Impacts of Temporary Habitat Fragmentation on Bats

Designing Effective Mitigation Strategies to Maintain Landscape Connectivity

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Contents

Abstract

Humans' ability to re-engineer the natural world to our own ends is seemingly boundless and the resulting destruction and fragmentation of habitats can lead to devastating effects for biodiversity. The process by which a landscape can be fragmented is well documented however most of the literature centres around permanent alterations to the landscape with temporary habitat fragmentation being far less studied. Temporary fragmentation of habitats may arise as a product of alterations to important habitat features or the introduction of ecological stressors that functionally fragment existing landscapes when they are in operation. In this thesis I explore questions related to the temporary fragmentation of habitats for bats and strategies deployed to mitigated anthropogenic pressures on nocturnal biodiversity. Chapter 2 investigates how the temporary hedgerow removal at a large linear infrastructure projects impacts local bat populations as well as assessing the effectiveness of mitigation measures deployed to maintain landscape connectivity. Whilst the temporary alterations to important habitat features represent a crucial factor when considering habitat fragmentation, anthropogenic activities can create a similar effect by introducing changes that fragment existing landscapes, in chapter 3 we investigate one of these activities in the form of acute noise pollution at music festivals. A well-known and important threat to global biodiversity conservation is artificial light at night, during chapters 4 and 5 we investigate the impact of light pollution in habitats that are important for bat species as well as assessing the effectiveness of mitigation strategies currently deployed in a bid to limit the harmful impacts of light pollution. Lastly in chapter 6 we explore rewilding habitats through nature-based solutions as a gold standard for restoring fragmented landscapes. Overall, this thesis provides an insight into the impact of temporary habitat fragmentation on bats and what we can do about it.

Chapter 1 | General Introduction

Overview of bats

The Chiroptera (bats) are the second-most speciose order of mammals comprising approximately 1,482 extant species (as of November 2023, Simmons & Cirranello, 2024) which makes up almost two thirds of all wild mammal individuals (Greenspoon et al., 2023).

However, despite their prevalence across the natural world, the nocturnal and often cryptic behaviour of bats has meant they are often some of the most difficult organisms to study. As a consequence, approximately 80% of bat species assessed by the IUCN have been highlighted as needing conservation or research attention (Frick, Kingston, & Flanders, 2020).

Bats have a unique combination of adaptations with many possessing sophisticated echolocation capabilities and are the only mammalian group to have achieved powered flight with a number of these characteristics convergently evolving among species. Bats have become highly specialised across the globe allowing them to colonize various and diverse ecological niches. they show considerable variation in roosting habits, diets, echolocation strategies and exhibit a diverse array of social systems varying from small groups to several million individuals (Fenton, 2010). However, in contrast to other mammals of a similar body size, bats are remarkedly long-lived species and share reproductive parallels with much larger organisms, including low fecundity (1-2 offspring per year; Dietz and Kiefer, 2016) as well as long gestation periods and infant dependency (Findley, 1993).

Landscape conservation

The extensive and ongoing re-engineering of the natural landscape often results in habitat destruction and fragmentation which can lead to devastating effects for local wildlife both directly and indirectly (Haddad et al., 2015). Centuries of agricultural intensification and urbanisation have left the UK as the one of the most nature-depleted countries in the world (Burns et al., 2023).

The modification of the natural landscape poses many challenges for biodiversity that are expected to be exacerbated by an increasingly unpredictable climatic future. Understanding the complex interactions between spatial heterogeneity and ecological processes is a key component of landscape ecological studies (Turner, 1989). Landscape ecology not only considers how spatial heterogeneity develops but also how this influences biotic and abiotic processes, including spatial and temporal interactions and exchanges across heterogeneous landscapes (Risser, Karr, & Forman, 1984). By approaching studies on the natural world more holistically by adopting a landscape ecological perspective, insights can be gained into the spatial scale at which the composition and configuration of landscape factors influence both individual and population responses (Jackson & Fahrig, 2012).

Bats are often considered an ideal model group for studying the consequences of landscape composition and modification due to their high mobility and reliance on multiple habitat features roosting and foraging to meet their roosting, foraging and mating requirements throughout the year (Abbott et al, 2012; Presley *et al*., 2019). Bats often utilise resources substantial distances from their roosts and therefore have home ranges larger than would be expected for a mammal of their body mass (Kelt & Van Vuren, 1999; Huang *et al*., 2021). As a result, the structure of a landscape and how this changes over time have significant implications on the location and suitability of both roosts and habitat patches for bats (Boughey *et al*., 2011; Tournant *et al*., 2013; Cable *et al*., 2021). Furthermore, responses of bats to a changing landscape are not only scale-dependent but also species- and guild-specific (Mendes *et al*., 2017; Ferreira *et al*., 2022). The structure and composition of habitat features within a landscape become even more important in fragmented landscapes, such as those commonly found across UK and Europe, whereby linear elements such as hedgerows, treelines, and woodland edges are vital for maintaining connectivity between habitat patches (Verboom & Huitema, 1997; Lesiński, 2008; Boughey *et al*., 2011). However, whilst the high functional connectivity of such habitats results in them being legally protected (e.g., EU Habitats Directive; 92/43/EEC [EC, 1992]), identifying these habitats as specific foraging and commuting routes if often difficult to do in practice and results in many of these features remaining unprotected.

Habitat fragmentation

Habitat fragmentation is one of the most important factors in biodiversity loss worldwide (Gonzalez et al., 2009) and the subsequent reorganisation of the spatial landscape not only affects individuals and their behaviours, but also the population dynamics of communities that rely on key habitat features such as hedgerows or woodlands for important life history traits such as foraging, commuting and dispersal across the wider landscape (Saunders et al., 1991; Krauss et al., 2010; Lindenmayer and Fischer, 2013).

The process by which suitable habitats can be fragmented is well documented and features recognisable components that include an overall loss of habitat, a reduction in its total area and an increased isolation of these habitats blocks across the landscape (Bennett, 1999; Reiter et al, 2013). The movement of individuals between isolated pockets of habitat within a fragmented landscape and the features utilised to achieve this, is becoming ever more important in both supporting the use of dispersed habitats blocks within home ranges and maintaining sufficient gene flow among populations (Abbott et al, 2012).

Extensive linear infrastructure works (e.g. roads, rail, water/powerlines), by their very nature, are often implicated in the fragmentation of habitats across the landscape. These man-made features can prevent the unimpeded movement of species across their home ranges, often leading to more limited dispersal opportunities as well as the potential to accrue additional energetic costs (Berthinussen and Altringham, 2015). Studies into the impacts of linear infrastructure projects increasingly highlight the detrimental effects they pose to biodiversity (e.g. Forman et al, 2003) and whilst much of the work in this area has focused on roads, recent studies are increasingly highlighting the negative impact this type of development has on the activity and movement of insectivorous bats (Berthinussen and Altringham, 2012; Kitzes and Merenlender, 2014; Abbott et al. 2015; Fensome and Mathews 2016

Many of the studies documenting the impacts of anthropogenic activities on habitat fragmentation for bats centre around the negative impacts of permanent fragmentation arising from road building projects (Zurcher et al., 2010; Berthinussen & Altringham 2012; Bennett & Zurcher 2013; Kitzes & Merenlender 2014; Abbott et al. 2015; Fensome & Mathews 2016). Roads are recognised as a significant threat to bat conservation and can impact bats directly as mortality sinks collision or indirectly through the degradation of important habitat features roosts or acting as potential flight barriers (Berthinussen & Altringham 2012; Frick, Kingston, & Flanders, 2020).

Whilst in recent decades the impacts on bats from permanent alterations to important habitat features have been studied, evidence on the impacts of temporary destruction of important bat foraging and commuting habitats is largely absent. Temporary fragmentation of habitats is a common occurrence across a range of development projects where it is common for linear habitat features such as hedgerows to be temporarily altered or removed for construction works to take place. As a result, these projects have the potential to sever extensive tracts of important ecological features, creating barriers to dispersal across the landscape. Due to the paucity of research on this form of impact and the fact that these features are expected to be reinstated to their former condition, little regard is given to this form of habitat fragmentation or how it impacts the favourable conservation status of bats with these areas.

In addition to the temporary fragmentation of landscapes that arise as a product of alterations to (or removal of) important habitat features, a range of anthropogenic activities have the potential to illicit a similar effect by introducing changes that functionally fragment existing landscapes during their operational stages, for example when wind turbines or lights are switched on. Using this definition of temporary habitat fragmentation allows the collation of a number of crucial areas of active conservation research as well as those that have not been extensively studied in regard to landscape connectivity of bat species.

Examples of temporary fragmentation in this context may include events or activities that significantly increase disturbance over a short period of time such as: music festivals, carnivals, sporting events and firework displays, or those that temporarily alter existing commuting and foraging habitats for limited time periods, such as fluctuations in river/stream water levels/quality as a result of drought or mismanagement, or significant changes in traffic volume on minor roads. These examples of events (and those similar) have the potential to further splinter commuting and foraging corridors in an increasingly fragmented landscape, however the effect of such activities are rarely studied. In the next chapter we will explore one of these under researched areas of temporary habitat fragmentation further.

Whilst many examples of temporary habitat fragmentation are understudied this is not true for all areas of bat research, with some examples of temporary fragmentation incorporated into much larger fields of study such as the environmental impacts of wind energy or light pollution (Arnett et al., 2016; Rowse et al., 2016). Understandably these fields incorporate a large body of research that aim to address the impact of these issues on our landscape and ecosystems, whilst also balancing the global priority of developing renewable energy alternatives and more efficient infrastructure in the face of a changing climate.

Harnessing energy from the wind is one of the fastest growing renewable energy sources worldwide and is considered a vital component in the fight against the long-term environmental impacts of fossil fuels (Shukla et al., 2022). However, the development of wind energy is far from environmentally neutral and an increasing number of studies document its impact on wildlife, either through direct mortality (i.e. collisions, barotrauma; Grodsky et al., 2011; Rollins et al., 2012) or indirect detrimental effects on habitat structure and function, temporarily fragmenting the landscape whilst in operation (Arnett 2012; Strickland et al. 2011). Depending on the location and layout of the wind farm, displacement could lead to the fragmentation of the habitat through virtual barriers that cannot be passed, or areas that are very complex to navigate (Rybicki and Hanski, 2013; Gaultier et al., 2023). The population-level impacts are of serious concern when it comes to bat fatalities regardless of the mechanism of death, as a result of a relatively slow natural population growth rate that limits their ability to recover from declines and maintain stable populations (Kunz and Fenton 2005).

In addition to the built infrastructure transforming the landscape around us, the use of artificial lighting at night is also rapidly increasing worldwide (annual rate of increase 6%; Cinzano et al., 2001; Hölker et al., 2010) much of it attributed to rampant urbanisation coupled with population growth and economic development (Hölker et al., 2010; Davies et al., 2012). Natural light cycles regulate fundamental aspects of organism physiology, ecology and behaviour with many species being finely tuned according to the timing, intensity and spectral composition of natural light. As a result, the hidden impacts of artificial lighting and the associated light pollution on biodiversity and ecosystem functioning has become a major concern for both species and habitat conservation (Rich & Longcore, 2006; Navara & Nelson, 2007; Hölker et al., 2010).

Ecological light pollution can affect the natural rhythms and activity patterns of populations with profound implications for individual fitness, sexual selection and reproductive success. This structural and functional biological interference is especially important in nocturnal fauna such as bats who use natural light regimes to synchronize their window of peak activity with environmental variables such as insect abundance (Gaston et al., 2013, 2014). Furthermore, whilst operational artificial lighting elicits a variety of species-dependent attraction/repulsion behaviours that profoundly affect the movement and distribution of populations across multiple spatial scales, condensing species in some areas whilst temporarily fragmenting others (Longcore & Rich, 2004).

Thesis outline

The ability for humans to profoundly change the landscape at a detriment of other species is seemingly boundless and so is our ingenuity at finding solutions to problems that we have created. Whilst many of the anthropogenic stressors on the natural world that lead to permanent fragmentation of habitats have been the subject of years of active research, temporary fragmentation of habitats and methods employed to mitigate these impacts have been research to a lesser extent. The aim of this thesis was to investigate some of the ways human activity can temporarily fragment important bat habitats as well as techniques employed to try and minimise or reverse fragmented landscapes. In chapter 2 I investigated how the temporary hedgerow removal at a large linear infrastructure project impacted local bat populations as well as assessing the effectiveness of mitigation measures deployed to maintain landscape connectivity.

Are festivals bad for bats? Noise pollution arising from music festivals is a source of potentially harmful noise which remains understudied. However, due to their temporary nature there is no specific legislation setting noise limits and there is little guidance to avoid impacting wildlife despite often occurring in areas important for local wildlife such as country parks, adjacent to woodlands and lakes. In chapter 3 I used an experimental survey design assess the impact of festival music on bat activity, disentangling the effect of music from other variables that effects bat activity such as lighting.

ALAN is a global problem with nearly a quarter of the world's land surface impacted by light pollution, a figure that is growing by ~2% per year in both radiance and extent. Bats are particularly susceptible to the detrimental effects of ALAN and as more research on its negative impacts continue to emerge local authorities are expanding the use of more flexible lighting technologies to mitigate impacts of light pollution on biodiversity. In chapters 4 and 5 I undertook studies examining the effectiveness of a number of methods currently deployed in an attempt to limit the impacts of temporary habitat fragmentation caused by light pollution in habitats that are important for both humans and bats.

Human efforts to return ecosystems to a favourable natural condition are often frustrated by conflicting aims of the surrounding populations and inadequate knowledge of historic ecology or baseline conditions. As a result, we are increasingly looking towards nature-based solutions for limiting our pressure of global resources and restoring ecologically degraded systems. In chapter 6 we explore the effectiveness of using nature-based solutions to unfragment landscapes by investigating the responses by bats from the reintroduction of a famed ecosystem engineer, the beaver.

CHAPTER 2 | Assessing the effectiveness of mitigation strategies designed to limit the impacts of temporary hedgerow removal on bats.

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Abstract

Bats are particularly sensitive to the many varieties of habitat loss and fragmentation that arise as a result of anthropogenic pressures on the natural world. Despite this, much of the research undertaken into the effects of habitat fragmentation arising from large linear infrastructure development is focused on permanent changes to the landscape. Throughout the construction phase of a development, it is common for linear habitat features that are important for a bats ability to disperse across the landscape to be temporarily altered or removed. However little regard is given to how long it takes for these features to be reinstated or the effectiveness of strategies employed to maintain landscape connectivity during these periods. In a multi-year study conducted along a large linear infrastructure project pre and post hedgerow removal we provide evidence of negative effects of hedgerow removal on Rhinolophus spp. activity of which none of the installed temporary bat flyway designs provided measurable benefits in mitigating potential impacts on severing bat commuting routes compared to no intervention at all. We demonstrate that the methods deployed to try and limit the harmful impacts of hedgerow removal on bats do not maintain landscape connectivity any better than leaving the gaps open and therefore should not be used a justified mitigation strategies for large infrastructure projects.

Introduction

Bats (Chiroptera) are particularly sensitive to the loss and fragmentation of habitat due to several life history traits. These include a home range larger than would be expected for a mammal of their body mass (Kelt & Van Vuren, 1999), the need to travel between habitats to meet their roosting, foraging and mating requirements throughout the year (Abbott et al, 2012), as well as living at low densities with patchy distributions making them more susceptible to local extinctions (Fensome and Mathews, 2016).

Furthermore, bats have a long-life expectancy and late maturation, which coupled with a low fecundity rate (1-2 offspring per year; Dietz and Kiefer, 2016) results in populations that are heavily dependent on adult survival (Medinas et al., 2013).

Despite this, studies into the effects of habitat fragmentation on bats as a result of large linear infrastructure projects are limited and largely centre around the negative impacts of permanent fragmentation arising from road building projects (Zurcher et al., 2010; Berthinussen & Altringham 2012; Bennett & Zurcher 2013; Kitzes & Merenlender 2014; Abbott et al. 2015; Fensome & Mathews 2016). Roads can impact bats directly through collision with vehicles, or indirectly through the damage and degradation of roosts and foraging areas and/or the severance of critical flight routes (Berthinussen & Altringham 2012). Mitigation measures that have been adopted to minimise the detrimental impacts on bats include the construction of overpasses (e.g. flight gantries), underpasses, and alterations and divergence to flight paths through habitat modification and improvements (e.g. hedge planting or the provision of artificial roosting sites; Møller et al., 2016; Claireau et al. 2019a; Claireau et al. 2019b).

However, studies on the effectiveness of such mitigation measures for bats are lacking, with most knowledge on the efficacy of deployed solutions based on anecdotic observations and descriptive studies. Only a few recent studies have adequately tested the effectiveness of measures designed to maintain landscape connectivity for bats (e.g. Abbott et al. 2012, Berthinussen et al., 2012, Berthinussen & Altringham 2015) with these studies showing that only a minority of bats used the structures to cross the roads safely. These mitigation structures are only considered successful at reducing the mortality risk and barrier effect of roads if they are used by a large proportion of the local bat populations, therefore a consequence of the insufficient knowledge on their effectiveness, or lack of available alternatives, is that local planning authorities may currently be implementing solutions which are ineffective and insufficient to protect and maintain viable bat populations (Møller et al., 2016).

Whilst the negative impacts associated with permanent alterations of important habitat features is starting to get more attention within the scientific literature, evidence on the impacts of temporary destruction of bat foraging and commuting habitats prior to reinstatement is largely absent. Temporary fragmentation of habitats is a prevalent occurrence across a range of development projects from small-scale housing developments to large linear infrastructure projects such as the installation of facilities (e.g. power lines, water pipes etc.) as well as rail and road construction.

Throughout the construction phase of a development, it is common for linear habitat features such as hedgerows, treeline, ditches etc. to be temporarily altered or removed in order for construction activities to take place after which the feature will be reinstated, for example removing sections of hedgerow to facilitate road access. As a result, these projects have the potential to sever extensive tracts of important ecological features, altering individual and colony behaviour, community composition and population dynamics at both the local and landscape scale. However, as these features are expected to be reinstated to their former condition, little regard is given to time lags involved with re-establishing vegetation or the effectiveness of mitigation strategies implemented on this temporary basis. These mitigation features may therefore be insufficient and ineffective in maintaining a favourable conservation status of bats with these areas.

In Britain all bat species and their roosts are legally protected by both domestic and international law through such legislation as the Habitats Directive (Council Directive 92/43/EEC), the Conservation of Habitats and Species Regulations 2017 and the Wildlife and Countryside Act 1981. As a result, all planned developments must demonstrate that sufficient consideration has been given to avoiding harm or minimising impacts, for example by limiting the timing, location or methodology of works due to be carried out (Berthinussen and Altringham, 2015). In most cases, projects are required to formulate a mitigation and compensation strategy in order to prevent, reduce and compensate for impacts that result in any loss of bat foraging or roosting habitats (Bezombes et al., 2017) and thereby maintain a favourable conservation status.

The North Somerset and Mendip Bats Special Area of Conservation (SAC: Fig. 1) is designated under the Habitats Directive 92/43/EEC, which is transposed into UK law under the Conservation of Habitats and Species Regulations 2010 (as amended) (‘Habitat Regulations). This means that the bat populations supported by this site are of international importance and therefore afforded high levels of protection, placing significant legal duties on decision-makers to prevent damage to bat roosts, feeding areas and the routes used by bats to travel between these locations. The North Somerset and Mendip Bats SAC is made up of 7 component Sites of Special Scientific Interest (SSSI):

- Compton Martin Ochre Mine SSSI
- Banwell Caves SSSI
- Banwell Ochre Mine SSSI
- Brockley Hall Stables SSSI
- King’s Wood and Urchin Wood SSSI

- The Cheddar Complex SSSI
- Wookey Hole SSSI

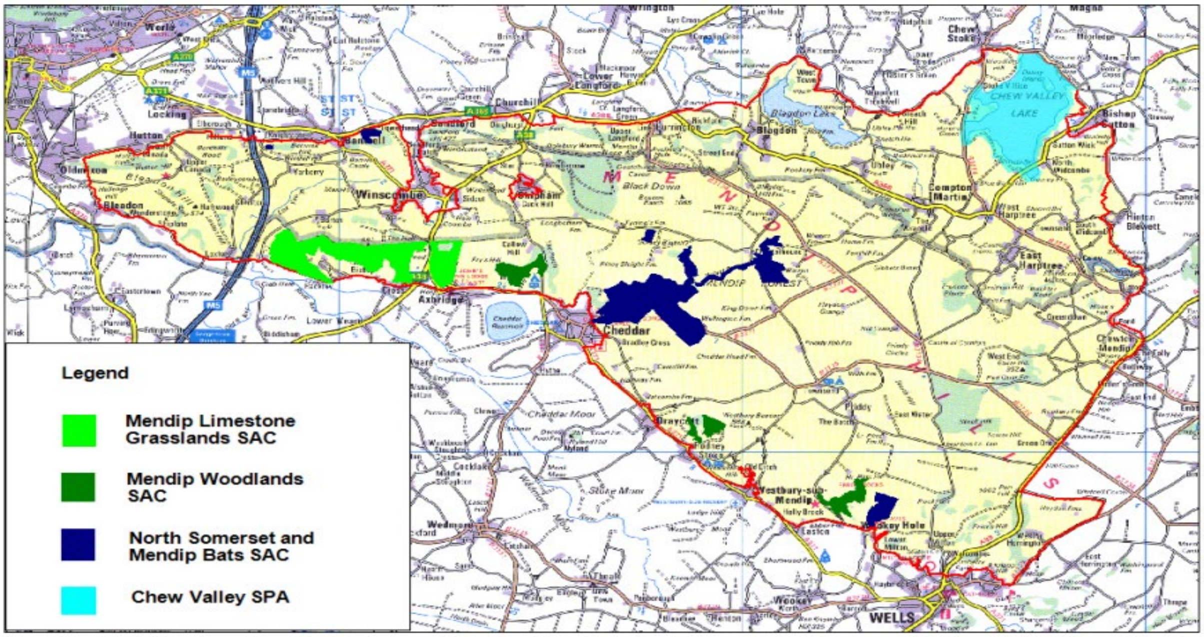


Figure 1. Location of Special Areas of Conservation (SAC) and Special Protection Areas (SPA) within the Mendip Hills Area of Outstanding Natural Beauty (AONB). The North Somerset and Mendip Bats SAC is made up of 7 component Sites of Special Scientific Interest (SSSI) that are designated based on their importance as roosting and feeding sites for the local bat populations.

This complex of sites across south-west England is designated on the basis of the size of the population represented (3% of the UK greater horseshoe bat *Rhinolophus ferrumequinum* population) as well as its good conservation of structure and function having both maternity and hibernation sites. For example, two greater horseshoe bat maternity roosts have been recorded at Brockley Hall Stables SSSI and King's Wood SSSI, maternity and hibernation roosts have been recorded in the Cheddar Complex SSSI and also hibernation roosts at Wookey Hole SSSI. Furthermore, the Mendips provide a range of hibernation sites for lesser horseshoe bats *Rhinolophus hipposideros* in the form of limestone cave complexes (North Somerset Council, 2018).

Table 1: Band width for horseshoe bats (North Somerset Council, 2018).

Band	Greater Horseshoe bat (metres)		Lesser Horseshoe bat (metres)	
	Maternity Roost	Other Roost	Maternity Roost	Other Roost
A	0 – 2200		0 - 600	
B	2201 - 4000	0 - 610	601 - 2500	0 - 300
C	4001 - 8000	611 – 2440	2501 - 4100	301 - 1250

As a result of this designation and following the accumulation of the best available data for these areas, Bat Consultation Zones (BCZ) have been identified and illustrate the geographic area in which horseshoe bats may be found. These are divided into three bands, A, B and C reflecting the density at which these bat species may be found in relation to a known roost site (Table 1: Figure 2).

Band A is shown in orange shading; Band B in yellow and Band C in pale yellow reflecting the decreasing density at which greater and lesser horseshoe bats are likely to occur away from the home roost. Within the BCZ any development with the potential to affect SAC bats must implement appropriate mitigation as dictated by specific guidance documents and survey information (North Somerset Council, 2018).

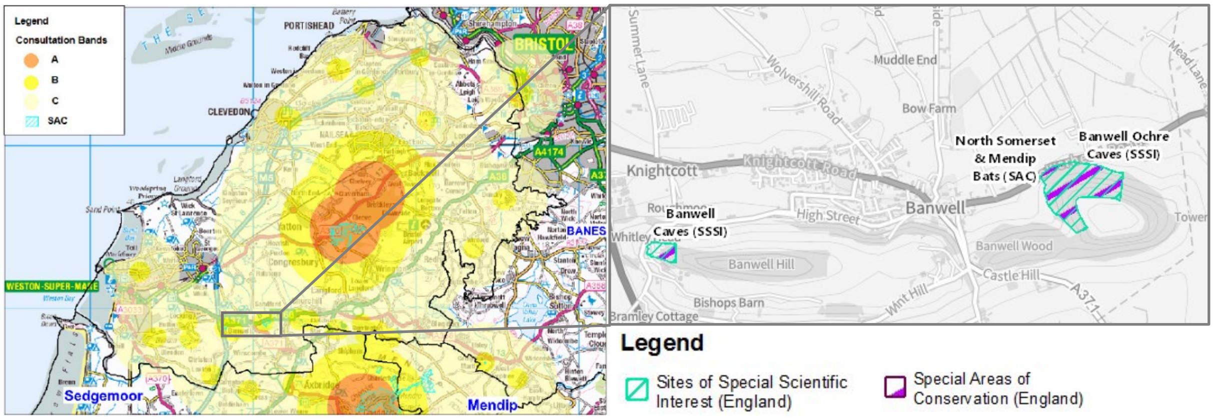


Figure 2. Map detailing Bat Consultation Zones for North Somerset and Mendip Bats SAC highlighting the specific parts of the SAC with relevance to the study site, Banwell Caves SSSI and Banwell Ochre Caves SSSI. Reproduced from OS map data by permission of the Ordnance Survey © Crown copyright 2023

National Grid is constructing a nationally significant infrastructure project to deliver a new 400kV electricity transmission connection between Bridgwater in Somerset and Seabank substation north of Avonmouth. The Environmental Statement and Habitats Regulations Assessment (HRA) for the project site identified potential for impacts to *R. hipposideros* and *R. ferrumequinum* associated with the North Somerset and Mendip Bats Special Area of Conservation (SAC) and the Mendip Limestone Grasslands SAC. The potential for impacts relate to the construction phase of the 400kV underground cables section of the development with runs for approximately 8.5km through the Mendip Hills AONB (Fig. 4).

The temporary loss of habitats resulting from the cable installation (ground clearance and hedge removal) in combination with the proximity of these works to the SACs identified a potential impact on horseshoe bats and hence National Grid committed to providing construction phase mitigation. Despite the importance of hedgerows for bats being well known, the mechanisms behind this importance are still not well understood. Specific aspects of field boundary structure are important for different bat species, corresponding to how different species utilise field boundaries, based on their echolocation and morphological adaptations (Jacobs and Bastian, 2016; Lacoeuilhe et al., 2018). Hedgerows support a diverse array of invertebrate prey items for bats (Merckx et al., 2009; Graham et al., 2018; Froidevaux et al., 2019), as well as offering shelter from wind and predators (Jones et al., 1995; Verboom and Spoelstra, 1999). For species with quiet or high frequency echolocation calls that attenuate quickly in air (e.g. *Rhinolophus* spp.; Altringham, 2011), these linear features may also act as navigational aids allowing them to travel across the landscape and are often one of the most important features in their home ranges (Foxley et al., 2023).

To our knowledge, no study has investigated the effects of temporary bat flyways in mitigating potential impacts on severing bat commuting routes (i.e. hedgerows) and associated bat activity, despite the commonplace removal of hedgerow to facilitate development works. Here we investigate the relationship between flyway design and hedgerow gap length on *Rhinolophus* spp. activity, with the aim of assessing the effectiveness of this mitigation approach and establishing other variables that may influence bat activity in these areas. We hypothesised that bats would respond positively to bat flyway designs compared to hedgerow gaps with no mitigation deployed, but that activity would be lower than activity measured pre hedgerow removal. We also predict a greater decrease in bat activity with increasing hedgerow gap length.

Materials and Methods

Passive acoustic monitoring was conducted at the National Grid Hinkley Point C Connection project site in southwest England between July 2018 and September 2021 (Fig.3) This study was carried out under ethical approval by the University of the West of England Animal Welfare and Ethics Sub Committee (licence no: 210716: AWESC: R189) under strict recommendations and guidance from government licensing departments Natural England. Each monitoring period was undertaken using eight acoustic bat

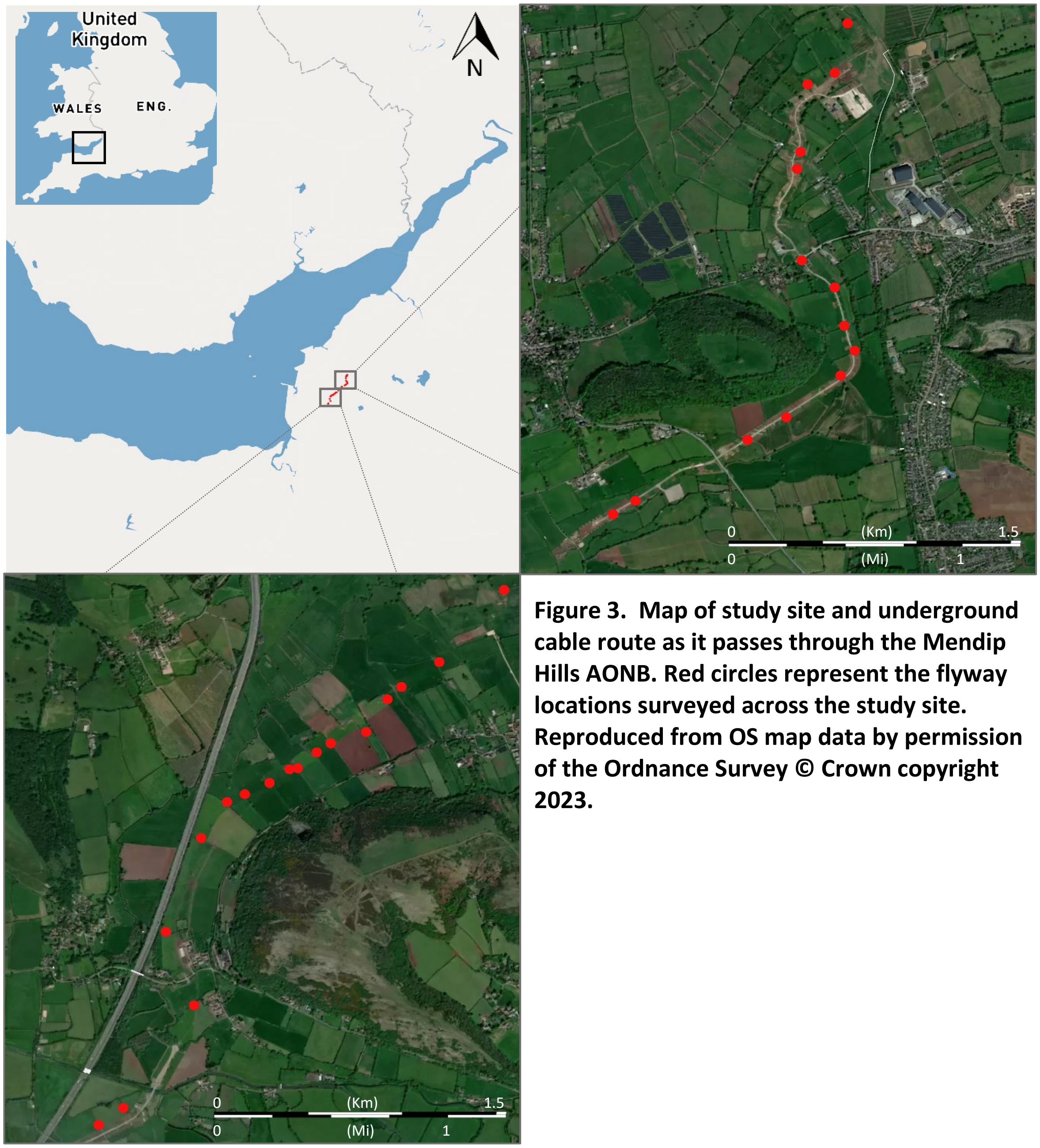
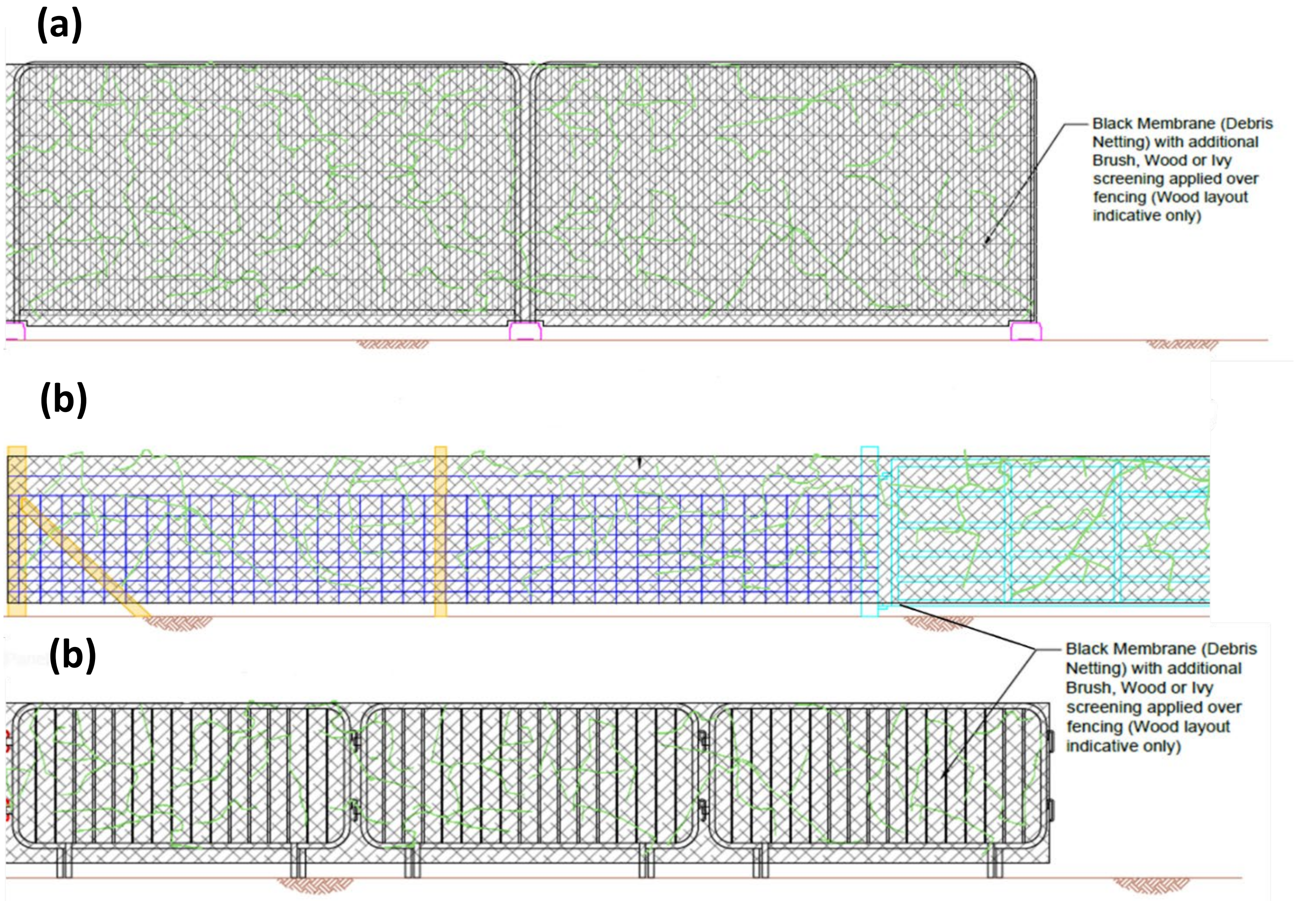


Figure 3. Map of study site and underground cable route as it passes through the Mendip Hills AONB. Red circles represent the flyway locations surveyed across the study site. Reproduced from OS map data by permission of the Ordnance Survey © Crown copyright 2023.

detectors at 48 fixed locations along the proposed cable route (Fig. 3) prior to the constructional phase of the development, commencing in July 2018 and repeated each subsequent month up to and including September 2018. Acoustic monitoring was then repeated using the same timetable during the operational phase of construction from July 2021 to September 2021 when sections of hedgerow has subsequently been removed and replaced by bat flyway gates or no flyway gate.

The size of the gap created as a result of hedgerow removal at the project site depends on the angle at which the cable route intersects with the hedgerow and ranges between 38m and 148m (mean = 64.5m, SD = 26.1m). While it is acknowledged that bats can cross gaps in linear habitat, it is widely accepted that most UK species prefer not to and even small gaps (e.g. <5m) can drastically affect the probability of bats crossing (BTHK, 2018; Claireau et al., 2019b). To mitigate impacts of severing potential commuting routes, the gaps arising from hedgerow removal would be spanned with temporary bat flyways of different designs, prior to reinstatement of hedgerows. Treatment designs consisted of fencing of different heights covered in netting with additional vegetation applied over the fencing in order to simulate a hedgerow. It was anticipated that the additional texture and width of these designs would allow bats to still echolocate effectively whilst also providing an element of shelter.

Treatment designs that were installed for removed hedgerow sections consisted of either flyway design 1 (n=3), tall 2m Heras panels covered in black membrane debris netting with additional brush, wood or ivy screening applied over the fencing (Fig. 4a) or design 2 (n=25), a short 1.2m crowd control barrier panel fencing or post and rail fence covered in black membrane debris netting with additional brush, wood or ivy screening applied over the fencing (Fig.4b). Flyway design 3 represented areas where hedgerow had been removed but no flyways were installed (n=3). The corresponding hedgerow gap for flyway design 1 averaged 48.7m (SD = 10m), for flyway design 2 gaps averaged 60.8m (SD = 21.2m) and for flyway design 3 gaps averaged 110.7m (SD = 26.4m).



Black Membrane (Debris Netting) with additional Brush, Wood or Ivy screening applied over fencing (Wood layout indicative only)

Black Membrane (Debris Netting) with additional Brush, Wood or Ivy screening applied over fencing (Wood layout indicative only)

Figure 4. Bat flyway designs installed at removed hedgerow sections across project site. (a) Flyway design 1 consists of a tall 2m Heras panels covered in black membrane debris with additional brush, wood or ivy screening applied over the fencing. (b) Flyway design 2 consists of a short 1.2m crowd control barrier panel fencing or post and rail fence covered in black membrane debris with additional brush, wood or ivy screening applied over the fencing.

The static monitoring locations were non-random as micro-siting was determined by the location of potential impacts (temporary loss of hedgerows) from the proposed cable route of the development. Monitoring locations were spread across a stretch of agricultural grassland that runs for 8.5km past areas of woodland in an approximate NE-SW direction. Each detector was deployed on a monthly basis for five consecutive nights after which the detectors would be moved to the next series of monitoring locations. In this way 8 acoustic bat detectors would cover the 48 monitoring locations every 30 days for a total of 90 days. Specific monitoring locations with the same deployment were orientated away from each other as much as possible ensure a collection of independent samples.

Field work was conducted in suitable conditions in accordance with Bat Conservation Trust guidance (2023; sunset temperature 10°C or above, no rain or strong wind). Mean nightly temperatures (°C) were recorded using thermometers within the bat detectors and mean nightly wind speed (mph) and total nightly rainfall (mm) were obtained from Met Office weather stations (http://www.metoffice.gov.uk) within 10 km of the site. As sites were surveyed on a continuous 5-night rotation, there may have been occasions where these conditions were not met, however as all monitoring locations are within a maximum distance of 8km of each other they would all experience similar local weather conditions, limiting any effect of weather and date.

Bat activity was recorded for 30 min before sunset to 30 min after sunrise using Anabat Express Bat Recorders (Titley Scientific, Brendale, QLD, Australia) positioned at the edge of the bat flyway gates. Pre-construction and during-construction monitoring locations were matched using GPS coordinates recorded using in-built GPS modules within Anabat Express Bat Recorders. Echolocation calls were analysed in Anabat Insight v.1.9.2 (Titley Scientific, Brendale, QLD, Australia) and identified manually using call parameters as described in Russ (2012). Number of bat passes per night per monitoring location was used as an index of relative bat activity with a single bat pass identified as a continuous sequence containing two or more echolocation pulses from a passing bat (Walsh and Harris, 1996). Bat passes from multiple bats were identified using distinguishable differences in pulse interval and/or peak frequency of overlapping echolocation pulse sequences. Calls were grouped into two species group: *R. ferrumequinum* and *R. hipposideros*, with all other species not included in subsequent analysis. We fitted bat activity as the dependent variable and included the fixed effects of treatment design (a factor with four levels: pre hedgerow removal, flyway design one, flyway design two and no flyway), distance to roost, flyway length , temperature, rain and wind. We included survey ID (a unique number for the specific deployment round at each flyway location) as a random effect in final models.
All analyses were performed in R v.4.0.4 (R Core Team, 2021) using the significance level $P < 0.05$. Relationships between different treatment flyway designs and bat activity were assessed by comparing the number of bat passes recorded per night at each monitoring locations featuring tall flyway design one, short design two or no flyway pre hedgerow removal activity. We analysed log transformed bat pass count data with generalized linear mixed effect models (GLMMs), with a Poisson family using the *glmmTMB* R Package (v1.0.1; Brookes et al., 2017). We followed the backwards step-wise model selection method to find the most parsimonious, yet best-fit model for the data (final model; Bolker et al., 2009). We removed terms sequentially from a more complicated model when likelihood ratio tests (LRT) were non-significant and retained significant terms in the final model. We present effect sizes and

standard errors for final models and post-hoc contrast test results in the text as *z*-statistics and *P*-values obtained using the *emmeans* package (v1.4–1; Lenth et al., 2023). We validated final models by simulation using the R package *DHARMa* (v.0.2.0; Hartig, 2024) using residual plots to check for overdispersion, heteroscedasticity and zero inflation.

Results

A total of 2947 bat passes belonging *Rhinolophus* spp. were recorded during the 90 days nights of monitoring. The majority of echolocation recordings belonged to *R. hipposideros* (1946 passes; 66%) with *R. ferrumequinum* making up the remaining 34% (1001 passes) of recordings.

			Bat Activity (passes)	
R. hipposideros				
Fixed Effects		**Estimate (± s.e)**	***z*- value**	***P* value**
Treatment			2.54	<0.0001***
Pre vs *Tall Flyway Design* 1		-1.04(±0.40)	-2.60	0.009**
Pre vs *Short Flyway Design* 2		-1.16(±0.16)	-7.19	<0.0001***
Pre vs *No Flyway*		-1.83(±0.65)	-2.82	0.005**
Tall Flyway Design 1 vs *Short Flyway Design* 2		0.13(±0.42)	0.30	0.766
Tall Flyway Design 1 vs *No Flyway*		0.79(±0.76)	1.05	0.295
Short Flyway Design 2 vs *No Flyway*		0.67(±0.66)	1.01	0.314
Rain		-0.08(±0.05)	-1.67	0.094
Distance to Roost		-0.22(±0.08)	-2.66	0.008**
Random Effects	**Variance**	**Std Dev.**		
Survey ID (*N*=90)	0.10	0.32		
R. ferrumequinum				
Fixed Effects		**Estimate (± s.e)**	***z*- value**	***P* value**
Treatment			2.53	<0.0001***
Pre vs *Tall Flyway Design* 1		-0.56(±0.32)	-1.74	0.082
Pre vs *Short Flyway Design* 2		-1.30(±0.19)	-6.93	<0.0001***
Pre vs *No Flyway*		-2.24(±0.85)	-2.62	0.009**
Tall Flyway Design 1 vs *Short Flyway Design* 2		0.75(±0.36)	2.09	0.036*
Tall Flyway Design 1 vs *No Flyway*		1.68(±0.90)	1.85	0.064
Short Flyway Design 2 vs *No Flyway*		0.93(±0.87)	1.07	0.283
Rain		-0.09(±0.05)	-1.77	0.076
Distance to Roost		-0.20(±0.08)	-2.51	0.012*
Random Effects	**Variance**	**Std Dev.**		
Survey ID (*N*=90)	5.834e-1	2.415e-05		

Table 2. Final model estimates and standard errors (± s.e), *z*- and *P*- values for fixed effects included in generalized linear mixed models and *post-hoc* comparisons relating bat activity to treatment flyway design (pre hedgerow removal vs treatment one, two or no flyway), rain and distance to roost, including variance and standard deviation (Std Dev.) of random effect terms.

We found statistically significant effects of hedgerow removal on bat activity for both *R. hipposideros* and *R. ferrumequinum* with activity being consistently lower for all flyway designs compared to activity surveys undertaken pre hedgerow removal. *R. hipposideros* activity was an average of 74.3% lower at removed hedgerow sections that featured tall flyway design 1 (Table 2; Fig. 5), an average of 77.2% lower at short flyway design 2 (Table 2; Fig. 5), and an average of 84.1% lower when no flyway was in place at all (Table 2; Fig. 5), compared to activity surveys undertaken pre hedgerow removal. We found no significant difference in *R. hipposideros* activity between any of the three flyway designs. *R. ferrumequinum* activity was an average of 73% lower at removed hedgerow sections that featured short flyway design 2 (Table 2; Fig. 2) and an average of 80% lower when no flyway was in place at all (Table 2; Fig. 2), compared to activity surveys undertaken pre hedgerow removal. However, in contrast to *R. hipposideros,* we only found marginally significant differences in *R. ferrumequinum* activity at tall flyway design 1 (46.6% decrease; Table 2; Fig. 2) compared to pre hedgerow removal activity levels which represented a significant difference in *R. ferrumequinum* activity between flyway design one and two. In addition, we found a significant effect of the distance to known roost sites, with bat activity for both *R. hipposideros* and *R. ferrumequinum* decreasing the further away the flyway location was situated from roost sites (Fig. 6).

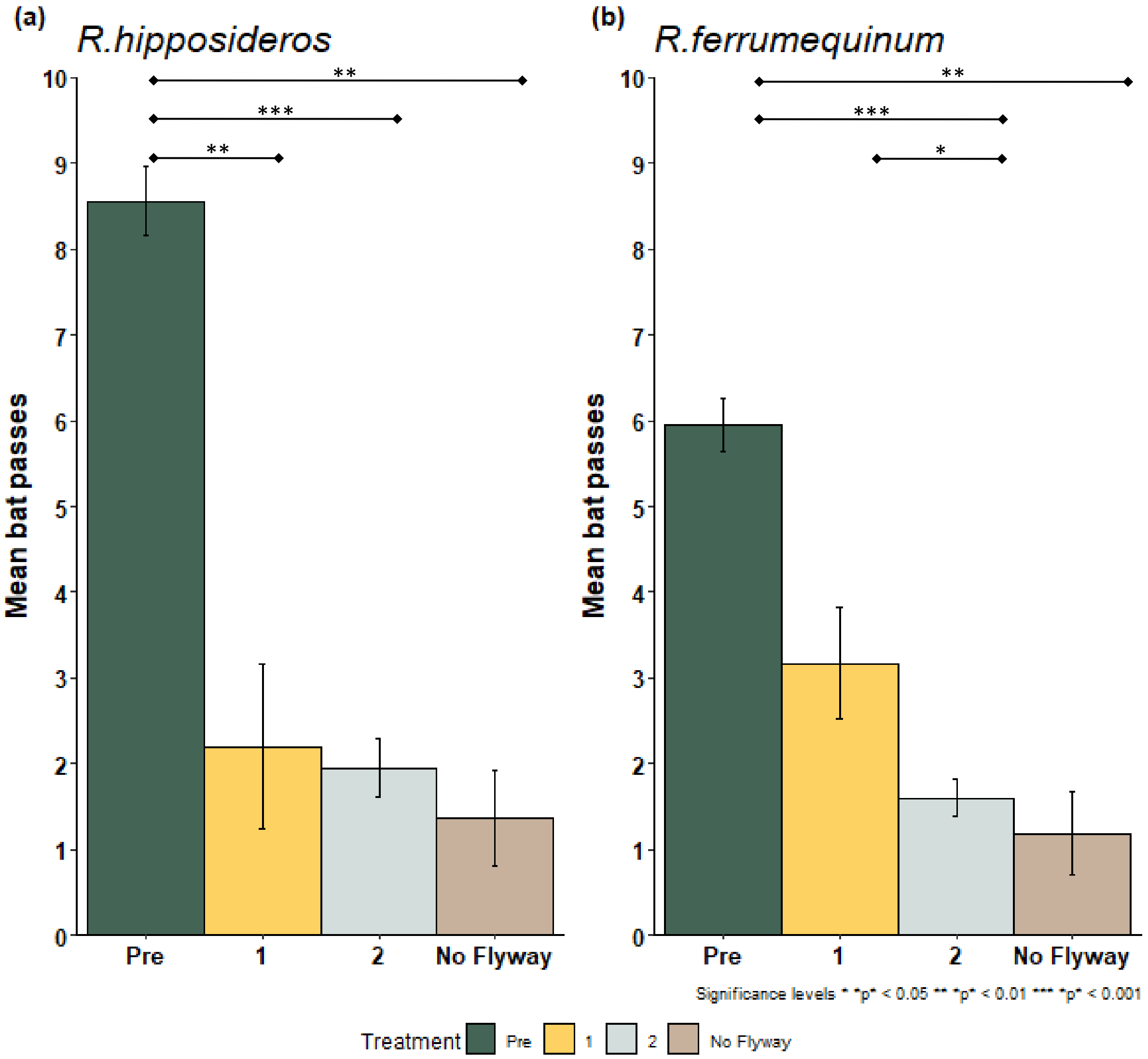


Figure 5. Bat activity (mean bat passes) by (a) *R. hipposideros* and (b) *R. ferrumequinum* at experimental flyway locations pre hedgerow removal and post hedgerow removal. Post hedgerow removal is represented by three treatment conditions corresponding to bat flyway designs one (tall) and two (short) and no flyway gate. Data is presented as mean ± SEM with significant within-subject differences during post hoc tests highlighted.

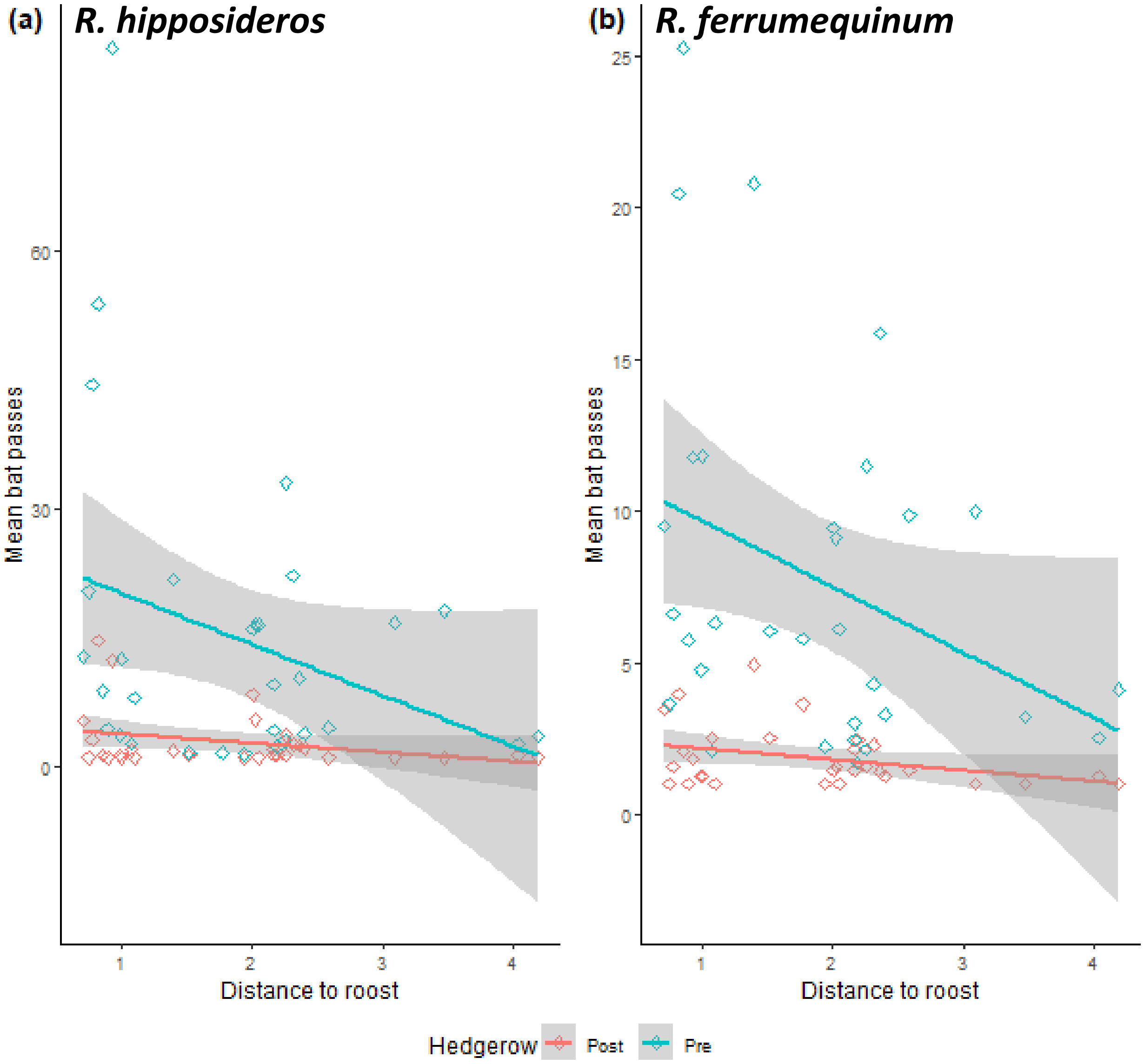


Figure 6. Bat activity (mean bat passes) by (a) *R. hipposideros* and (b) *R. ferrumequinum* at experimental flyway locations with differing distances to roost pre hedgerow removal and post hedgerow removal. Data is presented as mean with a linear regression trend line and confidence displayed in grey.

Discussion

To our knowledge, no study has investigated the effects of temporary bat flyways in mitigating potential impacts on severing bat commuting routes (i.e. hedgerows) and associated bat activity. Here we show that the removal of hedgerow sections to facilitate construction works had a significant effect on *Rhinolophus* spp. activity and this decrease was not mitigated through the installation of bat flyway gates of either design. Our results demonstrate that current methodologies deployed as safeguarding measures to limit the impacts of temporary hedgerow removal do not adequately mitigate negative effect leading to a degradation of functional connectivity across the landscape.

Our results show that activity for *Rhinolophus* spp. was consistently lower for all flyway designs compared to activity surveys undertaken pre hedgerow removal. This change in behaviour post hedgerow removal represents a significant or marginally significant decrease in activity for all flyway designs and shows that the installation of temporary bat flyways does not provide any benefit in limiting the harmful effects of linear habitat feature fragmentation. For both *R. hipposideros* and *R. ferrumequinum,* activity levels for both flyway design 1 (tall) and 2 (short) did not differ significantly from locations where no flyway was installed at all. This indicates that bats no longer identified these areas as having any benefits of the previous hedgerow but instead experienced these as hedgerow gaps regardless of what design was deployed. These findings support previous studies indicating the importance of hedgerow structure for *Rhinolophus* spp. (Ransome, 1996; Finch et al., 2020; Foxley et al. 2023). For *Rhinolophus* spp., activity is related to the physical structure of linear commuting features with tall, overgrown hedgerows being an important component of the landscape characteristics in their home range (Ransome, 1996). In addition, Finch et al., (2020) and Foxley et al. (2023) found that the number of trees within a linear feature was the most important aspect of field boundary structure for *R. ferrumequinum* and correlated with the highest rate of activity.

In agricultural landscapes, short-range echolocator species, such as *Rhinolophus* spp., mainly rely on linear features for commuting from their roost to foraging patches, and hedgerows with greater height, roughness and width may act as better acoustic landmarks (Limpens & Kapteyn, 1991; Froidevaux et al.,2019a). Furthermore, it is likely that *Rhinolophus* spp. favour foraging along tall outgrown hedgerows due to high prey availability. Tall hedgerows have found to be associated with greater abundance of dipterans and increased diversity of insect families, particularly moth abundance of specific guilds at both larval and adult stages a major food source for both *R. ferrumequinum* and *R. hipposideros* (Vaughan, 1997; Facey et al., 2014; Staley et al., 2016; Froidevaux et al., 2019b). This importance of height in linear features for *R. ferrumequinum* is supported to some degree by the findings of the current study, as we found a significantly higher activity level at tall flyway design 1 with a height of 2m compared to short flyway design 2 with a height of 1.2m.

We found no significant differences in *Rhinolophus* spp. activity between either of the flyway designs (1 and 2) and no flyway treatment. These results suggest that as the installed flyway designs represented a substantial reduction in both width and height compared to the removed hedgerows, bats experienced these sections as hedgerow gaps as opposed to hedgerows of decreased value. Previous studies in the US have shown that gaps of >2m in linear commuting features can cause bats to turn back either before, or while they are attempting to cross, with the frequency at which bats turn back increasing with the size of the gap (Bennett and Zurcher, 2013). A study undertaken in the United Kingdom has also demonstrated that a gap of only 10 m may disturb bat commuting (Entwistle et al., 2001). Furthermore, Pinaud et al. (2018) demonstrated that movements of *R. ferrumequinum* were significantly affected by gap width and the probability of bats crossing a gap dropped below 0.5 for gaps larger than 38 m, dropping drastically at gap widths exceeding 50m. As the hedgerow removal programme to enable works at the project site created gaps in linear features that exceeded this length (mean = 64.5m, SD = 26.1m), and the flyway designs that were deployed were not effective in maintaining bat activity, there is potential for the scheme to significantly alter connectivity for bats around the SACs. Additionally, this degradation of linear features may have associated impacts that could compromise the capacity of designated roost sites within the SAC namely Banwell Bone Caves SSSI and Banwell Ochre Mines SSSI. A study by Froidevaux et al. (2017) found that over larger scales, *R. ferrumequinum* colony size in the UK is positively related to density of linear features and therefore a reduction in this density may have knock on effects on the colony sizes in these roosts considering the duration in which it takes a hedgerow to reach a mature structure. For example, a common Hawthorn dominant hedgerow may take 7 years to become a 3m high hedgerow (Jones et al., 2002).

Lastly, we found a significant effect of the distance to roost on bat activity for both *R. hipposideros* and *R. ferrumequinum* with activity decreasing the further each monitoring location was away from the roost. This effect was more evident for bat activity recorded pre-hedgerow removal compared to post hedgerow removal which likely reflects the decrease in activity overall at all hedgerows due to the increase in what bats see as fragmented commuting corridors. The decrease in post -hedgerow bat activity in close proximity to the roost sites is particularly concerning as this may indicate that the construction enabling works to have led to an overall degradation of the roosts near the project site.

In the UK boundary features such as hedgerows are routinely removed to enable construction works to take place and currently no bat mitigation is formally advised for types of habitat fragmentation that are 'temporary' in nature. Our study highlights the extent of the impacts on bats in areas that have been designated as Special Areas of Conservation or Site of Special Scientific Interest and therefore receive higher levels of protection than elsewhere in the country. We also demonstrate that the methods deployed to try and limit the harmful impacts of hedgerow removal on bats do not maintain landscape connectivity any better than deploying no bat flyways. Whilst our study focused on the effects on *Rhinolophus* spp. due to the location of known roosts and associated statutory designations within close proximity, it is likely that other bat species are also negatively impacted by the removal of hedgerow sections, particularly species adapted to forage in cluttered environments (e.g. *Myotis bechsteinii*) that prefer large, overgrown field boundaries (Toffoli, 2016).

Acknowledgments

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CHAPTER 3 | Assessing the impact of festival music on bat activity.

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Abstract

Sound is a critical component of an animal's habitat, where it is used to glean important environmental information from their surroundings. The modification of natural soundscapes due to the global rise in anthropogenic noise pollution over recent decades can have serious negative impacts on species fitness and survival. Nocturnal species such as bats are reliant on sound for many aspects of their life history and are therefore highly sensitive to anthropogenic noise. Music festivals are a source of unregulated and potentially harmful, acute noise pollution however they have become ubiquitous across our landscapes throughout the summer months and are increasingly being held in settings important for wildlife. Using an experimental approach, we provide the first evidence of negative impacts of music festivals on bat activity in a habitat that represents a typical festival setting i.e. woodland edge. We found that loud music playback alone can reduce the activity of bats even in the absence of other anthropogenic factors commonly associated with music festivals such as lighting and habitat disturbance. Activity of *Nyctalus/Eptesicus* spp. was reduced along woodland edge habitats exposed to loud music whereas no effect was recorded for *Myotis* spp., *P. pygmaeus* and *P. pipistrellus* compared to quiet nights. We also provide the first evidence of the spatial scale of negative effects from festival music on activity for *P. pygmaeus* as well as highlighting differential responses between cryptic species.

Synthesis - In light of the paucity of research or guidance into acute noise impacts on nocturnal biodiversity, we outline the potential negative impacts of music festivals for bats. We show that music alone can reduce the activity of bats even in the absence of other anthropogenic factors commonly associated with music festivals which could potentially fragment important habitats for certain species, leading to a degradation of functional connectivity across the landscape.

Introduction

Throughout the natural world animals use acoustic cues to glean important environmental information from their surroundings. Environmental sound is a critical component of an animal's habitat, informing them of key resources such as food availability (Moss et al., 2006; Page & Ryan, 2006), eliciting anti-predator responses (Corcoran et al., 2009; Suzuki, 2011, Roca et al., 2016), aiding spatial orientation and navigation (Moss et al., 2006) and finding conspecifics and potential reproductive partners (Wenrick Boughman & Wilkinson, 1998; Duquette et al., 2019). As a result, modification of these natural soundscapes can have serious negative impacts on species fitness and survival, particularly in human-dominated environments.

The increase in urban development, resource extraction and transportation networks in the terrestrial environment have resulted in a global rise in anthropogenic noise over recent decades (Shannon et al., 2016). Anthropogenic changes to the acoustic environment include both chronically elevated ambient sound levels (e.g. traffic noise) and increases in acute high-intensity noise events (e.g. fireworks). These not only increase sound pressure levels within the local environment but can also differ from naturally occurring sounds in their frequency composition, spatial and temporal distribution and diurnal dynamics (Warren et al., 2006). Increases in man-made noise have created new soundscapes that can hinder an animals' ability to recognise and differentiate between natural acoustic cues in their environment as well as changing or disrupting active communication between individuals (Francis and Barber, 2013). This can result in attentional shifts and distraction away from correct information processing (Chan and Blumstein, 2011; Dominoni et al., 2020), masking of territorial and predatory alarm calls caused by a decreased ability to discriminate target stimulus (Chan et al., 2010; Nelson et al., 2017; Templeton et al., 2016; Dominoni et al., 2020) and hindrance of foraging capabilities due to misleading sensory pollutants provoking a inappropriate maladaptive response (Schaub et al., 2008; Purser and Radford, 2011; Luo et al., 2015; Dominoni et al., 2020). Furthermore, increased anthropogenic noise can reduce the distance over which acoustic signals can be perceived, reducing the functional connectivity of a landscape and exacerbating population level impacts posed by habitat fragmentation and wildlife responses to human presence (Barber et al., 2010; Kight and Swaddle, 2011; Francis and Barber, 2013).

Insectivorous bats, whether using echolocation, passive listening strategies or communicating between individuals, are reliant on sound for many aspects of their life history and therefore are particularly sensitive to anthropogenic ecosystem effects involving noise (Schnitzler and Kalko, 2001; Siemers and Swift, 2006). Anthropogenic noise can have a drastic impact on the ability of a bat to process their own signals as well as acoustic cues from their environment. Any subsequent changes in bat biology (e.g. malnutrition) and population dynamics can indicate habitat degradation and may allow bats to serve as important bioindicators for quantifying the ecological effects of noise pollution (Jones et al., 2009; Stahlschmidt & Brühl, 2012). In particular, noise pollution can have deleterious species-specific consequences on bats foraging capabilities depending on the mechanism of disturbance as well as the context and sound encountered (Luo et al., 2015). Some bats that regularly adopt a gleaning foraging strategy (e.g. *Plecotus* spp. and some *Myotis* spp.) rely on passive listening of prey-generated sounds, may be at risk from noise disturbance through mechanisms such as acoustic masking (Luo et al., 2015; Dietz and Kiefer, 2016). This process, whereby surrounding anthropogenic sounds interfere with the detection or recognition of a target prey sound, may hinder foraging due to prey-generated sound overlapping spectrally with anthropogenic noise (Schaub et al., 2008; Siemers and Schaub, 2011). In contrast, bat species who solely use echolocation emit calls that are generally higher in frequency than anthropogenic noise sources and therefore only some species who echolocate at lower frequencies (i.e. sonic spectrum, <20kHz) may be sensitive to acoustic masking (Luo et al., 2015). This may seem to suggest that bat species that echolocate at higher frequencies are immune to the effects of acoustic masking. However, the ability for bats to successfully analyse reflected echoes can also be impacted by anthropogenic noise and depending on the type of sound and environment in which they are encountered, changes in the spectral and temporal composition of reflected echoes (e.g. high frequency parts of the sound are more sensitive to transmission loss) can result in calls that are still vulnerable to masking (Stilz and Schnitzker, 2012).

Within a natural soundscape, a flexible responses of echolocation call structure may be particularly useful in the presence of both abiotic (e.g. flowing water; Gomes et al., 2021) and biotic noise sources (e.g. sounds of other animals; Gillam & McCracken, 2007) and has been observed in response to local environmental conditions such as proximity to prey (Griffin, 1958), presence of rain (Geipel et al., 2019) or amount of vegetative clutter (Kalko & Schnitzler, 1993; Obrist, 1995). This behavioural plasticity in echolocation call structure has also been recorded in response to artificial changes in ambient noise levels however, this has only been observed in response to chronically elevated ambient noise levels (e.g. Gillam and McCracken, 2007; Luo et al., 2016; Hage et al., 2013, 2014) as opposed to acute high-intensity noise events. Anthropogenic noises often constitute a novel, acute and often inconsistent source of disruption that can change in its characteristics as it travels across the landscape resulting in soundscapes that bats are ill-equipped to deal with. Previous studies have shown that noise pollution from sources such as road traffic (Schaub et al, 2008; Siemers and Schaub, 2011; Finch et al., 2020), passing trains (Jerem & Mathews, 2021) and industrial activities (Bunkley et al., 2015) can negatively impact both bat activity and important behaviours such as foraging.

Furthermore, the impact of anthropogenic noise is not limited to animals that rely intrinsically on sound and may constitute a source of disturbance through more general mechanisms such as reducing individual's attention (distraction) or acting as an unpredictable aversive stimulus that induces an avoidance response (Romero, 2004; Wright et al., 2007). For foraging animals, anthropogenic noise is a stimulus that requires additional allocation of cognitive resources (i.e. attention) and therefore may decrease the faculties available for tasks such as prey detection, navigation and decision making (Dukas, 2004; Chan and Blumstein, 2011).

Unlike noise produced by most human activities (e.g. traffic noise, industrial machinery, construction) in which the lowest possible sound level is the most desirable from a management perspective, noise pollution that arises as a result of entertainment such as outdoor music festivals is required to be at an audible level for humans that makes the events both viable and enjoyable (Parnell and Sommer, 2018). Music festivals are therefore a source of potentially harmful, acute anthropogenic noise which remains understudied. Furthermore, due to their temporary nature there is no specific legislation setting noise limits for audience exposure to noise at events in the UK (HSE, 2021) and there is little guidance for festival organisers as to the limit to set in order to avoid impacting wildlife. This is of particular concern due to the increasing number of both small and large-scale music events that are taking place annually (e.g. approx. 975 events in the UK in 2019; AIF, 2021) which often occur in areas important for local wildlife such as country parks, adjacent to woodlands and lakes.

To our knowledge, no study has experimentally tested the effect of loud music on free-living bat communities along woodland edge habitats or assessed the duration of impacts induced by music playback. Whilst there is a paucity in research on the impacts of loud music on bat communities, previous studies have recorded a significant decrease in successful drinking attempts by bats at remote desert waterbodies subjected to music (Domer et al., 2021) as well as significant delays in dusk emergence of bats roosting in a church priory adjacent to a local music festival (Shirley et al., 2001). In this study we used an experimental approach to assess the impact of loud music on bat activity in woodland edge habitat in order to disentangle any potential music impacts from other variables commonly present within a music festival setting e.g. light pollution, large crowds, other anthropogenic noise sources such as vehicles or generators. We compared activity levels of four bat species/groups (*P. pipistrellus, Pipistrellus pygmaeus, Nyctalus/Eptesicus* spp. and *Myotis* spp.) in response to loud music, assessing the impact and effect durations of music playback in addition to any potential avoidance behaviour. We hypothesised that bats would respond negatively to loud music according to species-specific differences in foraging strategy and echolocation call frequency. We predicted that activity would be reduced for all bat species with the greatest reduction recorded in species who rely more heavily on gleaning foraging strategies (i.e. *Myotis* spp.) due to spectral overlap between music frequencies and prey-generated sound (Schaub et al. 2008). Furthermore, we predicted that there would be a notable reduction in activity of *Nyctalus/Eptesicus* spp. that is not recorded in other fast aerial-hawking species (i.e. *Pipistrellus* spp.) due to the lower frequency at which *Nyctalus/Eptesicus* spp. echolocate and the potential for acoustic masking by loud music during the treatment cycle (Luo et al., 2015).

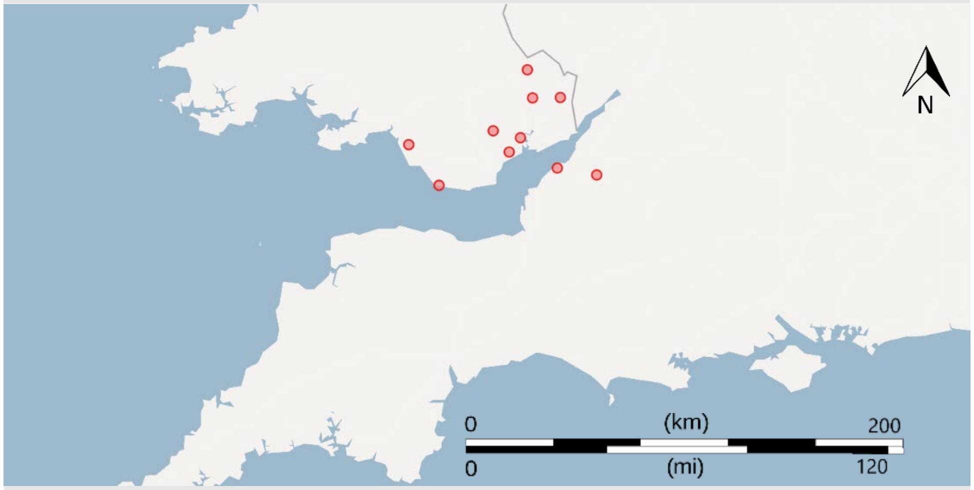
Materials and Methods

Acoustic experiments were conducted at 10 broadleaved woodland edges in south west England and south Wales between August and September 2021 (Fig.1). This study was carried out under ethical approval by the University of the West of England Animal Welfare and Ethics Sub Committee (licence no: 210716: AWESC: R189) under strict recommendations and guidance from government licensing departments Natural England and Natural Resource Wales. Each before-after-control-impact (BACI) experiment lasted for two nights and comprised of a single quiet (control) treatment on night one followed by loud music playback on night two. This design was used to study the effect of music on bat activity compared to quiet control nights alongside within-night variability during periods of ambient background noise (no music playback) and active music playback. Sites were located within dark semi-natural landscapes that were analogous to common festival locations and consisted of woodland edge and adjacent grassland or pasture habitat with sites separated by a minimum of 5km to ensure collection of independent samples.

Music broadcast during treatment nights consisted of five songs from five different genres featuring differing tempos and frequencies commonly emitted at a music festival (Appendix 1). One minute was selected from each of the songs and these segments were stitched together in two cycles of five minutes to form a total 10-minute medley of music (average F_{max} 15.5 kHz). Treatment cycles were repeated 5 times per night starting at sunset and consisted of 10 minutes of active music playback and 10 minutes of ambient background noise (average 42.82dB ± 2.50 SD) each separated by two minutes in which no bioacoustic recordings were undertaken so as to ensure clear delineation of treatment conditions. In order to ensure direct comparisons, the duration and program of recording periods was consistent between control and treatment nights.

Music cycles were played using a single portable wireless speaker (Partybox 310, JBL, Harman Audio, USA) that had an effective frequency response accuracy of 32.2 Hz - 19.1 kHz and could be operated at max volume (104.4 dB SPL) for >2 hours without recharging batteries. The speaker was positioned within woodland edge habitat on a tripod 1 m from the ground and 2 m from the woodland (defined as an area of continuous canopy dominated by trees >5 m in height; JNCC, 2010). Music volume was set at 100 dB (average 98.74dB ± 4.61 SD) 1 m from the speaker and 1.8 m from the ground and was calibrated before and after each experimental night using a sound level meter (ANSI S1.4 TYPE2 Meter, Soonda. Ltd, China). In lieu of any specific UK-based regulation on maximum event noise allowance, this decibel level represents a +4 dB increase over the threshold in which ‘Risk to hearing’ warnings are advised and comparable to noise levels experienced at music festivals. Field work was only conducted in suitable conditions in accordance with Bat Conservation Trust guidance (i.e. sunset temperature 10°C or above, no rain or strong wind). Mean nightly temperature (°C), mean nightly wind speed (mph) and mean nightly humidity (%) recorded on a weather station (Davis Vantage Vue 6250UK) positioned in open ground <10m from experimental woodland edge.

(a) Study sites surveyed across south west England, and south Wales, UK. Reproduced from OS map data by permission of the Ordnance Survey © Crown copyright 2016.



(b) Top view of standardized speaker and static ultrasonic detector (SD) experimental set up at woodland edge survey locations.

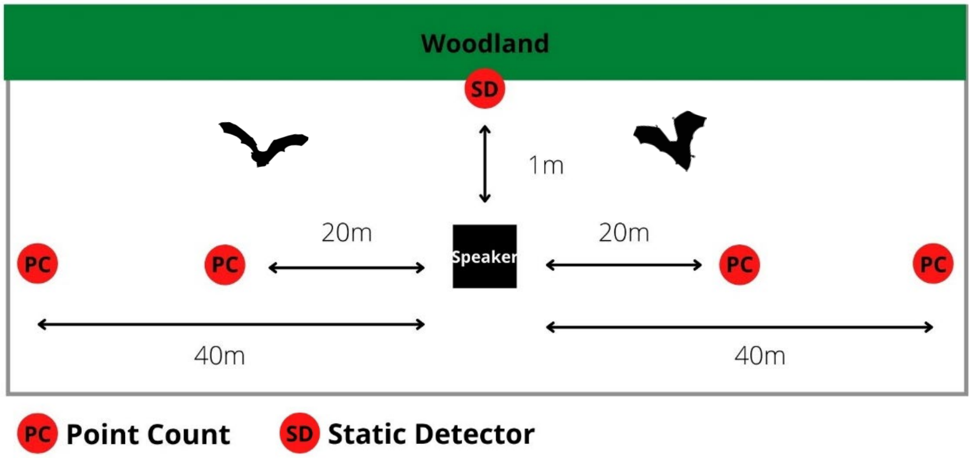


Figure 1. (a) Location of study sites surveyed within the south west of England and south Wales, UK, (b) a top view schematic of standardized speaker and point count locations with associated ultrasonic microphone experimental set up.

Bat activity was recorded for two hours starting at sunset using Anabat Swift Full Spectrum Bat Recorders (Titley Scientific, Brendale, QLD, Australia: triggered .wav recording; sample rate 500 kHz; minimum frequency 10 kHz; maximum frequency 250 kHz; minimum event time 2ms) positioned along the woodland boundary with omnidirectional microphones orientated away from the woodland understory. In order to study the impacts of music over a range of distances and decibel levels, point counts (i.e. ultrasound sampling at fixed position for predetermined time period) were also undertaken at 20 m (average dB 67.65 ± 2.69 SD) and 40 m (average dB 57.97 ± 3.78 SD) from the speaker using Anabat Swift Full Spectrum Bat Recorders (Titley Scientific, Brendale, QLD, Australia) with detector order being randomized between positions. Incremental distances of 20m were chosen, as previous research has shown that anthropogenic noise sources can affect bat activity at least 20m from noise source location (See Finch et al., 2020). Bat calls were recorded during music playback for three minutes per point count during four out of the five music treatment cycles conducting during each survey. Echolocation calls were analysed in Anabat Insight v.1.9.2 (Titley Scientific, Brendale, QLD, Australia) and identified manually using call parameters as described in Russ (2012). Mean number of bat passes per treatment night was used as an index of relative bat activity with a single bat pass identified as a continuous sequence containing two or more echolocation pulses from a passing bat (Walsh and Harris, 1996). Bat passes from multiple bats were identified using distinguishable differences in pulse interval and/or peak frequency of overlapping echolocation pulse sequences. Calls were grouped into four species/species groups: *P. pipistrellus*, *P. pygmaeus*, *Myotis* spp. and *Nyctalus/Eptesicus* spp.) with rarely recorded species such as *Rhinolophus ferrumequinum*, *Rhinolophus hipposideros* and *Plecotus* spp. (<1 % of overall bat activity), not included in subsequent analysis. Relative feeding activity of *P. pipistrellus* was examined by identifying diagnostic terminal phase calls (feeding buzzes) within recordings calculated as the ratio of feeding buzzes to total number of passes per species per night (buzz ratio: Vaughan et al., 1997). A buzz ratio of one indicates that on average every bat pass contains a feeding buzz.

All analyses were performed in R v.4.0.4 (R Core Team, 2021) using the significance level $P < 0.05$. Repeated measures general linear models (RMGLMs) were used to test for differences between environmental variables with treatment conditions fitted as a within-factor effect. As there were no significant differences in mean nightly temperature ($F_{1,9} = 0.14$, n = 10, $P = 0.72$), mean nightly humidity ($F_{1,9} = 0.01$, n = 10, $P = 0.93$) and mean nightly wind speed ($F_{1,9} = 1.65$, n = 10, $P = 0.23$) these variables were excluded from further analyses to achieve model simplification. To examine the effect of music treatment on bat activity (number of bat passes per night per species/species group), RMGLMs were fitted for counts of bat passes for each species group with log transformed data to meet assumptions of homoscedasticity and normality. Music treatment was fitted as a within-factor effect with 2 levels corresponding to the treatment (i.e. quiet control, music). RMGLMs with log transformed data were fitted for *P. pipistrellus, P. pygmaeus* and *Nyctalus/Eptesicus* spp. whilst *Myotis* spp. were tested using Friedman's non-parametric ANOVA due to their non-normal distribution despite data transformation attempts. *P. pipistrellus* were then assessed to examine the effect of music playback of bat feeding activity using Friedman's non-parametric ANOVA due to their non-normal distribution despite data transformation attempts. RMGLM statistics are presented as F and p values with effect sizes presented as Cohen's d or Kendall's W in the case of non-parametric ANOVAs.

To examine the effect durations of music playback on bat activity, RMGLMs were fitted for bat pass counts for each species/species group between periods of ambient background noise and music playback during treatment cycles (recorded during the music treatment nights only). Music playback was fitted as a within-factor effect with two levels corresponding to treatment condition (i.e. music on, music off). Counts of bat passes for each species group were log transformed to meet assumptions of homoscedasticity and normality.

To assess whether bats were avoiding the woodland edge during music playback, bat pass counts were recorded during point counts at varying distances (20m and 40m) and were examined compared to the speaker location (0m). This level of analysis was limited to *Pipistrellus* spp. as this was the only species group with a sufficient sample size to conduct statistical analysis. Distance was fitted as a within-factor effect with 3 levels corresponding to point count location (i.e. 0m, 20m and 40m). Counts of bat passes were log transformed to meet assumptions of homoscedasticity and normality. RMGLM statistics are presented as F and P values with effect sizes presented as Cohen's d or Kendall's W in the case of non-parametric ANOVAs.

Results

A total of 1,972 bat passes belonging to seven species/species groups were recorded during the 20 nights of monitoring. The majority of echolocation recordings belonged to *P. pipistrellus* (1,326 passes; 67.2%) followed by *P. pygmaeus* (276 passes; 13.9%), *Myotis* spp. (205 passes; 10.4%), *Nyctalus/Eptesicus* spp. (149 passes; 7.6%) with *Rhinolophus* spp. and *Plecotus* spp. <1% of species recorded.

We found significant effects of music on bat activity for *Nyctalus/Eptesicus* spp. between control and treatment nights. *Nyctalus/Eptesicus* spp. activity declined by an average of 47% along woodland edge during music treatment nights compared to quiet nights (*P* = 0.049; Table 1; Fig. 1). During music treatment nights there were no significant differences in *Nyctalus/Eptesicus* spp. activity between periods of music playback and ambient background noise within the treatment cycle (*P* = 0.286; Table 2; Fig. 2).

Table 1. Results for bat activity (mean bat passes) between control (quiet) and music treatments nights of *P. pipistrellus, P. pygmaeus, Nyctalus/Eptesicus* spp. and *Myotis* spp. species from repeated measures general linear models. RMGLM statistics are presented as F and P values with effect sizes presented as Cohen's d or Kendall's W in the case of non-parametric ANOVAs

Species/Species Group	**Bat Activity (passes)**		
	F	***d***	***P***
P. pipistrellus	1.977	0.220	0.193
P. pygmaeus	0.119	0.142	0.738
Nyctalus/Eptesicus spp.	5.156	0.519	0.049*
	F	***W***	***P***
Myotis spp.	0.111	0.011	0.739

There were no significant effects of music treatment on *Myotis* spp. (*P* = 0.739; Table 1; Fig. 1), *P. pygmaeus* (*P* = 0.738; Table 1; Fig. 1) and *P. pipistrellus*. (*P* = 0.201; Table 1; Fig. 1) activity compared to quiet nights. However, during the music treatment nights there were marginally significant reductions in *P. pipistrellus* activity between periods of music and ambient background noise within the treatment cycle (*P* = 0.071; Table 2; Fig. 2). *Pipistrellus pipistrellus* activity declined by an average of 32% during music playback compared to quiet periods.

Table 2. Results for bat activity (mean bat passes) between music playback and silent periods during music cycles on treatment nights of *Myotis* spp., *P. pygmaeus*. and *P. pipistrellus* and *Nyctalus*/*Eptesicus* spp. species from repeated measures general linear models. RMGLM statistics are presented as F and P values with effect sizes presented as Cohen's d.

Species/Species Group	**Bat Activity (passes)**		
	F	***d***	***P***
P. pipistrellus	4.202	0.168	0.071
P. pygmaeus	1.989	0.340	0.192
Nyctalus/Eptesicus spp.	1.288	0.387	0.286
Myotis spp.	0.043	0.061	0.84

We found no significant effects between *P. pipistrellus* activity recorded during point counts undertaken at 0m, 20m and 40m from the speaker (*F* = 0.044, n = 10, *W* = 0.004, *P* = 0.957) and while slight increases in bat activity were recorded at 20m (+ 15.79%) and 40m (+23.69%) from the speaker these were not significant compared to the music source location i.e. 0m (*P* = 1.000 and *P* = 0.672 respectively; Fig. 3). There were no significant effects of loud music playback on *P. pipstrellus* relative feeding activity (buzz ratio) compared to quiet nights (*F* = 0.5, n = 10, *W* = 0.05, *P* = 0.480).

We found significant effects of distance on *P. pygmaeus* activity during point counts undertaken at 0m, 20m and 40m from the speaker (*F* = 5.65, n = 10, *W* = 0.565, *P* = 0.004; Fig. 4). *P. pygmaeus* activity increased by an average of 130.6% at distances of 40m (*P* = 0.014) compared to the music source location, which also represented a significant increase over bat activity recorded at 20m (*P* = 0.033). We found no significant difference in activity levels between point counts undertaken at 20m and those undertaken at the music source location (*P* = 0.181).

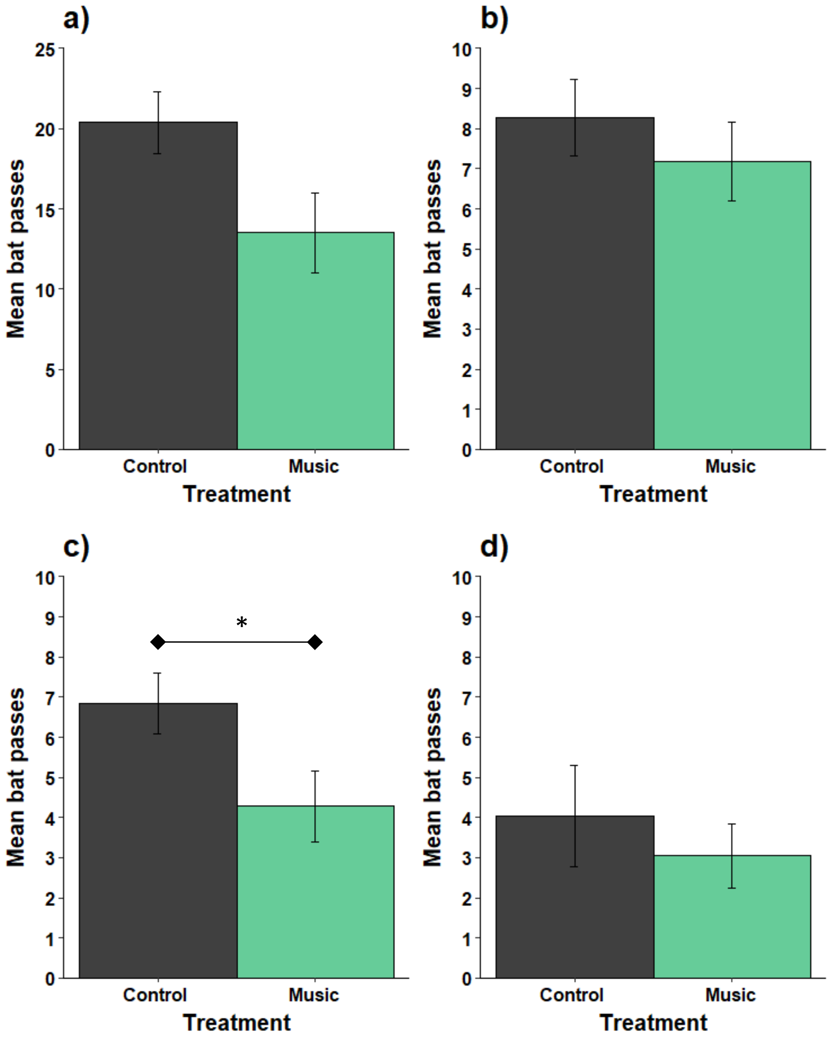


Figure 2. Bat activity (Mean bat passes) for a) *P. pipistrellus*, b) *P. pygmaeus*, c) *Nyctalus/Eptesicus* spp. and d) *Myotis* spp. species during quiet control and music treatment nights. Data are presented as mean ± SEM (Y-axis scaling different between graphs) with significant within-subject differences highlighted.

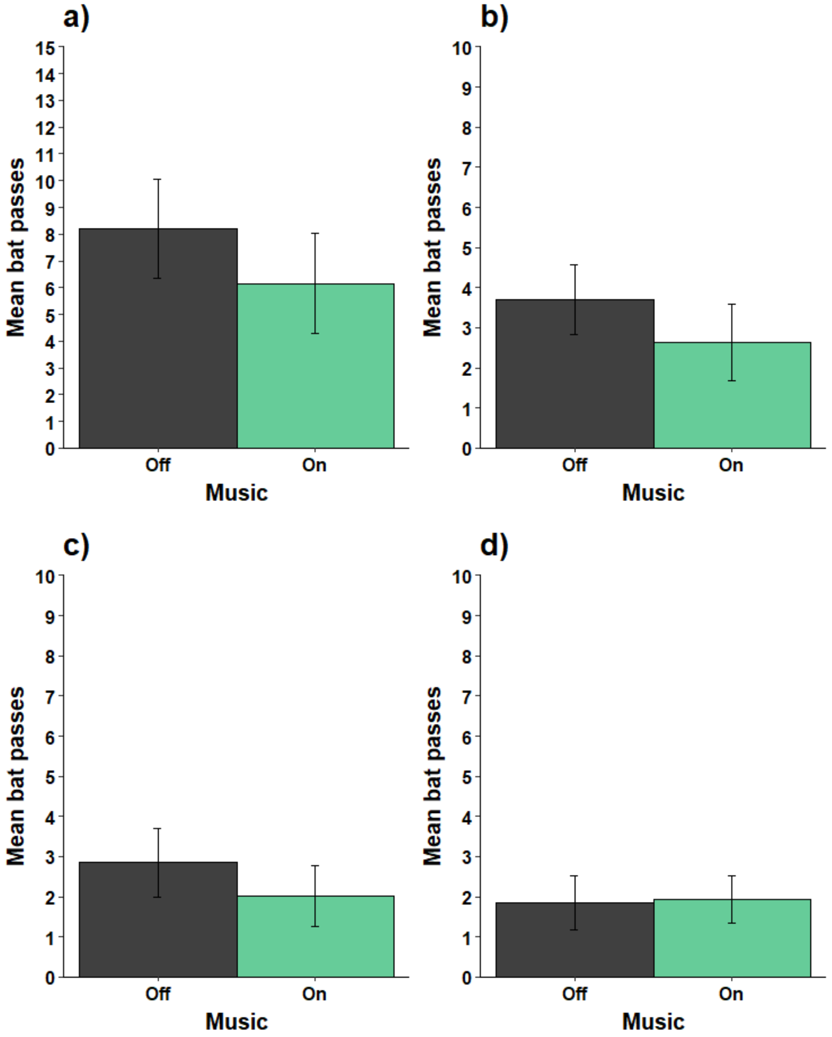


Figure 3. Bat activity (Mean bat passes) for a) *P. pipistrellus*, b) *P. pygmaeus*, c) *Nyctalus/Eptesicus* spp. and d) *Myotis* spp. species between music playback and silent periods during music cycles on treatment nights . Data are presented as mean ± SEM.

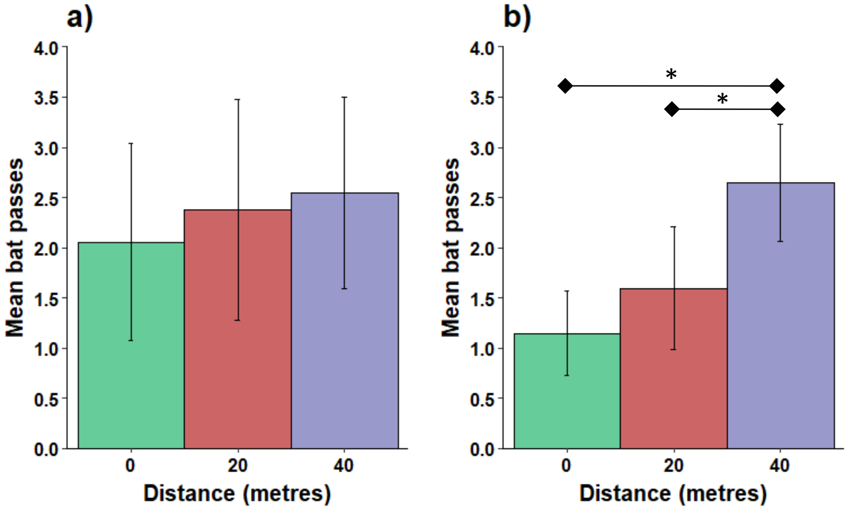


Figure 4. Bat activity (Mean bat passes) of a) *P. pipistrellus* and b) *P. pygmaeus* for point counts undertaken at 0m, 20m and 40m from the music source during music playback on treatment nights. Data are presented as mean ± SEM.

Discussion

To our knowledge this is the first study to experimentally test the impacts of loud music played along woodland edges on the activity of a bat assemblage. This is of particular importance as music festivals are rapidly growing in their scale and extent with ~5.2 million attendees attending close to 1,000 festivals during the 2019 UK season (AIF, 2021), many of which are set in areas that constitute important habitats for local wildlife such as country parks, woodlands and lakes. These globally renowned events make up a considerable part of the UK's £70 billion events industry (BVEP, 2020) and research into the potential impacts to wildlife are critical in securing a sustainable future for festivals that is in step with biodiversity targets. Here we show that loud music had a significant effect on the relative activity of certain bat species using woodland edge habitats. We also highlight species-specific responses in activity by bats dependent on the stage of the experimental cycle and corresponding music playback. Our results demonstrate that loud music played along woodland edges can present a species-specific risk to bats, and potentially other wildlife, and appropriate assessment and mitigation should be implemented during event planning and preparation.

We found that loud music playback alone can reduce the activity of bats even in the absence of other anthropogenic factors commonly associated with music festivals such as lighting and habitat disturbance. We recorded reduced activity for *Nyctalus/Eptesicus* spp. under music treatment conditions compared to quiet control nights, which represented a 47% reduction in activity levels. *Nyctalus/Eptesicus* spp. often emit echolocation calls at a lower frequency than other bats within the study area, particularly during cruising flight when bats are commuting to or from a roost (Jones, 1995). These long duration, low frequency calls can overlap spectrally with anthropogenic noise sources and are therefore sensitive to disruption when travelling through human-dominated landscapes. Whilst other bat species (e.g. *Myotis* spp.) can extensively modulate the frequency of their calls in response to their surroundings (Dietz & Keifer, 2016) the relatively little frequency modulation seen in *Nyctalus/Eptesicus* spp. are a result of a number of factors related to their respective flight morphology, foraging strategy and relative body mass (Jones & Rydell, 1994). Large aerial-hawking insectivorous bats such as *Nyctalus/Eptesicus* spp. have high wing loading and aspect ratios therefore often favour fast flight in open spaces where the increased detection distance and reduced attenuation of low-frequency wavelengths provide a benefit to the species (Norberg & Rayner, 1987; Jones, 1995; O'Mara et al., 2016). Furthermore, whilst *Nyctalus/Eptesicus* spp. are able to switch to using frequency modulated calls whilst searching for very small prey or foraging in clutter, their echolocation calls are optimized for low frequencies in order to receive echoes from their main target prey which comprises larger insect species (Pye, 1993; Jones & Rydell, 1994; Rydell & Arlettaz, 1994). This reliance on low-frequency calls in open habitats can put them at an increased risk of disturbance due to the spectral overlap with anthropogenic noise sources as well as downstream consequences including compromised foraging efficiency, spatial orientation and navigation(Schaub et al., 2008; Luo et al., 2015; Radford & Jones, 2021). Here we found that acute high-intensity noise events such as those witnessed at festivals, has the potential to disrupt echolocation behaviour in certain bat species through mechanism such as to acoustic masking, however, the role of acoustic masking of echolocation calls from anthropogenic noise sources for has not been fully addressed experimentally and there is still some question as to how this mode of disturbance fits alongside other mechanisms (e.g. reduced attention and noise avoidance) and its implications for specific bat behaviours (Luo et al., 2015).

During music treatment nights we found no significant differences in *Nyctalus/Eptesicus* spp. activity between periods of music playback and ambient background noise within the treatment cycle. This suggests that the mechanism of disturbance by loud music may constitute a general avoidance response that extended beyond periods of acute noise disturbance (Romero, 2004; Wright et al., 2007). This avoidance response can have varying magnitudes and stronger aversions can turn into stress responses, which are characterised both behavioural and physiological changes such as increased heart rate or concentration of steroid hormones (McEwen & Wingfield, 2003; Romero, 2004). If the experimental conditions within our study were causing a stress response, this could pose an additional negative impact reducing individual fitness of affected bat species whose echolocation calls overlap in frequency range of anthropogenic noise sources. Furthermore, whilst our experimental study represented a short-term impact and therefore any potential stress responses would be limited in its extent, music festivals over the course of several nights could produce a lasting and damaging stress response.

We did not find any significant effects of music treatment on *Myotis* spp., *P. pygmaeus* and *P. pipistrellus* activity compared to quiet control nights, suggesting that the relative activity of these bats recorded within the study sites were not impacted by loud music. As these species/species groups echolocate at higher frequencies than those found in songs included within our experimental music medley, this suggests that the frequency range of loud music did not mask the echolocation calls of the species present and therefore did not illicit an avoidance response (Luo et al., 2015). However, as the exact interplay between mechanisms of disturbance have yet to be fully understood, it may be that the lack of masking in these species, reduces the combined effect of disturbance mechanisms (i.e. acoustic masking, reduced attention and noise avoidance) resulting in a weaker overall effect but one that may be significant in studies representing larger bat communities or wider range of habitats. The response of these bats to loud music supports findings by Le Roux & Waas (2012) who found that activity of *Chalinolobus tuberculatus* did not decline in response to aircraft noise playback during experimental field studies. On the other hand, these results contrast with Finch et al. (2020) who found that playback of traffic noise in the sonic range (<20 kHz frequency noises) reduced activity for all functional groups of bats studied including species that have markedly different flight heights, speeds, foraging strategies, and with contrasting echolocation patterns (e.g. *Rhinopholus ferrumequinum*, *Nyctalus noctula*, *Myotis spp*. and *Pipistrellus spp*.). A similar response was also reported by Gilmour et al. 2021 who found significant reductions in activity across a range of UK bat species in response to acoustic deterrent playback. The range of effects found included increasing flight speed, reducing tortuosity of their flight paths as well as reduced echolocation call bandwidth and starting frequencies (Gilmour et al. 2021). This variation in response between studies may be illustrative of bats ability to adjust temporal echolocation parameters when encountering anthropogenic noise sources (Song et al., 2019). Such plasticity can be context dependent with both frequency range of stimulus and the acoustic characteristics of emitted pulses affecting the nature and magnitude of response (Tressler & Smotherman, 2009).

The results from the current study seem to suggest that acute loud music within the frequency range encountered at music festivals, has little effect on bat species who echolocate at higher frequencies, However, this finding may be confined to relative activity and not specific behaviours such as feeding or drinking. A number of studies have concluded that noise can specifically impact foraging efficiency (e.g. Schaub et al., 2008; Siemers & Schaub, 2011; Bunkley et al., 2015) even when the experimental noise does not overlap spectrally or temporally with bat echolocation calls (Luo et al., 2015). Furthermore, there is evidence to suggest that noise disturbance can impact the activity and diversity of bat species even when it does not overlap temporally, leading to longer term avoidance of affected habitats (Buxton et al. 2020). Within the current study we did not find any significant differences in feeding activity for *P. pipistrellus* which mirrors the response of loud music on overall activity levels for this species. This response indicates that *P. pipistrellus* are still able to forage in conditions where acute noise pollution is present, potentially a result of their habituation to anthropogenic stressors due to their prevalence within urban environments or a result of their terminal phase calls (feeding buzzes) being of a higher frequency range than those found on music tracks. In contrast to our findings, Domer et al. (2021) found that acute loud music reduced both the overall activity and foraging success of *Pipistrellus kuhlii,* whilst *Hypsugo ariel* showed an increase in unsuccessful drinking buzzes of 57% post-music playback despite no significant variance in bat activity pre and post music. This highlights the potential disconnect between number of bat passes and drinking or foraging success, as well as the species-specific responses to acute noise pollution such as loud music.

There were marginally significant differences in *P. pipistrellus* activity between periods of music playback and ambient background noise within the music treatment cycle . This suggests that *P. pipistrellus* may actively avoid an area during loud music but resume their activity quickly during quieter portions of the evening. Such species-specific differences in the effect duration of noise avoidance responses may constitute a crucial aspect in how festivals impact bats in increasingly wilder settings and should be a focus for future research. This would be of particular importance when considering that a real music festival scenario usually consists of multiple sources of music throughout the day and night with minimal rest periods, creating a heightened noise polluted environment which also has the potential to effect roosting bats.

Lastly, whilst we found no significant effect of distance and dB level on *P. pipistrellus* activity, we did record significant differences in activity levels for *P. pygmaeus* during point counts undertaken at 0m, 20m and 40m from the music source during playback on treatment nights. These results indicate that a reduction in dB level over these distances correlate with increased bat activity and are supported by previous findings from Finch et al. (2020) who reported a significant decrease in bat activity in response to traffic noise playback up to 20m from the speaker. These results give us an indication of the spatial scale of the impacts on *P. pygmaeus,* as well as highlighting differential responses to loud music even between two morphologically similar cryptic species.

Given that music festivals are increasingly being held in places that are important for local wildlife, such as country parks, woodland glades and adjacent to lakes, it is imperative that guidance relating to their planning and implementation is evidence-based and fully protects local biodiversity from any potential negative impacts. Using an experimental approach, we demonstrate that acute noise pollution in the form of loud music can produce species-specific impacts on local bat communities. Whilst many of the bat species do not seem to be too negatively impacted by music playback, possibly due to limited spectral overlap between echolocation and music track frequencies, we found a significant negative impact on *Nyctalus/Eptesicus* spp. activity that extended across the whole survey duration beyond periods of active music playback. Furthermore, our results indicate that some species are able to more readily resume their activity during periods of quiet as well as displaying differential responses to distance and dB level between even cryptic species. Whilst these results may seem to be a positive sign for music festivals, it is important to note that real music festival scenarios include multiple music sources playing consistently over a longer time frame and across a wider area and range of habitats potentially compounding impacts across local bat communities. Further research is needed to understand how this interacts with other anthropogenic stressors found at these events (e.g. lighting displays, recreational pressure on habitats, etc.), if we are to share these habitats with local biodiversity in a sustainable manner.

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CHAPTER 4 | Lighting up our waterways: Impacts of a current mitigation strategy on riparian bats.

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Abstract

Increasing levels of artificial light at night (ALAN) are a major threat to global biodiversity and can have negative impacts on a wide variety of organisms and their ecosystems. Nocturnal species such as bats are highly vulnerable to the detrimental effects of ALAN. A variety of lighting management strategies have been adopted to minimise the impacts of ALAN on wildlife, however relatively little is known about their effectiveness. Using an experimental approach, we provide the first evidence of negative impacts of part-night lighting (PNL) strategies on bats. Feeding activity of *Myotis* spp. was reduced along rivers exposed to PNL despite no reduction in overall bat activity. We also provide the first evidence of negative effects of PNL on both feeding and activity for *Pipistrellus pipistrellus* which has previously been recorded feeding under artificial light.

Despite having considerable energy-saving benefits, we outline the potential negative impacts of PNL schemes for bats in riparian habitats. PNL are unlikely to provide desired conservation outcomes for bats, and can potentially fragment important foraging habitats leading to a breakdown of functional connectivity across the landscape. We highlight the potential dichotomy for strategies which attempt to simultaneously address climate change and biodiversity loss and recommend alternative management strategies to limit the impacts of ALAN on biodiversity.

Introduction

Rapidly increasing urbanisation is regarded as a major threat to global biodiversity and a significant factor in current and future species extinctions (McKinney, 2006; McDonald et al., 2008). Urban expansion can create profound ecosystem changes, including shifts in local climate, habitat loss, fragmentation, and the introduction of ecological stressors such as anthropogenic noise, artificial illumination, disturbance and chemical and physical pollutants (e.g. Markovchick-Nicholls et al., 2008; Francis and Barber, 2013; Stone et al., 2009, 2012, 2015; Russo and Ancillotto, 2015; Voigt et al., 2021).

Artificial light at night (ALAN) associated with urban expansion ranks amongst the most important global threats to biodiversity conservation (Gaston et al., 2014; Gaston, Visser and Hölker, 2015; Davies and Smyth, 2017). ALAN is a global problem with nearly a quarter of the world’s land surface impacted by light pollution (Falchi et al., 2016). Negative impacts of ALAN have been demonstrated in a wide variety of organisms ranging from individual physiological responses to changes in ecosystem functioning which may trigger ecological effects spanning trophic levels (Hölker et al., 2010; Bennie et al., 2016; Knop et al., 2017; Bennie et al., 2018). Artificially lit areas are growing by ~2% per year in both radiance and extent (Kyba et al., 2017), therefore it is imperative to understand the impact of ALAN and test the effectiveness of mitigation strategies to minimise impacts on wildlife.

Nocturnal taxa such as bats are highly vulnerable to the detrimental effects of ALAN due to their evolutionary adaptations for dark environments, likely as a result of protection from diurnal predators, either perceived or real (Rydell and Speakman, 1995; Mikula et al., 2016). Bats exhibit differential sensitivity to light that can be both species and scale dependent (Lacoeuilhe et al., 2014; Stone et al., 2015; Rowse et al., 2018). Some light types, including newer technologies such as white metal halide and LED (e.g. Stone et al., 2015; Russo et al., 2017), can provide increased foraging opportunities for fast-flying bat species due to the accumulation of insects around lights along with a light-induced impairment for insects to evade predation by bats (Minaar et al., 2015; Wakefield et al., 2015, 2018; Voigt et al. 2021). These opportunistic bats may be able to forage and commute through illuminated areas as they are fast-flying, largely feed by aerial hawking on crepuscular prey and are able to escape diurnal predation more effectively (Matthews et al., 2015). These factors when taken together thereby lessen the risk at increased light levels. Overall, most bat species avoid sites that are subjected to ALAN due to its negative effect on roosting and foraging behaviour, the composition and abundance of insect prey sources as well as the increased risk of predation (e.g. Stone et al., 2009, 2012; Davies et al., 2012; Lewanzik and Voigt, 2017; Pauwels et al., 2021). Such light-induced habitat fragmentation can reduce the quality and availability of habitat as well as functional connectivity across the landscape (Azam et al., 2015; Pauwels et al., 2019; Laforge et al., 2019).

Linear habitat features such as waterways are important for bats, both as commuting corridors linking roosts and foraging/drinking areas (Smith and Racey, 2008; Lacoeuilhe et al., 2016; Pinaud et al., 2018); as well as being important foraging habitats in their own right, due to the increased insect biomass associated with riparian vegetation and water surfaces (Lintott et al., 2015; Laforge, 2019; Todd and Williamson, 2019). Urbanisation has increased the amount of light pollution along waterways due to light trespass from buildings as well as an increasing prevalence of security and aesthetic light installations. Despite the ecological importance of waterways, there is a paucity of research on the impacts of ALAN on riparian biodiversity with recent studies only just starting to quantify the extent of light pollution in aquatic environments and its impact on bat behaviour and distribution as well as ecosystem functioning (Russo et al., 2017, 2019; Jechow and Hölker, 2019; Barré et al., 2020). Waterways are particularly important areas for specialist bat species such as *Myotis daubentonii* which rely on these habitats for foraging and represent a genus that has been found to be negatively impacted by ALAN at the local and landscape level (Spoelstra et al., 2018; LaForge et al., 2019; Voigt et al., 2021).

As new research on the negative impacts of ALAN on nocturnal fauna emerges, local authorities are utilising more flexible lighting technologies to both reduce energy consumption in order to address climate change targets and mitigate potential negative impacts of light pollution on biodiversity (Bennie et al., 2014; Azam et al., 2015). Several policy and management responses have been proposed such as altering the spectrum or intensity of artificial lighting, reducing light trespass and the implementation of part-night lighting regimes (Gaston et al., 2012; Spoelstra et al., 2017; Bollinger et al., 2020). Part-night lighting (PNL) involves switching off streetlights during periods of low human activity and has been implemented widely in urban areas throughout Europe, primarily motivated by the need to reduce public expenditure and carbon emissions (Gaston, 2013). However, activity for many nocturnal species (including bats) peaks at dusk which corresponds with high human activity and demand for lighting , therefore the effectiveness of PNL for reducing negative impacts on biodiversity is questionable (Gaston et al., 2012). Simulations of PNL regimes (Day et al., 2015) and studies assessing the effectiveness of existing PNL regimes indicate they fail to mitigate the negative effects of ALAN for most bat species, despite some success for late- emerging species (Azam et al., 2015). However, previous studies have not assessed the impacts of PNL on feeding behaviours, nor have they focused on specific aquatic habitats or bat assemblages. Waterways represent a habitat of particular importance to a number of slow-flying bat species (e.g. *Myotis* spp.) that have echolocation and wing morphology adapted for cluttered, low-light environments, yet these habitats are increasingly subjected to ALAN (Norberg and Rayner, 1987; Stone et al., 2015). Increased light levels around these habitats may compromise crucial foraging areas as well as fragmenting dark corridor networks and limiting functional connectivity. For trawling bats (i.e. those who specialise in foraging over water) such as M. *daubentonii* echolocation plays a crucial role in detecting the water surface and surrounding environment in order to execute safe manoeuvres (Siemers and Swift, 2006; Russo et al. 2012). Under artificial illumination, bats rely more on vision than in the dark which reduces their ability to avoid obstacles (Orbach and Fenton, 2010). This shift in sensory ecology, along with higher potential predation risk could impair their ability to successfully forage which could have severe negative impacts for both individual bats and populations. This is especially important for those species who have low aspect ratios and wing loading (e.g. *Myotis* spp.), traits that correlate with an already heightened extinction risk (Jones et al., 2003).

To our knowledge no study has experimentally tested the effect of PNL on bat communities along waterways in riparian habitats or assessed its impact on specific behaviours such as feeding (despite some studies on the effect of ALAN on bat drinking behaviours, see Russo et al., 2017, 2019). In this study, we used an experimental approach to assess the impact of artificial lighting on bat activity and feeding behaviour in riverine ecosystems. We compared activity levels of four bat species/groups (*Myotis* spp., *Nyctalus/Eptesicus* spp. *P. pipistrellus*, *P. pygmaeus*) under dark (unlit), full-night lighting and different durations of PNL.

We hypothesised that bats would respond to PNL regimes according to species specific adaptations for flight and foraging (Stone et al., 2012; Zeale et al., 2016). We predicted that activity would be reduced during full-night lighting but activity would be higher during PNL for slower-flying species (i.e. *Myotis* spp.) due to the overall reduction in illuminated hours in which bats would perceive an increased predation threat (Rydell and Speakman, 1995). Furthermore, as *Myotis* spp. emerge later from roosts (Jones and Rydell, 1994) there is less potential overlap between bat activity and illuminated hours under PNL compared to full-night lighting. In contrast, we predicted no effects of light treatments on the activity of fast-flying species (i.e. *Pipistrellus* spp., *Nyctalus/Eptesicus* spp.) as operational hours for both PNL and full-night lighting would align with peak emergence and activity for these species (Spoelstra et al., 2017, Russo et al., 2018). In addition, fast-flying species are better adapted to increased light-levels due to their reduced perceived light-dependent predation risk and will often utilise illuminated sites opportunistically (Mathews et al., 2015).

Material and Methods

Lighting experiments were conducted along eight unconnected waterways in south west England (Bristol, Gloucestershire and Somerset; mean river width 5.5 m, SD = 2.39 m, range = 3-10 m, n = 8) between August and October 2020 (Fig. 1a). Each experiment lasted for four nights per site and comprised of a single dark unlit (control) treatment on night one followed by one of three lit treatments whereby lights were switched on at sunset for either 2 hours, 4 hours or for the full night until sunrise. The order of the lit treatments was randomized between sites to control for order effects and sites were separated by a minimum of 10 km to ensure collection of independent samples.

Table 1. Experimental treatment regime conducted at waterways (n=8). The sequence of light treatments was randomized among nights two to five to control for any potential order effects.

Night	Treatment	Description
1	Control (unlit)	Detectors installed at waterway, no lighting treatment
2	LED	Detectors installed, lighting units installed and illuminated for durations of 2-hr, 4-hr or full night. Sequence of lit treatments randomly selected at each site.
3	LED	As night 2 with second randomized light treatment.
4	LED	As night 2 with remaining light treatment.

Sites were located within dark (<0.05 lux) agricultural landscapes consisting predominantly of pasture, semi-natural woodland/scrub and managed grassland. Waterways were illuminated with three portable cool white RL20K LED Floodlights (Right Light, Chesterfield, Derbyshire, UK) that consist of 40 x 3 W high-powered LEDs powered by a 52 Ah Li-ion battery and dimmed to an output of 13,000 lumens (Pulse-width modulation 70 kHz). This LED lamp type was chosen due to its wide commercial usage for outdoor illumination owing to its energy efficiency and perceived benefit to nocturnal biodiversity (Davies and Smyth, 2018; Kyba et al., 2017). The lighting system did not emit any audible nor ultrasonic noise (assessed with Anabat Swift Full Spectrum Bat Recorder for a full-nights illumination) and therefore any potential noise effects as a result of the experimental protocol could be omitted from the study. At each site lights were placed 2 m from the top of the river bank and mounted 3 m above the ground on

(a) Study sites surveyed across south west England, UK. Reproduced from OS map data by permission of the Ordnance Survey © Crown copyright 2016.

(b) A photograph of a typical field site. Three LED street lights are positioned along a waterway illuminating river cross-section under different experimental light treatments.

(c) Top view schematic of standardized lighting column and ultrasonic microphone experimental set up at riverside survey locations.

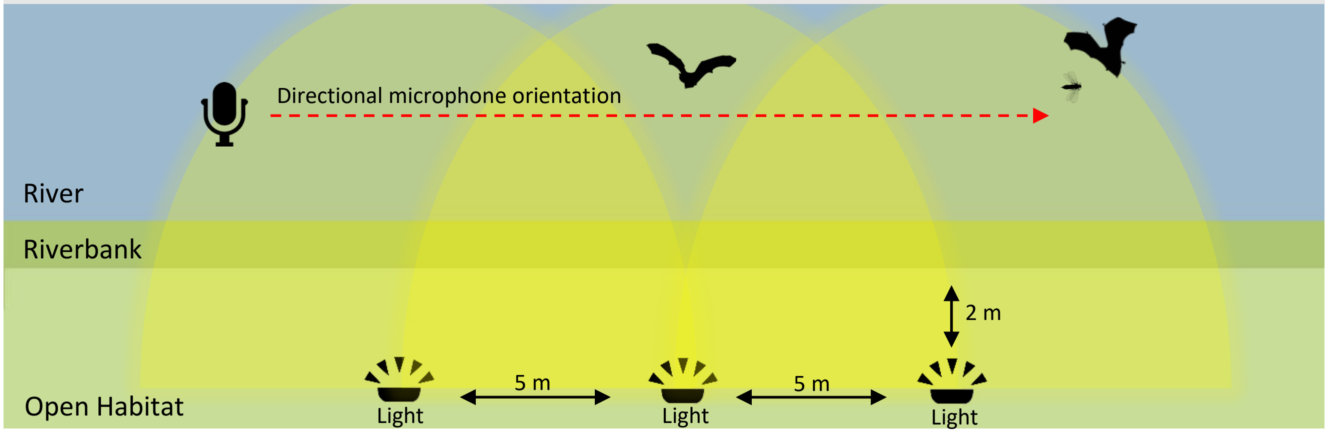


Figure 1. (a) Location of study sites surveyed within the south west of England, UK, (b) a photograph of a typical field site and (c) a top view schematic of standardized lighting columns and ultrasonic microphone experimental set up. Light columns were positioned at a height of 3 m and orientated downward toward river corridor.

portable columns and directed downwards. Light columns were placed 5 m apart from each other and we ensured that the entire cross section of the experimental stretch of river was illuminated. Due to the variation of lighting unit distances and orientations when deployed adjacent to waterways, lamp placement was ascertained based on overall illuminance (lux) (Fig. 1c).

Illuminance (in lux) was measured 1 hour after sunset using a T-10 illuminance metre (Konica Minolta Sensing Inc, Osaka, Japan) held horizontally 2 m from the edge of the river bank and 1 m above the water's surface in front of the lighting columns. Waterways were illuminated to a mean light intensity of 44.8 ± 6.8 lux which is in the range used during previous experiments utilising white LED (Stone et al., 2012; Zeale et al., 2018) and is equivalent to that emitted by street-lighting in public areas in the UK

(Stone et al., 2009). Field work was only conducted in suitable conditions in accordance with Bat Conservation Trust guidance (i.e. sunset temperature 10°C or above, no rain or strong wind). Mean nightly temperatures (°C) were recorded using in-built thermometers within the bat detectors and mean nightly wind speed (mph) and total nightly rainfall (mm) was obtained from Met Office weather stations (http://www.metoffice.gov.uk) within 15 km of each site (mean distance 10.24 km, SD 2.6 km).

Bat activity was recorded from 30 min before sunset to 30 min after sunrise using Anabat Swift Full Spectrum Bat Recorders (Titley Scientific, Brendale, QLD, Australia) with directional microphones orientated centrally down the river corridor to limit recordings from bats flying in adjacent habitats. Echolocation calls were analysed in Anabat Insight v.1.9.2 (Titley Scientific, Brendale, QLD, Australia) and identified manually using call parameters as described in Russ (2012). Mean number of bat passes per treatment night was used as an index of relative bat activity with a single bat pass identified as a continuous sequence from a passing bat containing two or more echolocation pulses within one second of each other (Fenton, 1970; Walsh and Harris, 1996). Bat passes from multiple bats of the same species were identified using distinguishable differences in pulse interval and/or peak frequency of overlapping echolocation pulse sequences. Calls were grouped into four species/species groups: *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus*, *Myotis* spp. and *Nyctalus/Eptesicus* spp. with rarely recorded species such as *Rhinolophus ferrumequinum, Rhinolophus hipposideros, Barbastella barbastellus* and *Plecotus* spp. (total 185 bat passes; 0.7% of overall bat activity), not included in subsequent analysis.

Relative feeding activity of recorded bat species was examined by identifying diagnostic terminal phase calls (feeding buzzes) within recordings calculated as the ratio of feeding buzzes to total number of passes per species per night (buzz ratio) (Vaughan et al., 1997). A buzz ratio of one indicates that on average every bat pass contains a feeding buzz.

All analyses were performed in R v.4.0.4 (R Core Team, 2021) using the significance level $p < 0.05$. Repeated measures general linear models (RMGLMs) were used to test for differences between environmental variables with treatment conditions fitted as a within-factor effect. As there were no significant differences in mean nightly temperature ($F_{3,21} = 0.97$, $n=8$, $P = 0.43$), total nightly rainfall ($F_{3,14} = 0.50$, $n = 8$, $P = 0.69$) and mean nightly wind speed ($F_{3,21} = 1.60$, $n = 8$, $P = 0.22$) across treatments these variables were excluded from further analyses to achieve model simplification. We fitted RMGLMs to examine the effect of light treatment on bat activity (number of bat passes per night per species/species group). Counts of bat passes for each species group were log transformed to meet assumptions of homoscedasticity and normality. Light treatment was fitted as a within-factor effect with 4 levels corresponding to the light treatment types (Unlit, 2-hour, 4-hour and full night). Species/species group were then assessed to examine the effect of lighting treatment of bat feeding activity. RMGLMs with log transformed data were fitted for *Myotis* spp. and *Nyctalus/Eptesicus* spp*.* whilst *P. pipistrellus* and *P. pygmaeus* were tested using Friedman's non-parametric ANOVA due to their non-normal distribution despite data transformation attempts. RMGLM statistics are presented as *F* and *p* values with effect sizes presented as Cohen's d or Kendall's W in the case of non-parametric ANOVAs.

Results

A total of 25,178 bat passes belonging to seven species/species groups were recorded during the 32 nights of monitoring. The majority of echolocation recordings belonged to *P. pygmaeus* (18,119 passes; 71.9%) followed by *P. pipistrellus* (3,837 passes; 15.2%), *Myotis* spp. (1,964 passes; 7.8%), *Nyctalus/Eptesicus* spp. (1,073 passes; 4.3%) with *Rhinolophus* spp. and *Plecotus* spp. <1% of species recorded. A total of 15,491 feeding buzzes were recorded from six species/species groups comprising *P. pygmaeus* (12,736 buzzes; 82.2% buzz ratio 0.70) followed by *P. pipistrellus* (1,206 buzzes; 7.8% buzz ratio 0.31), *Myotis* spp. (1,362 buzzes; 8.8% buzz ratio 0.69), *Nyctalus/Eptesicus* spp. (167 buzzes; 1.1% buzz ratio 0.16) with *Rhinolophus* spp. and *Plecotus* spp. making up the remaining <1% of feeding buzzes recorded.

Bat activity.

We found statistically significant effects of light on bat activity for *Myotis* spp., *P. pygmaeus* and *P. pipistrellus*. *Myotis* spp. activity declined by an average of 71% along waterways under full-night lighting compared to unlit nights (*P* = 0.033; Table 2; Fig. 2a) but did not decline significantly under PNL (2 or 4-hour PNL treatments) compared to unlit nights (2- hours *P* = 0.88 4-hours *P* =0.630; Table 2; Fig. 2a). *Myotis* spp. activity recorded under full-night lighting treatment was significantly lower compared to PNL (2- hours *P* = 0.044; 4-hours *P* =0.011; Table 2, Fig. 2a) with no significant differences between the 2-hour and 4-hour PNL treatments. In addition, we found temporal variation in *Myotis* spp. activity between unlit and lit treatments over the course of the night (Fig. 3). During unlit nights, peak bat activity occurred between 0-2 hours after sunset (35% of mean bat passes) whereas peak bat activity for both the 2-hour and 4-hour PNL treatments corresponded with hours following the lights being switched off (3-5 hours after sunset; 31% mean bat passes and 4-6 hours after sunset; 28% mean bat passes respectively). In contrast, under full-night lighting treatments bat activity was highest 0-2 hours after sunset (32% of mean bat passes) with no further peaks of activity throughout the night.

There was no significant effect of any light treatments on *P. pygmaeus* activity compared to unlit nights. However, significantly more *P. pygmaeus* passes were recorded (+ 164%) under the 4-hour PNL treatment compared to 2-hour PNL (*P* = 0.008; Table 2; Fig. 2c) which also represented an average 191% increase compared to full-night lighting treatments (*P* = 0.026; Table 2; Fig. 2c).

Table 2. Results for bat activity (mean bat passes) and relative feeding activity (mean buzz ratio) of *Myotis* spp., *P. pygmaeus*. and *P. pipistrellus* and *Nyctalus/Eptesicus* spp. species from repeated measures general linear models and within-subject differences during post-hoc comparisons.

	Bat Activity (passes)			**Feeding Activity (Buzz Ratio)**		
***Myotis* spp.**	***F***	***d***	***P***	***F***	***d***	***P***
Treatment	3.040	0.932	0.052	3.923	1.2729	0.023*
Control (Unlit) vs 2 hours		0.032	0.888		0.160	0.692
Control (Unlit) vs 4 hours		0.105	0.630		0.989	0.048*
Control (Unlit) vs Full night		0.544	0.033*		1.410	0.008*
2 hours vs 4 hours		0.130	0.534		0.819	0.103
2 hours vs Full night		0.474	0.044*		1.249	0.018*
4 hours vs Full night		0.619	0.011*		0.550	0.401
P. pygmaeus	***F***	***d***	***P***	***F***	***W***	***P***
Treatment	3.383	0.983	0.037*	3.32	0.415	0.019*
Control (Unlit) vs 2 hours		0.250	0.105			0.068
Control (Unlit) vs 4 hours		0.187	0.233			0.059
Control (Unlit) vs Full night		0.179	0.253			0.017*
2 hours vs 4 hours		0.450	0.008*			0.961
2 hours vs Full night		0.077	0.612			0.281
4 hours vs Full night		0.381	0.026*			0.761
P. pipistrellus	***F***	***d***	***P***	***F***	***W***	***P***
Treatment	2.817	0.969	0.068	3.077	0.440	0.026*
Control (Unlit) vs 2 hours		0.600	0.028*			0.011*
Control (Unlit) vs 4 hours		0.198	0.972			0.690
Control (Unlit) vs Full night		0.539	0.158			0.073
2 hours vs 4 hours		0.874	0.026*			0.196
2 hours vs Full night		0.031	0.369			0.912
4 hours vs Full night		0.755	0.149			0.550

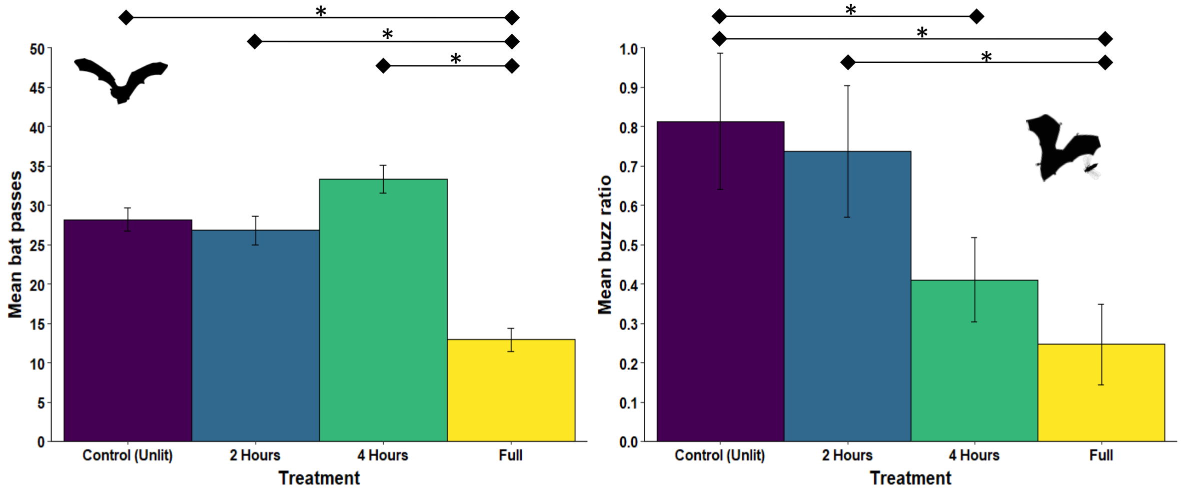
***Nyctalus/Eptesicus* spp.**	***F***	***d***	***P***	***F***	***W***	***P***
Treatment	0.679	0.44	0.575	1.000	0.125	0.392
Control (Unlit) vs 2 hours		0.100	0.658			0.281
Control (Unlit) vs 4 hours		0.315	0.205			1.000
Control (Unlit) vs Full night		0.037	0.870			0.787
2 hours vs 4 hours		0.202	0.399			0.181
2 hours vs Full night		0.066	0.780			0.423
4 hours vs Full night		0.285	0.266			0.423

Pipistrellus pipistrellus activity declined by an average of 79% under 2-hour PNL compared to unlit nights (*P* = 0.028; Table 2; Fig. 2e) but no significant differences in activity were recorded during the 4-hour PNL or the full-night lighting treatments compared to unlit nights (Table 2; Fig. 2e). A significant increase in *P. pipistrellus* activity was recorded for the 4-hour PNL compared to the 2-hour (*P* = 0.026; Table 2; Fig. 2e). We found no statistically significant effects of any light treatments on *Nyctalus/Eptesicus* spp. activity compared to unlit nights (*P* = 0.575; Table 2).

Bat feeding activity.

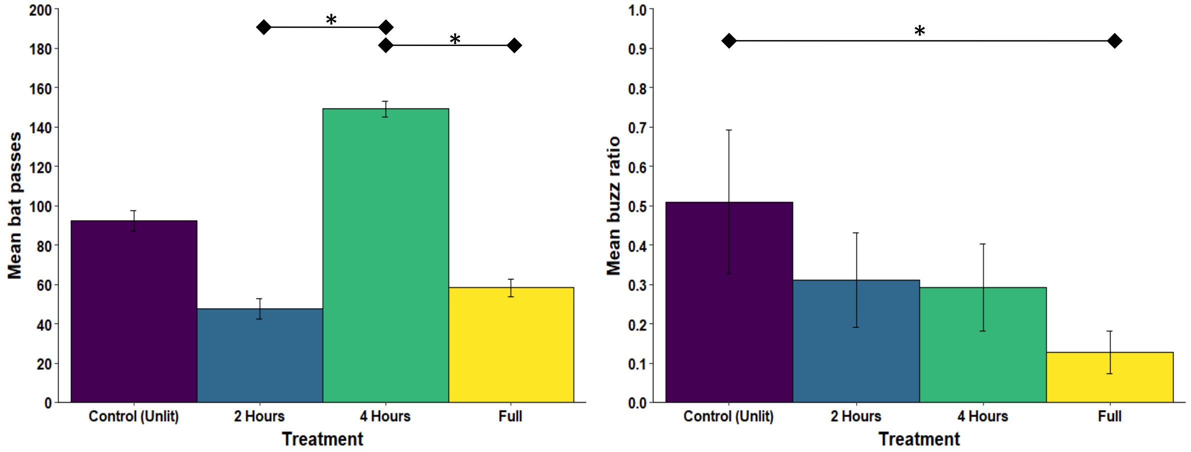
Relative feeding activity (buzz ratio) was lower for *Myotis* spp., *P. pygmaeus* and *P. pipistrellus* species under all lit treatments with significant (or marginally significant) negative effects recorded during both part-night and full-night lighting treatments. Relative feeding activity for *Myotis* spp. declined as the number of hours under lit treatments increased. Buzz ratios declined by an average of 50% during the 4-hour PNL (*P* = 0.048; Table 2; Fig. 2b) and by 70% in full-night lighting treatments (*P* = 0.008; Table 2; Fig. 2b) compared to unlit nights. *Myotis* spp. feeding activity was significantly higher during 2-hour PNL compared with full-night lighting treatments (*P* = 0.018; Table 2; Fig. 2b).

P. pygmaeus feeding activity declined by an average of 75% during full lit treatments compared to unlit nights (*P* = 0.017; Table 2; Fig. 2d). Marginally significant reductions in feeding activity were recorded in both 2-hour and 4-hour PNL treatments compared to unlit nights (*P* = 0.068 and *P* = 0.059 respectively; Table 2; Fig. 2d). *P. pipistrellus f*eeding activity declined by an average of 77% during 2-hour PNL compared to unlit nights (*P* = 0.011; Table 2; Fig. 2f) and marginally significant reduction in feeding activity were recorded under full-night lighting compared to unlit nights (*P* = 0.073; Table 2; Fig. 2f). We found no statistically significant effects of any light treatments on *Nyctalus/Eptesicus* spp. feeding activity compared to unlit nights (*P* = 0.392; Table 2).



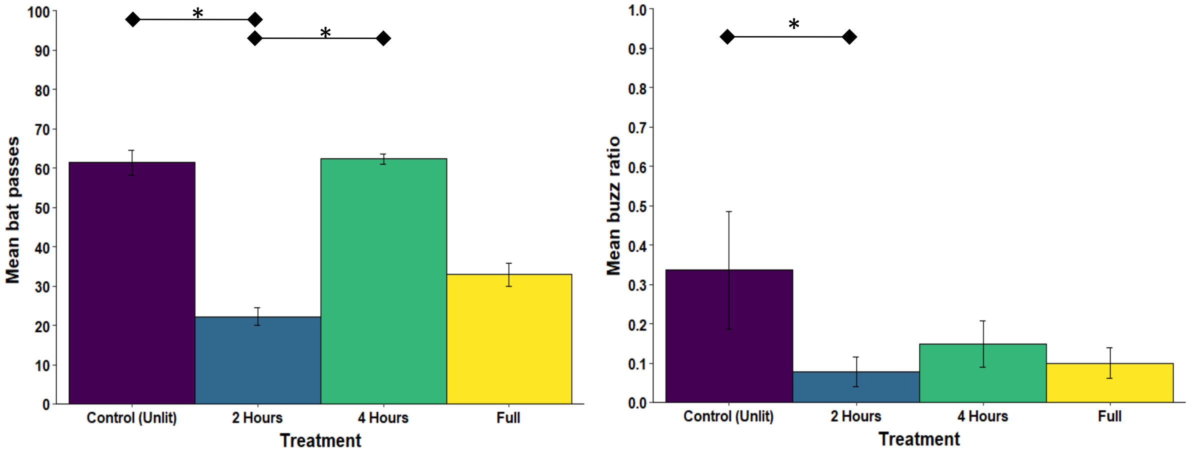
(a) *Myotis* spp. Overall activity

(b) *Myotis* spp. Feeding activity



(c) *P. pygmaeus* Overall activity

(d) *P. pygmaeus* Feeding activity



(e) *P. pipistrellus* Overall activity

(f) *P. pipistrellus* Feeding activity

Figure 2. Bat activity (Mean bat passes) and relative feeding activity (Mean buzz ratio) by (a,b) *Myotis* spp. (c,d) *P. pygmaeus*. and (e,f) *P. pipistrellus* along experimental waterways during dark control and three light treatment nights. Data are presented as mean ± SEM with significant within-subject differences during post hoc tests highlighted.

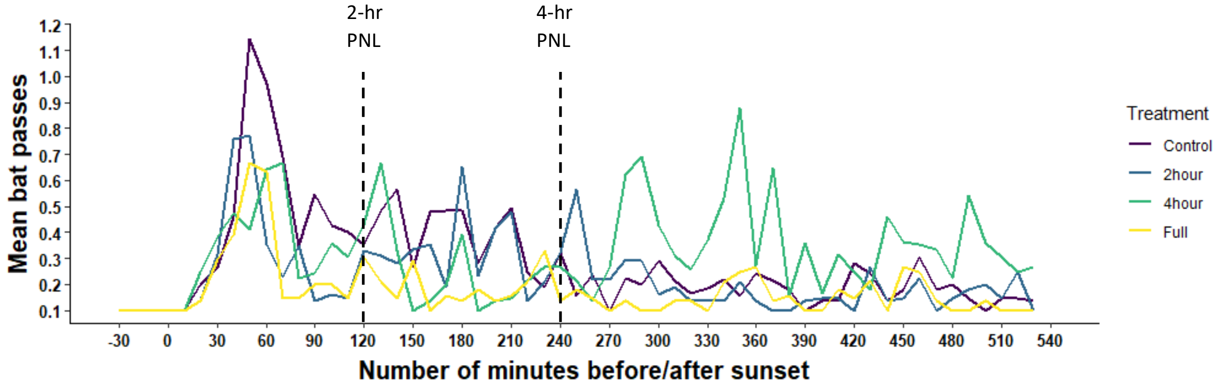


Figure. 3 Average number of *Myotis* spp. registrations recorded per 10-min period before and after sunset under control (unlit), 2-hour PNL, 4-hour PNL and full-night lighting treatments.

Discussion

To our knowledge this is the first study to experimentally test the effectiveness of part-night LED lighting schemes along waterways on the activity and behaviour of a bat assemblage. Here we show that light treatment had a significant or marginally significant effect on the overall activity and feeding behaviour of a riparian bat assemblage compared to unlit nights. Furthermore, we show species-specific responses in overall activity and feeding behaviour by bats to different light treatments. This is of particular importance as LEDs are rapidly replacing older lighting technologies and measures such as part-night lighting schemes are already being readily adopted in a bid to limit light pollution and mitigate the harmful impacts of urbanisation. Our results therefore demonstrate that part-night lighting still presents a risk to wildlife and appropriate assessment and mitigation should be deployed prior to their use.

Slow-flying *Myotis* spp. are generally considered to be less tolerant of lighting and therefore the reduction in relative activity under full-night lighting treatments was expected and is consistent with previous studies using both high pressure sodium (HPS) and LED lighting systems (e.g. Azam et al., 2015; Stone et al. 2012; Spoelstra et al., 2017). Overall activity under full-night light treatments was significantly lower in comparison to both unlit nights and PNL treatments. This suggests that, to some extent, PNL does limit the negative impacts of ALAN over the course of the night by allowing *Myotis* bats to have peaks of activity later in the night after lights are switched off (Fig. 3).

Superficially this may seem to highlight the efficacy of PNL as a mitigation method, however our results show that this is not true for all behaviours. Whilst no negative impact in overall *Myotis* spp. activity for PNL treatments was recorded, a 50% reduction in relative feeding activity occurred under the 4-hour part-night lighting treatment suggesting that PNL reduces the feeding activity window for these species.

Despite *Myotis* species being grouped together in a genera-wide category due to the similarities in call structure between species within the same genus (Schnitzler and Kalko, 2001), it is likely that the majority of the calls were of *M. daubentonii* given that this species is widespread throughout the study area and strongly associated with riverine habitats (Warren et al., 2000). *M. daubentonii* primarily feed on insects of the orders Diptera (most frequently those of the Chironomidae family), Trichoptera and Lepidoptera (Vaughan, 1997; Vesterinen et al., 2013; Todd and Waters, 2017) whose activity peaks in the evening and early part of the night (Holzenthal et al., 2015; Vebrová et al., 2018). Therefore, a delay in bat activity as a result of ALAN can create a mismatch with prey availability leading to an overall reduction in feeding. Previous studies assessing the effect of artificial lighting on *M. daubentonii* show that changes in food availability do not explain the decrease in foraging seen for this species under lit treatments as ALAN does not induce any significant qualitative or quantitative changes in typical prey abundance or availability (Russo et al., 2019).

The response of *Myotis* spp. to ALAN supports findings by Kuijper et al. (2008) who found that feeding activity of *M. dasycneme* reduced by more than 60% under lit conditions despite overall activity levels remaining unaffected and insect prey being in higher abundance. Our results suggest that *Myotis* species are more light-sensitive when foraging compared to commuting, likely due to their longer exposure to illumination and subsequent predation threat (Russo et al., 2019). This is consistent with findings by Spoelstra et al., 2018 who found that commuting *M. daubentonii* did not respond strongly to any of the four different light treatment combinations deployed in a choice experiment. Disturbances to bat foraging sites caused by ALAN can significantly impact the fitness and reproductive success of light-sensitive species especially *Myotis* spp. who are particularly sensitive to habitat fragmentation (Duverge et al., 2000; Safi and Kerth, 2004; Frey-Ehrenbold et al., 2013) and are typically of greater conservation concern than their light-opportunistic counterparts (Lacoeuilhe et al., 2014). The impacts of ALAN along waterways can be especially detrimental for specialist trawling bats who rarely move out of the river corridor whilst hunting (Nardone et al., 2015) and therefore any illumination constitutes a potential barrier, fragmenting their foraging habitat.

A similar reduction in *Myotis* spp. feeding activity was not found under the 2-hour PNL treatment, suggesting that a mitigation scheme of this duration may have little negative impact on overall activity and feeding for *Myotis* bats. This may be due to the limited overlap of operational lighting and peak activity windows as a result of their later emergence times (Mean emergence times for *M. daubentonii* from previous studies were found to be between 40 min and 73 min after sunset (see Warren et al., 2000 and Jones and Rydell, 1994). Despite the potential benefits of shorter PNL schemes (i.e. 2-hour PNL) to light-sensitive bats, this mitigation option is unlikely to be adopted as the hours in which street lighting would be turned off are also those most important to humans (Gaston et al., 2012).

Whilst our study showed no significant differences in overall activity between PNL treatments and unlit nights for *Myotis* spp., there is likely to be a species-specific response from this genus based on habitat preference and foraging guild. Species such as *M. daubentonii, M. capaccinii* and *M. dasycneme* constitute edge-space foragers that uses stretches of open water for commuting and foraging and therefore are likely to be more tolerant of ALAN than their narrow-space foraging counterparts who consistently avoid areas subjected to ALAN (Voigt et al, 2021). This differential response to ALAN by *Myotis* spp. is supported by findings from Azam et al., (2015) and our own study, showing that *Myotis* spp. in terrestrial ecosystems are more sensitive to PNL than those is aquatic or riparian ecosystems. These forest-dwelling bat assemblages are more likely to comprise narrow-space-foraging species such as *M. emarginatus* or *M. nattereri* who will avoid both commuting and foraging areas that are subjected to ALAN (Voigt et al., 2021).

Unlike *Myotis* spp. both *P. pipistrellus* and *P. pygmaeus* showed different overall activity responses to PNL dependent on the duration for which the lights were operational, with both species being significantly more active under the 4-hour than the 2-hour PNL treatment (*P. pygmaeus* 164% increase; *P. pipistrellus* 110% increase). For *P. pygmaeus* this also represented a significant 66% increase over full-night lighting treatments and may indicate a temporal delay in exploratory behaviour around these novel light sources after initial avoidance behaviour.

However, as with *Myotis* spp., changes in feeding activity do not always mirror changes in overall activity, as even though an increased amount of activity was recorded for both *P. pipistrellus* and *P. pygmaeus* under 4-hour PNL, feeding activity of both species was lower for all light treatments when compared to unlit nights. These findings are particularly important for this species group as while some previous studies highlight the negative impacts of ALAN on *Pipistrellus* spp. feeding behaviour (see Kerbiriou et al., 2020; Barré et al., 2020), it is commonly assumed that Pipistrelle bats represent a species group that benefit from increased feeding opportunities at artificial lighting due to increased insect biomass (e.g. Perkin et al., 2014; Wakefield et al., 2016; Spoelstra et al., 2017; Zeale et al., 2018). Our results add to the body of evidence highlighting the negative impacts of ALAN on *Pipistrellus* species through reducing feeding activity and may suggest that *Pipistrellus* spp. are responding to urbanisation through increasing individual flight speed through illuminated areas and transiting at commuting rather than foraging speed (Grodzinski et al., 2009; Polak et al., 2011; Barré et al., 2020). Our results therefore raise important questions about negative impacts of ALAN on supposedly “light-opportunistic” species and the implications for individual fitness and reproductive success.

Lastly, we found no significant effects of any light treatments on *Nyctalus/Eptesicus* spp. overall bat activity or foraging which is consistent with our hypothesis for fast-flying aerial hawking bat species that are known to emerge at dusk to coincide with crepuscular activity peaks of their prey species (Jones and Rydell, 1994). For this species group, prey availability rather than light levels will be a key driver of their activity patterns, due to their increased ability to escape diurnal predators, and they may even forage opportunistically at illuminated sites in order to exploit swarms of insects attracted by street lights (Mathews et al., 2015; Laforge et al., 2019; Voigt et al. 2020).

With increasing attention paid to the financial and environmental impacts of light pollution, the use of flexible management approaches such as PNL are an attractive option to limit the harmful impacts of ALAN on the nocturnal landscape. However, despite being a valuable approach in terms of reducing carbon emissions and public sector costs, we demonstrate that PNL schemes are unlikely to provide desired biodiversity benefits especially for bats due to species-specific impacts on activity and feeding. The use of PNL is particularly limited for light-sensitive bat species due to the standoff between humans' requirement for light and bats requirement for darkness occupying the same space in time. Therefore, if the aim it to limit the negative impacts of ALAN on biodiversity, it would be more beneficial to pursue alternative management strategies such as reducing light trespass, changing the intensity or spectrum of lighting and increasing dark corridor networks (Gaston et al., 2012; Pauwels et al., 2021).

Acknowledgments

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CHAPTER 5 | Reconciling urban bat conservation and public accessibility: spectrum dependent response to artificial light at night in urban green space.

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Abstract

Urbanisation is increasing rapidly and amongst the ecological stressors present within urban environments, ALAN ranks amongst the most important global risks to biodiversity conservation. Bats are particularly susceptible to the detrimental effects of ALAN. Improving urban green spaces so that bats can thrive is important both from a conservation perspective but also for human mental health and wellbeing. Long-wavelength red light has been proposed to mitigate the harmful impacts of ALAN on nocturnal biodiversity in areas like urban green spaces where human's requirement for light and bats requirement for darkness come into conflict however little is known about their effectiveness. Using an experimental approach, we provide evidence to the complex relationship between bats and lighting in urban ecosystems. For light-opportunistic *Pipistrellus* spp. red lighting did not affect overall activity or feeding compared to conventional white lighting. However, we found for *Nyctalus/Eptesicus* spp. overall activity was less under red lighting than white. Despite being shown to have some benefit for light-averse species at smaller scales, management options using spectral alterations are unlikely to provide comprehensive mitigation due to the species-specific and context dependent nature of response.

Introduction

Urbanisation is increasing rapidly, with 55-78% of the world's projected 8.5 - 9.9 billion population living in urban areas by 2050, which will place increasing demands on the global terrestrial surface (Kc and Lutz, 2017; Jiang and O'Neill, 2017; Li et al., 2022). The resulting land use change is a major threat to global biodiversity and will create profound ecosystem changes, including habitat loss and fragmentation as well as shifts in local climate (Grimm et al., 2008; Markovchick-Nicholls et al., 2008; Liu et al., 2016; van Vliet, 2019). Urban expansion has caused a global loss of ~50% of local within-site species richness and a 38% loss of total species abundance in heavily urbanised areas with further loss of natural habitats predicted to reach 11-33 million hectares by 2100 (Newbold et al., 2015; Li et al., 2022).

The detrimental impact of extensive land use change is further exacerbated by the introduction of ecological stressors such as anthropogenic noise, artificial illumination, disturbance and chemical and physical pollutants which place additional strain on the remaining fragmented natural habitats within urban areas (e.g. Markovchick-Nicholls et al., 2008; Francis and Barber, 2013; Stone et al., 2009, 2012, 2015; Russo and Ancillotto, 2015; Voigt et al., 2021). Bats represent a significant proportion of mammalian biodiversity and are particularly sensitive to environmental anthropogenic alteration threatening the survival of many species (Hutson et al., 2001; Park, 2015). Urbanisation can take a heavy toll on bat populations, influencing the behaviour and population dynamics of bats, with responses being highly species-specific subsequently altering the structure of bat communities (Russo and Ancillotto, 2015; Lewaznik et al., 2022). Mature woodland/tree specimens that possess the required roosting opportunities are often limited, whilst open water and green spaces that host the required arthropod prey are highly variable in both their size and quality, often being isolated and prone to deterioration (Hale et al., 2012; Lewaznik et al., 2022). These deficiencies in habitat and prey availability are further confounded by the addition of landscape scale barriers to connectivity such as large expanses of impervious, unvegetated surfaces and ubiquitous deployment of artificial lighting at night (ALAN) (Hale et al., 2012, 2015; Rowse et al., 2016; Voigt et al., 2021). While some generalist bat species show a strong degree of opportunism in urban habitats, readily adapting to roosting in buildings or foraging opportunities e.g. around streetlights (Rydell, 1992; Russo and Ancillotto 2015) even these species can suffer from ALAN (Davies et al., 2012; Lewanzik and Voigt, 2017; Pauwels et al., 2021; Lewaznik et al., 2022). For bat species that are specialised for particular natural habitats i.e. woodland, the increasing sprawl of urban landscapes creates irreparable losses in roosting and foraging opportunities that often lead to complete abandonment of heavily urbanised areas thereby increasing an already heightened extinction risk (Jones at al., 2003; Safi and Kerth, 2004).

However, like many issues facing the natural world, the impact of urbanisation is multifaceted, with the specific effects varying significantly both amongst and within cities (Beninde et al., 2015). Despite being a global threat to biodiversity, cities can be critical for native biodiversity conservation (Ives et al., 2016). This is particularly important in areas where other factors, such as agricultural intensification, has limited the viable habitat present to species across the landscape (Robinson and Sutherland, 2002; Hayhow et al., 2016; Winkler et al., 2021). While urbanisation can greatly reduce the amount of total habitat available it can also provide a network of urban green spaces (UGS) that constitute a more biodiverse habitat than the one it is replacing, e.g. former agricultural land, and have been shown to be a vital factor in enhancing and sustaining biodiversity (Sattler et al., 2010; Ives et al., 2016; Aronson et al., 2017).

Despite the potential benefits of well-designed UGS, urbanisation generally precedes a decrease in species diversity and homogenisation of species assemblages as a result of trait convergence in persisting species (McKinney, 2002; Shochat et al., 2006; Piano et al., 2020). This environmental filtering favours some generalist species or 'urban exploiters' due to the availability of resources in urban habitats whilst also excluding inflexible specialist species (Stochat et al., 2006; Concepcĭ on et al., 2015; Aronson et al., 2017 ; Callaghan et al., 2019; Santini et al., 2019).

Improving UGS so that bats, and nocturnal biodiversity in general, can thrive is of high importance both from a conservation perspective but also for human mental health and wellbeing (Reyes-Riveros et al., 2021; Methorst et al., 2021). Amongst the ecological stressors present within urban environments, ALAN ranks amongst the most important global risks to biodiversity conservation (Gaston et al., 2014, 2015; Davies and Smyth, 2017). ALAN is a global problem with nearly a quarter of the world's land surface impacted by light pollution, a figure that is growing by ~2% per year in both radiance and extent (Falchi et al., 2016; Kyba et al., 2017). Negative impacts of ALAN have been demonstrated in a wide variety of organisms ranging from individual physiological responses to changes in ecosystem functioning which can trigger ecological effects spanning trophic levels (Hölker et al., 2010; Bennie et al., 2016; Knop et al., 2017; Bennie et al., 2018).

Bats, like other nocturnal taxa, are particularly susceptible to the detrimental effects of ALAN due to their evolutionary adaptations for dark environments, which lessen the perceived or real predation risk from diurnal predators (Rydell and Speakman, 1995; Mikula et al., 2016). Despite this, bats can exhibit differential sensitivity to light that can be both species and scale dependent (Lacoeuilhe et al., 2014; Stone et al., 2015; Rowse et al., 2018), with some fast-flying bat species actively foraging in artificially illuminated habitats. Areas subjected to ALAN, including where modern lighting technologies such as LED have been installed (e.g. Stone et al., 2015; Russo et al., 2017), can increase foraging opportunities due to the accumulation of insects around lights along with a light-induced impairment of predation avoidance mechanisms innate in insects (Minaar et al., 2015; Wakefield et al., 2015, 2018; Voigt et al. 2021). These opportunistic species, which largely comprise edge- and open-space specialists, may be able to forage through lit areas as they are able to escape diurnal predation more effectively due to their increased flight speed and their preference for aerial hawking on crepuscular prey which decreases their predation risk at higher light levels (Matthews et al., 2015, Pauwels et al., 2021). Whilst opportunistic species have been able to exploit sources of ALAN, the majority of bat species will avoid artificially illuminated areas in most contexts due to its increased risk of predation, the alteration in composition and abundance of insect prey sources as well as the negative effect on roosting and foraging behaviour (e.g. Stone et al., 2009, 2012; Davies et al., 2012; Lewanzik and Voigt, 2017; Pauwels et al., 2021, Lewaznik et al., 2022). Habitat fragmentation caused by ALAN can reduce the quality and availability of habitat for bats as well as limiting the functional connectivity across the landscape (Azam et al., 2015; Pauwels et al., 2019; Laforge et al., 2019).

As new research on the negative impacts of ALAN on nocturnal fauna continue to emerge (e.g. Barré et al., 2022; Hooker et al., 2022; Mariton et al., 2022), local authorities are expanding the use of more flexible lighting technologies to reduce energy consumption in order to address climate change targets and mitigate potential negative impacts of light pollution on biodiversity (Bennie et al., 2014; Azam et al., 2015). Several policy and management responses have been proposed such as the implementation of part-night lighting regimes, reducing light trespass through design and placement and altering the spectrum or intensity of artificial lighting (Gaston et al., 2012; Spoelstra et al., 2017; Bollinger et al., 2020).

Alteration to the spectral composition of street lighting involves changing the proportion of different wavelengths that make up how visible light is perceived and usually involves adjusting the levels of UV light emitted, resulting in a change of colour. How bat species react to light often varies with light colour and similar to other mammals, altering the spectral composition of ALAN can alter a bat's behavioural response to light (Rydell, 1992; Stone et al., 2009; Spoelstra et al., 2017). More 'light-tolerant' species, are predominately drawn to the same light spectra as those attracting their insect prey – artificial lights emitting high UV levels and short-wavelength visual light (Minaar et al., 2015; Wakefield et al., 2015; Stone et al., 2015). Whereas bats are less active near lights emitting only longer-wavelength light, such as HPS and LPS lights, which attract up to 55% fewer insects (Rich and Longcore, 2006; Mathews et al., 2015).

Light-averse species avoid most lighting spectra, with very few lighting types causing deviations from behaviour (Stone et al., 2009, 2012, 2015; Straka et al., 2019). However, the precise mechanisms behind responses to spectral alteration are not well known and avoidance may depend on how well bat are able to see different light colours. Bats eyes have evolved to work optimally in dark environments with a high rod/cone ratio compared to diurnal mammal species (Piechl et al., 2005; Kim et al., 2008; Feller et al., 2009.) These specialised optics are reported to express opsins that are UV-sensitive and therefore may be particularly sensitive to blue light components of ALAN (Müller et al., 2009).

Of all light spectra, long-wavelength red light may be significantly less detrimental to bats compared to shorter wavelengths and recent studies have shown that utilising these wavelengths illicit similar behavioural responses to darkness when compared to amber or white LEDS (Downs et al., 2003; Spoelstra et al., 2017; Zeale et al., 2018; Straka et al., 2020). Red light could therefore potentially be used to mitigate the harmful impacts of ALAN on nocturnal biodiversity in areas like UGS where human’s requirement for light and bats requirement for darkness come into conflict. A number of local authorities have already adopted the use of red lighting in order to mitigate the harmful effect of ALAN in areas where bats forage or commute across the landscape (Worcestershire County Council, 2023).

To our knowledge no study has experimentally tested the effect of long-wave red lighting on bat communities within UGS ecosystems or assessed its impact on specific behaviours such as feeding. In this study, we used an experimental approach to assess the impact of artificial red lighting on bat activity and feeding behaviour in city centre parks or greenspace. We compared activity levels of four bat species/groups: (*Pipistrellus pipistrellus*, *Pipistrellus pygmaeus*, *Myotis* spp. and *Nyctalus/Eptesicus* spp.) under dark (unlit), white LED and ClearField red LED lighting.

We hypothesised that bats would respond to lighting spectrums according to species specific adaptations for flight and foraging (Stone et al., 2012; Zeale et al., 2016). We predicted that there would lower activity levels for slower-flying species (i.e. *Myotis* spp.) under white LED lighting but activity would be higher under ClearField Red LED lighting resulting from the overall reduction in UV light during which bats would perceive an increased predation threat (Rydell and Speakman, 1995; Müller, 2009). In contrast, we predicted no effects of light treatments on the activity of fast-flying species (i.e. *Pipistrellus* spp., *Nyctalus/Eptesicus* spp.) as fast-flying species are better adapted to increased light-levels due to their reduced perceived light-dependent predation risk and their ability to utilise illuminated sites opportunistically (Mathews et al., 2015).

Material and Methods

Lighting experiments were conducted along ten public footways within urban parks in south west England and south Wales between July and October 2021 (average park size 19.52 ha, SD 12.57, range 3.02-42.12, n = 10). Each experiment lasted for three nights per site and comprised of a single dark unlit (control) treatment on night one followed by one of two lit treatments whereby the footway was illuminated by either white LED or ClearField red LED streetlights. The order of the lit treatments was randomized between sites to control for order effects and sites were separated by a minimum of 10 km to ensure collection of independent samples.

Sites were located within dark urban parks (<0.05 lux) consisting predominantly of managed grassland (with scattered trees), formal and informal pathways, semi-natural woodland and amenity waterbodies. Urban parks were surrounded by residential or commercial development along with accompanying road networks thereby fragmenting them from additional greenspace in the area. Pathways were illuminated with white LED or ClearField red LED streetlight luminaires (Philips Signify, Guildford, England) powered by Ford FG2000iS 1.8kW Petrol inverter generator connected to the fixtures by waterproof cables and connectors at a distance of 25m behind the illuminated pathway. The generator was switched on for all experimental nights, including unlit, control nights and noise production was measured using a sound level meter (ANSI S1.4 TYPE2 Meter, Soonda. Ltd, China) to ensure standardisation between treatment conditions. We selected a generator with incorporated sound proofing insulation and the lowest noise output commercially available at the time of study (average 53.68 dB ± 2.64 SD).

This LED luminaire design was chosen due to its wide commercial usage for outdoor illumination and its strategic development in mitigating the harmful effects of light pollution through inclusion of red LED technologies. Both the white LED and red ClearField LED streetlights emit broad-spectrum light with negligible UV emissions, but the red ClearField LED streetlight has an increased red and reduced blue visible light emissions (See Spoelstra et al., 2015, 2017). The light level for each spectrum is perceived by humans as equally intense, with a nominal flux of 1800 Lumen and 7.6 + 1.2 Lux (1 s.e.m.) at ground level.

The lighting system did not emit any audible nor ultrasonic noise (assessed with Song Meter Mini Bat Full Spectrum Recorder for a full-nights illumination) and therefore any potential noise effects as a result of the experimental protocol could be omitted from the study. At each site three streetlights were placed 1 m from the edge of the pathway and were mounted 3.3 m above the ground on portable columns with luminaires directed downwards. Light columns were placed 30 m apart, ensuring that the entire cross section of the experimental pathway was illuminated, and thereby mimicking common streetlighting placement within the UK (Stone et al., 2009)

Illuminance (in lux) was measured 1 hour after sunset using a T-10 illuminance metre (Konica Minolta Sensing Inc, Osaka, Japan) held horizontally 2 m in front of the lighting columns and 1 m above the pathway surface. Pathways were illuminated to a mean light intensity of 49.0 ± 5.98 lux and 50.4 ± 5.10 lux for red and white lighting respectively which is in the range used during previous experiments utilising white LED (e.g. Stone et al., 2012; Zeale et al., 2018) and is equivalent to that emitted by street-lighting in public areas in the UK (Stone et al., 2009). Field work was only conducted in suitable conditions in accordance with Bat Conservation Trust (2016) guidance (i.e. sunset temperature 10°C or above, no rain or strong wind). Mean nightly temperatures (°C) were recorded using in-built thermometers within the bat detectors and mean nightly wind speed (mph), mean nightly humidity (%) and total nightly rainfall (mm) was obtained from Met Office weather stations (http://www.metoffice.gov.uk) within 2 km of each site (mean distance 0.92 km, SD 0.4 km).

Bat activity was recorded from sunset for 3.5 hours using Song Meter Mini Bat Full Spectrum Recorder (Wildlife Acoustics Inc. Maynard, MA, USA). Echolocation calls were analysed in Anabat Insight v.1.9.2 (Titley Scientific, Brendale, QLD, Australia) and identified manually using call parameters as described in Russ (2012). During two of the survey visits the full sampling periods could not be undertaken due to technical issues, the resulting reduced survey duration during these nights was then standardised across all treatment conditions by limiting the survey duration to 2 hours. Mean number of bat passes per treatment night was used as an index of relative bat activity with a single bat pass identified as a continuous sequence from a passing bat containing two or more echolocation pulses within one second of each other (Fenton, 1970; Walsh and Harris, 1996). Bat passes from multiple bats of the same species were identified using distinguishable differences in pulse interval and/or peak frequency of overlapping echolocation pulse sequences. Calls were grouped into four species/species groups: *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus*, *Myotis* spp. and *Nyctalus/Eptesicus* spp. with rarely recorded species such as *Plecotus* spp. (total 185 bat passes; <1% of overall bat activity), not included in subsequent analysis.

Relative feeding activity of recorded bat species was examined by identifying diagnostic terminal phase calls (feeding buzzes) within recordings calculated as the ratio of feeding buzzes to total number of passes per species per night (buzz ratio) (Vaughan et al., 1997). A buzz ratio of one indicates that on average every bat pass contains a single feeding buzz.

All analyses were performed in R v.4.0.4 (R Core Team, 2022) using the significance level p <0.05. Repeated measures general linear models (RMGLMs) were used to test for differences between environmental variables with treatment conditions fitted as a within-factor effect. As there were no significant differences in mean nightly temperature ($F_{2,18} = 0.68$, n=10, P = 0.52), mean nightly humidity ($F_{2,18} = 2.72$, n = 10, P = 0.09) and mean nightly wind speed ($F_{2,18} = 0.10$, n = 10, P = 0.91) across treatments, these variables were excluded from further analyses to achieve model simplification. Furthermore, in order to ensure that any differences between lighting technologies (i.e. white LED and ClearField red LED) were limited to spectral composition rather than intensity, RMGLMs were used to test for differences in illuminance across lit treatment conditions. As there were no significant differences in illuminance between the lit treatment conditions ($F_{1,9} = 0.07$, n = 10, P = 0.80), this variable was also excluded from further analyses.

We fitted RMGLMs to examine the effect of light treatment on bat activity (number of bat passes per night per species/species group). Counts of bat passes for *P. pipistrellus, P. pygmaeus* and *Nyctalus/Eptesicus spp*. were log transformed to meet assumptions of homoscedasticity and normality, whilst *Myotis spp*. were tested using Friedman's non-parametric ANOVA due to their non-normal distribution despite data transformation attempts. Light treatment was fitted as a within-factor effect with 3 levels corresponding to the light treatment types (Unlit, ClearField Red LED and white LED light). Species with a sufficient number of feeding buzzes were assessed using Friedman's non-parametric ANOVA to examine the effect of lighting treatment on bat feeding activity. RMGLM statistics are presented as F and p values with effect sizes presented as Cohen's d or Kendall's W in the case of non-parametric ANOVAs.

Results

A total of 7,904 bat passes belonging to five species/species groups were recorded during the 30 nights of monitoring. The majority of echolocation recordings belonged to *P. pipistrellus* (6,189 passes; 78.3%) followed by *P. pipistrellus* (894 passes; 11.3%), *Nyctalus/Eptesicus* spp. (723 passes; 9.2%) and *Myotis* spp. (82 passes; 1%), with *Plecotus* spp. making up the remaining <1% of species recorded. A total of 2,598 feeding buzzes were recorded from four species/species groups comprising *P. pipistrellus* (2,119 buzzes; 81.6%; buzz ratio 0.34) followed by *P. pygmaeus* (337 buzzes; 13%; buzz ratio 0.38), *Nyctalus/Eptesicus* spp. (128 buzzes; 4.9%; buzz ratio 0.18) with *Myotis* spp. making up the remaining <1% of feeding buzzes recorded.

Bat activity.

We found statistically significant effects of light treatment on bat activity for *Nyctalus/Eptesicus* spp. and *Myotis* spp. *Myotis* spp. activity recorded under white LED lighting declined by an average of 53% and was significantly lower compared to unlit nights (*P* =0.043; Table 1, Fig. 1a). Although a 37% decline in *Myotis* spp. activity was also recorded under ClearField red LED lighting, this did not represent a significant decline compared to unlit nights (*P* =0.157; Table 1, Fig. 1a). *Nyctalus/Eptesicus* spp. activity declined by an average of 46% within urban parks illuminated by ClearField red LED lighting compared to unlit nights (*P* = 0.043; Table 1; Fig. 1b), whereas bat activity did not significantly change under white LED lighting compared to unlit nights (*P* =0.423; Table 1; Fig. 1b).

We found no significant effects of light treatment on the activity of *Pipistrellus* spp. compared to unlit nights. There were no significant effects on *P. pipistrellus* activity during either white LED (*P* =0.460; Table 1, Fig. 1d) or ClearField red LED (*P* =0.600; Table 1, Fig. 1d) light treatments compared to unlit nights. Despite some average declines in activity under lit conditions, we found no significant effects on *P. pygmaeus* activity during white LED (*P* =0.153; Table 1, Fig. 1f) or ClearField red LED (*P* =0.201; Table 1, Fig. 1f) light treatments compared to unlit nights. In addition, there were no significant differences in activity levels between the white LED and ClearField red LED treatment conditions for either *P. pipistrellus* (*P* =0.214; Table 1, Fig. 1e) or *P. pygmaeus* (*P* =0.871; Table 1, Fig. 1f).

Bat feeding activity.

Relative feeding activity for *Nyctalus/Eptesicus* spp. declined during ClearField red LED lighting treatment compared to unlit and white LED treatments. Whilst not statistically significant compared to unlit nights (*P* =0.205; Table 1, Fig. 1c), there was a marginally significant reduction in feeding activity compared to white LED treatments (*P* =0.052; Table 1, Fig. 1c) and constitutes an average decline of 85% in feeding activity between ClearField red LED and white LED lighting treatments.

We found no statistically significant effects of any light treatments on relative feeding activity (buzz ratio) for *Pipistrellus* spp. compared to unlit nights. Relative feeding activity for *P. pipistrellus* was largely consistent across treatment conditions with no significant effects recorded for either white LED (*P* =0.846; Table 1, Fig. 1e) or ClearField red LED (*P* =0.557; Table 1, Fig. 1e) light treatments compared to unlit nights.

We found no statistically significant effects on *P. pygmaeus* feeding activity during either white LED (*P* =0.272; Table 1, Fig. 1g) or ClearField red LED (*P* =0.933; Table 1, Fig. 1g) light treatments compared to unlit nights.

Table 1. Results for bat activity (Mean bat passes) and relative feeding activity (Mean buzz ratio) of *Myotis spp., Nyctalus/Eptesicus spp. P. pipistrellus* and *P. pygmaeus* species from repeated measures general linear models and within-subject differences during post-hoc comparisons.

	Bat Activity (passes)			**Feeding Activity (Buzz Ratio)**		
Myotis spp.	***F***	***d***	***P***			
Treatment	3.160	0.316	0.042*			
Control (Unlit) vs White LED			0.043*			
Control (Unlit) vs Red LED			0.157			
White LED vs Red LED			0.838			
Nyctalus/Eptesicus spp.	***F***	***d***	***P***	***F***	***W***	***P***
Treatment	2.420	0.502	0.120	1.00	0.158	0.368
Control (Unlit) vs White LED			0.423			0.944
Control (Unlit) vs Red LED			0.043*			0.205
White LED vs Red LED			0.191			0.052
P. pipistrellus	***F***	***d***	***P***	***F***	***W***	***P***
Treatment	0.839	0.1796	0.449	0.700	0.070	0.497
Control (Unlit) vs White LED			0.460			0.846
Control (Unlit) vs Red LED			0.600			0.557
White LED vs Red LED			0.214			0.922
P. pygmaeus	***F***	***d***	***P***	***F***	***W***	***P***
Treatment	1.342	0.2708	0.286	0.234	0.023	0.792
Control (Unlit) vs White LED			0.153			0.272
Control (Unlit) vs Red LED			0.201			0.933
White LED vs Red LED			0.871			0.833

(a) *Myotis spp.* Overall activity

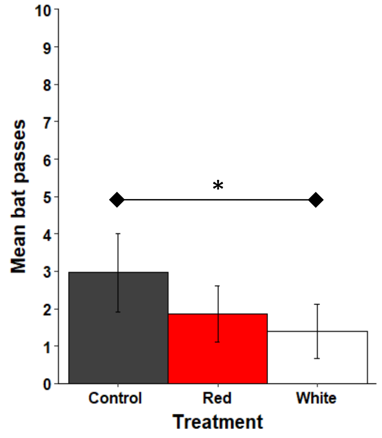
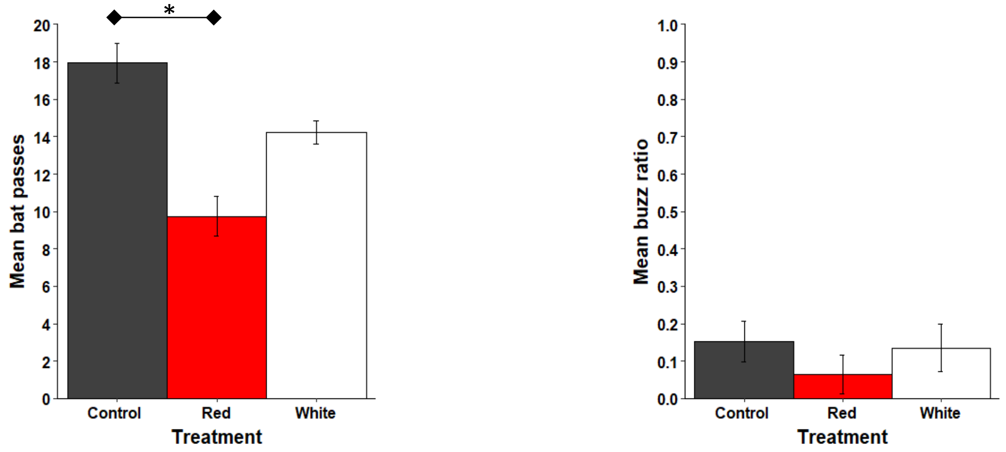
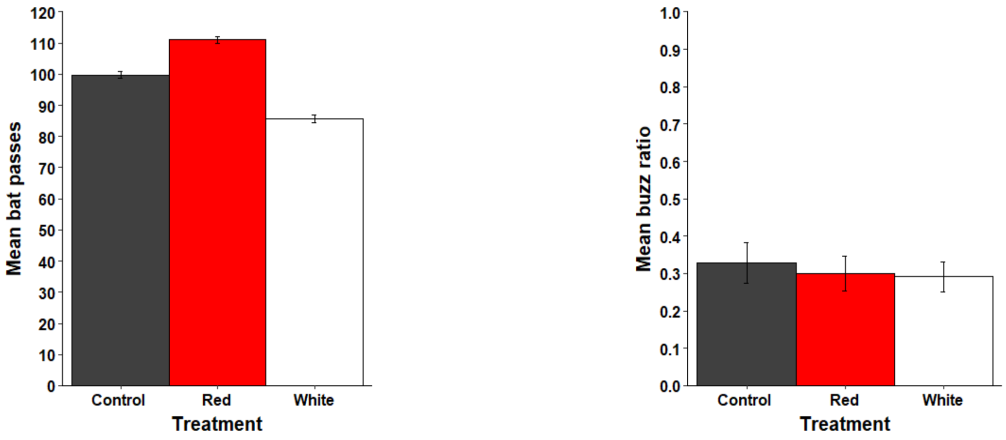


Figure 1. Bat activity (Mean bat passes) and relative feeding activity (Mean buzz ratio) by (a) *Myotis spp.*, (b,c) *Nyctalus/Eptesicus spp.*, (d,e) *P. pipistrellus* and (f,g) *P. pygmaeus* under experimental conditions within urban parks during unlit control, ClearField Red LED and white LED light treatment nights. Data are presented as mean ± SEM with significant within-subject differences during post hoc tests highlighted.

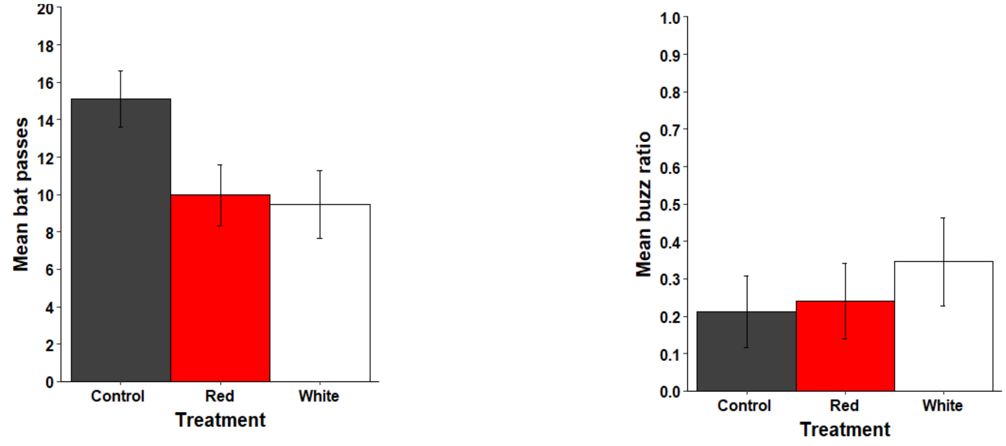
(b) *Nyctalus/Eptesicus spp.* Overall activity **(c)** *Nyctalus/Eptesicus spp.* Feeding activity



(d) *P. pipistrellus* Overall activity **(e)** *P. pipistrellus* Feeding activity



(f) *P. pygmaeus* Overall activity **(g)** *P. pygmaeus* Feeding activity



Discussion

As terrestrial land cover becomes more urbanised, UGS within built-up areas are increasingly more important as refuges for biodiversity, whilst also having to host a range of recreational activities known to benefit human well-being (Arnberger et al., 2012, Nielsen et al., 2017). The pressure on UGS to serve both biodiversity and human recreation is often a cause of conflict despite a substantial body of research has highlighted the positive effects of nature on human well-being with benefits positively related to faunal and floral species diversity (Cox et al,. 2017; Lindemann-Matthies and Matthies, 2018; Wood et al., 2018; Mavoa et al., 2019; Methorst et al., 2021). Unlike more natural habitats, the benefits of UGS are highly dependent on planning and management which are often based on the recreational needs of the surrounding human population. As a result, certain ecological stressors such as artificial lighting is deemed necessary and as such local authorities are expanding the use of more flexible lighting technologies to mitigate potential negative impacts of light pollution on biodiversity (Bennie et al., 2014; Azam et al., 2015). To our knowledge no study has experimentally tested the effect of long-wave ClearField red LED lighting on bat communities within UGS ecosystems or assessed its impact on specific behaviours such as feeding. Here we show that lighting had a significant effect on an urban bat assemblage with species-specific responses in overall activity, as well as marginally significant effects on bat feeding behaviour, recorded in response to different light spectrums. Our results demonstrate that spectral alteration of lighting may still present a risk to wildlife and appropriate assessment and mitigation should be deployed prior to its use.

Myotis spp. are generally considered to be less tolerant of lighting due to their evolutionary adaptations for cluttered, low-light environments which include low aspect ratios and wing loading, traits that correlate with an already heightened extinction risk (Norberg and Rayner, 1987; Jones et al., 2003). These species-specific adaptations result in slower flight speeds and foraging strategies, leading to a higher perceived predation risk in illuminated environments (Rydell, 1996; Mathews et al., 2015; Mikula et al., 2016). The reduction in relative activity under white LED lighting for *Myotis* spp. was expected and consistent with previous studies using LED lighting systems (e.g. Spoelstra et al., 2017, Azam et al., 2018; Hooker et al., 2022). Overall activity under white LED lighting was significantly lower in comparison to unlit control nights, which represents a 53% reduction in activity levels whilst, a similar significant reduction was not recorded on nights illuminated with ClearField red LED lighting. This suggests that, to some extent, replacing white LED bulbs with long-wave red LED bulbs does limit the negative impacts of ALAN on *Myotis* bats in UGS ecosystems. These findings are similar to previous studies that found that whilst *Myotis* bats appear to be sensitive to a wide spectrum of wavelengths, they may be more sensitive to artificial lights emitting high UV levels and short-wavelength visual light and therefore attenuation of these wavelengths under red LED lighting systems preserves overall activity to a greater extent in light-averse species (Müller et al., 2009; Spoelstra et al., 2017; Zeale et al., 2018; Straka et al., 2020).

That being said, there is likely to be species-specific responses to red LED lighting from this species group based on habitat preference and foraging guild and therefore may not represent the response of all species. Despite *Myotis* species being grouped together in a genera-wide category due to similarities in call structure (Schnitzler and Kalko, 2001), it is likely that the majority of calls were of *M. daubentonii* given that call registrations were only recorded at UGS with aquatic habitats present. The remaining *Myotis* spp. typically found within the study area (e.g. *M. nattereri*) comprising clutter adapted forest-dwelling populations that are unlikely to be found within UGS. These narrow-space foraging species such as *M.nattereri* will avoid both commuting and foraging areas that are subjected to ALAN (Voigt et al., 2021). As each study site is surrounded by urban development and isolated by connective habitat features, it is less likely they will be present in the UGS studied and therefore any lack of aversion to red LED lighting may not represent a comprehensive response from this species group. The response of *Myotis* spp. to ALAN appears to be context-dependent with bats being more light-sensitive when foraging compared to commuting, likely due to their longer exposure to illumination and subsequent predation threat (Spoelstra et al., 2018; Russo et al., 2019; Hooker et al. 2022). The response of *Myotis* spp. within our study supports findings by Barré et al (2021) who found that both red and white lighting increased the probability of bats sheltering inside the forest compared to dark control sites, which contrasts with the limited or absent effects of red lighting previously reported for these species (Spoelstra et al., 2017; Zeale et al., 2018).

We found a varying response of lighting treatment on *Nyctalus/Eptesicus* spp. activity, with red LED lighting causing a significant reduction in overall activity compared to unlit nights, which represents a 46% decline in activity levels. However, we did not record a significant reduction in activity on nights illuminated with white LED lighting and furthermore we only found a marginally significant reduction in feeding activity under red LED lighting compared to white LED lighting. These responses by *Nyctalus/Eptesicus* spp. may be explained by the relative presence of foraging opportunities in illuminated landscapes, as patterns of feeding activity under different lights mirrors overall activity.

Nyctalus/Eptesicus spp. are mostly repelled by ALAN but have been recorded foraging around street lights especially in areas away from roads or where bodies of water and high vegetation cover is present (Kronwitter, 1988; Rydell, 1992; Catto et al., 1996; Voigt et al., 2020). As our study was focused on UGS, our study sites represented valuable foraging habitat relative to the surrounding landscape, with larger areas of vegetation and presence of waterbodies. In particular, *Nyctalus noctula* will tolerate ALAN when foraging and are more likely to be present at waterbodies with high levels of ALAN, potentially as a result of the accumulation of insects at lights after having emerged from an aquatic larval stage into the winged adult stage (Voigt et al. 2020). Therefore, despite heavily urbanized areas generally being of low value for open-adapted species such as *N. noctula,* they will preferentially forage at these illuminated sites. This may explain the apparent aversion to UGS under the long-wavelength red LED lighting treatment as accumulation of insect prey is far lower than at artificial lights emitting high UV levels and short-wavelength visual light e.g. white LED lighting (Rich & Longcore, 2013; Van Langevelde et al., 2011; Van Grunsven et al., 2014). Due to their increased ability to escape diurnal predators, prey availability rather than light levels will be a key driver of activity patterns for *Nyctalus/Eptesicus* spp. and whilst red lighting may be beneficial for some bat species, our results indicate that this may not be the case for species who forage opportunistically at illuminated sites in order to exploit swarms of insects attracted by street lights (Mathews et al., 2015; Laforge et al., 2019; Voigt et al. 2020).

Whilst *Nyctalus/Eptesicus* spp. have been observed foraging opportunistically in areas subject to ALAN, the illuminated conditions where these bats have been recorded may be different from the small-scale lighting deployed at our experimental sites. In particular, *Nyctalus* species have very loud echolocation calls (range >100m) and are known to forage high above illuminated areas, therefore recorded activity levels of these species may not fully represent effects of our experimental lighting treatments, but may also include responses to variable ALAN levels associated with urban development that is ubiquitous surrounding our study sites and cannot be controlled for within our experimental setup.

Both *P. pipstrellus* and *P. pygmaeus* showed no significant differences in overall activity under treatment conditions compared to unlit nights, regardless of spectral composition of lighting. As *Pipistrellus* spp. are generally considered to be urban exploiters, opportunistically using ALAN as a foraging resource, these results are consistent with our hypothesis as fast-flying open- and edge-space foraging species are better adapted to increased light-levels due to their reduced perceived light-dependent predation risk and their ability to utilise illuminated sites opportunistically (Mathews et al., 2015; Pauwels et al., 2021). For *P. pipstrellus* and *P. pygmaeus* there were no significant effects on feeding activity between either of the lighting options compared to the unlit nights. This result was contrary to expectations as previous studies have reported increased foraging activity under white lighting due to the higher UV emissions of these shorter wavelength white LED bulbs attracting more insect biomass and therefore feeding opportunities (e.g. Perkin et al., 2014; Spoelstra et al., 2017; Wakefield et al., 2018; Zeale et al., 2018). A possible reason for this may be that each of our study sites were surrounded on all sides by illuminated urban development and therefore the insect density at our experimental lighting setup may be lower than studies conducted in darker landscapes due to a wider dispersal of these light-attracted insects. Whilst not being significant, it is worth noting that overall activity for *P. pygmaeus* was lower for both white LED and red LED lighting treatments compared to dark control. The responses to ALAN by open- and edge-space foraging bats such as *Pipistrellus* spp. have been shown to be antagonistic at different spatial scales, showing opportunism at the street-light scale but negatively impacted at the landscape-scale (Hale et al., 2015; Azam et al., 2016; Spoelstra et al., 2017; Zeale et al., 2018; Laforge et al., 2019; Pauwels et al., 2019). Furthemore, responses by these species have been shown to be context dependent with Barré et al. (2021) reporting that *Pipistrellus* spp. were significantly more likely to seek shelter in cluttered vegetation when exposed to ALAN regardless of colour spectrum, indicating the importance of landscape structure and habitat features when responding to light. As the exact mechanisms of disturbance by ALAN is not fully understood, the responses by supposedly 'light-opportunistic' bats can vary according to individual behaviour and habitat context and therefore results from our study may indicate a weaker overall effect but one that may be significant in studies representing larger bat communities or across a wider range of habitats (Kerbiriou et al., 2020; Barré et al., 2020; Voigt et al., 2021; Hooker et al., 2022).

LEDs are rapidly replacing older lighting technologies due to their flexibility in intensity and spectral composition, in addition to reducing carbon emissions and public sector costs. As a result, measures that capitalise on this new flexibility such as spectral alterations, are being adopted in a bid to limit light pollution and mitigate the harmful impacts of urbanisation. Our results add to the body of evidence documenting the complex relationship between bats and ALAN as well as highlighting that although lighting strategies that involve spectral alterations may provide some benefit for light-averse species at smaller scales, such management options are unlikely to provide comprehensive mitigation due to the species-specific and context dependent nature of responses as well as the antagonistic effects of ALAN at the landscape scale.

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CHAPTER 6 | Re-establishing historic ecosystem links through targeted species reintroduction: beaver-mediated wetlands support increased bat activity.

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Abstract

Despite the global significance of wetlands, conservation strategies often fall short in preserving these ecosystems due to failures in incorporating processes that sustain the ecosystem functioning, hydrological dynamics, ecological processes, and biodiversity of wetlands. Nature-based solutions, such as the reintroduction of beavers, have emerged as effective tools for promoting wetland restoration. Whilst the impact of beavers on wetland restoration is well known, their broader influence on ecosystem health, particularly in modifying habitats for other species, remains inadequately understood. Here we assess the impact that habitat modification through the reintroduction of beavers has on bat populations. There were significantly greater activity levels within beaver-modified wetland habitats for multiple bat species, including higher activity levels of 393% for *Barbastella barbastellus* and 313% for *Plecotus* spp.. Additionally, we observed positive effects on bat populations in the woodland habitat surrounding beaver-modified wetland for certain taxa. In the face of escalating challenges posed by climate change and habitat loss, addressing biodiversity loss necessitates a shift toward ecosystem-centric mitigation measures. Our study demonstrates that the reintroduction of keystone species like beavers can re-establish historical facilitative links between aquatic and terrestrial food webs, highlighting the importance of such interventions in fostering the resilience and sustainability of entire ecosystems.

Introduction

Global ecosystems are undergoing unprecedented transformation due to anthropogenic activities linked to food and fibre production, as well as the utilization of carbon-based resources for energy generation (Hong et al., 2021; Winkler et al., 2021). As the human population continues to grow and shift towards urban living, these environmental challenges are poised to escalate, placing greater demands on the global terrestrial surface (Kareiva et al. 2007; Li et al., 2022). Wetlands, recognised as crucial components of functionally connected landscapes (Keddy et al. 2009; He et al. 2019), face escalating anthropogenic pressures that modify or replace entire habitats (Reis et al. 2017). The long-term loss of natural wetlands averages between 54% and 57%, reaching up to 90% in some geographic regions (Junk et al. 2013). Despite their global and regional significance, conventional measures aimed at wetland protection, such as the 1971 Ramsar Convention, have proven insufficient in mitigating anthropogenic pressures on these habitats (Reis et al. 2017). There is therefore a critical need to determine effective approaches to protect wetlands, particularly with the growing need to incorporate nature-based solutions into these strategies.

In regions where wetland ecosystems have suffered terminal damage, the restoration or reconstruction of these habitats through ecological technology and engineering interventions, such as water division projects and the plugging of land drains, may represent the only viable option to reverse degraded or disappeared wetland habitats (Xu et al., 2019). Freshwater ecosystems can be at least partially restored through human intervention, such as re-meandering or the addition of large woody material to rivers, pond creation, reversing peatland drainage networks, reducing nutrient pressure or restoring riparian buffer zones to reduce diffuse nutrient loading (Phillips et al., 2005; Williams et al., 2008; Krause et al., 2008; González and Rochefort, 2014; Palmer et al., 2014). However, despite a growing base of case studies and empirical evidence, human efforts to return freshwater ecosystems to a favourable natural condition are often frustrated by inadequate knowledge of historical baseline conditions, a lack of biodiversity response and confounding stressors (Palmer et al., 2014; Moss, 2015). Consequently, despite substantial investments in planning, execution and monitoring, many restoration projects often fall short of achieving their intended objectives (Xu et al., 2019).

An important nature-based solution for restoring ecologically degraded wetland systems is to re-establish species that are famed for their ecosystem engineering activities. The beaver's (*Castoridae* spp.) ability to modify freshwater ecosystems as a primary agent of zoogeomorphic processes has no equivalent in the animal kingdom (Westbrook et al., 2011; Johnson et al., 2020; Brazier et al., 2020). The capacity of beavers to restore ecosystem function, habitat dynamics and heterogeneity to degraded habitats has created a rapidly developing interest in their use as restorative agents in both dryland and temperate environments, and the reintroduction of beavers across their former range is regarded as a critical component for restoration of freshwater ecosystems (Halley and Rosell, 2002; Burchsted at al., 2014; Pollock et al., 2014; Gibson et al., 2015).

In the northern hemisphere, beavers were hunted to near-extinction and in countries like Great Britain, the European Beaver (*Castor fiber*) was extirpated from the landscape ~400 years ago (Kitchener and Conroy, 1996). As a result, our collective memory of what beaver-inhabited freshwater ecosystems were like is very limited and similarly, our understanding of how other species co-existed with beavers, many of which may be dependent on beaver ponds, is restricted. Recent beaver reintroductions have therefore provided the opportunity to assess their role in creating ecosystems and shaping the composition of species that inhabit them and the surrounding landscape.

The primary focus on beaver restoration-oriented studies has been on their hydrological and geomorphic effects on the landscape. Despite biodiversity response being a key indicator of restoration effectiveness, it is only relatively recently that the ecological benefits of beaver occupancy have been demonstrated for a variety of organisms spanning trophic levels (e.g. waterbirds, Nummi and Holopainen, 2014; reptiles, Metts et al., 2001; invertebrates, Willby et al., 2018; amphibians, Dalbeck et al., 2020 and fish, Smith and Mather 2013). Bats, like other terrestrial consumers, depend on freshwater ecosystems such as wetlands for drinking water, with some species also relying heavily on these habitats as a foraging resource (Adams and Hayes, 2008; Salvarina, 2016). Several species of bat preferentially forage within wetlands (Dietz and Kiefer, 2016) and wetland cover positively impacts bat assemblage richness, diversity, and foraging activity compared with other habitats (e.g. Fukui et al., 2006; Flaquer et al., 2009; Lookingbill et al., 2010; Salsamendi et al., 2012; Šuba et al., 2012; Ciechanowski 2015, Straka et al. 2016, Blakey et al. 2017). The importance of wetlands also extends to urban environments, where they support higher bat activity and species richness than non-wetland habitats (Straka et al., 2016). Due to their importance as foraging and drinking sites, the management of wetland networks may be critical for the conservation of bat populations (Lookingbill et al., 2010).

In addition to the changes in wetland habitat seen in beaver-modified landscapes, the activities of beavers may also lead to benefits for adjacent habitats, such a woodland, because of their selective thinning of woody vegetation (Haarbery and Rosell, 2006). Not only can this create deadwood roosting habitats for bat species but also alters tree abundance and light availability, changing the woodland structure and allowing a diverse assemblage of plant communities to proliferate (Law et al., 2017). This in turn could lead to an increase in invertebrate species richness and prey availability for bats, whilst the reduction in closed canopy and woodland clutter (i.e. obstacles) may increase the habitat suitability for aerial hawking bat species who preferentially hunt in vegetation gaps (Zwolicki, 2005; Lloyd et al., 2006).

As habitat use by bats in freshwater ecosystems is linked to the spatial structure of riparian vegetation, physical characteristics of the current and water quality (Vaughan et al., 1997; Rydell et al., 1999; Warren et al., 2000; Downs and Racey 2006; Kalcounis-Rueppell et al., 2007; Biscardi et al., 2007), beaver-modified landscapes may have the potential to increase optimal foraging habitat for several bat species. Furthermore, as bats represent a mammal group with high trophic diversity that show clear reactions to environmental alterations (Jones et al., 2009; Russo et al., 2021), their response to landscape changes may be an effective indicator of biodiversity restoration in beaver-modified habitats. Indeed, a limited number of studies have found increased bat activity of certain species in areas where beavers have been reintroduced, however these studies were limited to study sites in the same local area with no clear delineation between control and treatment sites i.e. beavers were able to travel easily between waterbodies (<300m, Nummi et al., 2011) or surveys were conducted on the same watercourses (<1.7km) with transects divided into beaver-modified or unmodified sections (Ciechanowski et al., 2010).

To our knowledge, no study has investigated the effects of targeted species reintroduction on bat activity or assessed the importance of beaver-modified woodland and wetland habitats relative to control sites. Here we conducted a paired observational study to investigate changes in bat activity at enclosed beaver (*Castor fiber*) reintroduction projects across England and Wales. In the absence of suitable baseline bat data for each beaver reintroduction site, we chose independent control locations that were of comparable habitat to those present prior to the release of beavers. We compared activity levels of eight bat species/groups (*P. pygmaeus*, *P. pipistrellus*, *Myotis* spp., *Nyctalus/Eptesicus* spp., *B. barbastellus*, *R. ferrumequinum*, *R. hipposideros* and *Plecotus* spp.) in beaver reintroduction enclosures and paired control locations, with activity levels recorded in separate woodland and wetland habitats.

We hypothesised that bats would respond positively to localised reintroduction of beavers according to species-specific differences in foraging strategy and habitat preference. We predicted that activity would be higher in beaver enclosures compared to paired control sites for all species due to the increased heterogeneity of woodland and wetland habitat. This includes improved spatial structure of riparian vegetation, physical characteristics of the current and water quality as well as increases in abundance and diversity of invertebrate biomass (Salvarina, 2016; Puttock et al., 2017; Russo et al., 2021). Furthermore, we predicted that increases in activity would be most prevalent in wetland habitats due to the transformative nature of beavers engineering capabilities on watercourses. However, we do not predict there to be negative impacts seen on woodland bat assemblages due to beavers discriminate approach to tree felling.

Materials and Methods

Passive acoustic monitoring was conducted at 12 beaver reintroduction project sites across England and Wales between June and September 2022 (Fig.1). This study was carried out under ethical approval by the University of the West of England Animal Welfare and Ethics Sub Committee (licence no: 210716: AWESC: R214) under strict recommendations and guidance from government licensing departments Natural England and Natural Resource Wales. Each monitoring period lasted for 7 nights (with the exception of one site that was monitored for 6 nights due to equipment failure) and comprised two full spectrum ultrasonic detectors deployed at wetland and woodland habitats within the beaver reintroduction enclosure. A further two detectors were deployed in paired control locations outside of the beaver enclosure (four detectors in total per site).

We determined the location of control detectors based on habitat suitability, choosing locations that were comparable to beaver enclosure locations prior to species introduction and subsequent change in habitat management (Table 1). We located the control detector as far away from the beaver enclosures as possible, while still being within the boundary of land managed by the same landowner. As there were no significant differences in landscape cover across detector locations, these variables were excluded from further analyses to achieve model simplification. An exception to this were differences recorded in UKCEH aggregate land cover category LC8 which represents freshwater habitats and were therefore anticipated to be distinct from control sites due to the damming and flooding activity of beavers (see supplementary material for statistical analyses of landscape variables for paired locations).

Beaver reintroduction sites comprised fenced off enclosures of various sizes (mean 11.15 ha, SD 15.96 ha) based around a pre-existing water source i.e. a stream or lake in a variety of different landscape settings including broadleaved and coniferous woodland, culm grassland, former agricultural land and wildlife reserves operated by various non-governmental organisations (NGOs). Beaver enclosures were only chosen as study sites if the beavers had been present for >6 months to ensure sufficient time for beavers to make changes to habitat composition and structure.

Field work was conducted in suitable conditions in accordance with Bat Conservation Trust guidance (2016; i.e. sunset temperature 10°C or above, no rain or strong wind). Mean nightly temperatures (°C) were recorded using in-built thermometers within the bat detectors and mean nightly wind speed (mph), mean nightly humidity (%) and total nightly rainfall (mm) were obtained from Met Office weather stations (http://www.metoffice.gov.uk) within 8 km of each site (mean distance 2.83 km, SD 1.87 km). As sites were surveyed continuously for 7 nights each, there may have been occasions where these conditions were not met, however our experimental design ensured paired sites were surveyed on the same nights and would therefore experience the same local weather conditions, controlling for any effects of weather and date.

Table 1: Summary of landscape metrics—the mean and SD for habitat area cover within 2500m of the paired beaver enclosure and control locations across 12 reintroduction project sites. Spatial analysis of landscape variables was undertaken in QGIS using habitat data extracted from UK CEH Land Cover Map 2021 (Marston et al, 2022).

UKCEH Aggregate Land Cover	Beaver Wetland m^2	Control Wetland m^2	Beaver Woodland m^2	Control Woodland m^2
Broadleaf woodland	367 (289)	383 (308)	369 (291)	380 (310)
Coniferous woodland	132 (219)	129 (206)	131 (219)	126 (199)
Arable	403 (519)	398 (512)	407 (523)	402 (513)
Improved grassland	812 (437)	823 (466)	802 (443)	822 (467)
Semi-natural grassland	53.1 (121)	39.9 (76.5)	55.4 (128)	42.5 (83.6)
Mountain, heath and bog	21 (35.1)	18.9 (31.1)	21.2 (35.4)	18.3 (29.8)
Saltwater	0.25 (0.87)	0.26 (0.89)	0.34 (1.16)	0.20 (0.69)
Freshwater	35.8 (79.1)	34.8 (78.5)	36.2 (79.8)	34.1 (77.8)
Coastal	21.3 (73.9)	21.3 (73.9)	22.3 (77.2)	20.2 (70.1)
Built-up areas and gardens	115 (151)	114 (139)	116 (159)	115 (145)

Bat activity was recorded for 30 min before sunset to 30 min after sunrise using Anabat Swift full spectrum bat detectors (Titley Scientific, Brendale, QLD, Australia; triggered .wav recording; sample rate 500 kHz; minimum frequency 10 kHz; maximum frequency 250 kHz; minimum event time 2ms) positioned either at the edge of wetland habitat or within woodland understory using omnidirectional microphones. Automated species identification was necessary as manual classification would have been prohibitively time consuming. We used BatClassify (Scott, 2012) to classify bat calls by species or species groups and consistent with recommendations (Lopez-Baucells et al., 2019; Russo and Voigt, 2016; Rydell et al., 2017) classifications were manually verified using Anabat Insight v.1.9.2 (Titley Scientific, Brendale, QLD, Australia) using call parameters as described in Russ (2012) and following Barré et al. (2019) to quantify classification error rates (see Appendix 2 for detail of error rate modelling approach).

Rather than providing positive and negative classifications for recordings, error rate modelling returns a probability of a correct classification (by species). Following Barré et al. (2019) we removed acoustic data with a maximum error rate tolerance (MERT) of 0.5 (i.e. 50% correct classification probability). Number of bat passes per night per detector location was used as an index of relative bat activity and calls were grouped into eight species/species groups: *P. pipistrellus*, *P. pygmaeus*, *Myotis* spp., *Nyctalus/Eptesicus* spp., *R. ferrumequinum, R. hipposideros, B. barbastellus* and *Plecotus* spp. Call identifications were grouped together in a genera-wide category for *Myotis* spp. and *Plecotus* spp. due to similarities in call structure between species within the same genus preventing robust manual verification (Schnitzler and Kalko, 2001). In addition, *Nyctalus* spp. and *Eptesicus* spp. are automatically grouped together by BatClassify. *Pipistrellus nathusii* is not classified by BatClassify so were grouped with *P. pipistrellus*. All analyses were performed in R v.4.0.4 (R Core Team, 2021) using the significance level $P < 0.05$. Relationships between beaver-modified habitats and bat activity were assessed by comparing the number of bat passes recorded per night in wetland and woodland habitats present within beaver reintroduction enclosures with paired control locations. We analysed log transformed bat pass count data with generalized linear mixed effect models (GLMMs), with a Poisson family using the *glmmTMB* R Package (v1.0.1; Brookes et al., 2017). We fitted the number of bat passes per species/species group per night as the dependent variable, detector location (a factor with two levels: beaver-modified and control) as a fixed effect and site as a random effect. We present effect sizes and standard errors for final models and post-hoc contrast test results in the text as *z*-statistics and *P*-values obtained using the *emmeans* package (v1.4–1; Lenth et al., 2023). We validated final models by simulation using the R package *DHARMa* (v.0.2.0; Hartig, 2024) using residual plots to check for overdispersion, heteroscedasticity and zero inflation.

Figure 1. Location of study sites surveyed across England and Wales, UK including photographs of example field site recording positions. Reproduced from OS map data by permission of the Ordnance Survey © Crown copyright 2023.

Results

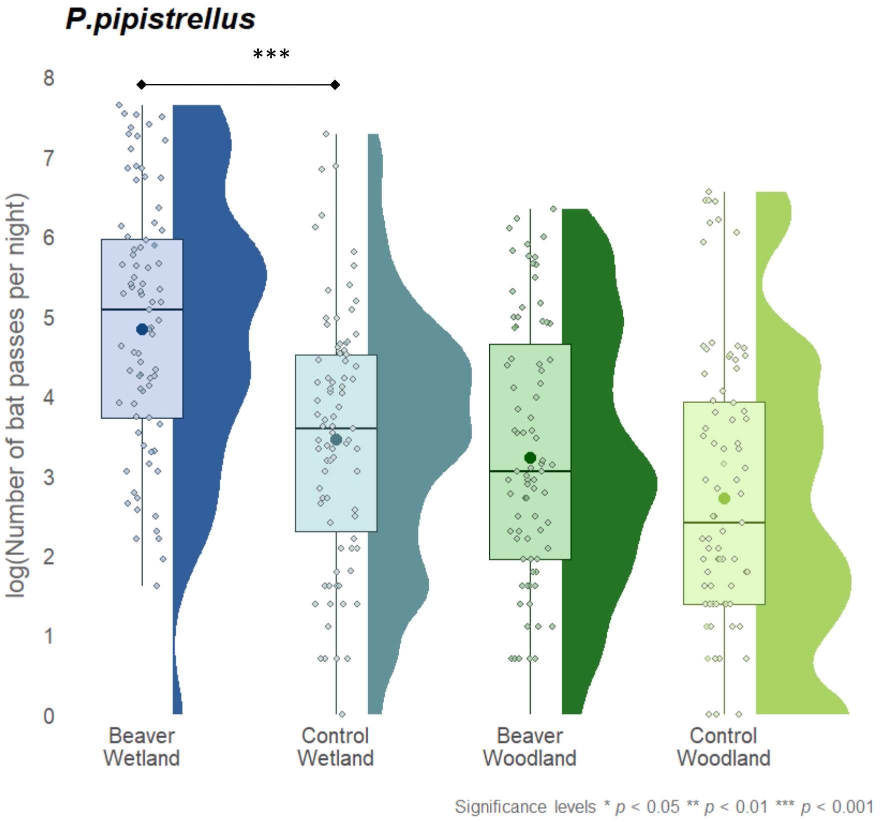
A total of 144,548 bat passes belonging to eight species/species groups were recorded during the 83 nights of monitoring using a MERT of 0.5 in automated identification. The majority of echolocation recordings belonged to *P. pygmaeus* (63,965 passes; 44.3%) and *P. pipistrellus* (52,687 passes; 36.5%), followed by *Myotis* spp. (16,018 passes; 11.1%), *Nyctalus/Eptesicus* spp. (10,531 passes; 7.3%) with *B. barbastellus*, *Rhinolophus* spp. and *Plecotus* spp. <1% of species recorded.

We found statistically significant effects of paired detector location on bat activity within wetland and woodland habitats for *P. pipistrellus, P. pygmaeus*, *Nyctalus/Eptesicus* spp., *Myotis* spp., *B. barbastellus* and *Plecotus* spp. *Pipistrellus pipistrellus* activity was an average of 40% higher in beaver-modified wetland habitats compared to paired wetland control locations (*P* <0.001; Table 2; Fig. 2), with marginally significant differences in bat activity also recorded between beaver-modified woodland and paired control locations (*P* = 0.06 Table 2; Fig. 2). *P. pygmaeus* activity was an average of 54% higher in beaver-modified wetland habitats compared to paired control locations (*P* <0.001; Table 2; Fig. 2), with significantly higher level of bat activity also recorded between beaver-modified woodland and paired control locations (*P* <0.001; Table 2; Fig. 2). *Nyctalus/Eptesicus* spp. activity recorded in beaver-modified wetland habitats was significantly higher than paired control locations representing a 21% higher activity level (*P* 0.05; Table 2; Fig. 2) although no significant differences in activity levels were found between beaver-modified woodland habitat and paired control locations(*P* 0.69; Table 2; Fig. 2). *Myotis* spp. activity was an average of 35% higher in beaver-modified wetland habitats compared to paired control locations (*P* <0.001; Table 2; Fig. 2), however no significant differences in bat activity were recorded between beaver-modified woodland and paired control locations (*P* 0.27; Table 2; Fig. 2). *B. barbastellus* activity was an average of 393% higher in beaver-modified wetland habitats compared to paired control locations (*P* <0.001; Table 2; Fig. 2), however no significant differences in bat activity were recorded between beaver-modified woodland and paired control locations (*P* 0.33; Table 2; Fig. 2). *Plecotus* spp. activity recorded in beaver-modified wetland habitats was significantly higher than paired control locations representing a 313% increase in overall activity (*P* <0.001; Table 2; Fig. 2) although no significant differences activity levels were found between beaver-modified woodland habitat and paired control locations(*P* 0.64; Table 2; Fig. 2). Lastly we found no statistically significant effects of paired detector location on *Rhinolophus* spp. activity in either of the wetland or woodland habitats (*R. ferrumequinum P* = 0.73; *P* = 0.25, *R. hipposideros P* = 0.94; *P* = 0.98 respectively; Table 2; Fig. 2).

Table 2. Parameter estimates and standard errors (± s.e), *z*- and *P*- values for fixed effects included in generalized linear mixed models and *post-hoc* comparisons relating bat activity to paired detector location (beaver vs control wetland, beaver vs control woodland) including variance and standard deviation (Std Dev.) of random effect terms.

	Bat Activity (passes)		
P. pipistrellus			
Fixed Effects	**Estimate (± s.e)**	***z*- value**	***P* value**
Lo. ion (Beaver Wetland vs Control Wetland)	-0.34 (±0.08)	4.35	<0.001***
Location (Beaver Woodland vs Control Woodland)	0.17 (±0.09)	1.90	0.06
Random Effects	**Variance**	**Std Dev.**	
Site (*N*=12)	0.10	0.33	
P. pygmaeus			
Fixed Effects	**Estimate (± s.e)**	***z*- value**	***P* value**
Location (Beaver Wetland vs Control Wetland)	0.43 (±0.08)	5.56	<0.001***
Location (Beaver Woodland vs Control Woodland)	0.26 (±0.09)	2.75	<0.01**
Random Effects	**Variance**	**Std Dev.**	
Site (*N*=12)	0.15	0.38	
***Nyctalus/Eptesicus* spp.**			
Fixed Effects	**Estimate (± s.e)**	***z*- value**	***P* value**
Location (Beaver Wetland vs Control Wetland)	0.19 (±0.10)	1.94	0.05*
Location (Beaver Woodland vs Control Woodland)	-0.04 (±0.11)	-0.40	0.69
Random Effects	**Variance**	**Std Dev.**	
Site (*N*=12)	0.29	0.54	
***Myotis* spp.**			
Fixed Effects	**Estimate (± s.e)**	***z*- value**	***P* value**
Location (Beaver Wetland vs Control Wetland)	0.30 (±0.09)	3.46	<0.001***
Location (Beaver Woodland vs Control Woodland)	0.12 (±0.10)	-0.40	0.27
Random Effects	**Variance**	**Std Dev.**	
Site (*N*=12)	0.07	0.26	
B. barbastellus			
Fixed Effects	**Estimate (± s.e)**	***z*- value**	***P* value**
Location (Beaver Wetland vs Control Wetland)	1.60 (±0.31)	5.09	<0.001***
Location (Beaver Woodland vs Control Woodland)	0.28 (±0.28)	0.98	0.33
Random Effects	**Variance**	**Std Dev.**	
Site (*N*=12)	1.77	1.33	
***Plecotus* spp.**			
Fixed Effects	**Estimate (± s.e)**	***z*- value**	***P* value**
Location (Beaver Wetland vs Control Wetland)	1.42 (±0.29)	4.96	<0.001***
Location (Beaver Woodland vs Control Woodland)	0.23 (±0.48)	0.47	0.64
Random Effects	**Variance**	**Std Dev.**	
Site (*N*=12)	0.56	0.75	
R. ferrumequinum			
Fixed Effects	**Estimate (± s.e)**	***z*- value**	***P* value**
Location (Beaver Wetland vs Control Wetland)	0.19 (±0.55)	0.35	0.73
Location (Beaver Woodland vs Control Woodland)	0.71 (±0.62)	0.47	0.25
Random Effects	**Variance**	**Std Dev.**	

Site (*N*=12)	68.28	8.26	
R. hipposideros			
Fixed Effects	**Estimate (± s.e)**	***z*- value**	***P* value**
Location (Beaver Wetland vs Control Wetland)	0.02 (±0.26)	0.08	0.94
Location (Beaver Woodland vs Control Woodland)	-0.01 (±0.62)	-0.02	0.98
Random Effects	**Variance**	**Std Dev.**	
Site (*N*=12)	25.53	5.05	



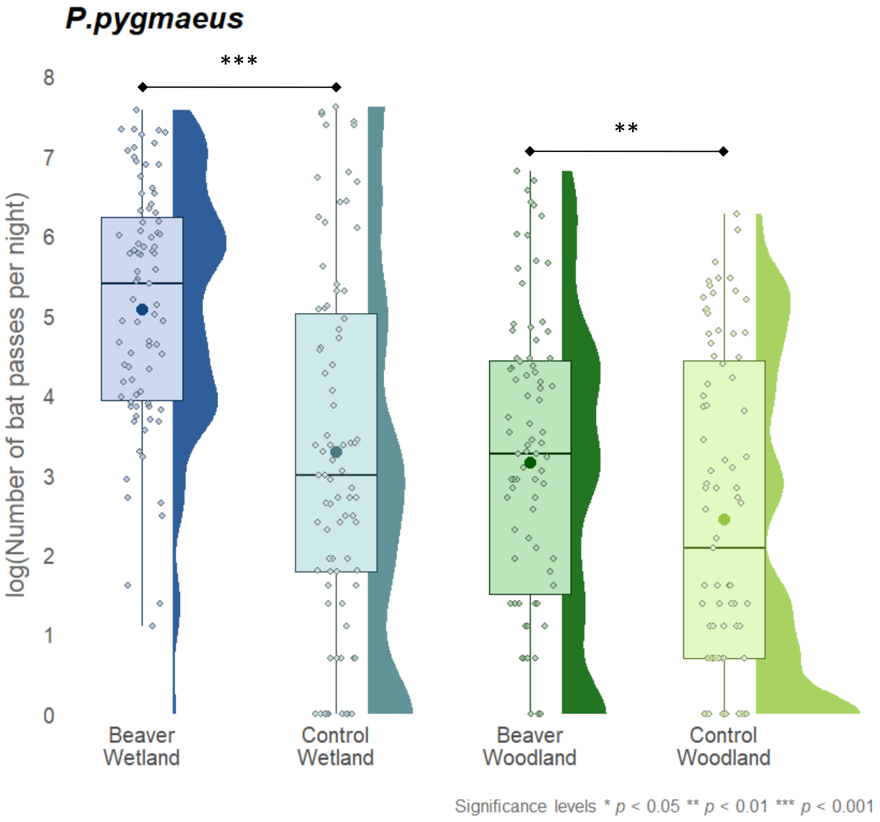
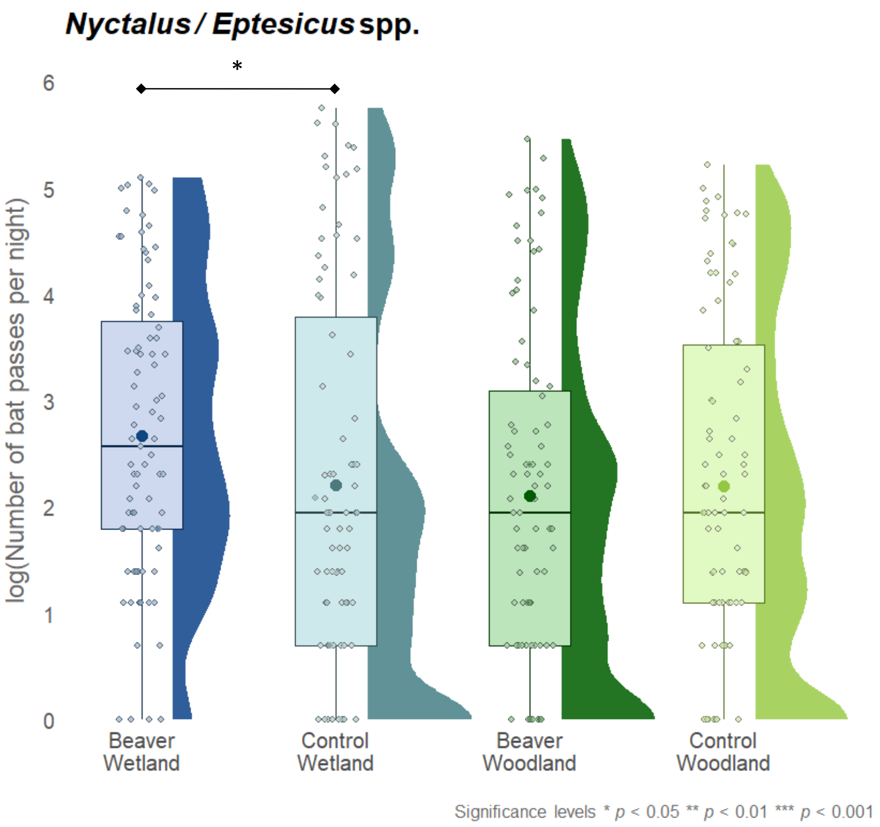
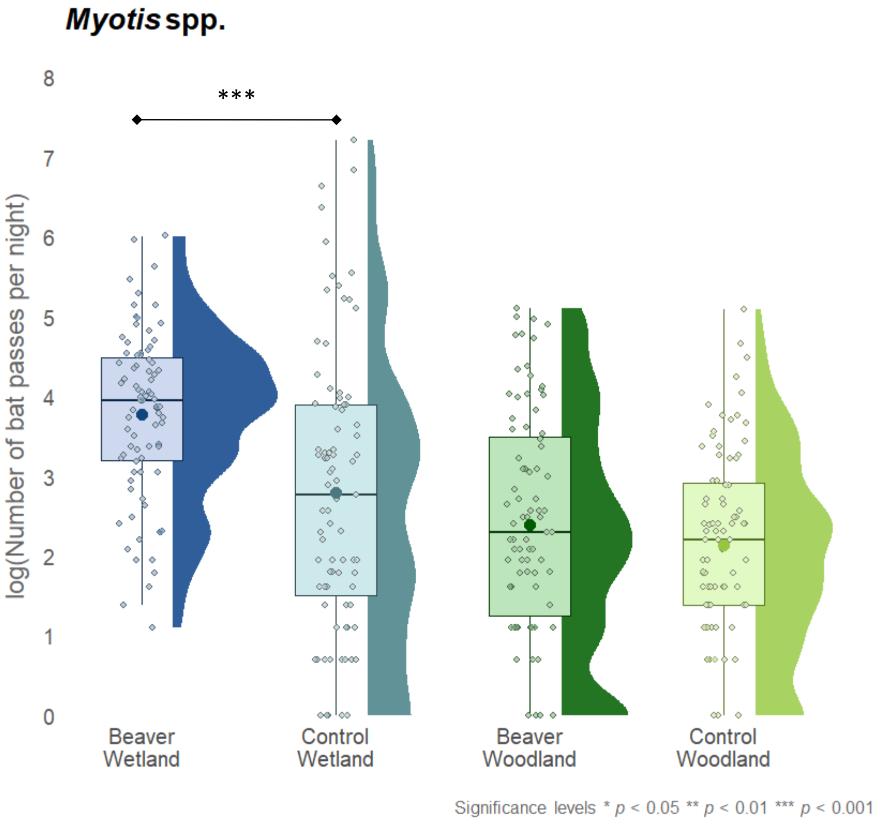


Figure 2. Raincloud plots displaying data distribution, probability density and summary statistics of nightly bat activity by *P. pipistrellus, P. pygmaeus*, Nyctalus/Eptesicus spp. and *Myotis spp.* at beaver-modified wetland and woodland habitats compared to paired control locations. Data is presented as log(Number of bat passes per night) with significant within-subject differences during post hoc tests highlighted. Individual dark points indicate mean values across sites (*N*=12).


Nyctalus / Eptesicus spp.


Myotis spp.

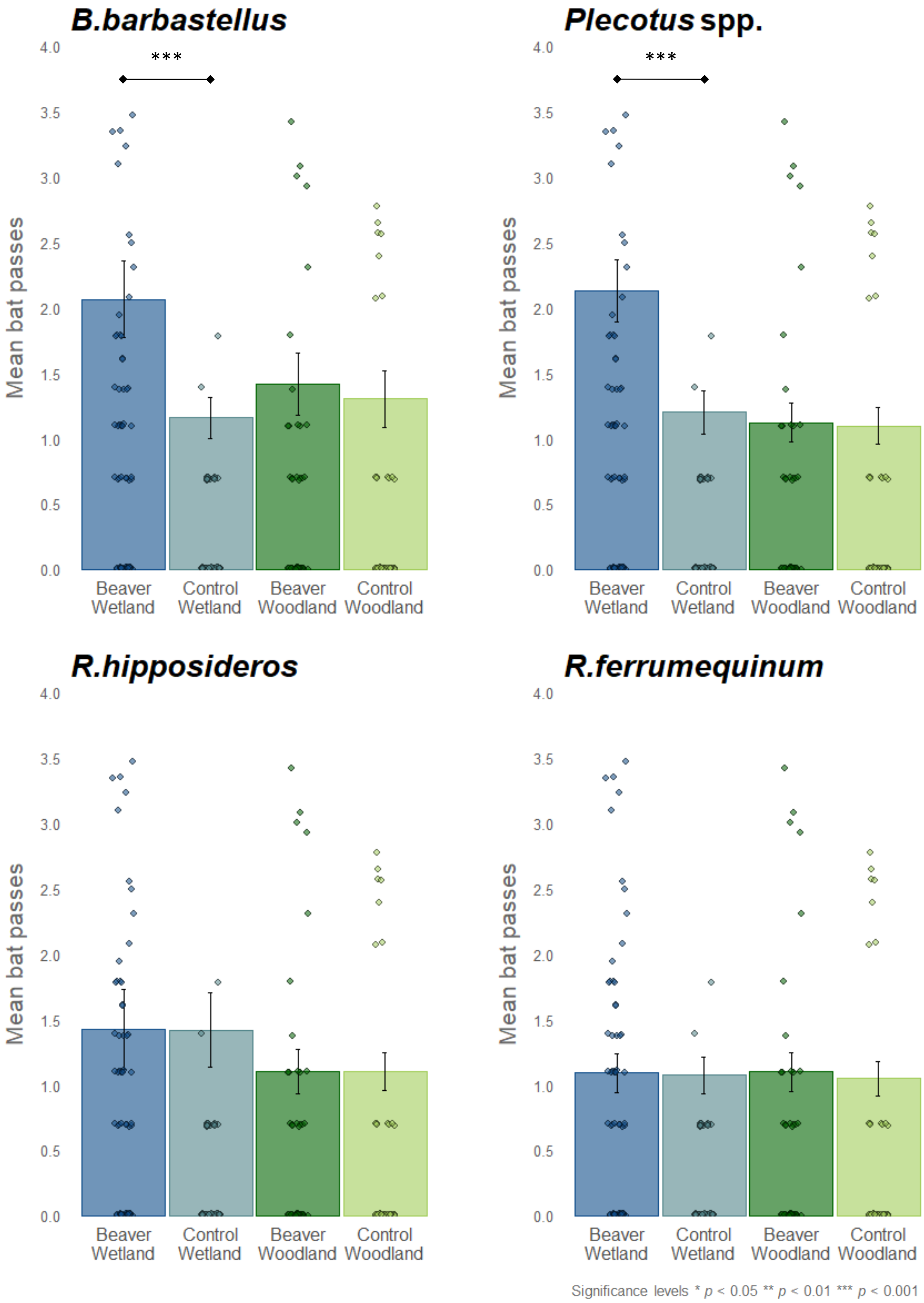


Figure 3. Bat activity (mean bat passes) by *B. barbastellus, Plecotus* spp., *R. hipposideros* and *R. ferrumequinum* at beaver-modified wetland and woodland habitats compared to paired control locations. Data is presented as mean ± SEM with significant within-subject differences during post hoc tests and individual data points highlighted.

Discussion

To our knowledge, no study has investigated the effects of targeted species reintroduction on bat activity or assessed the potential differences in responses between modified and conventional habitats. As countries grapple with the dual threats of climate and biodiversity breakdown, these results are of particular significance as the reintroduction of native fauna is an important nature-based solution for restoring and rewilding areas that have been subject to centuries of anthropogenic pressures and resulting extinction events. Here we show that the release of European beavers (*Castor fiber*) into enclosures at sites across England and Wales had a significant effect on the overall activity of local bat assemblages compared to paired control locations of comparable habitat unimpacted by beavers. We also highlight species-specific responses in activity dependant on the habitat surveyed within the reintroduction enclosures. Our results demonstrate that targeted species reintroductions could be an effective strategy in rewilding degraded landscapes for a variety of species as well as re-establishing historic links between aquatic and terrestrial ecosystems.

We found that the presence of beavers in waterbodies at reintroduction enclosures resulted in a higher level of bat activity recorded over wetland habitats compared to paired controls for the majority of species/species groups studied. We also found no negative impacts on bat activity in woodland habitats resulting from the presence of beavers and indeed found a significant or marginally significant higher level of activity for *Pipistrellus* spp.

As a keystone species, beavers significantly modify the structure, hydrology, geomorphology and biotic community composition of their local environment, affecting almost all elements of the aquatic and terrestrial interface which they inhabit (Brazier et al., 2021). Beavers engineer ecosystems in various ways, but most fundamentally through the construction of dams. These dams are constructed from felled wood, stones and mud placed perpendicular to water flow, creating ponds full of sediment and nutrients which slow the flow of water, reducing peaks flows downstream, storing and gently releasing water in times of drought (Hood and Bayley, 2008; Puttock et al., 2017). By creating depositional pond environments and excavating canals, beaver dams have pronounced effects on both aquatic and terrestrial biota and their trophic interactions, as well as enhancing wetland connectivity, and geomorphic dynamism (Correll et al., 2000; Pollock et al., 2014; Gorczyca et al., 2018). In this study, we demonstrate that the modification of wetland habitats by European beaver can have a dramatic positive impact on the surrounding ecosystem and re-establish historic facilitative links between aquatic and terrestrial food webs. Our results indicate that the resulting habitat improvements following beaver reintroductions also lead to improvements in habitats, furthermore, as bats display sensitivity to alterations in the environment, their heightened activity in beaver-modified habitats may be an effective indicator of biodiversity restoration when rewilding degraded landscapes (Jones et al., 2009; Russo et al., 2021).

We recorded increased activity over wetland habitats for *P. pipistrellus* (+40%)*, P. pygmaeus* (+54%), *Nyctalus/Eptesicus* spp. (+21%), *Myotis* spp. (+35%) which comprise the most common species/species groups of bats in the UK and are therefore amongst the largest consumers of insect biomass. Increased activity of *P. pipistrellus, P. pygmaeus*, *Nyctalus/Eptesicus* spp. in wetland habitats aligns with our predictions, as these species are all known to prefer waterbodies or riparian zones, highlighting the regenerative impact the beavers have had on the quality and extent of wetland habitats (Rachwald 1992; Rydell et al. 1994; Vaughan et al. 1997; Mickevičiené and Mickevičius 2001; Russ and Montgomery 2002; Downs and Racey 2006; Kaňuch et al. 2008; Nummi et al., 2011; Ciechanowski et al., 2011). Furthermore, despite *Myotis* species being grouped together in our analysis due to the similarities in echolocation call structure between species within the same genus (Schnitzler and Kalko, 2001), it is likely that the majority of the calls were of *M. daubentonii* given that this species is widespread throughout the study area and are also strongly associated with riparian habitats (Warren et al., 2000). As the positive impact on bat activity by localised reintroduction of beavers' ranges across bat species/species groups, it is likely that the drivers behind these increases represent a multi-faceted response according to species-specific differences in foraging strategy and habitat preference.

When beavers flood former terrestrial ecosystems they extend the riparian zone and increase the heterogeneity of stream depth, flow velocity, and benthic habitats such as silty substrates as well as submerged and emergent vegetation (Clifford, Wiley, and Casey, 1993; France, 1997; Rolauffs, Hering, and Lohse, 2001). These alterations in turn support increased invertebrate abundance, biomass and/or density and support more lentic species including bats' main aquatic prey, Diptera (especially the family Chironomidae) and Trichoptera (Collen and Gibson, 2000; Rosell et al., 2005; Salvarina, 2016; Osipov et al., 2018; Willby et al., 2018) which can improve the habitat quality and foraging opportunities for bats (Benke, Ward, and Richardson, 1999; Bush and Wissinger, 2016; Law et al., 2019).

Despite the significant benefits brought about by beaver reintroductions, there is potential for beavers to cause an overall decrease in diversity of animal assemblages or population sizes of particular species. Modification of habitat conditions by beavers can result in ponds that are dominated by unique invertebrate assemblages that thrive in the typically homogeneous benthic habitat that result from increased fine sediment deposition (Descloux, Datry, and Usseglio-Polatera, 2014; Pulley et al., 2019), however these impacts would likely only arise as a consequence of limiting beavers to defined areas. At broader scales in which beavers are not confined to enclosures, spatial and temporal variation in successional stages increases the taxonomic, trophic, and/or β-diversity of aquatic invertebrate communities compared to environments lacking beaver modification (Margoslis et al., 2001; Law et al., 2016; Bush, Stenert, Maltchik, and Batzer, 2019). Encouraging the wider dispersal of beavers throughout the landscape would further increase the positive impacts of beaver reintroductions on food web dynamics supporting a range of both lotic and lentic invertebrate prey species for bats as well as avoiding the potential creation of homogenous habitats (Law et al., 2016; Bush et al., 2019; Pollock et al., 2017; Willby et al., 2018; Brazier et al., 2021). A similar response was also reported by Ciechanowski et al. (2011) who found that the number of bat passes was significantly higher in the stream sections modified by beavers than in the unmodified sections for *P. nathusii*, *P. pipistrellus*, *P. pygmaeus*, and *N. noctula.* Whilst the experimental design of this study did not quantify levels of beaver modification between study and control sites or indeed control for beavers being able to freely move between the two, their findings do suggest that activity of some species was concentrated in areas where habitat modifications by beaver was most evident.

In addition to the more obvious benefits that result from the beaver presence in waterbodies, such as increased foraging opportunities, the change in hydrological conditions can have direct species-specific benefits for bats. Trawling bat species such as *M. daubentonii* benefit from an acoustic mirror effect when waterbodies transition from turbulent shallow and narrow streams to still beaver ponds (Siemers et al. 2005). This aids surface-based prey detection as acoustically smooth backgrounds such a beaver pond surfaces facilitate echolocation calls that receive no or very low background echo (Siemers et al., 2001, 2005). Indeed, previous observational and playback experiments have found that noise from turbulent water could interfere with foraging efficiency in bats that forage close to water surfaces indicating a direct benefits of beaver presence for these species (von Frenckell and Barclay, 1987; Mackey and Barclay, 1989; Rydell et al., 1999; Schaub et al., 2008). In our study, the positive response in wetland habitats by bats with different foraging strategies, habitat and prey preferences suggests that the mechanisms behind the increase in activity in beaver-modified landscapes is context and species-dependent, relying on an interplay of factors that improve the quality and extent of habitat available to bats.

In addition to the increase in activity levels of bat species with an affinity to water, we also recorded significant increases in activity for species that are woodland specialists such as the *B. barbastellus*

(+393%) and *Plecotus* spp. (+313%) in beaver-modified wetland habitats compared to paired control locations. Whilst we did not find any significant differences in activity level of these species in woodland habitats, our results suggest an overall improvement in habitat quality within the reintroduction enclosures. The narrow ecological niche of *B. barbastellus* is largely defined by a preference for roosting in features of old or dead tree trunks, such as under loose bark or within crevices, resulting in populations that are highly dependent on mature broadleaved woodlands (Sierro and Arlettaz, 1997; Russo et al., 2004). However, in lieu of age-related senescence in the creation of deadwood habitats, beavers can create copious amounts of this habitat by raising water levels, with the subsequent inundation causes extensive die-off of trees within woodlands in the flood zone (Thompson et al., 2016). This formation of new deadwood on a short rotation cycle in beaver-created flood sites, coupled with *B. barbastellus* preference for trees in close proximity to water, may constitute an important habitat creation process for these rare bat species (Thompson et al., 2016; Carr et al., 2018). A similar rationale may also be a driver behind the increase in *Plecotus* spp. activity recorded within beaver enclosures. As *P. auritus* (the most likely species present within our study area) will roost within trees in natural habitats (Ancillotto and Russo, 2020) the formation of new deadwood by beaver flooding is likely to benefit this species. However, unlike *B. barbastellus, P*. *auritus* regularly adopt a gleaning foraging strategy and rely more heavily on passive listening of prey-generated sounds, increasing the risk from noise disturbance through mechanisms such as acoustic masking (Luo et al., 2015; Dietz and Kiefer, 2016). Previous studies have found that natural noise sources can cause difficulties for gleaning bat species and therefore the transition from turbulent shallow and narrow streams to still beaver ponds may constitute an improvement in the soundscape for these species (Schaub et al., 2008; Gomes et al., 2021). However, this result should be interpreted with caution as these species have very soft echolocation calls that are often not detected even when bats are present (Dekker et al., 2022).

The results from the current study suggest that beaver reintroduction also has a beneficial effect on bat activity in woodland habitats for some species, with a significant or marginally significant increase in activity recorded for *Pipistrellus* spp. Importantly, given the widespread potential conflicts that arise from tree-cutting by beavers including the potential decrease in tree cover adjacent to beaver habitat (Campbell-Palmer et al., 2016), no negative impacts on bat activity were recorded in woodland habitats for any of the bat species recorded. Whilst beavers do remove cut trees for foraging, building, and as means to wear down their continually growing teeth (Baker and Hill 2003; Johnston, 2017), they discriminately select trees based on species, size and location as opposed to clearing large areas (Haarberg and Rosell, 2006). This selective thinning of woody plants decreases canopy cover, increasing the amount of sunlight available to understory vegetation and therefore diversifying the spatial structure and species composition of plant communities (Rosell et al., 2005; Zwolicki, 2005; Law et al., 2017). Forest and woodland structure are an important influence on activity patterns of bats and increased levels of forest-associated clutter are a serious limitation for aerial hawking species such as *Pipistrellus* spp. Previous studies have shown that most aerial hawking bats avoid internal parts of dense, intact stands with their activity being negatively correlated with the area of closed canopy and density of trees (Rachwald 1992; Erickson and West 2003; Kusch et al., 2004; Lloyd et al. 2006; Fuentes-Montemayor et al., 2013; Froidevaux et al., 2021). In managed forests that are subject to commercial logging, aerial hawkers use either stream corridors or artificial areas of low clutter, which include thinned stands, clear-cuts and trails (Patriquin and Barclay 2003; Lloyd et al. 2006), whilst in unmanaged forests, the same group of bats have to use canopy gaps created by natural processes such as tree senescence, windthrows or outbreaks of phytophagous insects, fungi or disease (Weiskittel and Hix 2003; Worrall et al. 2005; Jochner-Oette et al., 2021). The selective cutting of trees by beavers therefore may have a similar function in wooded areas in which they inhabit.

Wetland ecosystems are highly productive and biodiverse ecosystems that provide essential regulation, provision and support of critical ecosystem services as well as social and cultural services. Yet despite this, most wetland habitats face numerous and mounting anthropogenic pressures resulting in a vast decline of both area and ecological condition, with international legislation and conventions aimed at recognising the importance of wetlands and promoting their conservation largely failing to mitigate anthropogenic pressures on these habitats. There is a growing understanding that the actions required to protect and restore wetland ecosystems will require nature-based solutions. The capacity of beavers to restore ecosystem function, habitat dynamics and heterogeneity in degraded landscapes has created a rapidly developing interest in their use as restorative agents, with their reintroduction now regarded as a critical component for restoration of freshwater ecosystems. We demonstrate that rewilding areas using beavers can provide a natural and long-term solution to restoring degraded landscapes which not only modifies the structural composition and functional connectivity of a landscape but also increases the species activity found within it. We found that the reintroduction of beavers to wetland habitats resulted in significant increases in bat activity for the majority of species recorded, with significant benefits are also described for aerial-hawking species in woodland habitats. The increase in activity across a range of bat species/species groups that have different foraging strategies, habitat and prey preferences suggests the positive impacts of beavers on a landscape represent a dynamic and multifaceted solution to restore degraded wetland ecosystems.

Acknowledgements

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Chapter 7 | General Discussion

The impacts of the biodiversity crisis the world is now facing is being witnessed in every habitat on earth and whilst unprecedented, are now fully entrenched and a daily reality for many species. Despite the contributing factors being well known and highlighted consistently by Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), the International Union for Conservation of Nature (IUCN) and the Convention on Biological Diversity targets to reduce or halt biodiversity declines are perpetually missed by governments.

Habitat fragmentation can lead to devastating effects for wildlife both directly and indirectly and the subsequent reorganisation of the spatial landscape not only affects individual behaviour, but population dynamics of whole communities and the complex ecosystems they are a part of. Bats are particularly sensitive to the loss and fragmentation of habitat due to several life history traits making them more susceptible to local extinctions.

Whilst the negative impacts associated with permanent alterations of important habitat features is starting to get more attention, evidence on the impacts of temporary habitat fragmentation and mitigation strategies deployed to limit these impacts is limited. Temporary fragmentation of habitats is a prevalent occurrence and may consist of the temporary removal of habitat features such as hedgerows, treeline, ditches etc. to be reinstated later or through a range of anthropogenic activities that have the potential to illicit a similar effect by introducing changes that functionally fragment existing landscapes during their operational stages. As a result, these factors have the potential to sever extensive tracts of important ecological features, altering individual and colony behaviour, community composition and population dynamics at both the local and landscape scale. However, often little regard is given to the effectiveness of mitigation strategies implemented to limit temporary impacts, or the scope of mitigation does not adequately account for the full range of effects from temporary habitat fragmentation. Here we present results highlighting the detrimental effects of temporary habitat fragmentation in a variety of forms and evaluate a number of strategies deployed to mitigate the harmful effects of habitat fragmentation on bats and maintain or restore landscape connectivity.

In chapter 2 we begin by investigating the impacts of temporary destruction of bat foraging and commuting habitats prior to reinstatement at large linear infrastructure projects including assessing the effectiveness of mitigation measures deployed to try and maintain landscape connectivity during these periods of development. It could be argued that these forms of fragmentation are not temporary in nature due to the time lags involved with restoring these important habitat features to their former condition. However, within the planning systems such construction activities are deemed temporary as there is not the intention to remove the habitats permanently. This form of temporary habitat fragmentation is a common occurrence across a range of development projects from small-scale housing developments to large linear infrastructure projects such as the installation of facilities (e.g. power lines, water pipes etc.) as well as rail and road construction. Whilst the majority of instances of this form of fragmentation do not legally require any mitigation to be adopted the Environmental Statement and Habitats Regulations Assessment (HRA) for the project site identified potential for impacts due to the proximity of the site to the North Somerset and Mendip Bats Special Area of Conservation (SAC) and the Mendip Limestone Grasslands SAC which contain important maternity and hibernation sites for both *R. hipposideros* and *R. ferrumequinum.* As a result, and despite having little evidence base to support the effectiveness of such mitigation, National Grid developed a series of temporary bat flyway designs to act as surrogate hedgerows during the construction phase of the development.

During the study we found that the removal of hedgerow sections to facilitate construction works had a significant effect on *Rhinolophus* spp. activity which was consistently lower for all flyway designs compared to activity surveys undertaken pre hedgerow removal. Furthermore, this decrease was not mitigated through the installation of bat flyway gates of any design and suggests that bats experienced these sections as hedgerow gaps and did not utilise these flyways in the same way as the removed hedgerows or even hedgerows of decreased value. Our results demonstrate that current methodologies deployed as safeguarding measures to limit the impacts of temporary hedgerow removal do not adequately mitigate the negative effect of removing hedgerows and should not be used as a rationale for large infrastructure developments in order to get through the planning process. This degradation of functional connectivity across the landscape is particularly important for areas surveyed within this study that represent nationally significant breeding and overwintering sites for rare bat species. The degradation of linear features could have significant detrimental impacts that could compromise the capacity of designated roost sites within the SAC and lead to negative impacts on the favourable conservation status of these bat populations.

Using this study as a foundation, future research should seek to experimentally test new flyway designs in order to minimise the reductions in activity as much as possible thereby maintaining landscape connectivity during construction works. Species such as *Rhinolophus* spp., favour foraging along tall outgrown hedgerows due to high prey availability and rely on linear features with greater height, roughness and width which act as better acoustic landmarks when travelling across a landscape. Future designs should be grounded in scientific evidence using these attributes as a starting point, after which economic viability can be optimised.

Whilst the temporary fragmentation of landscapes can arise as a product of direct alterations to important habitat features, anthropogenic activities may create a similar effect by introducing changes that functionally fragment existing landscapes during their operational stages. In chapter 3 we investigate one of these activities in the form of acute noise pollution in sensitive habitats.

Increases in man-made noise have created new soundscapes that can significantly hinder an animals' ability to recognise and differentiate between natural acoustic cues in their environment. For bats this is particular problematic owing to their reliance on environmental sounds and echolocation for many of their life history traits. Anthropogenic noises often constitute a novel, acute and often inconsistent source of disruption that bats are ill-equipped to deal with and music festivals are a source of unregulated and potentially harmful, acute noise pollution which are now ubiquitous across our landscapes throughout the summer months and are increasingly being held in settings important for wildlife. During this study we used an experimental approach to assess the impact of loud music on bat activity by introducing festival music to natural habitats in order to disentangle any potential music impacts from other variables commonly present within a music festival setting e.g. light pollution, large crowds, other anthropogenic noise sources such as vehicles or generators. This study provides evidence that loud music playback alone can reduce the activity of bats even in the absence of other anthropogenic factors commonly associated with music festivals and therefore should be more regulated with more evidence-based guidance relating to their planning and implementation to ensure limitation of detrimental impacts to bat species in these areas. Our findings show that these impacts may be particularly important for bat species who echolocate at lower frequencies as these calls have the potential to overlap spectrally with anthropogenic noise sources and are therefore more sensitive to disruption when travelling through human-dominated landscapes.

Given that music festivals are increasingly being held in places that are important for local wildlife, such as country parks, woodland glades and adjacent to lakes future research should focus on the species-specific and context-dependent responses from bat species as well as how these responses may change with habitats. Furthermore, whilst the results from the current study seem to suggest that loud festival music had little effect on bat species who echolocate at higher frequencies, further research is required to understand whether specific behaviours such as feeding or drinking may be impacted indifferent ways.

Artificial light at night (ALAN) associated with urban expansion ranks amongst the most important global threats to biodiversity conservation and bats are highly vulnerable to the detrimental effects of ALAN due to their evolutionary adaptations for dark environments. Bats exhibit differential sensitivity to light that can be both species and scale dependent but in general it is understood that most bats are negatively impacted by artificial in some way. Light-induced habitat fragmentation is a form of temporary habitat fragmentation that can not only reduce the quality and availability of habitat but also degrade the functional connectivity across the landscape. Consequently, a number of management responses have been proposed such as the implementation of part-night lighting regimes and altering the spectrum or intensity of artificial lighting. During chapters 4 and 5 we investigate the impact of light pollution in habitats i.e. waterways and urban green spaces, that are important for bat species as well as assessing the effectiveness of these mitigation strategies currently deployed in a bid to limit the harmful impacts of light pollution. Using an experimental approach, we provide further evidence to the complex relationship between bats and lighting including the first evidence of negative impacts of lighting mitigation schemes on bats. During chapter 4 we show that part-night lighting still presents a risk to bats through disruption of specific behaviours such as feeding even when it may seem as though general activity has been maintained. Our results suggest that certain species such as *Myotis* spp. are more light-sensitive when foraging compared to commuting, likely due to their longer exposure to illumination and subsequent predation threat. This can be especially detrimental for specialist trawling bats such as *M. daubentonii* who rarely move out of the river corridor whilst hunting therefore any illumination constitutes a potential barrier, fragmenting their foraging habitat.

A similar complex relationship with lighting and deployed lighting mitigation methods was also found during the work undertaken within urban ecosystems as detailed in chapter 5. During this study alteration to the spectral composition of street lighting was assessed as a mitigation methods in habitats whereby a reconciliation between bat conservation and public accessibility to urban green spaces is required. Of all light spectra, long-wavelength red light is thought to be less detrimental to bats and illicit similar behavioural responses to darkness when compared to amber or white LEDS. As such a number of local authorities have already adopted the use of red lighting in order to mitigate the harmful effect of ALAN in areas where human's requirement for light and bats requirement for darkness come into conflict. However, during our study we show that lighting had a significant effect on an urban bat assemblage with species-specific responses in overall activity, as well as marginally significant effects on bat feeding behaviour. During this study we also found unusual responses from bat species that were contrary to expectations. We found a varying response of lighting treatment on *Nyctalus/Eptesicus* spp. activity, with red LED lighting causing a significant reduction in overall activity although did not record a significant reduction in activity on nights illuminated with white LED lighting. Furthermore for *P. pipstrellus* and *P. pygmaeus* there were no significant effects on feeding activity between either of the lighting options compared to the unlit nights despite previous studies reporting increased foraging activity under white lighting due to the higher UV emissions attracting more insect biomass and therefore feeding opportunities. These contrasting results highlight the complexity of responses by bats to ALAN and the mitigation methods employed alleviate this stress on the nocturnal environment. As the exact mechanisms of disturbance by ALAN is not fully understood, the responses by bats may vary according to individual behaviour and habitat context and therefore further research is required from a range of studies representing larger bat communities or across a wider range of habitats to establish what context mitigation methods may be useful. However, it is likely that part-night lighting schemes or spectral alterations to lighting unlikely to provide desired comprehensive biodiversity benefits due to species-specific impacts on activity and feeding. Therefore, if the aim it to limit the negative impacts of ALAN on biodiversity, it would be more beneficial to pursue alternative management strategies such as reducing light trespass and increasing dark corridor networks.

In regions where ecosystems have suffered terminal damage, the restoration or reconstruction of these habitats through ecological technology and engineering interventions may represent the only viable option to reverse fragmented or lost habitats. Human efforts to return ecosystems to a favourable natural condition are often frustrated by a lack of resources, conflicting aims and inadequate knowledge of complex ecological interactions which often leads to projects falling short of their intended outcomes. As a result, we are increasingly looking towards nature-based solutions for restoring ecologically degraded systems. In chapter 6 we explore the effectiveness of using nature-based solutions to unfragment landscapes by looking towards the biodiversity response in beaver restoration-oriented studies as an indicator of restoration effectiveness for bats. During this study we investigated the effects of targeted species reintroduction on bat activity by assessing the importance of beaver-modified habitats relative to control sites in a paired observational study in the absence of suitable baseline bat data for each beaver reintroduction site. During this study we show that the release of beavers into enclosures demonstrates that targeted species reintroductions could be an effective strategy in restoring fragmented landscapes for a variety of species as well as re-establishing historic links between aquatic and terrestrial ecosystems. We recorded increased activity over wetland habitats for *P. pipistrellus, P. pygmaeus*, *Nyctalus/Eptesicus* spp. and *Myotis* spp. which comprise the most common species/species groups of bats in the UK and are therefore amongst the largest consumers of insect biomass. As the extensive positive impact of beaver reintroductions was recorded bat across a range bat species/species groups, it is likely that the drivers behind these increases represent a multi-faceted response according to species-specific differences in foraging strategy and habitat preference. The apparent success of beaver reintroductions to restore fragmented landscape adds to a growing evidence base of mitigating harmful impacts on the environment through rewilding portions of the landscape as opposed to relying on expensive and costly human interventions and may represent a gold standard in terms of mitigation strategies. Contrary to many human interventions' rewilding areas using nature-based solutions provides a shift toward ecosystem-centric mitigation measures that can provide a natural and long-term strategy to restoring fragmented or lost landscapes which can drastically improve the structural composition and functional connectivity of a landscape and in turn increase the species activity found within it. In order to provide a comprehensive understanding of the benefits of beaver reintroductions on bat activity, further research should be conducted comparing beaver-made wetlands and human-made wetlands including a breakdown of costs and timeframes involved with their inception and ongoing maintenance.

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Chapter 1 | General Introduction

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Appendix 1

Assessing the impact of festival music on bat activity | Track List for music treatment conditions

Artist	**Track**	**Genre**	**Time stamps**
Destiny’s Child	Bootylicious	R&B, Pop	0:19 – 1:19
C3B	Untold Stories	Jungle, D&B, Tekno	0:21 – 1:21
Black Sabbath	War Pigs	Heavy Metal	2:59 – 3:59
Ed Solo & Skool of Thought	Life Gets Better	Electro, HipHop, Breakbeat	1:01 – 2:01
Sharon Van Etten	Seventeen	Indie, Rock, Folk	2:00 – 3:00

Appendix 2

Re-establishing historic ecosystem links through targeted species reintroduction: beaver-mediated wetlands support increased bat activity | Spatial analysis of landscape variables.

Table S1: Statistical Analysis of Variance (ANOVA) model outputs of land cover types LC1-LC10 within 2500m of paired beaver enclosure and control locations across reintroduction project sites. Spatial analysis of landscape variables was undertaken in QGIS using habitat data extracted from UK CEH Land Cover Map 2021 (Marston et al, 2022). Mixed models were fit (land cover type ~ detector location) using the aov_4 function with site included as a random effect. Post-hoc pairwise comparisons were undertaken using the *emmeans* package (v1.4–1).

LC1

```
contrast                           estimate    SE df t.ratio p.value

 beaver.wetland - control.wetland     -15.64 12.57 11  -1.244  0.2393
 beaver.woodland - control.woodland   -10.93 11.27 11  -0.970  0.3530
```

LC2

```
contrast                           estimate    SE df t.ratio p.value

 beaver.wetland - control.wetland      3.241 4.797 11   0.676  0.5132
 beaver.woodland - control.woodland    4.976 6.968 11   0.714  0.4900
```

LC3

```
contrast                           estimate    SE df t.ratio p.value

 beaver.wetland - control.wetland       5.44  8.32 11   0.653  0.5270
 beaver.woodland - control.woodland     4.73 10.77 11   0.440  0.6687
```

LC4

```
contrast                           estimate    SE df t.ratio p.value

 beaver.wetland - control.wetland     -10.87 17.59 11  -0.618  0.5491
 beaver.woodland - control.woodland   -20.22 16.02 11  -1.262  0.2329
```

LC5

```
contrast                           estimate    SE df t.ratio p.value

 beaver.wetland - control.wetland      13.21 13.87 11   0.953  0.3612
 beaver.woodland - control.woodland    12.91 13.73 11   0.941  0.3671
```

LC6

```
contrast                           estimate    SE df t.ratio p.value

 beaver.wetland - control.wetland      2.068 3.427 11   0.603  0.5585
 beaver.woodland - control.woodland    2.853 1.833 11   1.557  0.1477
```

LC7

```
contrast                           estimate      SE df t.ratio p.value

 beaver.wetland - control.wetland   -0.00693 0.00693 11  -1.000  0.3388
 beaver.woodland - control.woodland  0.13795 0.13795 11   1.000  0.3388
```

LC8

```
contrast                           estimate    SE df t.ratio p.value

 beaver.wetland - control.wetland      0.910 0.413 11   2.204  0.0498
 beaver.woodland - control.woodland    2.143 1.064 11   2.013  0.0693
```

LC9

```
contrast                           estimate      SE df t.ratio p.value

 beaver.wetland - control.wetland   -0.00618 0.00618 11  -1.000  0.3388
 beaver.woodland - control.woodland  2.02718 2.02718 11   1.000  0.3388
```

LC10

```
contrast                           estimate    SE df t.ratio p.value

 beaver.wetland - control.wetland      1.395  8.22 11   0.170  0.8684
 beaver.woodland - control.woodland    0.889  8.29 11   0.107  0.9165
```

Bat Call Analysis and Error Rate Modelling

Recordings were analysed using open-source software BatClassify (Scott, 2012) which automatically assigns a species classification and confidence score (0-1) for every species/species groups identified in the recording. Threshold values are then determined by the user, in which species ID are either considered positive or negative (e.g. accepting all scores above 0.7 as positive IDs).

Following Barré et al. (2019), we manually analysed 2,400 random recordings, 25 recordings for every confidence score value at 0.1 intervals (0.1, 0.2, 0.3 etc) for every species/species group, and recorded the result (0/1, incorrect/correct ID). If less than 25 recordings were available, then all files were used. We then performed a logistic regression (correct/incorrect ID ~ confidence score) to estimate the probability of a given confidence score containing a correct identification. All manual sound analysis was conducted blind whereby the confidence score was hidden when performing manual ID. It was not possible to differentiate *Myotis* spp. manually, so all *Myotis* calls were merged, keeping the highest confidence score. At a 50% probability of a correct ID, it is expected that the results will contain approximately the same number of false positives as false negatives, meaning that the results for the entire dataset will be accurate (Barré et al., 2019).

We filtered the dataset at two confidence score thresholds corresponding to a predicted maximum error rate tolerance (MERT) of 0.5 and 0.3. This allowed us to perform statistical analyses at different maximum error rate thresholds to check for consistency of results. A 0.5 threshold tolerates more false positives but keeps more bat passes, while a more restrictive 0.3 threshold limits false positives at the cost of discarding more true positives, leading to a potential loss of statistical power. In this paper we present results based on the 0.5 threshold, having confirmed consistency of results at the 0.3 threshold and only make conclusive interpretation when both are consistent (Barré et al., 2019).

Table S2: Comparison of model estimates between 0.5 MERT and 0.3 MERT datasets using generalized linear mixed models and post-hoc comparisons relating bat activity to paired detector location (beaver vs control wetland, beaver vs control woodland). Included are parameter estimates, standard errors (± s.e), z- and P- values for fixed effects in addition to variance and standard deviation (Std Dev.) of random effect terms ('*' p-value <0.05; '' p-value <0.01; '***' p-value <0.001).**

	Bat Activity (passes)					
P.pipistrellus	**MERT 0.5**			**MERT 0.3**		
Fixed Effects	**Estimate (± s.e)**	***z*- value**	***P* value**	**Estimate (± s.e)**	***z*- value**	***P* value**
Location (Beaver Wetland vs Control Wetland)	-0.34 (±0.08)	4.35	<0.001***	-0.36 (±0.08)	4.51	<0.001***
Location (Beaver Woodland vs Control Woodland)	0.17 (±0.09)	1.90	0.06	0.20 (±0.09)	2.10	0.04*
Random Effects	**Variance**	**Std Dev.**		**Variance**	**Std Dev.**	
Site (*N*=12)	0.10	0.33		0.17	0.41	
P.pygmaeus						
Fixed Effects	**Estimate (± s.e)**	***z*- value**	***P* value**	**Estimate (± s.e)**	***z*- value**	***P* value**
Location (Beaver Wetland vs Control Wetland)	0.43 (±0.08)	5.56	<0.001***	0.45 (±0.08)	5.66	<0.001***
Location (Beaver Woodland vs Control Woodland)	0.26 (±0.09)	2.75	<0.01**	0.27 (±0.10)	2.83	<0.01**
Random Effects	**Variance**	**Std Dev.**		**Variance**	**Std Dev.**	
Site (*N*=12)	0.15	0.38		0.16	0.40	
***Nyctalus/Eptesicus* spp.**						
Fixed Effects	**Estimate (± s.e)**	***z*- value**	***P* value**	**Estimate (± s.e)**	***z*- value**	***P* value**
Location (Beaver Wetland vs Control Wetland)	0.19 (±0.10)	1.94	0.05*	0.21 (±0.11)	1.94	0.05*
Location (Beaver Woodland vs Control Woodland)	-0.04 (±0.11)	-0.40	0.69	-0.02 (±0.11)	-0.21	0.84
Random Effects	**Variance**	**Std Dev.**		**Variance**	**Std Dev.**	
Site (*N*=12)	0.29	0.54		0.43	0.66	
***Myotis* spp.**						
Fixed Effects	**Estimate (± s.e)**	***z*- value**	***P* value**	**Estimate (± s.e)**	***z*- value**	***P* value**
Location (Beaver Wetland vs Control Wetland)	0.30 (±0.09)	3.46	<0.001***	0.27 (±0.09)	3.00	<0.01**
Location (Beaver Woodland vs Control Woodland)	0.12 (±0.10)	-0.40	0.27	0.15 (±0.11)	1.40	0.16
Random Effects	**Variance**	**Std Dev.**		**Variance**	**Std Dev.**	
Site (*N*=12)	0.07	0.26		0.10	0.31	
B.barbastellus						
Fixed Effects	**Estimate (± s.e)**	***z*- value**	***P* value**	**Estimate (± s.e)**	***z*- value**	***P* value**
Location (Beaver Wetland vs Control Wetland)	1.60 (±0.31)	5.09	<0.001***	1.69 (±0.33)	5.05	<0.001***
Location (Beaver Woodland vs Control Woodland)	0.28 (±0.28)	0.98	0.33	0.10 (±0.30)	0.33	0.74
Random Effects	**Variance**	**Std Dev.**		**Variance**	**Std Dev.**	
Site (*N*=12)	1.77	1.33		1.70	1.32	
***Plecotus* spp.**						
Fixed Effects	**Estimate (± s.e)**	***z*- value**	***P* value**	**Estimate (± s.e)**	***z*- value**	***P* value**
Location (Beaver Wetland vs Control Wetland)	1.42 (±0.29)	4.96	<0.001***	1.64 (±0.47)	3.49	<0.001***
Location (Beaver Woodland vs Control Woodland)	0.23 (±0.48)	0.47	0.64	-0.49 (±1.21)	-0.40	0.69
Random Effects	**Variance**	**Std Dev.**		**Variance**	**Std Dev.**	
Site (*N*=12)	0.56	0.75		1.56	1.25	

R. ferrumequinum

Fixed Effects	**Estimate (± s.e)**	***z*- value**	***P* value**	**Estimate (± s.e)**	***z*- value**	***P* value**
Location (Beaver Wetland vs Control Wetland)	0.19 (±0.55)	0.35	0.73	0.19 (±0.55)	0.35	0.73
Location (Beaver Woodland vs Control Woodland)	0.71 (±0.62)	0.47	0.25	0.71 (±0.62)	1.14	0.25
Random Effects	**Variance**	**Std Dev.**		**Variance**	**Std Dev.**	
Site (*N*=12)	68.28	8.26		68.28	8.26	

R. hipposideros

Fixed Effects	**Estimate (± s.e)**	***z*- value**	***P* value**	**Estimate (± s.e)**	***z*- value**	***P* value**
Location (Beaver Wetland vs Control Wetland)	0.02 (±0.26)	0.08	0.94	-0.03 (±0.26)	-0.10	0.92
Location (Beaver Woodland vs Control Woodland)	-0.01 (±0.62)	-0.02	0.98	-0.01 (±0.50)	-0.02	0.98
Random Effects	**Variance**	**Std Dev.**		**Variance**	**Std Dev.**	
Site (*N*=12)	25.53	5.05		24.62	4.96	

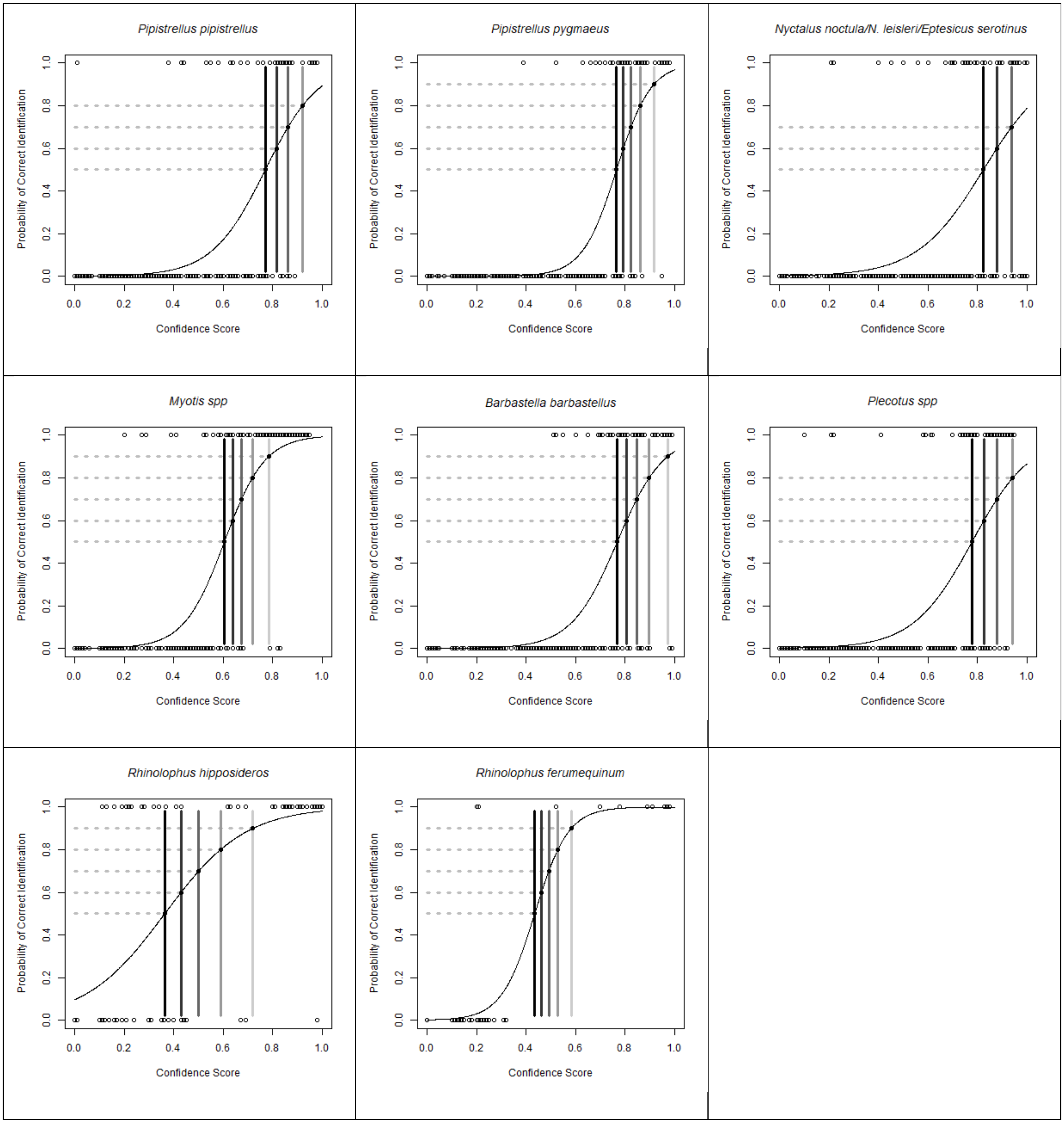

Figure S1: Predicted logistic regression curves showing success probability of correct ID and confidence score of automatic identification for the 8 species/species groups studied (False Positive Tolerances). Horizontal dotted lines show identification success probabilities corresponding to the maximum error risk tolerance thresholds used in the error rate modelling analysis and corresponding confidence thresholds (vertical solid lines).