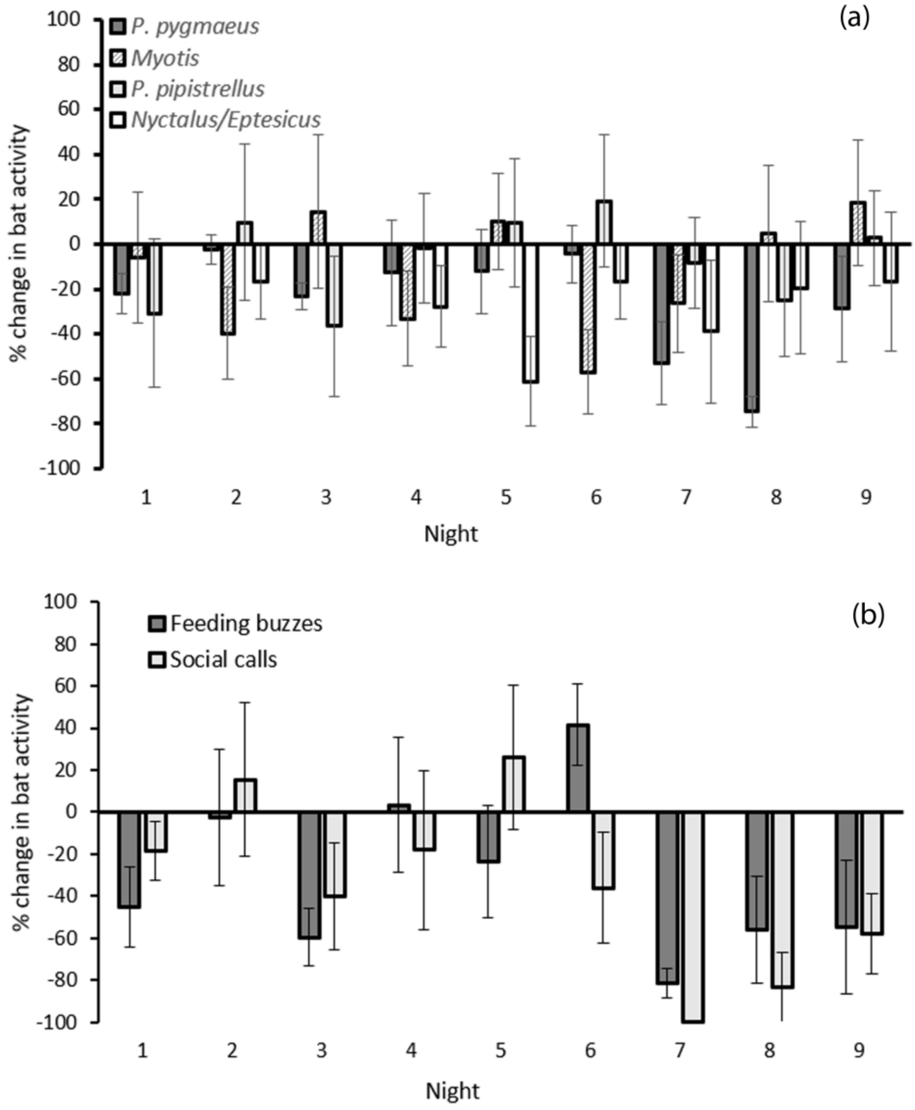


**Figure 4.6** Mean % change from control to deterrent treatments in counts of (a) bat passes of four species/groups and (b) feeding buzzes and social calls of *Pipistrellus pygmaeus*. Species included *Pipistrellus pygmaeus*, *Myotis* species, *Pipistrellus pipistrellus* and *Nyctalus* and *Eptesicus* species. Bars were calculated as the mean (± SE error bars) of the % difference between counts for control and deterrent treatment for each time block on each night, including three nights at each site (N=6 10 min time blocks containing 5 min control and treatment periods). A negative %, below zero on the *y* axis represents a reduction in bat activity and a positive, an increase in bat activity.

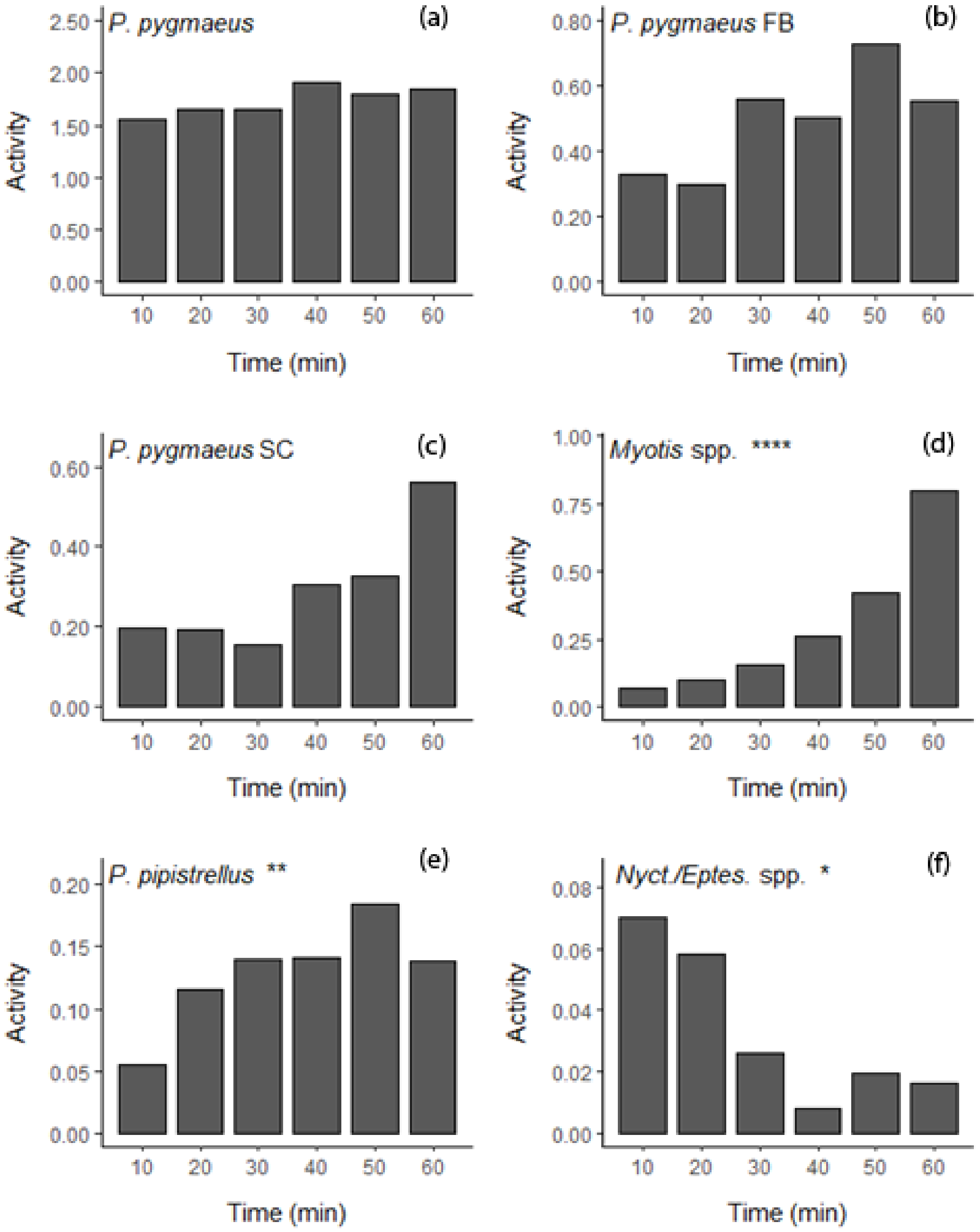


**Figure 4.7** Temporal activity of bat species over experiment hour. Including mean number of passes per 10 s file, for each 10 min period for: (a) *Pipistrellus pygmaeus* passes, (b) *P. pygmaeus* feeding buzzes, (c) *P. pygmaeus* social calls, (d) *Myotis* spp. passes (e) *P. pipistrellus* passes and (f) *Nyctalus* and *Eptesicus* spp. passes. Significant effect of time block from GLMM analysis indicated by significance stars (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, **** = $p < 0.0001$).

**Table 4.2.** Final model estimates, SE and *z* statistics from final models for *Pipistrellus pygmaeus* data, including passes (p), feeding buzzes (fb) and social calls (sc). Likelihood ratio test (LRT) statistics (including *p* values) are presented for significant and non-significant terms. Variance, standard deviation and percentage of total variance are presented for random effects. Model selection statistics presented in Supplementary Material Table S4.3.

| **Species** | **Model terms** | **Estimate** | **SE** | ***z*** | **χ2** | **df** | ***p*** |
|---|---|---|---|---|---|---|---|
| ***P. pygmaeus* (p)** | (Intercept) | 0.61 | 0.23 | 2.64 | | | |
| | **Deterrent treatment** | **-0.46** | **0.11** | **-4.13** | **15.92** | **1** | **< 0.0001** |
| | Time block order | | | | 3.43 | 1 | 0.06 |
| | **Random effects** | **Variance** | **SD** | **% total** | | | |
| | Time block (in night) (*N* = 12) | 0.28 | 0.53 | 66.28 | | | |
| | Night (in site) (*N* = 9) | 0.00 | 0.00 | 0.00 | | | |
| | Site (*N* = 3) | 0.14 | 0.38 | 33.72 | | | |
| ***P. pygmaeus* (fb)** | (Intercept) | -1.17 | 0.25 | -4.69 | | | |
| | **Deterrent treatment** | **-0.71** | **0.28** | **-2.48** | **5.99** | **1** | **< 0.05** |
| | Time block order | | | | 0.27 | 1 | 0.60 |
| | **Random effects** | **Variance** | **SD** | **% total** | | | |
| | Time block (in night) (*N* = 12) | 1.76 | 1.33 | 93.74 | | | |
| | Night (in site) (*N* = 9) | 0.07 | 0.27 | 3.96 | | | |
| | Site (*N* = 3) | 0.04 | 0.21 | 2.30 | | | |
| ***P. pygmaeus* (sc)** | (Intercept) | -2.21 | 0.29 | -7.48 | | | |
| | **Deterrent treatment** | **-1.04** | **0.42** | **-2.50** | **6.34** | **1** | **< 0.05** |
| | Time block order | | | | 0.79 | 1 | 0.37 |
| | **Random effects** | **Variance** | **SD** | **% total** | | | |
| | Time block (in night) (*N* = 12) | 3.28 | 1.81 | 98.78 | | | |
| | Night (in site) (*N* = 9) | 0.04 | 0.20 | 1.22 | | | |
| | Site (*N* = 3) | 0.00 | 0.00 | 0.00 | | | |

**Table 4.3.** Final model estimates, SE and *z* statistics for *Myotis* species, *Pipistrellus pipistrellus* and *Nyctalus* and *Eptesicus* species group pass count data. Likelihood ratio test (LRT) statistics (including *p* values) are presented for significant and non-significant terms. Variance, standard deviation and percentage of total variance are presented for random effects. Model selection statistics presented in Supplementary Material Table S4.3.

| Species | Model terms | Estimate | SE | *z* | χ2 | df | *p* |
|---|---|---|---|---|---|---|---|
| ***Myotis* spp. (p)** | (Intercept) | -3.65 | 0.35 | -10.35 | | | |
| | **Deterrent** | **-0.74** | **0.21** | **-3.48** | **11.28** | **1** | **< 0.001** |
| | **Time block order** | **0.29** | **0.03** | **8.91** | **65.32** | **1** | **< 0.0001** |
| | **Random effects** | **Variance** | **SD** | **% total** | | | |
| | Time block (in night) (*N* = 12) | 0.74 | 0.86 | 63.68 | | | |
| | Night (in site) (*N* = 9) | 0.40 | 0.64 | 34.92 | | | |
| | Site (*N* = 3) | 0.02 | 0.13 | 1.40 | | | |
| ***P. pipistrellus* (p)** | (Intercept) | -3.63 | 0.53 | -6.82 | | | |
| | **Time block order** | **0.13** | **0.04** | **3.25** | **10.90** | **1** | **< 0.01** |
| | Deterrent | | | | 0.74 | 1 | 0.39 |
| | **Random effects** | **Variance** | **SD** | **% total** | | | |
| | Time block (in night) (*N* = 12) | 1.01 | 1.00 | 63.82 | | | |
| | Night (in site) (*N* = 9) | 0.01 | 0.09 | 0.49 | | | |
| | Site (*N* = 3) | 0.56 | 0.75 | 35.69 | | | |
| ***Nyctalus* and *Eptesicus* spp. (p)** | (Intercept) | -3.98 | 0.93 | -4.27 | | | |
| | **Deterrent** | **-0.98** | **0.50** | **-1.96** | **4.29** | **1** | **< 0.05** |
| | **Time block order** | **-0.17** | **0.07** | **-2.36** | **5.94** | **1** | **< 0.05** |
| | **Random effects** | **Variance** | **SD** | **% total** | | | |
| | Time block (in night) (*N* = 12) | 1.89 | 1.37 | 41.42 | | | |
| | Night (in site) (*N* = 9) | 1.87 | 1.37 | 41.02 | | | |
| | Site (*N* = 3) | 0.80 | 0.89 | 17.57 | | | |

### 4.4.3 Bat call parameter data

I extracted echolocation call parameter measurements from 300 *Pipistrellus pygmaeus* passes (900 individual calls) from five pairs of 5-min time blocks (150 passes per control and treatment blocks). Calls ranged in frequency of maximum energy from 49.40 to 63.70 kHz, with a mean ± standard deviation of 55.75 ± 2.38 kHz (Table 4.4). Start and end frequency ranged from 55.30 to 113.40 kHz and 47.80 to 60.80 kHz respectively, with means and standard deviations of 83.05 ±13.65 and 53.41 ±2.09 kHz respectively (Table 4.4). Call duration ranged from 1.80 to 9.80 ms (4.83 ± 1.27) and pulse interval from 6.30 to 164.00 ms (75.29 ±16.04).

Bandwidth and start frequency were significantly reduced by 5.79 and 5.68 kHz respectively during the deterrent treatment (Table 4.4;

Table **4.5**), but there was no effect of treatment on call duration, pulse interval, peak or end frequency when data were analysed using LMMs (Duration: χ2 = 0.63, df = 1, p = 0.43; IPI: χ2 = 0.83, df = 1, p = 0.36; Peak F: χ2 = 0.06, df = 1, p = 0.81; end F:  χ2 = 0.30, df = 1, p = 0.58) (see Table S4.4 for model selection statistics). A higher number of bats in a pass significantly increased both bandwidth and start frequency and was a significant effect in an LMM.

**Table 4.4.** *Pipistrellus pygmaeus* echolocation call parameter statistics for control and deterrent treatments and total. Including mean ± standard deviation, *p* value from linear mixed effect model likelihood ratio tests between models with and without deterrent treatment and adjusted *p* values calculated using Bonferroni correction. Model selection statistics presented in Supplementary Material Table S4.4.

| **Call parameter** | **Control** | **Deterrent** | **Total** | ***p*** | ***p* adjusted** |
|---|---|---|---|---|---|
| **Bandwidth (kHz)** | **32.53 ± 13.42** | **26.74 ± 12.44** | **29.63 ± 13.25** | 0.0028 | 0.017 |
| **Start F (kHz)** | **85.89 ± 13.87** | **80.21 ± 12.82** | **83.05 ± 13.65** | 0.0044 | 0.026 |
| **End F (kHz)** | 53.36 ± 2.09 | 53.46 ± 2.09 | 53.41 ± 2.09 | NS | NS |
| **Peak F (kHz)** | 55.83 ± 2.45 | 55.67 ± 2.32 | 55.75 ± 2.38 | NS | NS |
| **IPI (ms)** | 75.35 ± 17.43 | 75.22 ± 14.54 | 75.29 ± 16.04 | NS | NS |
| **Duration (ms)** | 4.85 ± 1.27 | 4.82 ± 1.26 | 4.83 ± 1.27 | NS | NS |

**Table 4.5.** Final model estimates, SE and *t* statistics for significant *Pipistrellus pygmaeus* echolocation call parameter measurements, bandwidth and start frequency. Fixed effects included deterrent treatment (control or deterrent) and the number of bats in a pass (one or two). Likelihood ratio test (LRT) statistics (including *p* values) are presented for significant and non-significant terms. Variance, standard deviation and percentage of total variance are presented for random effects. Model selection statistics presented in Supplementary material Table S4.4.

| **Model** | **Model terms** | **Estimates** | **SE** | ***t*** | **χ2** | **df** | ***p*** |
|---|---|---|---|---|---|---|---|
| **Bandwidth** | (Intercept) | 27.37 | 3.04 | 9.01 | | | |
| | **Deterrent** | **-5.62** | **1.79** | **-3.13** | **8.93** | **1** | **< 0.01** |
| | **No of bats** | **3.84** | **1.28** | **3.00** | **8.76** | **1** | **< 0.01** |
| | Time block order | | | | 4.47 | 4 | 0.35 |
| | **Random effects** | **Variance** | **SD** | **% total** | | | |
| | Sequence (in time block) | 64.66 | 8.04 | 37.86 | | | |
| | Time block (in time block pair) (*N* = 10) | 40.69 | 6.38 | 23.83 | | | |
| | Time block pair (in night) (*N* = 6) | 27.12 | 5.21 | 15.88 | | | |
| | Night (in site) (*N* = 9) | 0.00 | 0.00 | 0.00 | | | |
| | Site (*N* = 3) | 13.81 | 3.72 | 8.09 | | | |
| | Residual | 24.50 | 4.95 | 14.35 | | | |
| **Start F** | (Intercept) | 79.95 | 3.03 | 26.36 | | | |
| | **Deterrent** | **-5.45** | **1.83** | **-2.98** | **8.13** | **1** | **< 0.01** |
| | **No of bats** | **4.42** | **1.33** | **3.32** | **10.58** | **1** | **< 0.01** |
| | Time block order | | | | 2.35 | 1 | 0.12 |
| | **Random effects** | **Variance** | **SD** | **% total** | | | |
| | Sequence (in time block) | 72.20 | 8.50 | 66.30 | | | |
| | Time block (in time block pair) (*N* = 10) | 40.85 | 6.39 | 37.51 | | | |
| | Time block pair (in night) (*N* = 6) | 30.32 | 5.51 | 27.84 | | | |
| | Night (in site) (*N* = 9) | 0.00 | 0.00 | 0.00 | | | |
| | Site (*N* = 3) | 12.74 | 3.57 | 11.70 | | | |
| | Residual | 24.99 | 5.00 | 22.95 | | | |

## 4.5 Discussion

I have shown that bats altered their echolocation calls and flew significantly faster during deterrent broadcast and therefore foraged less (Figure 4.5; Table 4.4), matching my predictions and supporting the interpretation that the mechanism underpinning acoustic deterrence is a masking effect on echolocation (Jones & Rayner 1988, 1991; Jones 1995; Grodzinski et al. 2009; Polak et al. 2011). However, the small reduction in tortuosity further away from the deterrent (~25-30 m) during noise playback (1.25%, Table 4.1) may have been due to a bridge being present at the edge of the treatment area at each site, at which bat activity was generally higher. In the absence of deterrent noise, it is likely that bats foraged around the bridge with more tortuous flight paths, compared to during deterrent treatment where they flew more directly, perhaps under the bridge to get away from the sound and with less of an area to manoeuvre.

Overall, bat activity was reduced by 30% when the deterrent noise was broadcast, which is what we would expect for distances up to 30-40 m from the deterrent, in support of findings in Chapters 2 and 3 of this thesis. Indeed, the experiment was set up purposefully in order to record enough bats to see an effect, but not so far away to be beyond the zone of influence. The range of the cameras field of view (FOV) covered ~5-30 m and as the deterrent speakers were placed a further 10 m behind this, the treated airspace was ~15-40 m from the deterrent. A stronger effect on trajectory measurements and bat call activity and characteristics would therefore likely have been recorded nearer the deterrent (at < 15 m).

Species deterred by the noise included *Pipistrellus pygmaeus*, *Myotis* species (likely *Myotis daubentonii*) and *Nyctalus* and *Eptesicus* species (Figure 4.6). There was no effect of the deterrent on *P. pipistrellus* passes, but this may have been due to the small sample size of calls recorded. *P. pipistrellus* is also a generalist species, that will forage in a range of habitats, but preferring deciduous woodland edge overall, whereas *P. pygmaeus* is more of a riparian specialist (Davidson-Watts et al. 2006). *P. pipistrellus* passes were also significantly reduced by the acoustic deterrent in Chapter 2 and in the larger scale experiment in Chapter 3. Therefore, I cannot rule out a deterrent effect on *P. pipistrellus* from this study, as the focus on river habitats, may have reduced the ability to record the species, resulting in a small sample size. *Nyctalus* and *Eptesicus* species are usually high fliers (Jones 1995) and unlikely to have been recorded on thermal cameras and incorporated into trajectory analysis. However, it is likely deterrence effects extend into the vertical plane as well as just in front of the speakers, as there was a significant (68%) reduction in *Nyctalus* and *Eptesicus* species passes during deterrent broadcast (Figure 4.6).

*P. pygmaeus* feeding buzzes were also reduced by 38%, but there was less of a reduction in social calls (23%), relative to the 28% reduction in passes. Social calls of bats deterred from the treatment area, but still in the vicinity, may have still been recorded, reducing the effect of the deterrent on social calls. *P. pygmaeus* social calls are louder and of lower frequency than echolocation calls and so can travel further in the environment and are therefore more likely to be recorded (Pfalzer & Kusch 2003; Middleton et al. 2014). *P. pygmaeus* social calls can also have an aversive effect on conspecifics when insect densities are low, in line with the food patch defence hypothesis (Barlow & Jones 1997). An increase in bats moving into an already occupied patch, outside of the treatment area, but close enough to be recorded, could also have decreased the likelihood of detecting a greater effect. I also can not rule out any deterrent effect on amplitude, frequency characteristics or vocal complexity of social calls, as I did not measure these call characteristics (Jiang et al. 2019; Song et al. 2019).

As predicted, the deterrent noise acted like other sources of ambient ultrasound, to mask *P. pygmaeus* echolocation calls, resulting in shift in their signal structure (Gillam & McCracken 2007; Tressler & Smotherman 2009; Hage & Metzner 2013; Bunkley et al. 2015; Song et al. 2019). *P. pygmaeus* reduced bandwidth and start frequency of echolocation search phase calls in response to deterrent noise, probably to increase the signal to noise ratio of signals and discern echoes more easily (Table 4.4) (Tressler & Smotherman 2009; Bunkley et al. 2015). Due to the energetic costs of echolocation, bats either focus their energy in a narrower band or spread it over a wider range of frequencies, depending on the situation (Schnitzler & Kalko 2001; Chiu et al. 2009). Therefore, by focussing energy into a louder, more narrowband call, bats are more likely to detect their echoes against the background noise of the deterrent. A potential confound is that bats will increase their bandwidth when more conspecifics are present in an area, due to the surrounding airspace representing a more complex environment similar to clutter (Chiu et al. 2009; Cvikel et al. 2015; Gotze et al. 2016). Therefore, the reduction in start frequency and bandwidth recorded during deterrent periods could be due to less bats being present in a pass (and therefore the surrounding area). However, I analysed passes where there were one or two bats present and controlled for number of bats in analyses. The number of bats present did significantly increase bandwidth and start frequency as predicted from the literature (Chiu et al. 2009; Cvikel et al. 2015; Gotze et al. 2016) (Table 4.4), but despite this, there was still a significant negative effect on both call parameters when the deterrent was deployed.

Deterrent noise could have also acted as an aversive stimulus as well as a masking one (Luo et al. 2015; Zeale et al. 2016). For example, foraging efficiency of *Myotis daubentonii* was significantly reduced during playbacks of traffic noise that both did and did not overlap with its echolocation call spectral range, but search effort was not affected (Luo et al. 2015). Therefore, as I did not measure echolocation call characteristics of *Myotis* bats, it is possible the reduction in activity seen in this species is due to the deterrent acting as an aversive or uncomfortable stimulus, rather than a masking one.

In conclusion, I have shown that the mechanism underpinning acoustic deterrence in bats is likely to be due to auditory masking and the impact is a reduction in foraging activity, due to the masking noise precluding the use of echolocation. Bats foraging in areas such as around wind turbine blades and on or nearby roads are at high risk of mortality (Mathews et al. 2016; Rydell et al. 2016; Foo et al. 2017). Acoustic deterrence could be used to deter bats from these areas and mitigate for the impacts of these structures (Arnett et al. 2013). However, the building and operation of these structures may already be causing a reduction in available foraging habitats, due to for example traffic and construction noise pollution, light pollution, habitat loss/destruction and barrier effects (Arnett & Baerwald 2013; Altringham & Kerth 2016; Arnett et al. 2016; Fensome & Mathews 2016; Barre et al. 2018). Introducing deterrence could reduce available foraging habitat even further and may contribute another pollutant into an already increasingly noisy environment. However, this may be the lesser of two evils if bats are at direct risk of mortality (Altringham & Kerth 2016; Frick et al. 2017). As with any mitigation measure, a case-by-case approach is important, weighing up any loss of foraging habitat against the threat of mortality and other potential impacts.

# Supplementary material

**Table S4.1** Model selection statistics for significant bat trajectory measurement models

**Table S4.2** Model selection statistics for non-significant trajectory measurement models

**Table S4.3** Model selection statistics for acoustic bat pass, feeding buzz and social call data

**Table S4.4** Model selection statistics for bat echolocation call parameter data

**Table S4.1** Model selection statistics for significant final models of trajectory measurement data. Models arranged by AICc weight (AICc Wt) and include number of model parameters (K), cumulative AICc weight (Cum. Wt).

| Measurement | Model | Distribution | Link | K | AICc | ΔAICc | AICc Wt | Cum. Wt |
|---|---|---|---|---|---|---|---|---|
| **Speed** | Deterrent + block number | Gaussian | NA | 7 | 2922.174 | 0 | 0.974 | 0.97 |
| | Deterrent + depth + block number | Gaussian | NA | 8 | 2929.521 | 7.3 | 0.025 | 1.00 |
| | Deterrent + depth * block number | Gaussian | NA | 9 | 2936.13 | 14 | 0.001 | 1.00 |
| | Block number | Gaussian | NA | 6 | 2943.108 | 20.9 | 0.001 | 1.00 |
| | Deterrent | Gaussian | NA | 6 | 2945.363 | 23.2 | 0.001 | 1.00 |
| | Deterrent + depth | Gaussian | NA | 7 | 2952.642 | 30.5 | 0.001 | 1.00 |
| | Deterrent * depth * block number | Gaussian | NA | 12 | 2955.425 | 33.3 | 0.001 | 1.00 |
| **Tortuosity** | Deterrent * distance | beta-binomial | cloglog | 8 | -10329784.19 | 0 | 1 | 1.00 |
| | Deterrent * distance | beta-binomial | logit | 8 | -10329678.14 | 106 | < 0.001 | 1.00 |
| | Deterrent * distance + block number | beta-binomial | logit | 9 | -10329676.27 | 107.9 | < 0.001 | 1.00 |
| | Deterrent * distance | beta-binomial | probit | 8 | -10329448.02 | 336.2 | < 0.001 | 1.00 |
| | Deterrent + distance | beta-binomial | logit | 7 | -10327031.42 | 2752.8 | < 0.001 | 1.00 |
| | Deterrent + distance + block number | beta-binomial | logit | 8 | -10327029.45 | 2754.7 | < 0.001 | 1.00 |
| | Deterrent * height + block number | beta-binomial | logit | 9 | -10320815.84 | 8968.3 | < 0.001 | 1.00 |
| | Deterrent * distance | beta-binomial | logit | 8 | 12914.25 | 10342698.4 | < 0.001 | 1.00 |
| **Distance** | Deterrent | Gaussian | NA | 6 | 6239.36 | 0 | 0.868 | 0.87 |
| | Deterrent + block number | Gaussian | NA | 7 | 6243.694 | 4.3 | 0.099 | 0.97 |
| | Deterrent * block number | Gaussian | NA | 8 | 6246.415 | 7.1 | 0.026 | 0.99 |
| | null | Gaussian | NA | 5 | 6249.013 | 9.7 | 0.007 | 1.00 |

**Table S4.2** Model selection statistics for final models of non-significant trajectory measurement data. Models arranged by AICc weight (AICc Wt) and include number of model parameters (K), cumulative AICc weight (Cum. Wt).

| **Measurement** | **Model** | **Distribution** | **Link** | **K** | **AICc** | **ΔAICc** | **AICc Wt** | **Cum. Wt** |
|---|---|---|---|---|---|---|---|---|
| **Length** | null | Gaussian | NA | 5 | 9.995264 | 0 | 0.971 | 0.97 |
| | Deterrent | Gaussian | NA | 6 | 17.04132 | 7 | 0.029 | 1.00 |
| | Deterrent + distance | Gaussian | NA | 7 | 27.00289 | 17 | 0 | 1.00 |
| | Deterrent + distance + block number | Gaussian | NA | 8 | 38.6426 | 28.6 | 0 | 1.00 |
| | Deterrent * distance + block number | Gaussian | NA | 9 | 46.47199 | 36.5 | 0 | 1.00 |
| **Height** | null | Gaussian | NA | 5 | 314.6157 | 0 | 0.952 | 0.95 |
| | Deterrent | Gaussian | NA | 6 | 320.6235 | 6 | 0.047 | 1.00 |
| | Deterrent + block number | Gaussian | NA | 7 | 329.2744 | 14.7 | <0.001 | 1.00 |
| | Deterrent * block number | Gaussian | NA | 8 | 336.5071 | 21.9 | <0.001 | 1.00 |

**Table S4.3** Model selection statistics for pass data of *Pipistrellus pygmaeus*, *P.* pipistrellus, *Myotis* spp., *Nyctalus* and *Eptesicus* spp. and *P. pygmaeus* feeding buzz (fb)/social call (sc) data. Models arranged by AICc weight (AICc Wt) and include number of model parameters (K), cumulative AICc weight (Cum. Wt).

| **Species** | **Model** | **link** | **Distribution** | **K** | **AICc** | **ΔAICc** | **AICc Wt** | **Cum. Wt** |
|---|---|---|---|---|---|---|---|---|
| *P. pygmaeus* | Deterrent | log | Poisson | 6 | 6723.37 | 0.00 | 0.60 | 0.60 |
| | Deterrent + time block | log | Poisson | 5 | 6724.78 | 1.40 | 0.29 | 0.89 |
| | Deterrent | log | Negative binomial | 6 | 6726.82 | 3.50 | 0.11 | 1.00 |
| | null | log | Poisson | 4 | 6738.70 | 15.30 | 0.00 | 1.00 |
| *Myotis* spp. | Deterrent + time block | log | Poisson | 6 | 2702.84 | 0.00 | 0.73 | 0.73 |
| | Deterrent + time block | log | Negative binomial | 7 | 2704.84 | 2.00 | 0.27 | 0.99 |
| | Time block | log | Poisson | 5 | 2712.10 | 9.30 | 0.01 | 1.00 |
| | Deterrent | log | Poisson | 5 | 2766.15 | 63.30 | 0.00 | 1.00 |
| *P. pipistrellus* | Time block | log | Poisson | 5 | 1732.04 | 0.00 | 0.58 | 0.58 |
| | Deterrent + time block | log | Poisson | 6 | 1733.31 | 1.30 | 0.31 | 0.89 |
| | Deterrent + time block | log | Negative binomial | 7 | 1735.33 | 3.30 | 0.11 | 1.00 |
| | Deterrent | log | Poisson | 5 | 1742.20 | 10.20 | 0.00 | 1.00 |
| *Nyctalus* and *Eptesicus* spp. | Deterrent + time block | log | Poisson | 6 | 572.99 | 0 | 0.508 | 0.51 |
| | Time block | log | Poisson | 5 | 574.735 | 1.7 | 0.213 | 0.72 |
| | Deterrent + time block | log | Negative binomial | 7 | 575.017 | 2 | 0.185 | 0.91 |
| | Deterrent | log | Poisson | 5 | 576.381 | 3.4 | 0.094 | 1.00 |
| *P. pygmaeus* (fb) | Deterrent + time block | log | Negative binomial | 6 | 3889.00 | 0.00 | 0.64 | 0.64 |
| | Deterrent | log | Negative binomial | 7 | 3890.74 | 1.70 | 0.27 | 0.91 |
| | Deterrent | log | Negative binomial | 5 | 3892.97 | 4.00 | 0.09 | 1.00 |
| | null | log | Poisson | 6 | 3934.89 | 45.90 | 0.00 | 1.00 |
| *P. pygmaeus* (sc) | Deterrent | log | Negative binomial | 6 | 2540.75 | 0.00 | 0.60 | 0.60 |
| | Deterrent + time block | log | Negative binomial | 7 | 2541.96 | 1.20 | 0.33 | 0.93 |
| | null | log | Negative binomial | 5 | 2545.08 | 4.30 | 0.07 | 1.00 |
| | Deterrent | log | Poisson | 6 | 2782.80 | 242.10 | 0.00 | 1.00 |

**Table S4.4** Model selection statistics for final models of bat echolocation call parameter data. Models arranged by AICc weight (AICc Wt) and include number of model parameters (K), cumulative AICc weight (Cum. Wt).

| Parameter | Model | Distribution | K | AICc | ΔAICc | AICc Wt | Cum. Wt |
|---|---|---|---|---|---|---|---|
| Bandwidth | Deterrent + no of bats + time block | Gaussian | 10 | 6202.54 | 0.00 | 0.53 | 0.53 |
| | Deterrent + no of bats | Gaussian | 9 | 6202.80 | 0.30 | 0.46 | 0.99 |
| | Deterrent + time block | Gaussian | 9 | 6211.61 | 9.10 | 0.01 | 1.00 |
| | No of bats | Gaussian | 8 | 6212.70 | 10.20 | 0.00 | 1.00 |
| Peak F | null | Gaussian | 7 | 3366.28 | 0.00 | 0.75 | 0.75 |
| | Deterrent | Gaussian | 8 | 3368.82 | 2.50 | 0.21 | 0.96 |
| | Deterrent + time block + no of bats | Gaussian | 10 | 3373.37 | 7.10 | 0.02 | 0.98 |
| | Deterrent + time block | Gaussian | 9 | 3373.95 | 7.70 | 0.02 | 1.00 |
| Duration | null | Gaussian | 7 | 2139.23 | 0.00 | 0.78 | 0.78 |
| | Deterrent | Gaussian | 8 | 2142.56 | 3.30 | 0.15 | 0.92 |
| | Deterrent + no of bats | Gaussian | 9 | 2143.91 | 4.70 | 0.07 | 1.00 |
| | Deterrent + no of bats + time block | Gaussian | 10 | 2150.72 | 11.50 | 0.00 | 1.00 |
| IPI | Deterrent + time block + no of bats | Gaussian | 10 | 7185.86 | 0.00 | 0.55 | 0.55 |
| | Deterrent + time block | Gaussian | 9 | 7186.98 | 1.10 | 0.31 | 0.86 |
| | null | Gaussian | 8 | 7188.60 | 2.70 | 0.14 | 1.00 |
| | Deterrent | Gaussian | 8 | 7198.11 | 12.20 | 0.00 | 1.00 |
| Start F | Deterrent + no of bats | Gaussian | 9 | 6240.43 | 0.00 | 0.50 | 0.50 |
| | Deterrent + time block + no of bats | Gaussian | 10 | 6240.43 | 0.00 | 0.50 | 0.99 |
| | No of bats | Gaussian | 8 | 6249.57 | 9.10 | 0.01 | 1.00 |
| | Deterrent + block number | Gaussian | 9 | 6251.51 | 11.10 | 0.00 | 1.00 |
| End F | No of bats | Gaussian | 8 | 2892.87 | 0.00 | 0.76 | 0.76 |
| | Deterrent + no of bats | Gaussian | 9 | 2895.27 | 2.40 | 0.23 | 0.98 |
| | Deterrent + time block + no of bats | Gaussian | 10 | 2901.13 | 8.30 | 0.01 | 1.00 |
| | Deterrent + time block | Gaussian | 9 | 2903.84 | 11.00 | 0.00 | 1.00 |

# CHAPTER 5

## General Discussion

## 5.1 Thesis overview

Bat deterrence methods have shown potential for their use in reducing risk to bats at wind turbines (Nicholls & Racey 2007, 2009; Arnett et al. 2013), and in removing roosting bats from areas in historic buildings when they can cause problems (Zeale et al. 2016). Therefore, in this thesis, I aimed firstly to test and compare methods to deter bats and secondly, to investigate bat responses to deterrence. For the latter, I focussed on acoustic deterrence methods, which showed potential in reducing bat activity when compared to radar in the first experiment, which had no effect. For this thesis, I also developed a thermal bat tracking technique (with help from M.W Holderied), which I implemented at riparian foraging sites to record counts of 2-dimensional (2D) bat trajectories with increasing distance from an acoustic deterrent. I then developed the tracking methods further to record 3-dimensional responses of bats, to investigate the mechanisms underpinning acoustic deterrence and its impact on foraging behaviour. Therefore, in the following sections, I discuss applications, welfare implications and future research recommendations for acoustic deterrence for bat conservation and the reduction of human impacts on bats. I also briefly outline possible applications for the 2D tracking and stereo thermal videogrammetry methods developed for this thesis.

## 5.2 Are bat deterrence methods effective?

In Chapter 2 of this thesis, I show that acoustic, but not radar deterrents are effective at reducing bat activity and foraging at riparian foraging sites in the UK. This study is the first to test and compare bat deterrence methods in Europe and acts as proof-of-concept for the use of acoustic deterrence to reduce impacts of human activities and/or structures, for example wind turbines (Rydell et al. 2010a; Rydell et al. 2010b; Mathews et al. 2016; Rydell et al. 2016), roads (Altringham & Kerth 2016; Fensome & Mathews 2016) and in buildings where bats roost (Zeale et al. 2016). In Chapter 3, I show that the efficacy of an acoustic deterrent decreases with distance at a fine-scale (15-30 m) and in a larger scale experiment over 100 m. I conclude that bats are unlikely to hear and respond to the deterrent beyond 40 m, as sound pressure levels are likely to be at or below hearing thresholds of bats (20-30 dB SPL), but closer to the speaker units there was a significant reduction in bat activity (80% at 15 m). In Chapter 4, I show that the mechanism for acoustic deterrence is likely masking of bat echolocation calls, which in turn reduces bat foraging behaviour. However, it is possible that the deterrent is also acting as a generally aversive stimulus in some species (Luo et al. 2015). Therefore, acoustic deterrents warrant further research and development and in the next two sections I discuss potential welfare implications and possible applications of these methods.

## 5.3 Welfare implications

Despite its potential, acoustic bat deterrence may have welfare implications that need to be considered when weighing up its use against alternative mitigation methods. Acoustic deterrence usually involves the use of an aversive, distractive or masking stimulus and therefore has potential to reduce access to habitats and resources and/or could cause stress or even direct pain in some animals (Schakner & Blumstein 2013).

Bats are likely to respond to an acoustic deterrent stimulus in a similar way to that from an anthropogenic source, such as traffic or gas compressor noise (Bunkley & Barber 2015; Bunkley et al. 2015; Luo et al. 2015). Anthropogenic noise can induce measurable stress responses in some animals such as an increase in cortisol levels or heart rate (Kight & Swaddle 2011). However, Brazilian free-tailed bats (*Tadarida brasiliensis*) had lower cortisol levels and parasite load when roosting below road bridges compared to in their natural cave roosts (Allen et al. 2011). Therefore, future research should address whether bats exposed to deterrent noise show elevated levels of stress hormones and other short and/or longer-term physiological indicators such as parasite load and other measures of body condition. However, any results of stress indication should also be weighed up against the short and long-term effects of the human activity being mitigated for, which may cause more harm to bats in the long term.

Mechanisms for response to acoustic deterrence in this thesis were likely to be a masking effect on echolocation by the deterrent sound, which also may have had a generally aversive effect (Luo et al. 2015). A sudden high amplitude sound can cause temporary threshold shifts (TTS) and even permanent damage in some animals (Schakner & Blumstein 2013). However, as bats have evolved in relatively loud and complex acoustic environments, often being exposed to the close-range high intensity calls of their conspecifics, they may not be so sensitive to these effects (Simmons et al. 2016). Understanding hearing thresholds in bats in more detail is therefore an important basis for further deterrent research, including the exploration of species-specific effects of different deterrent frequencies and amplitudes on bat ears.

Bat deterrence, by its design, acts to move bats out of an area, which may mean a reduction in access to foraging resources or habitat features such as roosts or commuting routes. If these resources are rare in the remaining habitat not affected by deterrence, or if the noise degrades surrounding habitats due to overspill effects, this could lead to unwanted impacts on the target species (and non-target species). However, small-scale movement of bats to new roosts within churches using acoustic deterrence did not affect where radio-tracked bats from the same church went to forage and also had no other obvious impacts on behaviour (Packman et al. 2015; Zeale et al. 2016). In comparison, light deterrents, which were also initially included for testing in churches in the same study were abandoned in early trials, due to entombment of bats in roosts (Zeale et al. 2016). The detrimental effects on bat colonies of the illeagal use of light in churches is also widely reported (Stone 2013; Rydell et al. 2017). In comparison, acoustic deterrence may allow the movement of bats to new areas within a building, without the significant detrimental effects on behaviour seen with the use of light.

Other wild mammals such as rodents, polecats and otters all have the ability to hear high frequency sounds of > 20 kHz and therefore could be affected by noise overspill of bat deterrence methods (Heffner & Heffner 2008). Therefore, future research and implementation should focus on ensuring that acoustic bat deterrence devices are as targeted as possible, reducing any effects on non-target bat species and species from other taxa. In the next section, I discuss possible applications, refinements to the system and future research.

## 5.4 Applications and future research

### 5.4.1 Wind turbines

Human activities and development put many bat species at risk and human-bat conservation conflicts and impacts are an increasing concern for governments and non-government organisations wishing to protect this enigmatic and ecologically important group (Altringham & Kerth 2016; Arnett et al. 2016; Rowse et al. 2016; Voigt & Kingston 2016). For example, wind energy development and construction pose a significant risk to bat populations and large numbers of fatalities have been documented in North America over the last few decades (Arnett et al. 2008; Cryan 2008; Baerwald et al. 2014). Fatalities in Europe are not documented on such a large scale, but still have the potential to cause deleterious effects to resident bat populations and those that migrate in from further afield (Amorim et al. 2012; Camina 2012; Georgiakakis et al. 2012; Santos et al. 2013; Lehnert et al. 2014; Lintott et al. 2016; Mathews et al. 2016). Wind energy development is listed as one of the key threats and conservation issues in the recent EU Bats Action Plan for 2018 to 2024 and guidelines specifically considering bats in wind developments such as the EUROBATS guidelines have been published (Rodrigues et al. 2015; Marchais & Thauront 2018). Along with mortality from direct collision, bats entering the roto-swept zone of turbines may be subject to pressure changes, which can result in damage to internal organs (barotrauma) (Baerwald et al. 2008; Rollins et al. 2012). Wind farms may also displace bats from important foraging habitats or commuting and migration routes (Roscioni et al. 2013; Lehnert et al. 2014; Roscioni et al. 2014). Bat fatalities were significantly reduced by up to 50-60% at a wind farm in North America, when acoustic deterrents were used (Arnett et al. 2013). Therefore, acoustic deterrence is a method that requires further exploration for use at wind turbines, along with other post-construction operational mitigation measures such as the increase in cut-in speeds (starting the movement of turbine blades at higher wind speeds, often called ‘feathering’) (Arnett et al. 2010; Arnett & Baerwald 2013). Feathering has been shown to reduce bat mortality at wind farms in North America, with nightly reductions in bat fatalities ranging from 44-93% (Arnett et al. 2010). However, deterrence may be a cheaper alternative mitigation strategy, as after initial costs of installation, costs of powering the speakers are likely to be negligible, compared to the economic losses incurred by feathering the blades at lower wind speeds (Arnett et al. 2013). Future research should therefore focus on implementation of acoustic deterrence at wind farm sites in Europe and evaluation of the effectiveness in reducing causalities compared to and/or in combination with operational mitigation.

This thesis has shown that a broadband ultrasonic deterrent is effective up to about 40 m for bats with echolocation call frequencies of around 50 kHz. Current development of a second-generation speaker system by Bat Conservation International (BCI) (batcon.org) and NRG Systems (nrgsystems.com) may result in a more targeted speaker system, similar to those used on birds (Mahjoub et al. 2015; Swaddle et al. 2016; Schlichting et al. 2017). A speaker with a tuneable, relatively more narrowband output may allow deterrence over larger distances and a more species-specific effect. For example, bats killed in the greatest numbers at wind turbines in Europe tend to be the bigger, migratory species such as *Nyctalus* and *Eptesicus* species, that have relatively low frequency echolocation calls of < 30 kHz (Rydell et al. 2010a; Mathews et al. 2016). Therefore, tuning deterrent speakers to these frequencies may yield a greater deterrent effect on these species and a resultant reduction in causalities. However, this method would not necessarily cause a deterrent effect in species that call at higher frequencies such as *Pipistrellus* species, which are also killed in significant numbers at turbines in Europe (Rydell et al. 2010a; Mathews et al. 2016). Therefore, a broadband deterrent speaker, similar to that tested in this thesis may be more appropriate in the European context.

High frequency sound is subject to frequency-dependent absorption in air, with higher frequencies attenuating more quickly, especially with higher temperatures and humidity (Bazley 1976). As turbine blades are becoming increasingly longer, broadcasting the higher frequency components of a deterrent sound with sufficient power, so that it reaches the edge of the rotor-swept zone is a challenging engineering problem. In this thesis, I found evidence for a masking effect on echolocation as a potential mechanism for the deterrent effect seen on *Pipistrellus pygmaeus* bats at foraging sites. However, as the deterrent I tested produced broadband sound that overlapped with the species' main call frequency (55 kHz), aversive effects of non-overlapping lower frequency elements of the deterrent broadcast cannot be ruled out. If a strong aversive effect of a lower frequency deterrent sound (e.g. ~20 kHz) is sufficient for deterrence, higher frequency sounds that are harder to project as far may not be necessary. Therefore, an important next step will be to understand the species-specific mechanisms underpinning deterrence in more depth for species that are at risk at wind turbines. For example, studies using the new tuneable deterrent will allow a comparison of the effects of overlapping and non-overlapping deterrent frequencies on species with different echolocation call frequencies.

Another important avenue for future research is whether bats habituate to the deterrent sound at wind turbines and in other potential application scenarios. Zeale et al. (2016) found no habituation of *Myotis nattereri* to the same acoustic deterrent used in this thesis over a 21-day experimental period. However, a follow-on study also in churches found some evidence of habituation in *Pipistrellus pygmaeus*, with some individuals returning to roosts above the deterrent, after initial exclusion (Packman et al. 2015). Differences in habituation effects may therefore be species-specific in bats that roost in churches and may also be related to their echolocation call structure. Motivation to return to a roosting site may also be influenced by availability and quality of other potential roost sites. There was no habituation effect to the same deterrents in a study at wind turbines in North America, although this was not tested directly (Arnett et al. 2013). In this thesis, I did not document any habituation to the deterrent in three experiments at foraging sites, however I also did not directly test this. As the experiments were short (1 hour per night) and designed to capture a peak in bat activity after sunset, any changes in activity over the experiment were likely due to normal activity patterns of different species at that time of night. Future research should therefore focus on species-specific habituation effects to the deterrents over a longer period and in different applications where they have potential for reducing risk to bats.

### 5.4.2 Roads and other transport networks

Despite extensive studies on other taxa, such as birds (Lowry et al. 2012; McClure et al. 2013; Ware et al. 2015; McClure et al. 2017), the impacts of roads and other transport infrastructure on bats is relatively understudied and current mitigation is largely ineffective or undeveloped (Berthinussen & Altringham 2012; Altringham & Kerth 2016). Road impacts range from direct mortality from collision, to a destruction or degradation of important habitat by noise, light and even potentially chemical pollution (Lesinski 2007; Kerth & Melber 2009; Altringham & Kerth 2016; Fensome & Mathews 2016). Roads can cause barrier effects due to a reduction in access to important habitats (Altringham & Kerth 2016; Fensome & Mathews 2016), either directly (Kerth & Melber 2009) or by noise or light degrading habitat quality (Bennett & Zurcher 2013; Fensome & Mathews 2016). However, both barrier effects and collision risk seem to be species-specific (Fensome & Mathews 2016). For example, woodland species are at increased collision risk, but suffer less barrier effects, especially in areas where roads intersect favourable woodland habitat (Lesinski 2007; Fensome & Mathews 2016). Therefore, future research could test whether acoustic deterrence could divert bats away from potentially dangerous flight routes over roads, allowing them to take safer alternative routes, for example over green bridges or through underpasses. However, as bats may respond to acoustic deterrence in a similar way to anthropogenic noise (Bunkley & Barber 2015; Bunkley et al. 2015; Luo et al. 2015), it would be important to weigh up whether adding another potential noise pollutant into an already degraded habitat is detrimental to local bat populations.

### 5.4.3 Movement of roosting bats

Conflict between groups wishing to conserve bat populations and those with more human-focussed interests can arise when bats roost in areas where they cause damage or hygiene issues in human dwellings, schools, workplaces or historical buildings such as churches or temples (Mgode et al. 2014; Zeale et al. 2016). Bats may also be impacted by construction activities at bridges or in buildings where they roost. Therefore, deterrence provides a non-invasive method of moving bats either temporarily or permanently to another roosting site (when alternatives are available) to alleviate human-bat impacts and conservation conflicts. For example, Natterer's bats (*Myotis nattereri*) were successfully moved away from areas where they were causing problems with their urine and faeces to new roosting sites within churches in Norfolk, UK, using the same broadband ultrasonic deterrent device as tested in this thesis (Zeale et al. 2016). Short- and long-term deterrence did not exclude bats completely from the buildings and there was no measurable effect on foraging in radio-tracking experiments. Therefore, future research could focus on implementation of acoustic deterrence systems in other buildings or structures where bats roost (such as schools or workplaces), whilst monitoring impacts on behaviour.

### 5.4.4 Applications and limitations of thermal bat tracking methods

Thermal imaging and image-based tracking are methods that have incredible potential for studying bat behaviour and ecology (Hristov et al. 2008; Betke et al. 2017). Automated counting methods allow bat activity to be quantified with increasing accuracy and detail (Dell et al. 2014) and have applications in studying the emergence, foraging behaviour and responses of bats to human structures and/or activities (Betke et al. 2008; Hristov et al. 2008; Hristov et al. 2010; Yang et al. 2013; Betke et al. 2017). Stereo thermal videogrammetry also allows individual bat flight trajectory measurements such as speed, tortuosity and turning angles to be measured and therefore has applications in the study of bat flight and energetics (Holderied et al. 2005; Yang et al. 2013). Future research and mitigation applications are therefore broad ranging and are only limited by the possibilities of the system. For example, bat flight lines could be mapped around road networks, allowing appropriate mitigation to be developed for specific infrastructure networks. Thermal tracking methods could also be used to predict casualties at wind farms and allow appropriate real-time mitigation, such as operation of deterrents or limiting turbine operation during peaks in bat activity. Detailed exploration of bat flight behaviour during foraging or in tandem flights with conspecifics could allow investigation into these behaviours.

However, a current limitation of the tracking system developed for this thesis and similar systems, is the requirement for large amounts of data storage, due to the recording of uncompressed video files (Dell et al. 2014). 3D tracking also requires accurately synchronised cameras and precise calibration methods, which limit the systems portability and ease of use (Dell et al. 2014). Further refinement of the technology involved in these systems to allow real-time compression and upload of data would therefore significantly increase their application potential.

## 5.5 Conclusions

In this thesis, I have shown that acoustic bat deterrents are a viable method to mitigate for human impacts on bats and further research should focus on their refinement and application. However, due to the mechanisms underpinning noise avoidance in bats, these methods may have a number of potentially unwanted effects. Therefore, I recommend that these methods should always be used with caution and should not made commercially available for use, without a government licence where possible. I also suggest that acoustic deterrents are used on a case-by-case basis, with careful consideration in each application, following specialist guidance. Providing this is the case, acoustic bat deterrents will be a useful tool in reducing human-bat conservation conflicts and impacts and contribute to the conservation of bat populations in a variety of scenarios.

# References

Allen LC, Turmelle AS, Widmaier EP, Hristov NI, McCracken GF, Kunz TH. 2011. Variation in physiological stress between bridge- and cave-roosting Brazilian free-tailed bats. Conservation Biology **25**:374-381.

Altringham J, Kerth G. 2016. Bats and roads. Pages 35-62 in Voigt CC, and Kingston T, editors. Bats in the Anthropocene: conservation of bats in a changing world. Springer Open, Berlin.

Amichai E, Blumrosen G, Yovel Y. 2015. Calling louder and longer: how bats use biosonar under severe acoustic interference from other bats. Proceedings of the Royal Society B-Biological Sciences **282**:20152064.

Amorim F, Rebelo H, Rodrigues L. 2012. Factors influencing bat activity and mortality at a wind farm in the Mediterranean region. Acta Chiropterologica **14**:439-457.

Arnett EB, Baerwald EF. 2013. Impacts of wind energy development on bats: implications for conservation. Pages 435-456 in Adams RA, and Pedersen SC, editors. Bat evolution, ecology and conservation. Springer, New York.

Arnett EB, Baerwald EF, Mathews F, Rodrigues L, Rodríguez-Durán A, Rydell J, Villegas-Patraca R, Voigt CC. 2016. Impacts of wind energy development on bats: a global perspective. Pages 295-323 in Voigt C, and Kingston T, editors. Bats in the Anthropocene: conservation of bats in a changing world. Springer Open, Switzerland.

Arnett EB, Brown W, Erickson WP, Fiedler JK, Hamilton BL, Henry TH, Jain A, Johnson GD, Kerns J, Koford RR. 2008. Patterns of bat fatalities at wind energy facilities in North America. The Journal of Wildlife Management **72**:61-78.

Arnett EB, Hein CD, Schirmacher MR, Huso MM, Szewczak JM. 2013. Evaluating the effectiveness of an ultrasonic acoustic deterrent for reducing bat fatalities at wind turbines. PLoS ONE **8**:e65794.

Arnett EB, Huso MM, Schirmacher MR, Hayes JP. 2010. Altering turbine speed reduces bat mortality at wind-energy facilities. Frontiers in Ecology and the Environment **9**:209-214.

Attanasi A, et al. 2014. Collective behaviour without collective order in wild swarms of midges. PLoS Computational Biology **10**:e1003697.

Aziz SA, Olival KJ, Bumrungsri S, Richards GC, Racey PA. 2016. The conflict between pteropodid bats and fruit growers: species, legislation and mitigation. Pages 377-426 in Voigt C, and Kingston T, editors. Bats in the Anthropocene: Conservation of bats in a changing world. Springer, Cambridge, UK.

Baerwald EF, D'Amours GH, Klug BJ, Barclay RM. 2008. Barotrauma is a significant cause of bat fatalities at wind turbines. Current Biology **18**:R695-R696.

Baerwald EF, Patterson WP, Barclay RMR. 2014. Origins and migratory patterns of bats killed by wind turbines in southern Alberta: evidence from stable isotopes. Ecosphere **5**:17.

Ballerini M, et al. 2008. Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study. Proceedings of the National Academy of Sciences of the United States of America **105**:1232-1237.

Barber JR, Crooks KR, Fristrup KM. 2010. The costs of chronic noise exposure for terrestrial organisms. Trends in Ecology & Evolution **25**:180-189.

Barber JR, Razak KA, Fuzessery ZM. 2003. Can two streams of auditory information be processed simultaneously? Evidence from the gleaning bat *Antrozous pallidus*. Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology **189**:843–855.

Barlow KE, Jones G. 1997. Function of pipistrelle social calls: Field data and a playback experiment. Animal Behaviour **53**:991-999.

Barre K, Le Viol I, Bas Y, Julliard R, Kerbiriou C. 2018. Estimating habitat loss due to wind turbine avoidance by bats: Implications for European siting guidance. Biological Conservation **226**:205-214.

Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B, Grothendieck G. 2015. lme4: linear mixed-effects models using 'Eigen' and S4. R package version 1.1-9.

Bates ME, Stamper SA, Simmons JA. 2008. Jamming avoidance response of big brown bats in target detection. Journal of Experimental Biology **211**:106-113.

Bauer S, et al. 2019. The grand challenges of migration ecology that radar aeroecology can help answer. Ecography **42**:861-875.

Bazley EN. 1976. Sound absorption in air at frequencies up to 100 kHz. NPL Acoustics Report Ac 74, National Physical Laboratory, Teddington, England.

Bennett VJ, Zurcher AA. 2013. When corridors collide: road-related disturbance in commuting bats. Journal of Wildlife Management **77**:93-101.

Berthinussen A, Altringham J. 2012. Do bat gantries and underpasses help bats cross roads safely? PLoS ONE **7**:e38775.

Betke M, Hedrick T, Theriault D. 2017. Multi-camera videography methods for aeroecology. Pages 239-257 in Chilson PB, Frick WF, Kelly JF, and Liechti F, editors. Aeroecology. Springer, Cham, Switzerland.

Betke M, et al. 2008. Thermal imaging reveals significantly smaller Brazilian free-tailed bat colonies than previously estimated. Journal of Mammalogy **89**:18-24.

Bittencourt L, Lima IMS, Andrade LG, Carvalho RR, Bisi TL, Lailson-Brito J, Azevedo AF. 2017. Underwater noise in an impacted environment can affect Guiana dolphin communication. Marine Pollution Bulletin **114**:1130-1134.

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution **24**:127-135.

Brooks M, Kristensen K, van Benthem K, Magnusson A, Berg C, Nielsen A, Skaug HJ, Maechler M, Bolker BM. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal **9**:378-400.

Bunkley JP, Barber JR. 2015. Noise reduces foraging efficiency in pallid bats (*Antrozous pallidus*). Ethology **121**:1116-1121.

Bunkley JP, McClure CJ, Kleist NJ, Francis CD, Barber JR. 2015. Anthropogenic noise alters bat activity levels and echolocation calls. Global Ecology and Conservation **3**:62-71.

Burger J. 1983. Bird control at airports. Environmental Conservation **10**:115-124.

Camina A. 2012. Bat fatalities at wind farms in northern Spain - lessons to be learned. Acta Chiropterologica **14**:205-212.

Carretta JV, Barlow J. 2011. Long-term effectiveness, failure rates, and "dinner bell" properties of acoustic pingers in a gillnet fishery. Marine Technology Society Journal **45**:7-19.

Chan A, Blumstein DT. 2011. Attention, noise, and implications for wildlife conservation and management. Applied Animal Behaviour Science **131**:1-7.

Chan A, Giraldo-Perez P, Smith S, Blumstein DT. 2010. Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. Biology Letters **6**:458-461.

Chapman J, Reynolds D, Smith A, Smith E, Woiwod I. 2004. An aerial netting study of insects migrating at high altitude over England. Bulletin of Entomological Research **94**:123-136.

Chapman JW, Reynolds DR, Smith AD, Riley JR, Pedgley DE, Woiwod IP. 2002. High - altitude migration of the diamondback moth *Plutella xylostella* to the UK: a study using radar, aerial netting, and ground trapping. Ecological Entomology **27**:641-650.

Chauhan P, Verma HN, Sisodia R, Kesari KK. 2017. Microwave radiation (2.45 GHz)-induced oxidative stress: whole-body exposure effect on histopathology of Wistar rats. Electromagnetic Biology and Medicine **36**:20-30.

Chaverri G, Quiros OE. 2017. Variation in echolocation call frequencies in two species of free-tailed bats according to temperature and humidity. Journal of the Acoustical Society of America **142**:146-150.

Chiu C, Reddy PV, Xian W, Krishnaprasad PS, Moss CF. 2010. Effects of competitive prey capture on flight behavior and sonar beam pattern in paired big brown bats, *Eptesicus fuscus*. Journal of Experimental Biology **213**:3348-3356.

Chiu C, Xian W, Moss CF. 2009. Adaptive echolocation behavior in bats for the analysis of auditory scenes. Journal of Experimental Biology **212**:1392-1404.

Ciechanowski M, Zajac T, Bilas A, Dunajski R. 2007. Spatiotemporal variation in activity of bat species differing in hunting tactics: effects of weather, moonlight, food abundance, and structural clutter. Canadian Journal of Zoology **86**:236-236.

Cilulko J, Janiszewski P, Bogdaszewski M, Szczygielska E. 2013. Infrared thermal imaging in studies of wild animals. European Journal of Wildlife Research **59**:17-23.

Clark CW, Ellison WT, Southall BL, Hatch L, Van Parijs SM, Frankel A, Ponirakis D. 2009. Acoustic masking in marine ecosystems: intuitions, analysis, and implication. Marine Ecology Progress Series **395**:201-222.

Codarin A, Wysocki LE, Ladich F, Picciulin M. 2009. Effects of ambient and boat noise on hearing and communication in three fish species living in a marine protected area (Miramare, Italy). Marine Pollution Bulletin **58**:1880-1887.

Corcoran AJ, Barber JR, Conner WE. 2009. Tiger moth jams bat sonar. Science **325**:325-327.

Corcoran AJ, Barber JR, Hristov NI, Conner WE. 2011. How do tiger moths jam bat sonar? Journal of Experimental Biology **214**:2416-2425.

Corcoran AJ, Conner WE. 2012. Sonar jamming in the field: effectiveness and behavior of a unique prey defense. Journal of Experimental Biology **215**:4278-4287.

Corcoran AJ, Moss CF. 2017. Sensing in a noisy world: lessons from auditory specialists, echolocating bats. Journal of Experimental Biology **220**:4554-4566.

Crawley MJ 2007. The R book. John Wiley & Sons, Sussex, UK.

Cryan PM. 2008. Mating behavior as a possible cause of bat fatalities at wind turbines. The Journal of Wildlife Management **72**:845-849.

Cryan PM, et al. 2014. Behavior of bats at wind turbines. Proceedings of the National Academy of Sciences of the United States of America **111**:15126-15131.

Cullinan VI, Matzner S, Duberstein CA. 2015. Classification of birds and bats using flight tracks. Ecological Informatics **27**:55-63.

Cvikel N, Levin E, Hurme E, Borissov I, Boonman A, Amichai E, Yovel Y. 2015. On-board recordings reveal no jamming avoidance in wild bats. Proceedings of the Royal Society B-Biological Sciences **282**.

D'Andrea JA, Adair ER, de Lorge JO. 2003. Behavioral and cognitive effects of microwave exposure. Bioelectromagnetics **6**:S39-S62.

Davidson-Watts I, Walls S, Jones G. 2006. Differential habitat selection by *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus* identifies distinct conservation needs for cryptic species of echolocating bats. Biological Conservation **133**:118-127.

Dawson S, Northridge SP, Waples D, Read A. 2013. To ping or not to ping: the use of active acoustic devices in mitigating interactions between small cetaceans and gillnet fisheries. Endangered Species Research **19**:201-221.

de Jong K, Amorim MCP, Fonseca PJ, Fox CJ, Heubel KU. 2018a. Noise can affect acoustic communication and subsequent spawning success in fish. Environmental Pollution **237**:814-823.

de Jong K, Amorim MCP, Fonseca PJ, Heubel KU. 2018b. Noise affects multimodal communication during courtship in a marine fish. Frontiers in Ecology and Evolution **6**:113.

Dechmann DKN, Heucke SL, Giuggioli L, Safi K, Voigt CC, Wikelski M. 2009. Experimental evidence for group hunting via eavesdropping in echolocating bats. Proceedings of the Royal Society of London B Biological Sciences **276**:2721-2728.

Dell AI, et al. 2014. Automated image-based tracking and its application in ecology. Trends in Ecology & Evolution **29**:417-428.

Dell'Aglio DD, Stevens M, Jiggins CD. 2016. Avoidance of an aposematically coloured butterfly by wild birds in a tropical forest. Ecological Entomology **41**:627-632.

Dieter CD, Warner CS, Ren C. 2014. Evaluation of foliar sprays to reduce crop damage by Canada geese. Human-Wildlife Interactions **8**:139-149.

Dorado-Correa AM, Zollinger SA, Brumm H. 2018. Vocal plasticity in mallards: multiple signal changes in noise and the evolution of the Lombard effect in birds. Journal of Avian Biology **49**:e01564.

Dukas R, Kamil AC. 2000. The cost of limited attention in blue jays. Behavioral Ecology **11**:502-506.

Elder JA, Chou CK. 2003. Auditory response to pulsed radiofrequency energy. Bioelectromagnetics **6**:S162-S173.

Evangelista D, Fernandez MJ, Berns MS, Hoover A, Dudley R. 2010. Hovering energetics and thermal balance in Anna's hummingbirds (*Calypte anna*). Physiological and Biochemical Zoology **83**:406-413.

Fawcett K, Ratcliffe JM. 2015. Clutter and conspecifics: a comparison of their influence on echolocation and flight behaviour in Daubenton's bat, *Myotis daubentonii*. Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology **201**:295-304.

Fensome AG, Mathews F. 2016. Roads and bats: a meta-analysis and review of the evidence on vehicle collisions and barrier effects. Mammal Review **46**:311-323.

Fenton MB. 1970. A technique for monitoring bat activity with results obtained from different environments in southern Ontario. Canadian Journal of Zoology **48**:847-851.

Foo CF, Bennett VJ, Hale AM, Korstain JM, Schildt AJ, Williams DA. 2017. Increasing evidence that bats actively forage at wind turbines. Peerj **5**:e3985.

Foote AD, Osborne RW, Hoelzel AR. 2004. Environment- whale-call response to masking boat noise. Nature **428**:910-910.

Francis CD, Barber JR. 2013. A framework for understanding noise impacts on wildlife: an urgent conservation priority. Frontiers in Ecology and the Environment **11**:305-313.

Francis CD, Ortega CP, Cruz A. 2009. Noise pollution changes avian communities and species interactions. Current Biology **19**:1415-1419.

Francis CD, Ortega CP, Cruz A. 2011. Noise pollution filters bird communities based on vocal frequency. PLoS ONE **6**:e27052.

Frick WF, Baerwald EF, Pollock JF, Barclay RMR, Szymanski JA, Weller TJ, Russell AL, Loeb SC, Medellin RA, McGuire LP. 2017. Fatalities at wind turbines may threaten population viability of a migratory bat. Biological Conservation **209**:172-177.

Gazo M, Gonzalvo J, Aguilar A. 2008. Pingers as deterrents of bottlenose dolphins interacting with trammel nets. Fisheries Research **92**:70-75.

Geipel I, Smeekes MJ, Halfwerk W, Page RA. 2019. Noise as an informational cue for decision-making: the sound of rain delays bat emergence. Journal of Experimental Biology **222**:jeb192005.

Georgiakakis P, Kret E, Carcamo B, Doutau B, Kafkaletou-Diez A, Vasilakis D, Papadatou E. 2012. Bat fatalities at wind farms in north-eastern Greece. Acta Chiropterologica **14**:459-468.

Gillam EH, Hristov NI, Kunz TH, McCracken GF. 2010. Echolocation behavior of Brazilian free-tailed bats during dense emergence flights. Journal of Mammalogy **91**:967-975.

Gillam EH, McCracken GF. 2007. Variability in the echolocation of *Tadarida brasiliensis*: effects of geography and local acoustic environment. Animal Behaviour **74**:277-286.

Gillam EH, McCracken GF, Westbrook JK, Lee YF, Jensen ML, Balsley BB. 2009. Bats aloft: variability in echolocation call structure at high altitudes. Behavioral Ecology and Sociobiology **64**:69-79.

Gillam EH, Ulanovsky N, McCracken GF. 2006. Rapid jamming avoidance in biosonar. Proceedings of the Royal Society B: Biological Sciences **274**:651-660.

Giuggioli L, McKetterick TJ, Holderied M. 2015. Delayed response and biosonar perception explain movement coordination in trawling bats. PLoS Computational Biology **11**:e1004089-e1004089.

Goerlitz HR. 2018. Weather conditions determine attenuation and speed of sound: Environmental limitations for monitoring and analyzing bat echolocation. Ecology and Evolution **8**:5090-5100.

Gomes DGE, Page RA, Geipel I, Taylor RC, Ryan MJ, Halfwerk W. 2016. Bats perceptually weight prey cues across sensory systems when hunting in noise. Science **353**:1277-1280.

Gomez-Marin A, Partoune N, Stephens GJ, Louis M. 2012. Automated tracking of animal posture and movement during exploration and sensory orientation behaviors. PLoS ONE **7**:e41642.

Gorresen PM, Cryan PM, Dalton DC, Wolf S, Johnson JA, Todd CM, Bonaccorso FJ. 2015. Dim ultraviolet light as a means of deterring activity by the Hawaiian hoary bat *Lasiurus cinereus semotus*. Endangered Species Research **28**:249-257.

Gotze S, Koblitz JC, Denzinger A, Schnitzler HU. 2016. No evidence for spectral jamming avoidance in echolocation behavior of foraging pipistrelle bats. Scientific Reports **6**:13.

Griffin DR. 1971. The importance of atmospheric attenuation for the echolocation of bats (Chiroptera). Animal Behaviour **19**:55-61.

Griffin DR, McCue JJG, Grinnell AD. 1963. The resistance of bats to jamming. Journal of Experimental Zoology **152**:229-250.

Grodzinski U, Spiegel O, Korine C, Holderied MW. 2009. Context-dependent flight speed: evidence for energetically optimal flight speed in the bat *Pipistrellus kuhlii*? Journal of Animal Ecology **78**:540-548.

Guinet C, Tixier P, Gasco N, Duhamel G. 2015. Long-term studies of Crozet Island killer whales are fundamental to understanding the economic and demographic consequences of their depredation behaviour on the Patagonian toothfish fishery. ICES Journal of Marine Science **72**:1587-1597.

Hage SR, Metzner W. 2013. Potential effects of anthropogenic noise on echolocation behavior in horseshoe bats. Communicative & integrative biology **6**:e24753.

Hamer DJ, Childerhouse SJ, Gales NJ. 2012. Odontocete bycatch and depredation in longline fisheries: a review of available literature and of potential solutions. Marine Mammal Science **28**:E345-E374.

Hansen SC, Stolter C, Jacob J. 2016. Effect of plant secondary metabolites on feeding behavior of microtine and arvicoline rodent species. Journal of Pest Science **89**:955–963.

Hartig F. 2018. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.2.0.

Hase K, Kadoya Y, Maitani Y, Miyamoto T, Kobayasi KI, Hiryu S. 2018. Bats enhance their call identities to solve the cocktail party problem. Communications Biology **1**:39.

Hedges S, Gunaryadi D. 2010. Reducing human–elephant conflict: do chillies help deter elephants from entering crop fields? Oryx **44**:139-146.

Heffner HE, Heffner RS. 2008. High-frequency hearing. Pages 55-60 in Dallos P, Oertel D, and Hoy R, editors. Handbook of the senses: audition. Elsevier, New York, USA.

Holderied MW, Baker CJ, Vespe M, Jones G. 2008. Understanding signal design during the pursuit of aerial insects by echolocating bats: tools and applications. Integrative and Comparative Biology **48**:74-84.

Holderied MW, Jones G. 2009. Flight dynamics. Pages 459–475. Ecological and Behavioral Methods for the Study of Bats. Johns Hopkins University Press, Baltimore, USA.

Holderied MW, Korine C, Fenton MB, Parsons S, Robson S, Jones G. 2005. Echolocation call intensity in the aerial hawking bat *Eptesicus bottae* (Vespertilionidae) studied using stereo videogrammetry. The Journal of Experimental Biology **208**:1321-1327.

Holderied MW, von Helversen O. 2003. Echolocation range and wingbeat period match in aerial-hawking bats. Proceedings of the Royal Society B-Biological Sciences **270**:2293-2299.

Horn JW, Arnett EB, Jensen M, Kunz TH. 2008a. Testing the effectiveness of an experimental acoustic bat deterrent at the Maple Ridge wind farm. Report submitted to The Bats and Wind Energy Cooperative and Bat Conservation International, Austin, Texas.

Horn JW, Arnett EB, Kunz TH. 2008b. Behavioral responses of bats to operating wind turbines. The Journal of Wildlife Management **72**:123-132.

Hothorn T, Bretz F, Westfall P, M. HR, Schuetzenmeister A, Scheibe S. 2015. Multcomp: simultaneous inference in general parametric models. R package version 1.4-1.

Hristov NI, Betke M, Kunz TH. 2008. Applications of thermal infrared imaging for research in aeroecology. Integrative and Comparative Biology **48**:50-59.

Hristov NI, Betke M, Theriault DEH, Bagchi A, Kunz TH. 2010. Seasonal variation in colony size of Brazilian free-tailed bats at Carlsbad Cavern based on thermal imaging. Journal of Mammalogy **91**:183-192.

Hristov NI, Conner WE. 2005. Sound strategy: acoustic aposematism in the bat–tiger moth arms race. Naturwissenschaften **92**:164-169.

Hurley S, Fenton M. 1980. Ineffectiveness of fenthion, zinc phosphide, DDT and two ultrasonic rodent repellers for control of populations of little brown bats (*Myotis lucifugus*). Bulletin of Environmental Contamination and Toxicology **25**:503-507.

Jarvis J, Jackson W, Smotherman M. 2013. Groups of bats improve sonar efficiency through mutual suppression of pulse emissions. Frontiers in Physiology **4**:140.

Jiang TL, Guo X, Lin AQ, Wu H, Sun CN, Feng J, Kanwal JS. 2019. Bats increase vocal amplitude and decrease vocal complexity to mitigate noise interference during social communication. Animal Cognition **22**:199-212.

Johnson CN, Balmford A, Brook BW, Buettel JC, Galetti M, Lei GC, Wilmshurst JM. 2017. Biodiversity losses and conservation responses in the Anthropocene. Science **356**:270-274.

Johnson JB, Ford WM, Rodrigue JL, Edwards JW. 2012. Effects of acoustic deterrents on foraging bats. Research Note NRS-129, Northern Research Station, United States Department of Agriculture Forest Service, Washington D.C., USA.

Jones G. 1995. Flight performance, echolocation and foraging behaviour in noctule bats *Nyctalus noctula*. Journal of Zoology **237**:303-312.

Jones G, Rayner JMV. 1988. Flight performance, foraging tactics and echolocation in free-living Daubenton's bats *Myotis daubentoni* (Chiroptera: Vespertilionidae). Journal of Zoology **215**:113-132.

Jones G, Rayner JMV. 1991. Flight performance, foraging tactics and echolocation in the trawling insectivorous bat *Myotis adversus* (Chiroptera: Vespertilionidae). Journal of Zoology **225**:393-412.

Kerth G, Melber M. 2009. Species-specific barrier effects of a motorway on the habitat use of two threatened forest-living bat species. Biological Conservation **142**:270-279.

Kight CR, Swaddle JP. 2011. How and why environmental noise impacts animals: an integrative, mechanistic review. Ecology Letters **14**:1052-1061.

King LE, Douglas ‐ Hamilton I, Vollrath F. 2011. Beehive fences as effective deterrents for crop ‐ raiding elephants: field trials in northern Kenya. African Journal of Ecology **49**:431-439.

King LE, Lala F, Nzumu H, Mwambingu E, Douglas ‐ Hamilton I. 2017. Beehive fences as a multidimensional conflict ‐ mitigation tool for farmers coexisting with elephants. Conservation Biology **31**:743-752.

Kleist NJ, Guralnick RP, Cruz A, Francis CD. 2016. Anthropogenic noise weakens territorial response to intruder's songs. Ecosphere **7**:e02159.

Kuhn RA, Meyer W. 2009. Infrared thermography of the body surface in the Eurasian otter *Lutra lutra* and the giant otter *Pteronura brasiliensis*. Aquatic Biology **6**:143-152.

Kunc HP, Lyons GN, Sigwart JD, McLaughlin KE, Houghton JDR. 2014. Anthropogenic noise affects behavior across sensory modalities. American Naturalist **184**:E93-E100.

Lawrence BD, Simmons JA. 1982. Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. Journal of the Acoustical Society of America **71**:585-590.

Lehnert LS, Kramer-Schadt S, Schonborn S, Lindecke O, Niermann I, Voigt CC. 2014. Wind farm facilities in Germany kill noctule bats from near and far. PLoS ONE **9**:e103106.

Leopold BD, Hutchins M. 2016. Impact of wind energy on wildlife: synthesis. Human-Wildlife Interactions **10**:81-82.

Lesinski G. 2007. Bat road casualties and factors determining their number. Mammalia **71**:138-142.

Lewanzik D, Goerlitz HR. 2018. Continued source level reduction during attack in the low-amplitude bat *Barbastella barbastellus* prevents moth evasive flight. Functional Ecology **32**:1251-1261.

Lintott PR, Richardson SM, Hosken DJ, Fensome SA, Mathews F. 2016. Ecological impact assessments fail to reduce risk of bat casualties at wind farms. Current Biology **26**:R1135-R1136.

Loss SR, Will T, Marra P. 2015. Direct mortality of birds from anthropogenic causes. Annual Review of Ecology Evolution and Systematics **46**:99-120.

Lowry H, Lill A, Wong BBM. 2012. How noisy does a noisy miner have to be? Amplitude adjustments of alarm calls in an avian urban 'adapter'. PLoS ONE **7**:e29960.

Luo J, Siemers BM, Koselj K. 2015. How anthropogenic noise affects foraging. Global Change Biology **21**:3278-3289.

Mackey RL, Barclay RMR. 1989. The influence of physical clutter and noise on the activity of bats over water. Canadian Journal of Zoology **67**:1167-1170.

Madden F. 2004. Creating coexistence between humans and wildlife: global perspectives on local efforts to address human–wildlife conflict. Human dimensions of wildlife **9**:247-257.

Mahjoub G, Hinders MK, Swaddle JP. 2015. Using a "sonic net" to deter pest bird species: excluding European starlings from food sources by disrupting their acoustic communication. Wildlife Society Bulletin **39**:326-333.

Marchais G, Thauront M. 2018. Action plan for the conservation of all bat species in the European Union 2018-2024 in Barova S, and Streit A, editors. European Commission Report. European Commission & UNEP/EUROBATS, Paris, France.

Marker LL, Dickman AJ, Macdonald DW. 2005. Perceived effectiveness of livestock-guarding dogs placed on Namibian farms. Rangeland Ecology & Management **58**:329-336.

Marques AT, Batalha H, Rodrigues S, Costa H, Pereira MJR, Fonseca C, Mascarenhas M, Bernardino J. 2014. Understanding bird collisions at wind farms: an updated review on the causes and possible mitigation strategies. Biological Conservation **179**:40-52.

Mason JT, McClure CJW, Barber JR. 2016. Anthropogenic noise impairs owl hunting behavior. Biological Conservation **199**:29-32.

Mathews F, Richardson S, Lintott P, Hosken D. 2016. Understanding the risk to European protected species (bats) at onshore wind turbine sites to inform risk management. Defra, Winchester, UK.

Matsumoto J, Urakawa S, Takamura Y, Malcher-Lopes R, Hori E, Tomaz C, Ono T, Nishijo H. 2013. A 3D-video-based computerized analysis of social and sexual interactions in rats. PLoS ONE **8**:e78460.

Matthews SG, Miller AL, Plotz T, Kyriazakis I. 2017. Automated tracking to measure behavioural changes in pigs for health and welfare monitoring. Scientific Reports **7**:17582.

Matzner S, Cullinan VI, Duberstein CA. 2015. Two-dimensional thermal video analysis of offshore bird and bat flight. Ecological Informatics **30**:20-28.

McCafferty DJ. 2013. Applications of thermal imaging in avian science. Ibis **155**:4-15.

McClure CJW, Ware HE, Carlisle J, Kaltenecker G, Barber JR. 2013. An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. Proceedings of the Royal Society B-Biological Sciences **280**:20132290.

McClure CJW, Ware HE, Carlisle JD, Barber JR. 2017. Noise from a phantom road experiment alters the age structure of a community of migrating birds. Animal Conservation **20**:164-172.

McGill BJ, Dornelas M, Gotelli NJ, Magurran AE. 2015. Fifteen forms of biodiversity trend in the Anthropocene. Trends in Ecology & Evolution **30**:104-113.

Meijaard E, et al. 2011. Quantifying killing of orangutans and human-orangutan conflict in Kalimantan, Indonesia. PLoS ONE **6**:e27491.

Metzner W, Müller R. 2016. Ultrasound production, emission, and reception. Pages 55-91 in Fenton MB, Grinnell AD, Popper AN, and Fay RR, editors. Bat Bioacoustics. Springer Handbook of Auditory Research. Springer, New York, USA.

Mgode GF, Mbugi HA, Mhamphi GG, Ndanga D, Nkwama EL. 2014. Seroprevalence of L*eptospira* infection in bats roosting in human settlements in Morogoro municipality in Tanzania. *Tanzania Journal of Health Research* **16**:1-7.

Middleton N, Froud A, French K 2014. Social calls of the bats of Britain and Ireland. Pelagic Publishing Ltd, Exeter, UK.

Mooney TA, Pacini AF, Nachtigall PE. 2009. False killer whale (*Pseudorca crassidens*) echolocation and acoustic disruption: implications for longline bycatch and depredation. Canadian Journal of Zoology-Revue Canadienne De Zoologie **87**:726-733.

Mooney TA, Yang WC, Yu HY, Ketten DR, Jen IF. 2015. Hearing abilities and sound reception of broadband sounds in an adult Risso's dolphin (*Grampus griseus*). Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology **201**:751-761.

Moore BCJ 2013. An introduction to the psychology of hearing. Emerald Group Publishing, Leiden, the Netherlands.

Morris-Drake A, Bracken AM, Kern JM, Radford AN. 2017. Anthropogenic noise alters dwarf mongoose responses to heterospecific alarm calls. Environmental Pollution **223**:476-483.

Morris-Drake A, Kern JM, Radford AN. 2016. Cross-modal impacts of anthropogenic noise on information use. Current Biology **26**:R911-R912.

Møhl B. 1988. Target detection by echolocating bats. In: Nachtigal, PE, & Moore, PWB Animal sonar: processes and performance, Plenum Press, New York, USA **156**:435–450.

Nicholls B, Racey PA. 2007. Bats avoid radar installations: could electromagnetic fields deter bats from colliding with wind turbines? PLoS ONE **2**:e297.

Nicholls B, Racey PA. 2009. The aversive effect of electromagnetic radiation on foraging bats—a possible means of discouraging bats from approaching wind turbines. PLoS ONE **4**:e6246.

Noatch MR, Suski CD. 2012. Non-physical barriers to deter fish movements. Environmental Reviews **20**:71-82.

Nyhus PJ. 2016. Human-wildlife conflict and coexistence. Annual Review of Environment and Resources **41**:143-171.

Olsen KE, Asen W. 2017. Bridging the gap between civilian and military passive radar. IEEE Aerospace and Electronic Systems Magazine **32**:4-12.

Packman C, Zeale M, Harris S, Jones G 2015. Management of bats in churches- a pilot. English Heritage, Swindon, UK.

Patrick PH, Christie A, Sager D, Hocutt C, Stauffer J. 1985. Responses of fish to a strobe light/air-bubble barrier. Fisheries Research **3**:157-172.

Pena JL, Gutfreund Y. 2014. New perspectives on the owl's map of auditory space. Current Opinion in Neurobiology **24**:55-62.

Pennycuick CJ. 1975. Mechanics of flight. Pages 1–75. Avian Biology Academic Press, London, UK.

Persons MH, Walker SE, Rypstra AL, Marshall SD. 2001. Wolf spider predator avoidance tactics and survival in the presence of diet-associated predator cues (Araneae : Lycosidae). Animal Behaviour **61**:43-51.

Peste F, et al. 2015. How to mitigate impacts of wind farms on bats? A review of potential conservation measures in the European context. Environmental Impact Assessment Review **51**:10-22.

Pfalzer G, Kusch J. 2003. Structure and variability of bat social calls: implications for specificity and individual recognition. Journal of Zoology **261**:21-33.

Polak T, Korine C, Yair S, Holderied MW. 2011. Differential effects of artificial lighting on flight and foraging behaviour of two sympatric bat species in a desert. Journal of Zoology **285**:21-27.

Purser J, Radford AN. 2011. Acoustic noise induces attention shifts and reduces foraging performance in three-spined sticklebacks (*Gasterosteus aculeatus*). PLoS ONE **6**:e17478.

Radford AN, Kerridge E, Simpson SD. 2014. Acoustic communication in a noisy world: can fish compete with anthropogenic noise? Behavioral Ecology **25**:1022-1030.

Rayner JMV. 1999. Estimating power curves of flying vertebrates. Journal of Experimental Biology **202**:3449-3461.

Read AJ. 2008. The looming crisis: Interactions between marine mammals and fisheries. Journal of Mammalogy **89**:541-548.

Read AJ, Drinker P, Northridge S. 2006. Bycatch of marine mammals in US and global fisheries. Conservation Biology **20**:163-169.

Redpath SM, Bhatia S, Young J. 2015. Tilting at wildlife: reconsidering human-wildlife conflict. Oryx **49**:222-225.

Redpath SM, et al. 2013. Understanding and managing conservation conflicts. Trends in Ecology & Evolution **28**:100-109.

Roca IT, Desrochers L, Giacomazzo M, Bertolo A, Bolduc P, Deschesnes R, Martin CA, Rainville V, Rheault G, Proulx R. 2016. Shifting song frequencies in response to anthropogenic noise: a meta-analysis on birds and anurans. Behavioral Ecology **27**:1269-1274.

Rodrigues L, et al. 2015. Guidelines for consideration of bats in wind farm projects-Revision 2014. Secretriat UE, Bonn, Germany.

Rollins KE, Meyerholz DK, Johnson GD, Capparella AP, Loew SS. 2012. A forensic investigation into the etiology of bat mortality at a wind farm: barotrauma or traumatic injury? Veterinary Pathology Online **49**:362-371.

Roscioni F, Rebelo H, Russo D, Carranza ML, Di Febbraro M, Loy A. 2014. A modelling approach to infer the effects of wind farms on landscape connectivity for bats. Landscape Ecology **29**:891-903.

Roscioni F, Russo D, Di Febbraro M, Frate L, Carranza ML, Loy A. 2013. Regional-scale modelling of the cumulative impact of wind farms on bats. Biodiversity and Conservation **22**:1821-1835.

Rowse EG, Lewanzik D, Stone EL, Harris S, Jones G. 2016. Dark matters: the effects of artificial lighting on bats. Pages 187-213 in Voigt CC, and Kingston T, editors. Bats in the Anthropocene: conservation of bats in a changing world Springer Open, Berlin.

Russ J 2012. British bat calls: a guide to species identification. Pelagic publishing, Exeter.

Rydell J. 1992. Exploitation of insects around streetlamps by bats in Sweden. Functional Ecology **6**:744-750.

Rydell J. 2006. Bats and their insect prey at streetlights. Pages 43 – 60 in Rich C, and Longcore T, editors. Ecological consequences of artificial night lighting. Island Press, Washington, DC, USA.

Rydell J, Bach L, Dubourg-Savage M-J, Green M, Rodrigues L, Hedenström A. 2010a. Bat mortality at wind turbines in northwestern Europe. Acta Chiropterologica **12**:261-274.

Rydell J, Bach L, Dubourg-Savage M-J, Green M, Rodrigues L, Hedenström A. 2010b. Mortality of bats at wind turbines links to nocturnal insect migration? European Journal of Wildlife Research **56**:823-827.

Rydell J, Bogdanowicz W, Boonman A, Pettersson S, Suchecka E, Pomorski JJ. 2016. Bats may eat diurnal flies that rest on wind turbines. Mammalian Biology **81**:331-339.

Rydell J, Eklof J, Sanchez-Navarro S. 2017. Age of enlightenment: long-term effects of outdoor aesthetic lights on bats in churches. Royal Society Open Science **4**:161077.

Rydell J, Miller LA, Jensen ME. 1999. Echolocation constraints of Daubenton's Bat foraging over water. Functional Ecology **13**:247-255.

Rydell J, Wickman A. 2015. Bat activity at a small wind turbine in the Baltic Sea. Acta Chiropterologica **17**:359-364.

Santos H, Rodrigues L, Jones G, Rebelo H. 2013. Using species distribution modelling to predict bat fatality risk at wind farms. Biological Conservation **157**:178-186.

Sapir N, Horvitz N, Dechmann DKN, Fahr J, Wikelski M. 2014. Commuting fruit bats beneficially modulate their flight in relation to wind. Proceedings of the Royal Society B-Biological Sciences **281**:20140018.

Schakner ZA, Blumstein DT. 2013. Behavioral biology of marine mammal deterrents: a review and prospectus. Biological Conservation **167**:380-389.

Schaub A, Ostwald J, Siemers BM. 2008. Foraging bats avoid noise. Journal of Experimental Biology **211**:3174-3180.

Scherberich J, Hummel J, Schoneich S, Nowotny M. 2017. Functional basis of the sexual dimorphism in the auditory fovea of the duetting bushcricket *Ancylecha fenestrata*. Proceedings of the Royal Society B-Biological Sciences **284**:20171426.

Schlichting PE, Holland AE, Beasley JC, Bryan AL, Kennamer RA, Devault TL, Blackwell BF, Rhodes OE. 2017. Efficacy of an acoustic hailing device as an avian dispersal tool. Wildlife Society Bulletin **41**:453-460.

Schnitzler HU, Kalko EKV. 2001. Echolocation by insect-eating bats. Bioscience **51**:557-569.

Schnitzler HU, Moss CF, Denzinger A. 2003. From spatial orientation to food acquisition in echolocating bats. Trends in Ecology & Evolution **18**:386-394.

Senzaki M, Kadoya T, Francis CD, Ishiyama N, Nakamura F. 2018. Suffering in receivers: negative effects of noise persist regardless of experience in female anurans. Functional Ecology **32**:2054-2064.

Shannon G, et al. 2016. A synthesis of two decades of research documenting the effects of noise on wildlife. Biological Reviews **91**:982-1005.

Sharma A, Kesari KK, Saxena VK, Sisodia R. 2017. Ten gigahertz microwave radiation impairs spatial memory, enzymes activity, and histopathology of developing mice brain. Molecular and Cellular Biochemistry **435**:1-13.

Shen YY, Liang L, Li GS, Murphy RW, Zhang YP. 2012. Parallel evolution of auditory genes for echolocation in bats and toothed whales. PLoS Genetics **8**:e1002788.

Siemers BM, Stilz P, Schnitzler HU. 2001. The acoustic advantage of hunting at low heights above water: behavioural experiments on the European 'trawling' bats *Myotis capaccinii*, *M. dasycneme* and *M. daubentonii*. Journal of Experimental Biology **204**:3843-3854.

Sienkiewicz Z. 1998. Biological effects of electromagnetic fields. Engineering Science & Education Journal **7**:127-134.

Simmons AM, Hom KN, Warnecke M, Simmons JA. 2016. Broadband noise exposure does not affect hearing sensitivity in big brown bats (*Eptesicus fuscus*). Journal of Experimental Biology **219**:1031-1040.

Simpson SD, Radford AN, Nedelec SL, Ferrari MCO, Chivers DP, McCormick MI, Meekan MG. 2016. Anthropogenic noise increases fish mortality by predation. Nature Communications **7**:10544.

Smith TM, et al. 2016. Multi-radar multi-sensory (MRMS) severe weather and aviation products: initial operating capabilities. Bulletin of the American Meteorological Society **97**:1617-1630.

Song S, Lin A, Jiang T, Zhao X, Metzner W, Feng J. 2019. Bats adjust temporal parameters of echolocation pulses but not those of communication calls in response to traffic noise. Integrative Zoology **14**:1749-4877.

Spanjer G. 2006. Responses of the big brown bat, *Eptesicus fuscus*, to a proposed acoustic deterrent device in a lab setting. Report submitted to the Bats and Wind Energy Cooperative and the Maryland Department of Natural Resources, Austin, Texas, USA.

Stone EL. 2013. Bats and lighting: overview of current evidence and mitigation. Bristol, UK.

Stone EL, Jones G, Harris S. 2009. Street lighting disturbs commuting bats. Current Biology **19**:1123-1127.

Stone EL, Jones G, Harris S. 2012. Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats. Global Change Biology **18**:2458-2465.

Stone EL, Wakefield A, Harris S, Jones G. 2015. The impacts of new street light technologies: experimentally testing the effects on bats of changing from low-pressure sodium to white metal halide. Philosophical Transactions of the Royal Society B-Biological Sciences **370**:7.

Straw AD, Branson K, Neumann TR, Dickinson MH. 2011. Multi-camera real-time three-dimensional tracking of multiple flying animals. Journal of the Royal Society Interface **8**:395-409.

Sueur J, Aubin T, Simonis C. 2008. Seewave, a free modular tool for sound analysis and synthesis. Bioacoustics **18**:213-226.

Swaddle JP, Moseley DL, Hinders MK, Smith EP. 2016. A sonic net excludes birds from an airfield: implications for reducing bird strike and crop losses. Ecological Applications **26**:339-345.

Szewczak JM, Arnett E. 2006. Preliminary field test results of an acoustic deterrent with the potential to reduce bat mortality from wind turbines. An investigative report submitted to the Bats and Wind Energy Cooperative. Bat Conservation International. Austin, Texas, USA.

Szewczak JM, Arnett EB. 2007. Field test results of a potential acoustic deterrent to reduce bat mortality from wind turbines. Unpublished report. Bat Conservation International. Austin, Texas, USA.

Takahashi E, Hyomoto K, Riquimaroux H, Watanabe Y, Ohta T, Hiryu S. 2014. Adaptive changes in echolocation sounds by *Pipistrellus abramus* in response to artificial jamming sounds. Journal of Experimental Biology **217**:2885-2891.

Taylor LR. 1963. Analysis of the effect of temperature on insects in flight. Journal of Animal Ecology **32**:99-117.

Teeling EC, Jones G, Rossiter SJ. 2016. Phylogeny, genes, and hearing: implications for the evolution of echolocation in bats. Pages 25-54 in Fenton MB, Grinnell AD, Popper AN, and Fay RR, editors. Bat bioacoustics. Springer, New York, USA.

Tidau S, Briffa M. 2019. Anthropogenic noise pollution reverses grouping behaviour in hermit crabs. Animal Behaviour **151**:113-120.

Tressler J, Smotherman MS. 2009. Context-dependent effects of noise on echolocation pulse characteristics in free-tailed bats. Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology **195**:923-934.

Viscido SV, Parrish JK, Grunbaum D. 2004. Individual behavior and emergent properties of fish schools: a comparison of observation and theory. Marine Ecology Progress Series **273**:239-249.

Voigt CC, Kingston T. 2016. Bats in the Anthropocene. Pages 1-9 in Voigt CC, and Kingston T, editors. Bats in the Anthropocene: conservation of bats in a changing world. Springer Open, Berlin.

Voigt CC, Phelps KL, Aguirre LF, Schoeman MC, Vanitharani J, Zubaid A. 2016. Bats and Buildings: The Conservation of Synanthropic Bats. Pages 427-462 in Voigt CCK, Tigga, editor. Bats in the Anthropocene: Conservation of Bats in a Changing World. Springer Open, Berlin.

Voigt-Heucke SL, Zimmer S, Kipper S. 2016. Does interspecific eavesdropping promote aerial aggregations in European *Pipistrelle* bats during autumn? Ethology **122**:745-757.

Wakefield A, Broyles M, Stone EL, Harris S, Jones G. 2018. Quantifying the attractiveness of broad-spectrum street lights to aerial nocturnal insects. Journal of Applied Ecology **55**:714-722.

Wale MA, Simpson SD, Radford AN. 2013. Noise negatively affects foraging and antipredator behaviour in shore crabs. Animal Behaviour **86**:111-118.

Wang JH, Fisler S, Swimmer Y. 2010. Developing visual deterrents to reduce sea turtle bycatch in gill net fisheries. Marine Ecology Progress Series **408**:241-250.

Ware HE, McClure CJW, Carlisle JD, Barber JR. 2015. A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. Proceedings of the National Academy of Sciences of the United States of America **112**:12105-12109.

Warren RD, Waters DA, Altringham JD, Bullock DJ. 2000. The distribution of Daubenton's bats (*Myotis daubentonii*) and pipistrelle bats (*Pipistrellus pipistrellus*) (Vespertilionidae) in relation to small-scale variation in riverine habitat. Biological Conservation **92**:85-91.

Wiley RH, Richards DG. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behavioral Ecology and Sociobiology **3**:69-94.

Wright AJ, et al. 2007. Anthropogenic noise as a stressor in animals: a multidisciplinary perspective. International Journal of Comparative Psychology **20**:250-273.

Yahav S, Shinder D, Tanny J, Cohen S. 2005. Sensible heat loss: the broiler's paradox. Worlds Poultry Science Journal **61**:419-434.

Yang XY, et al. 2013. Study of bat flight behavior by combining thermal image analysis with a LiDAR forest reconstruction. Canadian Journal of Remote Sensing **39**:S112-S125.

Yin XY, Muller R. 2019. Fast-moving bat ears create informative Doppler shifts. Proceedings of the National Academy of Sciences of the United States of America **116**:12270-12274.

Zaugg S, Saporta G, Van Loon E, Schmaljohann H, Liechti F. 2008. Automatic identification of bird targets with radar via patterns produced by wing flapping. Journal of the Royal Society Interface **5**:1041-1053.

Zeale MRK, Stone E, Bennitt E, Newson S, Parker P, Haysom K, Browne WJ, Harris S, Jones G. 2014. Improving mitigation success where bats occupy houses and historic buildings, particularly churches. Defra, UK, www.defra.gov.uk.

Zeale MRK, Bennitt E, Newson SE, Packman C, Browne WJ, Harris S, Jones G, Stone E. 2016. Mitigating the impact of bats in historic churches: The response of Natterer's bats *Myotis nattereri* to artificial roosts and deterrence. PLoS ONE **11**:e0152531.

Zhou Y, Radford, A. N., & Magrath, R. D. 2019. Why does noise reduce response to alarm calls? Experimental assessment of masking, distraction and greater vigilance in wild birds. Functional Ecology **33**:1280-1289.

Zwicker E, Fastl H 1990. Psychoacoustics: facts and models. Springer-Verlag, Berlin, Germany.