The distribution and habitat preferences of bats in a temperate urban landscape

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Declaration

I hereby declare that this thesis has been composed by myself and that it embodies the results of my own research. Where appropriate, I have acknowledged the nature and extent of work carried out in collaboration with others.

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Paul Lintott

Summary

Urbanisation is a key driver in the loss, fragmentation and modification of natural habitats resulting in the global loss of biodiversity. As the human population, and consequently the rate of urbanisation, continues to increase exponentially it is important to understand how to sustain and enhance biodiversity within the built environment. Cities comprise a complex assortment of habitat types yet relatively little is known of how its composition and spatial configuration can influence species presence or foraging activities. It is therefore necessary to examine habitat use and biodiversity patterns at multiple spatial scales to fully understand how species are responding to the urban matrix. There are few other orders of animals that are as strongly associated with people as bats (*Chiroptera*); for some bat species human habitations provide roosts and adaptations of the environment provide food sources. However bat species richness generally declines with increasing urbanisation indicating that many species are not able to persist in highly urbanised areas. In this thesis, I show that the behaviour, habitat preferences, and distribution of bats are strongly influenced by the built environment at both a local and landscape scale. Although many animal species are known to exhibit sex differences in habitat use, adaptability to the urban landscape is commonly examined at the species level without consideration of potential intraspecific differences. I found that female *Pipistrellus pygmaeus* show greater selectivity in foraging locations within urban woodland in comparison to males at both a local and landscape scale. There was a lower probability of finding females within woodlands which were poorly connected, highly cluttered, with a high edge: interior ratio and fewer mature trees. The results have important implications for our understanding of how to manage areas for breeding females and highlight the need to supplement acoustic monitoring with trapping data to assess sex differences in habitat use. Determining how morphological or behavioural traits can influence species adaptability to the built environment may enable us to improve the effectiveness of conservation efforts. The morphological similarities between *P. pygmaeus* and *P. pipistrellus* suggest that both species should respond similarly to the urban matrix, however I found differential habitat use occurring within a variety of urban habitats (e.g. woodland and waterways) and at a landscape scale. In urban woodland there was a higher probability of *P. pygmaeus* activity relative to *P. pipistrellus* in woodlands with low clutter and understory cover which were surrounded by low levels of built environment. Many bat species are strongly associated with aquatic or adjacent riparian habitats yet we know little about the utilisation of urban waterways by bats. After surveying urban waterways throughout the UK, I was able to show that the built environment can negatively affect a variety of bat species from the riparian zone up to 3km from a waterway. This indicates that beneficial urban waterway rehabilitation schemes for bats require management at multiple spatial scales, from retaining a vegetated riparian zone at the local scale to highlighting the necessity for conservation funding to be spent on the implementation of landscape scale environmental improvement schemes that encompass the entire urban matrix. Undertaking surveys to confirm species presence or to estimate population sizes can be difficult, particularly for elusive species such as bats. I was able to demonstrate a variety of ways to increase surveying efficiency (e.g. the use of an acoustic lure to increase bat-capture rate and a significant relationship between bat activity and the relative abundance of certain species of bat which can maximise the knowledge of diversity in an area whilst minimising wildlife disturbances.

Urbanisation has also had strong negative effects on many insect groups, such as moths, which are important components of the diets of many bat species. I found that woodland vegetation characteristics were more important than the surrounding landscapes in determining the abundance, species richness, and species diversity of moth assemblages within urban woodland. This indicates that management at a local scale to ensure provision of good quality habitat may be more beneficial for moth populations than improving habitat connectivity across the urban matrix. The findings presented in this thesis have important implications for our understanding of the adaptability of species to the built environment and for the management and monitoring of bat populations. It also highlights that even common bat species are negatively affected by urbanisation and much greater attention should be paid to securing their future within the urban landscape.

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Chapter 1

General Introduction

A legacy of our modern society will surely be the growth of urbanisation. Few other human activities have created such profound changes to natural ecosystems or, in many cases, are as homogenising as urbanisation. Understanding how to sustain and enhance biodiversity whilst mitigating the worst effects of urbanisation in conjunction with ever increasing levels of urban expansion should therefore be at the forefront of conservation science as the human population, and therefore the rate of urbanisation, continues to increase exponentially (Faulkner 2004).

1.1 Global biodiversity loss: the role of urbanisation

Human actions are disrupting the Earth's ecosystems, eliminating genes, species and biological traits at a rapid and alarming rate (Cardinale et al. 2012). Conserving biodiversity is essential given its importance in supporting ecosystem services (e.g. climate regulation or protection against natural hazards) and for its provision of vital resources (e.g. biochemical, food, fibre and fuel; Diaz et al. 2006). Despite recent efforts (e.g. the Convention on Biological Diversity) most indicators of the state of biodiversity including species' population trends, habitat extent and condition, and extinction risk show significant negative declines (Butchart et al. 2010). Rates of species extinction greatly outpace background rates suggested from the fossil record which may result in the sixth mass extinction on Earth within the next 250 years (Barnosky et al. 2011). The loss, fragmentation and modification of natural habitats are regarded as some of the strongest drivers of species extinctions (Pullin et al. 2013). Understanding the behaviour, life history and ecology of how species respond to human-modified landscapes is therefore critical in identifying the actions that are required to reverse this negative trend.

Urbanisation (alongside agricultural intensification) is a key global driver in the modification of land use, and is probably the main one in Europe (Reginster & Rounsevell 2006). Rapid urbanisation is a consequence of the exponential growth of the human population coupled with the high percentage of the population living in urban areas. In 1950, over two-thirds of the global human population lived in rural settlements but by 2007, for the first time in history, the global urban population exceeded the global rural population. By 2050 it is projected that two-thirds of the global population will be living within urban areas (United Nations 2014). Urbanisation not only leads to land use change, but can result in other alterations such as modification of the regional climate, increased prevalence of exotic species, and increased pollution levels; all of which have biological consequences. The urban heat island effect elevates air temperatures within the built environment resulting in seasonality shifts in the timing of greening, flowering, and dormancy of vegetation (Neil & Wu 2006; Zhang et al. 2004). Decreased permeability in urban areas increases precipitation runoff which impacts upon the morphology of urban streams, thereby altering the composition of riparian vegetation (Pickett et al. 2001). These abiotic modifications to the landscape have required animal species to either adapt or face rapid extinction within the urban environment.

Traditionally, the total species pool of an area was determined by evolutionary mechanisms, however anthropogenic changes to ecosystems occur at faster rates and exert stronger pressures than evolutionary adaptation allows (Duchamp & Swihart 2008). Urban areas should therefore favour species whose traits enable them to adapt to new, human-altered environments (Duchamp & Swihart 2008). As a consequence, the majority of studies have found that species associated with highly urbanised areas are 'generalists' that can tolerate and may even respond positively to a wide range of conditions, whilst 'specialist species' are rarely found within the urban landscape (Lizée et al. 2011). Specialisation can lead to dependence on a specific resource which can result in extinction if the resource becomes depleted (Harcourt et al. 2002), as is often the case during dramatic land use change as a result of urbanisation. Understanding how species respond to urbanisation is therefore critical in identifying species which require conservation effort. Species are commonly classified into three distinct categories following Blair's (2001) terms which reflect their response to anthropogenic modification (Figure 1.1).

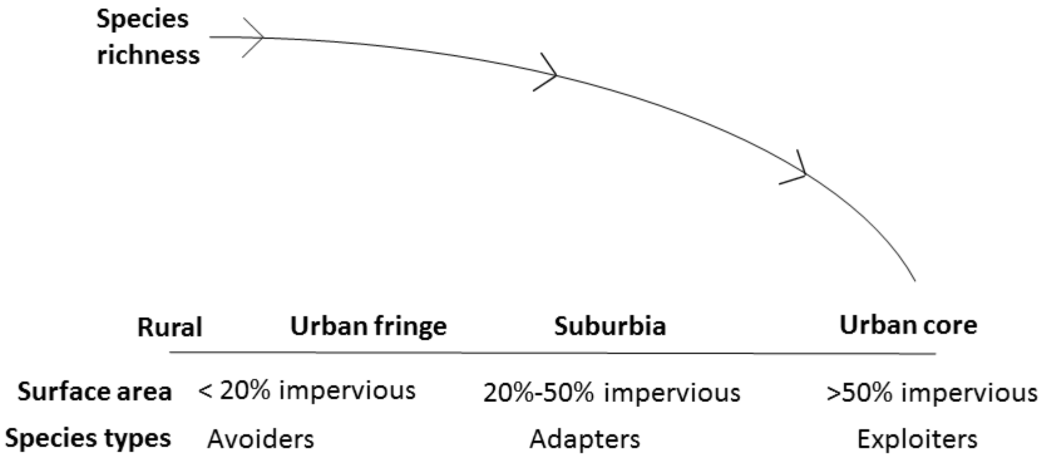

Figure 1.1 Generalised and simplified diagram showing species composition across an urban-rural gradient (Adapted from McKinney 2002).

Urban avoiders are those species that are very sensitive to human persecution and/or habitat disturbances. Avian urban avoiders include those species requiring large, old mature forests (McKinney 2002) and those possessing particular life history traits (e.g. allocating more energy to reproduction to the detriment of adaptation to the built environment; Croci et al. 2008). Urban adapters frequently exploit urban resources but additionally require natural/semi-natural habitats to survive. For example, foxes *(Vulpes vulpes*) forage on discarded human food supplies but require adjacent forest fragments for shelter (McKinney 2002). Urban exploiter species are well adapted to intensely modified urban environments due to a combination of traits including diet, sedentariness, degree of sociality and preferred nesting sites (Kark et al. 2007).

The adaptability of a species to the urban landscape is frequently assessed by determining its occurrence within the built environment (e.g. Ordeñana et al. 2010). Records of presence indicate that, to at least some extent, individuals of a species have the capacity to explore the urban environment. However, successful colonisation of urban habitats can only be achieved by species with sufficient rate of dispersal to establish a permanent population (Clobert et al. 2001). Recording the occasional presence of a rare species within the city only indicates its adaptability to urbanisation as much as inferring that an exotic bird blown off course onto British shores is actually a resident. Similarly, urban areas display complex habitat heterogeneity (Wu et al. 2013) and so inferring species adaptability to the built environment based upon species presence within particular areas of a city without an understanding of what local and landscape factors are influencing their distribution may overstate adaptability. Therefore investigating measures of adaptability such as relative activity levels, demographic differences within a population in their response to urbanisation or the presence of breeding populations within towns or cities will give a better indication of the true level of how adept a species is at adjusting to the urban environment.

There are a wide variety of motivations to conserve urban nature which can include those which produce human benefits that often resonate more strongly to members of the general public (Figure 1.2; Dearborn & Kark 2010). Traditional ecological concepts developed in a “human-free” ecosystem (e.g. interspecific competition) increasingly leads to inadequate explanations of ecosystem processes in a human-dominated Earth (Alberti et al. 2003). In this thesis, I investigate how the behaviour and habitat preferences of a variety of species are modified within the built environment.

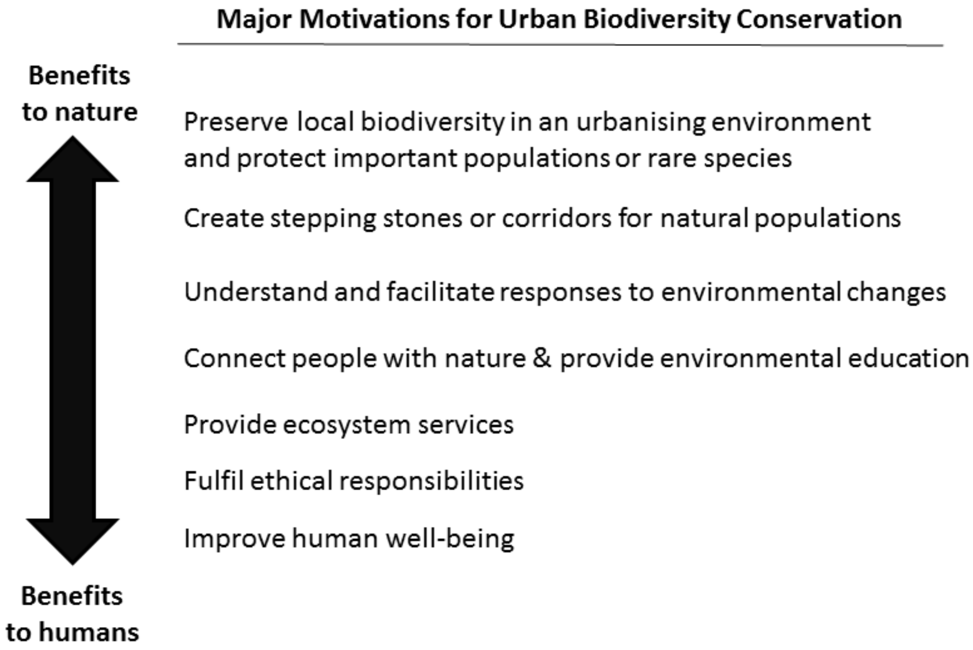

Figure 1.2 Motivations to conserve urban nature ranging from the direct benefit for nature to reasons that directly connect human welfare and wildlife conservation. (Adapted from Dearborn & Kark 2010).

1.2 Understanding urban ecology at multiple spatial scales

A key approach which drives current research into the ecology and biodiversity of cities and towns is the importance of examining habitat use and biodiversity patterns at multiple spatial scales (local to landscape).

Urbanisation can affect taxa differently according to their dispersal ability. At a local scale, the vegetation characteristics of a fragmented patch of semi-natural habitat may determine which species are able to use it for sleeping, foraging, or commuting. For example, Yui et al. (2001) found that ant species richness within urban woodland positively correlates with the number of microhabitat types such as stones and herbaceous patches. Similarly, small patches of green space are vital for snail populations due to their small range and ability to utilise small remnants of native vegetation as refugia (Clark 2004). Local vegetation characteristics can also influence larger taxa; shrub density and average canopy height of urban woodlands are important factors in determining bird species diversity (Tilghman 1987). It is therefore apparent that conservation strategies targeted at the local scale (i.e. management of small parklands) will be beneficial for those species with small home range sizes where surrounding anthropogenic disturbances may not impact upon their behaviour or habitat use. Additionally, local scale management is important for wider ranging taxa that have particular foraging or roosting requirements that may intensively use particular habitats within the urban matrix.

At a wider spatial scale, fauna are influenced by the size and shape of the habitat patch (Natuhara & Hashimoto 2009). A comparison of woodlands in Brussels found that the largest woodland contained the highest flora species richness in comparison to 11 smaller patches (Godefroid & Koedam 2003). Similarly, bird species richness within Greater London was positively correlated with larger public green spaces (Chamberlain et al. 2007). Strong species-area relationships are a reflection that larger urban habitat patches have reduced edge effects and therefore can support larger, more stable, populations (Evans et al. 2008). For example, insectivorous species adapted to exploit woodland edge habitat are less sensitive to anthropogenic disturbances and will generally be found within any urban woodland regardless of its size. However species adapted to the conditions found within the woodland interior will only be found in those fragments which are of suitable size and shape to buffer from surrounding disturbances (Natuhara & Hashimoto 2009). Although habitat area is an important factor in influencing species richness and composition, in practice, increasing the size of existing semi-natural habitats (e.g. urban woodland or wetlands) is very difficult (Fernández-Juricic and Jokimäki 2001). It is therefore important to consider additional factors such as connectivity amongst semi-natural habitats which can strongly influence how species are able to use the urban matrix.

The composition, spatial configuration and heterogeneity of the urban matrix coupled with species phylogeny, morphology and behavioural traits determine biodiversity levels within the urban landscape (Riedinger et al. 2013). For example, small and medium sized mammals including water voles (*Arvicola amphibious*) and dormice (*Muscardinus avellanarius*) require semi-natural greenway corridors to disperse among woodland refuges in the urban matrix (Angold et al. 2006). Similarly, vegetated streets connecting urban parks act as important corridors and contain a higher diversity of avian species than streets without vegetation (Fernández-Jurici 2000).

Carabid beetle richness within urban woodland is positively associated with the proportion of woodland in the surrounding 5 km and negatively related to the extent of built environment in the landscape (Sadler et al. 2006). Although the vast majority of conservation effort is focused on managing remnant patches of semi-natural habitats, connectivity within the urban matrix is also reliant on backyard habitats, wooded streets, and utility rights of way (e.g. canals or railways; Rudd et al. 2002). At an even wider scale, assessments of biodiversity in cities must be contextualised by comparing it with the surrounding landscape. For example, urban areas in Midwestern United States (e.g. Chicago) have been identified as biodiverse 'islands' when contrasted with the large areas of intensive agricultural production that surround them (Gehrt and Chelsvig 2004).

In this thesis I therefore focus on how species respond to habitat characteristics at multiple spatial scales and attempt to contrast the relative importance of local versus landscape management strategies.

1.3 Management Strategies

Although the response of organisms to the urban landscape is interesting from a theoretical perspective, the vast majority of studies strive to derive applications from their results which can influence the management of the urban ecosystem. The first management efforts in cities date back to the 1970s when there was a rising social awareness of the value of nature in the city and the realisation that extensive losses of wildlife had already taken place (Breuste 2009). Yet ecological research in the urban setting was slow to catch up, between 1993 and 1997 only 25 of 6157 papers (0.4%) published in ecological journals dealt either with urban wildlife or were set within the built environment (Collins et al. 2000). Ecologists have only recently begun to address this oversight and started to investigate how overall ecosystem structure and functions are shaped by urban developments (Berry 2008). As a consequence, research has progressed beyond that of patterns of species abundance and diversity to include studies on behavioural ecology, species interactions, genetics and evolution (Shochat et al. 2006). Savard et al. (2000) considered there to be three biodiversity concepts which should be considered when managing urban ecosystems:

1) hierarchy of scale (ranging from genetic diversity to species diversity and community diversity);

2) the role of individual species within the community and how they interact with humans (e.g. umbrella and flagship species);

3) understanding the effect on wildlife of habitat fragmentation and habitat quality.

These concepts, particularly (2) indicate the role that humans play in developing unique ecosystems and how management strategies need to take this into account. For example, focusing on flagship species (i.e. charismatic species) can attract attention and galvanise public support for wider conservation efforts (Savard et al. 2000). The regular use of urban infrastructure (e.g. tower blocks and telephone masts) by peregrine falcon (*Falco peregrinus*) has provided plenty of opportunities for public education and raising awareness about falcons and the problems facing endangered wildlife (Cade & Bird 1990). Yet, maintaining urban biodiversity will inevitability lead to land use conflicts. For example, scrub cover is important for many song birds and other small vertebrates within the urban landscapes, yet the public will frequently not tolerate what they perceive to be ‘untidiness’ in open urban green space which is also used for recreational purposes (Soulé 2008). Human perceptions of landscape aesthetic beauty are set by cultural identity and evolutionary preferences and are frequently for Savannah-like environments that are open and offer easy navigation (Sadler et al. 2011). For example, the public show a strong preference for urban woodland containing vegetation of an open character with low density undergrowth due to perceived safety within these habitats (Jansson et al. 2013). One study in Brisbane, Australia showed that the public do not preferentially visit those parks with greater vegetation cover despite these areas holding the potential for improved nature-based experiences and greater wellbeing benefits. Only people who had a passion for nature were prepared to travel further for vegetated green spaces (Shanahan et al. 2015). Yet in the city environment, for ecological management strategies to be effective, the public should appreciate and value biodiversity mitigation and enhancements schemes (Sadler et al. 2011). Therefore efforts to enhance biodiversity should incorporate community involvement and environmental education to increase the desire to support biodiversity (Sadler et al. 2011). This is of particular importance for less known or traditionally less popular species (e.g. insects; Hunter & Hunter 2008) and occasions where ecological requirements may result in a design/management plan that creates less preferred landscapes. Encouraging public engagement with urban wildlife will not only facilitate support for maintaining biodiversity but can have considerable benefits for human mental and physical health.

1.4 Urban ecology and human health

Urban green space is strongly associated with providing and maintaining the environmental conditions that make cities habitable (i.e. climate, air pollution removal), however there is also a direct link to human health benefits (Tzoulas & Greening 2011). The use of urban green space by urban residents can have a key role in preventing disease including cardiovascular disease, some forms of cancer, and type II diabetes (Tzoulas & Greening 2011). Similarly, contact with (semi-) natural environments is positively associated with mental health benefits including psychological restoration, improved mood, improved attention and reduced stress and anxiety (e.g. Barton & Pretty 2010; Ward Thompson et al. 2012). Additionally, Kuo (2003) found that urban green space can improve social relationships and enhance community spirit (with subsequent improvements to the well-being of individuals) by fostering social ties between neighbours when working together to maintain residential green space. Creating imaginative and appealing green space which will encourage community engagement and people to use it recreationally is important for supporting a healthy urban population; the urban ecologist is therefore required to incorporate this information into conservation management plans.

1.5 Methods to improve urban biodiversity

The development of green technologies has increased the diversity of ways that urban habitat can be restored, improved, and created. This can range from local, small scale initiatives such as affordable nest and roost boxes which the homeowner can purchase for their garden or have their builder fit internal nest boxes into the design of their building. At a larger scale, initiatives such as green walls, living walls, and permeable pavements can be used to increase habitat availability and connectivity within the urban matrix (Sadler et al. 2011). Green roofs are frequently adapted as a tool to mitigate the inhospitality of urban areas because (i) unoccupied space at ground level is scarce in city environments, (ii) roofs comprise more than 30% of the total surface area of cities, and (iii) they represent an opportunity to increase public participation in environmental issues as they can be created directly by citizens or companies (Madre et al. 2014). The integration of green roofs in urban spatial planning has potential to increase connectivity between patches of green spaces for communities of low-mobility species (e.g. carabids and spiders, Braaker et al. 2014; bats, Pearce & Walters 2012). Similarly, there is potential to enhance and create habitats for wildlife in both public (e.g. woodlands, canals) and private (e.g. urban gardens) spaces. However, there is currently limited information transfer between ecological research, practical conservation and town planning (Sadler et al. 2011). Additionally, the vast majority of guidance currently available focuses on a few taxa (e.g. birds; Fernandez-Juricic & Jokimäki 2001, Fontana et al. 2011, Jokimäki et al. 2011) with many taxa (e.g. bats, moths) frequently underrepresented in studies.

1.6 The response of bats to urbanisation

Bats (Chiroptera) are one of the most numerous and diverse orders of mammals. Globally distributed, with the exception of the polar regions and some isolated oceanic islands, bats fill a wide array of ecological niches (Jones et al. 2009). The evolution of powered flight has contributed to a wide variety of feeding, roosting, and reproductive strategies and social behaviours (Simmons & Conway 2003). The diet breadth of bats includes those which are carnivorous (e.g. eating fish, amphibians, reptiles and mammals), hematophagous, nectarivorous and frugivorous (Altringham 1996).

However, the vast majority of bats (approximately 70% of all species) are insectivorous and have many important ecological and economic roles including the control of many crop and forest pests (Boyles et al. 2011; Kalka et al. 2008).

Bat populations are declining almost everywhere in the world in response to a series of environmental stresses, many of which are caused by humans (Jones et al. 2009). Human induced threats include roost site loss and disturbance (e.g. the resumption of open cast mining in abandoned underground mines or the modification of cave ecosystems for tourists), persecution (e.g. culling of Australian flying foxes due to the perception that they cause agricultural damage) and climate change (Mickleburgh et al. 2002; Rebelo et al. 2009). However, habitat loss and modification is currently the greatest threat to bats (Chaverri & Kunz 2011; Mickleburgh et al. 2002).

There are few other orders of animals that are so strongly associated with people as Chiroptera. Human habitations provide roosts, while adaptations of the environment provide food sources (e.g. insects swarming around artificial light sources or fruits in orchards; Fenton 2003). Historically, bats appear to have been abundant in many urban areas including Greater London; one contributory factor is thought to be the higher density of insects as a consequence of poorer living conditions (Guest et al. 2002). Subsequent reductions in insect abundance, disturbance and increased persecution all contributed to a decline in the abundance of many bat species.

The prevalence of a species within the urban landscape not only depends on its ability to survive and adapt within a highly modified environment, it can also be influenced by human tolerance and conflict (Baker & Harris 2007). A widespread fear of bats amongst humans can be explained by the association between bats and disease, and the representation by the media of bats as animals that should be feared (Prokop et al. 2009). In Brazil the association between bats and the rabies virus has resulted in indiscriminate acts of bat poisoning and roost destruction (Mayen 2003). Education is the key to changing perceptions, for example urban encounters with wildlife often form the basis of attitudes and motivation for urban inhabitants to become involved in wider conservation and environmental issues (Randler et al. 2007). Bats are frequent visitors to urban gardens (Baker & Harris 2007); the opportunity therefore exists to use these regular encounters as a beneficial mechanism for bat conservation. Similarly, the Congress Avenue Bridge in Austin, Texas, home to 1.5 million Mexican free-tailed bats attracts nearly 140,000 visitors each year, the majority of whom leave more informed and with a positive impression of bats (Pennisi et al. 2004).

Habitat loss and modification as a consequence of urbanisation has arguably the greatest impact on species, including bats, within the urban landscape. The reduction in semi-natural habitats such as woodland has strongly impacted those bat species with low wing-loading and low aspect-ratio (e.g. *Myotis nattereri* and *Plecotus auritus*; Jong 1995). Habitat modification such as the replacement of low density housing with new high density housing estates has reduced foraging opportunities for bats (Gaisler et al. 1998). Similarly, the drive for well insulated and energy efficient housing has led to the loss of roosting space for those bat species adapted to roost within buildings (Waring et al. 2012).

Connectivity (the degree to which a landscape can facilitate or restrain movement of organisms amongst resource patches) can influence dispersal rates, home range movements, colonisation rates, and extinction risk (Tischendorf & Fahrig 2000). Urban landscapes are particularly vulnerable to fragmentation due to habitat loss and high anthropogenic disturbances which can prevent movement within the matrix (Schippers et al. 1996). Although the mobility of bats gives them greater flexibility than many other taxa in fragmented landscapes, many species are constrained by features present within the urban matrix. The complex system of road networks found across towns and cities can be a major source of bat mortality (Lesiński et al. 2010). Road networks also contribute to noise pollution which has the greatest impact on bats using a 'passive listening' foraging strategy (e.g. *Myotis myotis*; Schaub et al. 2008). Similarly, the impact of light pollution on bats is species specific. Slower flying species with a higher perceived risk of predation actively avoid floodlit areas of habitat (e.g. *Rhinolophus hipposideros*; Stone et al. 2009), whilst, faster flying species can exploit the high concentration of prey species which occur around artificial light sources (e.g. *Nyctalus noctula*; Bartonicka 2003).

Although urbanisation has had a strong negative effect on many bats, certain species, often those with generalist foraging and roosting behaviour are able to persist within the built environment and profit from the resources it provides (Johnson et al. 2008). Products of urbanisation such as sewage treatment works are beneficial to both insectivorous birds and bats due to high macroinvertebrate densities (Vermonden et al. 2009; Park & Cristinacce 2006; but see Park et al. 2009). The introduction of exotic vegetation to urban landscapes has provided fruit and nectar for Australian fruit bats (e.g. *Pteropus poliocephalus*) during the winter period when naturally there would be a period of food scarcity (Williams et al. 2006). The presence of conspicuous linear structures such as terraced housing are utilised by *Pipistrellus pipistrellus* as they provide shelterbelts for foraging and form territorial boundaries (Sachteleben & von Helversen 2006).

Efforts to determine the impact of urbanisation on bats frequently use spatial gradients ranging from city centres, to suburbia, to agricultural land and finally 'natural' landscapes to determine relative habitat use among areas (Hourigan et al. 2010). These typically find that species diversity, foraging rates, and reproductive success are greater in rural locations than nearby urban localities (e.g. Kurta & Teramino 1992; Gaisler et al. 1998). Categorising urban and rural landscapes has grown increasingly complicated as the development and expansion of cities during the late 20th century has altered the spatial layout of cities which now consist of mosaics of interspersed habitats such as densely built areas, parkland, vegetation remnants and agricultural areas (Hourigan et al. 2010). Understanding what factors influence bat presence within each of these habitats is therefore essential in understanding how to conserve bats within the urban landscape.

Conservation strategies for urban areas are inevitably constrained by funding, it is therefore imperative to optimise the efficiency and effectiveness of management actions. The response of many species to the urban landscape is currently unclear therefore species are often grouped together using their morphological traits to infer the risk of exclusion from highly modified landscapes (Safi & Kerth 2004). Bats have previously been categorised as either urban exploiters, adapters or avoiders based upon their morphological traits (e.g. Jung & Kalko 2011; Threlfall et al. 2012a), although in reality there is likely to be a continuous spectrum of adaptability. In this thesis I examine where along this spectrum a variety of British bat species lie, alongside examining if using morphological traits to make this assessment is a reliable method.

1.7 Invertebrate responses to urbanisation

The utility of urban areas by bats is influenced by multiple factors including roost availability, microclimate, habitat structure, energetic requirements and the availability and abundance of prey species (Fukui et al. 2006, Threlfall et al. 2012b). Understanding which local and landscape factors influence the distribution of prey species within the urban matrix is therefore important to help explain the distribution of bat species.

Alongside representing important food resources for many mammalian and bird species, insects play critical roles in ecosystem function. They fill many roles including nutrient recyclers, pollinators, detritivores, parasites, and predators. Despite being abundant and diverse, relatively little is known of how insects respond to environmental change caused by anthropogenic activity (Schowalter 2006). Investigations along an urban gradient have shown that the abundance and species richness of butterflies (Blair 1999) and carabid beetles (Ishitani et al. 2003) decrease significantly from rural to urban sites. In contrast, no difference was found between urban and rural environments for bee species diversity (Banaszak-Cibicka & Żmihorski 2011), or spider abundance and species richness (Alaruikka et al. 2002). Habitat fragmentation and the changing quality of habitat that remains within the urban matrix are also known to affect insects (Rickman & Connor 2003). Changes in habitat quality due to fragmentation can impact upon insects by altering host-plant quality, adjusting soil attributes, introducing exotic species and changing light, nutrient and water regimes (Connor et al. 2002). Reduced insect availability within fragmented semi-natural habitats such as urban woodland may therefore severely affect many bat species.

The most diverse insect orders and those which form an important component in the diet of insectivorous bats are Coleoptera, Diptera, and Lepidoptera (Vaughan 1997). Of these, despite their abundance and diversity across Britain, relatively little is known of how Lepidoptera (with the exception of butterflies; Blair 1999) respond to urbanisation (Fox 2013). In comparison to other common insect taxa, Lepidoptera are relatively easy to sample and to identify to species level. It is for these reasons that a chapter of this thesis is given to investigating how moth abundance, diversity, and species richness is determined within the urban landscape.

1.8. Study aims and thesis outline

Despite the growing awareness that urbanisation is likely to have a negative effect on many bat species, relatively little research has been conducted to ascertain how urbanisation directly impacts the behaviour, habitat use and distribution of bat populations. The percentage of the British population living within urban areas is projected to reach almost 90% by 2050 (United Nations 2014), which will result in increased infrastructure, extra demands for housing and additional pressure on wildlife, including bats. This thesis therefore includes datasets collected from a range of spatial scales (e.g. central Scotland to Britain) with the purpose of assessing the relative importance of a variety of key habitat types found within the urban matrix for bats and to produce recommendations which will improve the effectiveness of urban conservation strategies at both a local and landscape scale.

In particular, the aims of this study are to:

- assess the effectiveness of a variety of surveying techniques in determining bat community composition within woodland, with the aim of increasing surveying efficiency to improve the accuracy of targeted conservation decisions (chapter 2).
- examine if two cryptic, and largely sympatric, bat species exhibit differential responses in their use of fragmented urban woodland and the surrounding urban matrix. These results will indicate how plausible it is to assess the adaptability of species to urbanisation by grouping morphologically similar species together (chapter 3).
- assess whether bats exhibit sex differences in habitat use within the built environment. These findings will have important implications for our understanding of the adaptability of species to urbanisation (chapter 4).
- examine the relative importance of vegetation characteristics (e.g. woodland canopy cover), patch configuration (e.g. woodland size and shape) and the composition, spatial configuration and heterogeneity of the surrounding landscape on moth abundance, species richness, and diversity within fragmented urban woodland (chapter 5).
- assess how the activity of a variety of bat species on urban waterways within the British Isles is influenced by the local vegetation characteristics and the surrounding habitat types at both a local and landscape scale. These results will provide management strategies to protect and improve urban waterway habitats for the benefit of a variety of bat species (chapter 6).

- investigate the extent to which bat species are using urban gardens and how the vegetation and environmental characteristics of the garden and its surrounding landscape determine use. These results will allow for the creation of more coherent landscape plans for the urban matrix coupled with recommendations of how individual gardens can be managed to increase bat use (chapter 7).
- use data from the National Bat Monitoring Programme, a citizen science scheme, to assess how two cryptic, and morphologically similar, species are responding to the built environment at a landscape scale. Additionally I consider how the negative response towards urbanisation by relatively common species should shape future conservation policies (chapter 8).

Chapter 2

Testing the effectiveness of surveying techniques in determining bat community composition within woodland

An adapted version of this chapter has been published as:

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2.1 Summary

Determining the biodiversity of an area is essential for making targeted conservation decisions. Undertaking surveys to confirm species presence or to estimate population sizes can be difficult, particularly for elusive species. Bats are able to detect and avoid traps, making it difficult to quantify abundance. Although acoustic surveys using bat detectors are often used as a surrogate for relative abundance, the implicit assumption that there is a positive correlation between activity levels and abundance is rarely tested. I assessed the effectiveness of surveying techniques (i.e. trapping and acoustic monitoring) for detecting species presence and tested the strength of collinearity among methods. In addition, I tested whether the use of an acoustic lure (a bat-call synthesiser) increased bat-capture rate and therefore species detectability. Surveying was carried out over 3 years in central Scotland (Britain), in 68 woodlands within predominantly agricultural or urban landscapes. There was a significant positive relationship between bat activity recorded on ultrasonic detectors and the relative abundance of *Pipistrellus pygmaeus* and *P. pipistrellus*, but not those in the genus *Myotis*. In general, acoustic monitoring was more effective than trapping at determining species presence; however, to ensure rarer or quiet species are recorded, a complementary approach is required. Broadcasting four different types of echolocation call resulted in a 2–12-fold increase in trapping success across four species of insectivorous bat found in the study region. Whereas lure effectiveness remained unchanged for female *P. pygmaeus* over time, there was a marked increase in the number of males captured using the lure throughout the summer (May to September). I have demonstrated a variety of ways to increase surveying efficiency,

which can maximise the knowledge of diversity in an area, minimise wildlife disturbance, and enhance surveying effectiveness.

2.2 Introduction

Obtaining accurate quantitative information on the species richness of an area is difficult, yet it is essential to identify highly biodiverse areas for conservation prioritisation (Brooks et al. 2006). Species can remain undetected despite extensive surveying, and presence records can be spatially biased towards localities that are easier to survey or are more frequented by recorders (Rondinini et al. 2006). Estimates of species frequency of occurrence or relative abundance are also often used as indices of species persistence to gain a better understanding of how species use habitats (Araújo and Williams 2000). Abundance has been used to form area-based priority-setting criteria for a range of taxa (Gauthier et al. 2010). However, assessing abundance for rare or elusive species can involve high levels of uncertainty, and failure to detect species within an area may influence future planning decisions and leave sites vulnerable to habitat loss. Many species of European bat have undergone population declines in the past few decades as a result of habitat loss and degradation, a consequence of pressure on resources from increasing human populations (Mickleburgh et al. 2002). Bats are becoming increasingly important as bioindicators, therefore gaining accurate estimates of bat population sizes is critical to quantify the extent of population changes (Jones et al. 2009). The size of bat populations can be estimated by counting individuals emerging from summer roosts (Jones et al.1996) or in hibernacula (O’Shea et al.2003); however, roosts are often difficult to find and inaccessible. Acoustic surveys using bat detectors are widely used in studies to determine species presence and quantify activity of foraging bats (e.g. Roche et al. 2011; Fuentes-Montemayor et al. 2013). However, call intensity varies among species; gleaning species such as *Plecotus* spp. emit calls of short duration, high frequency and low intensity, which may not be detected by acoustic surveys (Waters and Jones 1995). In cluttered habitats, such as woodland, bats emit quieter echolocation calls, which can reduce detection rate and make species identification from ultrasonic recordings more difficult (Russ 1999; Schnitzler and Kalko 2001). Therefore, it is often necessary to confirm species presence within an area by capturing and examining individuals in the hand.

Mist-netting and harp-trapping are two of the most common methods used to capture bats (O'Farrell and Gannon 1999). However, as with acoustic surveys, inherent biases exist within these sampling techniques, including interspecies differences in capture rates (Berry et al. 2004), avoidance-learning behaviour in bats (Larsen et al. 2007), and ambient light levels altering net detectability (Lang et al. 2004). Habitat characteristics can also determine capture rates; trapping is most effective in locations with dense vegetation containing discrete flyways (Duffy et al. 2000; Hourigan et al. 2008). However, some species, such as *Myotis bechsteinii*, rarely use tracks or rides, which would therefore decrease their capture rate when surveying within woodland habitat (Hill and Greenaway 2005). Additionally, trapping requires specialist skills, and can cause stress to the animals (Flaquer et al. 2007).

A complementary approach, using a combination of acoustic surveys and trapping techniques, may maximise detection efficiency (Duffy et al. 2000; MacSwiney G. et al. 2008; Meyer et al. 2011), yet is not always practical due to limitations in expertise, expense and time requirements (Hourigan et al. 2008). Therefore, several previous studies have used measurements of bat activity assessed by acoustic monitoring as a surrogate for relative abundance (e.g. Kalko et al. 2008; Razgour et al. 2011; Berthinussen and Altringham 2012). However, to our knowledge, the relationship between foraging activity and abundance has never been explicitly tested (but see Parsons et al 2009).

Broadcasting natural or synthetic auditory stimuli has been used to increase detection rates by provoking a response that makes individuals more easily detectable. Such 'playback' calls have been used to estimate population sizes in a range of amphibian, avian and mammalian species, including *Bufo marinus* (Schwarzkopf and Alford 2007), *Loxia scotica* (Summers and Buckland 2011) and *Panthera leo* (Brink et al. 2013). Behavioural studies have demonstrated that broadcasting bat-feeding buzzes and social calls can attract both conspecific and heterospecific bats (Russ et al. 1998; Wilkinson and Boughman 1998); this led to the development of an acoustic lure, the Sussex AutoBat (Hill and Greenaway 2005). Field testing showed that the capture rate of different bat species, including the rare *M. bechsteinii*, increased with the use of the lure (Hill and Greenaway 2005; Goiti et al. 2007; Hill and Greenaway 2008); however, the extent to which this enhances capture rates in comparison to traditional trapping techniques has not, to our knowledge, been systematically tested.

Here, I quantify and compare the effectiveness of traditional surveying methods (acoustic surveys, mist-netting and harp-trapping) and novel techniques (mist-netting and harp-trapping with the addition of an acoustic lure), with the aim of informing future surveys for insectivorous temperate bat species. I address the following five specific questions:

(1) is bat activity, as measured by acoustic surveys, a good surrogate for relative bat abundance;

(2) which surveying method (acoustic surveys or trapping) is most effective at determining species presence within temperate woodland;

(3) to what extent does an acoustic lure enhance capture rate in comparison to traditional trapping techniques;

(4) does the type of synthesised bat-call broadcast determine capture rate; and

(5) what is the effect of sex, age, and season on trapping success with an acoustic lure?

2.3 Materials and Methods

2.31 Site Selection

Ordinance survey digital maps (EDINA Digimap Ordnance Survey Service 2012) were used to select 68 broadleaved and mixed woodland patches of different size (0.1–30 ha) and shape (ranging from compact to complex) within central Scotland, Great Britain (Appendix 2.1). This region comprises a highly modified and densely populated landscape that is dominated by agriculture, large conurbations, coniferous plantations and fragmented patches of semi-natural habitat including broadleaved woodland. Each woodland was surveyed once during the summers of 2009 (June to August, 20 sites), 2010 (May to July, 14 sites) and 2011 (May to August, 34 sites). Surveying was conducted in dry weather, when the temperature remained ≥ 8°C throughout the surveying period, and wind speed ≥ 4 on the Beaufort scale. Surveying commenced 30–45 min after sunset and continued for the following 4 h, this being the shortest period between sunset and sunrise in this area. A combination of acoustic surveys and trapping was used to determine species presence, relative abundance and activity within each woodland patch.

2.32 Bat abundance estimates using trapping

An estimate of relative abundance was determined by placing an Austbat harp trap (2.4 × 1.8 m) and three Ecotone mist nets (2.4 × 6 m each) within each woodland. Traps were placed ≥ 20 m from the woodland edge, ≥ 40 m from each other and positioned to avoid paths. A single acoustic lure (The Autobat, Sussex University, Brighton UK) and speaker was positioned alongside a trap (<1 m from the centre of the trap and at 2-m height) and moved between traps every 30 min for the duration of surveying (Hill and Greenaway 2005). Ultrasound was broadcast from two Polaroid Series 600 Environmental Grade transducers (SensComp, Livonia, Michigan, United States) mounted in a custom-built ultrasound distributor (built by F. Greenaway, described in Murphy 2012), which enabled the sound to be emitted across 360 degrees in the horizontal plane. Preliminary testing using a frequency-division bat detector indicated that the sound emitted by the acoustic lure was detectable from a maximum of 20 m away, although it is likely that bats can hear them from a greater distance (i.e. Murphy 2012). Four different synthesised bat-call types were played (*Pipistrellus* spp. mix, *Myotis* spp. mix, *Nyctalus leisleri* and *M. nattereri*), which are known to attract a variety of bat species (F. Greenaway, pers. comm.). Call sequences were switched every 15 min and played in the same sequence each night. Traps were checked every 15 min to extract any captured bats, which were then identified to species, aged, sexed, measured, weighed and marked temporarily by fur clipping.

2.33 Bat activity estimates using acoustic surveys

Bat activity was quantified using a frequency division bat detector (Anabat SD1, Titley Electronics, Coppull, Lancashire, UK) fixed on a 1-m-high pole, with the microphone pointing upward. The detector was positioned adjacent to the centre of the trap (<1 m away) and rotated between traps every 30 min. The sequence of rotation ensured that the detector did not record at the same net as where the acoustic lure was positioned. All bat recordings were analysed using Analook W (Corben 2006). One bat pass was defined as a continuous sequence of at least two echolocation calls from a passing bat (Walsh and Harris 1996). All nine species of four bat genera present within the study area (*Myotis*, *Nyctalus*, *Pipistrellus* and *Plecotus*) can be identified from detector recordings on the basis of the search-phase of their echolocation call (Russ 1999). However, it can often be difficult to distinguish among *Myotis* species because of similarities in call structure, particularly within cluttered environments (Schnitzler and Kalko 2001). As a consequence, recordings of *Myotis* species known to be present in the area (*M. daubentonii*, *M. mystacinus* and *M. nattereri*) were grouped together as *Myotis* spp. The three *Pipistrellus* species in this area (*P. pipistrellus*, *P. pygmaeus* and *P. nathusii*) can be determined by the characteristic frequency (Fc = the frequency at the right-hand end of the flattest portion of a call; Corben 2006) of their search-phase echolocation calls. Bat passes with a Fc of between 49 and 51 kHz were classed as unknown *Pipistrellus* spp.

2.34 Data analysis

Statistical analyses were conducted using the statistics package R version 2.14 (R Core Team 2012) run within the R Studio interface (R Studio 2012) and using the package ggplot2 (Wickham 2009). Total captures per site was converted to captures per hour per site (with /without the acoustic lure) because the lure was operating only at one of the four traps at a time within each site. Total bat passes per site was converted to passes per hour. I performed a series of linear regression models for *P. pygmaeus*, *P. pipistrellus*, and *Myotis* spp. to determine whether an association exists between bat-capture rate and bat activity and whether this changes through the season. Bat captures per hour per site was used as the response variable for each species /genus. Bat activity, date and the interaction between them were included as predictor variables in each of the models. Each model was fitted with a Gaussian distribution and, if required, the capture and activity rates were logged to achieve normality. Non-significant interactions or variables were removed from the model by using a stepwise method, whereby explanatory variables were dropped or retained using $P > 0.05$ as a threshold. Model validation was conducted by the examination of residuals (Zuur et al. 2009). To determine how the effectiveness of each surveying strategy varied among species, I compared the number of woodlands in which species presence was confirmed by trapping (with and without the lure), acoustic surveys, or both methods combined. A Mann–Whitney U-test was used to determine whether the number of species detected per site differed between trapping versus acoustic surveys. A two-sided Wilcoxon paired test was used to assess trapping success with and without the acoustic lure for each species /genus. The relative effectiveness of the four different synthesised bat-call types broadcast by the acoustic lure was tested using a chi-square test. To determine whether trapping success (with and without the acoustic lure) varied between sex or age (adult /juvenile), two-sided Wilcoxon paired tests were conducted on *P. pygmaeus* only because there were insufficient numbers of other species captured. I also tested whether the effect of the lure on male and female *P. pygmaeus* changed with date throughout the active season, by using linear regressions for males and females separately. Regression models were validated by visual examination of residuals (Crawley 2007).

2.4 Results

2.4.1 Bat activity and abundance

I captured a total of 376 bats in 64 of the 68 woodlands, and recorded a total of 16 121 usable bat passes (i.e. identifiable to species / *Myotis* spp. level), with activity recorded in 66 of the 68 woodlands. I identified the following five species / genera by acoustic surveys: *P. pygmaeus*, *P. pipistrellus*, *P. nathusii*, *P. auritus* and *Myotis* spp. Six species were identified by trapping, namely, *P. pygmaeus*, *P. pipistrellus*, *P. auritus*, *M. nattereri*, *M. daubentonii* and *M. mystacinus.* With the exception of *M. mystacinus*, all species were captured in traps both with and without the use of an acoustic lure (Table 2.1). Abundance of *M. mystacinus* and *M. daubentonii* was insufficient to conduct analyses at species level; therefore, abundance of all *Myotis* species was grouped together and analysed at the genus level. *P. nathusii* was recorded only at one site and therefore excluded from further analysis.

2.4.2 Correspondence between acoustic surveys and capture rates

There was a positive association between both bat activity and date and the capture rate of *P. pygmaeus*. Bat activity was a marginally significant positive predictor of *P. pipistrellus* capture rate; however, there was no relationship between capture rate and date. Neither activity nor date was a significant predictor of *Myotis* spp. capture rate (Table 2.2, Figure 2.1). *P. auritus* was not included in this analysis because of its presence at relatively few sites (Table 2.1).

Table 2.1 Summary of species presence determined by trapping, acoustic surveys or combined methods at 68 woodlands in central Scotland. The percentage increase of the combined approach is calculated from the addition of sites where a species was detected by trapping but not by acoustic monitoring to sites where a species was only detected by acoustic monitoring.

Species	% of sites (number of sites) at which species presence was confirmed					% increase of combined approach
	Trapping			Acoustic survey	Combined approach	
	Lure	No lure	Total			
P. pygmaeus	80.9 (55)	38.2 (26)	82.4 (56)	91.2 (62)	94.2 (64)	3.2
P. pipistrellus	19.1 (13)	8.8 (6)	22.1 (15)	77.9 (53)	79.4 (54)	1.9
Myotis spp.	20.6 (14)	16.2 (11)	27.9 (19)	41.2 (28)	44.1 (30)	7.1
of which:						
M. nattereri	19.1 (13)	14.7 (10)	25 (17)			-
M. daubentonii	1.5 (1)	2.9 (2)	4.4 (3)			-
M. mystacinus	1.5 (1)	0 (0)	1.5 (1)			-
P. auritus	8.8 (6)	7.4 (5)	13.2 (9)	13.2 (9)	23.5 (16)	77.7

Table 2.2 Summary of results for linear regression models for *P. pygmaeus*, *P. pipistrellus*, and *Myotis* spp. to assess the association between bat capture rate (response variable) and bat activity and whether this changes with date.

			95% CI			
Species	Predictor variable	Estimate	Lower	Upper	*p*	R^2
P. pygmaeus	Activity	0.041	0.028	0.055	0.003	–
	Date	0.468	0.333	0.603	0.001	–
	Model	–	–	–	0.001	24.02%
P.pipistrellus	Activity	0.017	0.009	0.026	0.052	–
	Date	-0.023	-0.112	0.067	0.802	–
	Model	–	–	–	0.052	7.19%
Myotis spp.	Activity	-0.102	-0.187	-0.016	0.245	–
	Date	0.477	0.122	0.831	0.190	–
	Model	–	–	–	0.218	1.06%

2.4.3 Effectiveness of surveying methods at determining species presence

On average, acoustic surveying detected one more species per site than did trapping (*n* = 64, *U* = 2983, *P* = 0.001). Of the 68 survey sites, acoustic surveying recorded more species at 41 of the sites, trapping detected more species at two sites, whereas both methods recorded the same species at 19 sites. *P. pipistrellus* showed the greatest difference in detection between methods, with acoustic surveys detecting this species at an additional 38 sites compared with trapping (Table 2.1). Trapping added only one additional site to those where *P. pipistrellus* presence had already been confirmed through acoustic surveys (Table 2.1). In contrast, for *P. auritus*, trapping increased the number of sites at which it was detected by seven (of a total of 16) woodlands.

2.4.4 Effect of an acoustic lure on capture rate

The acoustic lure significantly increased capture rates for all species. *P. pygmaeus* showed the strongest response (*n* = 56, *v* = 1593, *P* = 0.001), with a 12-fold increase in individuals caught using the acoustic lure. Likewise, 7.5 times more *P. pipistrellus* were caught when the lure was adjacent to a trap (*n* = 15, *v* = 117, *P* = 0.001). The acoustic lure increased the capture rate of both *M. nattereri* (*n* = 17, *v* = 127, *P* = 0.017) and *P. auritus* (*n* = 9, *v* = 39, *P* = 0.055) by 2.25- and 3.5-fold, respectively (Figure 2.2).

2.4.5 Effect of broadcasting different types of synthesised bat call on capture rate

There were significant differences in the effectiveness of the type of call sequences broadcast by the lure in attracting *P. pygmaeus* (χ^2 = 63.91, d.f. = 3, *P* = 0.001), *P. pipistrellus* (χ^2 = 8.67, d.f. = 3, *P* = 0.034) and *P. auritus* (χ^2 = 7.86, d.f. = 3, *P* = 0.049) (Figure 2.3). *P. pipistrellus* and *P. pygmaeus* responded more strongly than expected by chance to synthesised calls of *N. leisleri*, *Myotis* spp. mix and *Pipistrellus* spp. playback calls, whereas very few were captured with synthesised calls of *M. nattereri*. In contrast, *P. auritus* was not trapped at all when *M. nattereri* or *Pipistrellus* spp. playback calls were broadcast, but showed a strong response to *Myotis* spp. mix and *N. leisleri* calls. There was a marginal difference in the effectiveness of each of the call sequences in attracting *M. nattereri* (χ^2 = 6.6, d.f. = 3, *P* = 0.086), with the calls of *N. leisleri* instigating the greatest response.

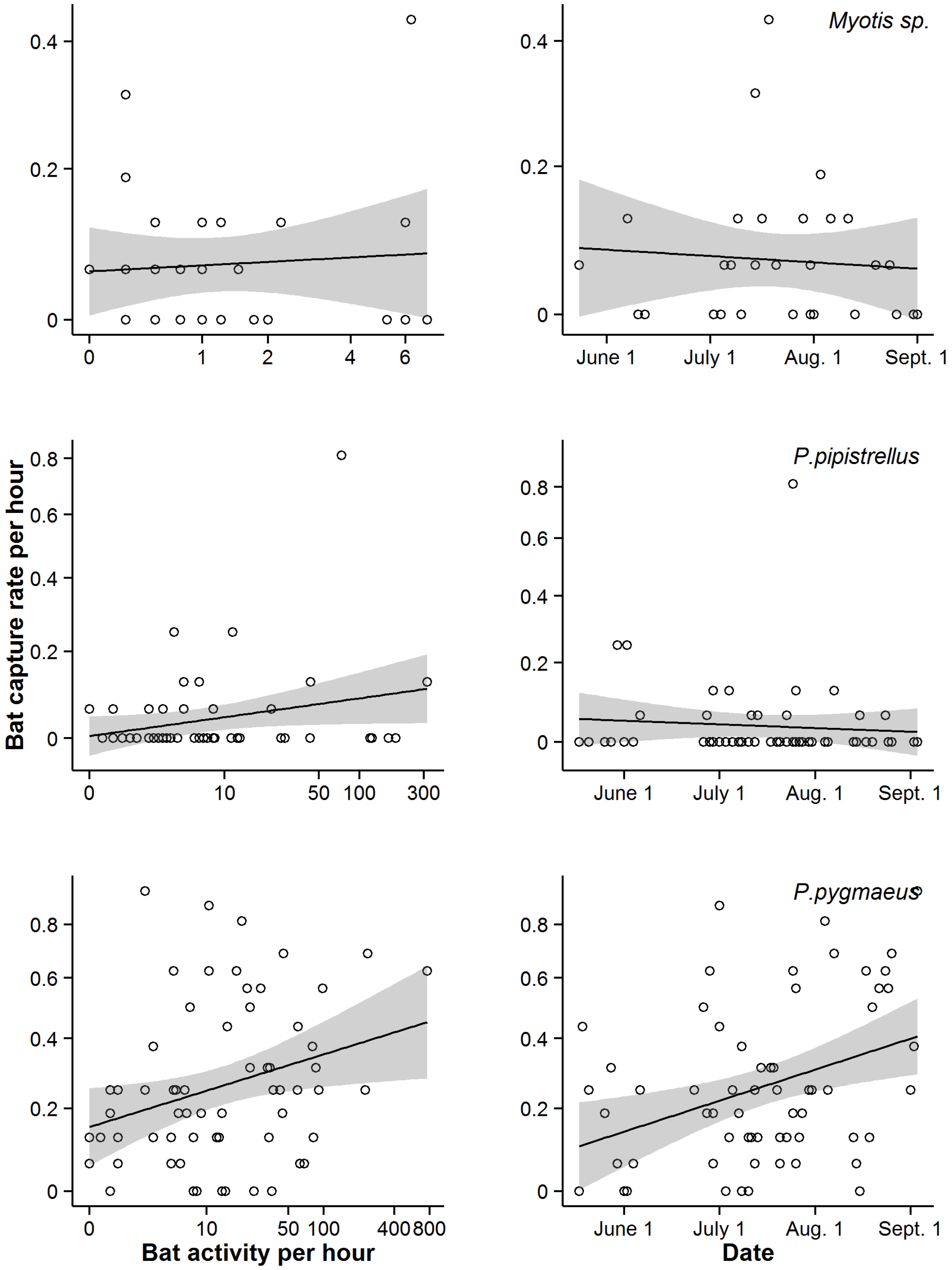


Figure 2.1 Linear regression models for *P. pygmaeus*, *P. pipistrellus*, and *Myotis* spp. to assess the association between bat capture rate and bat activity and whether this changes through the season. The shaded area represents 95% confidence intervals for each model. Note the difference in axis scales between species.

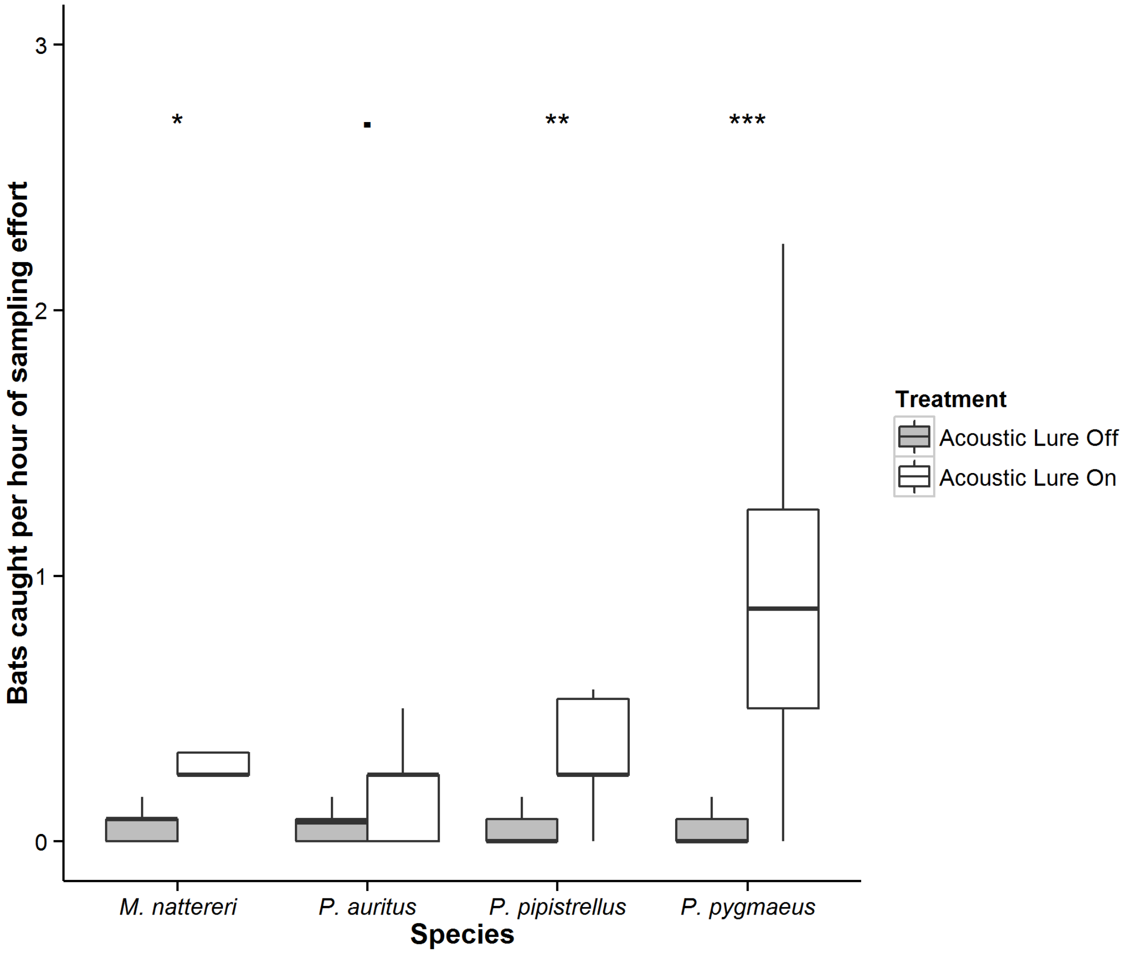


Figure 2.2 Bat captures per hour for four species, with and without the lure. The upper and lower hinges correspond to the first and third quartiles, while the upper and lower whiskers extend to the value that is within 1.5 times of the interquartile range of the hinge (Wickham 2012). Outliers are excluded from this graph. Significance codes: p ≤ 0.001***, p ≤ 0.01**, p≤ 0.05*, p≤ 0.1▪

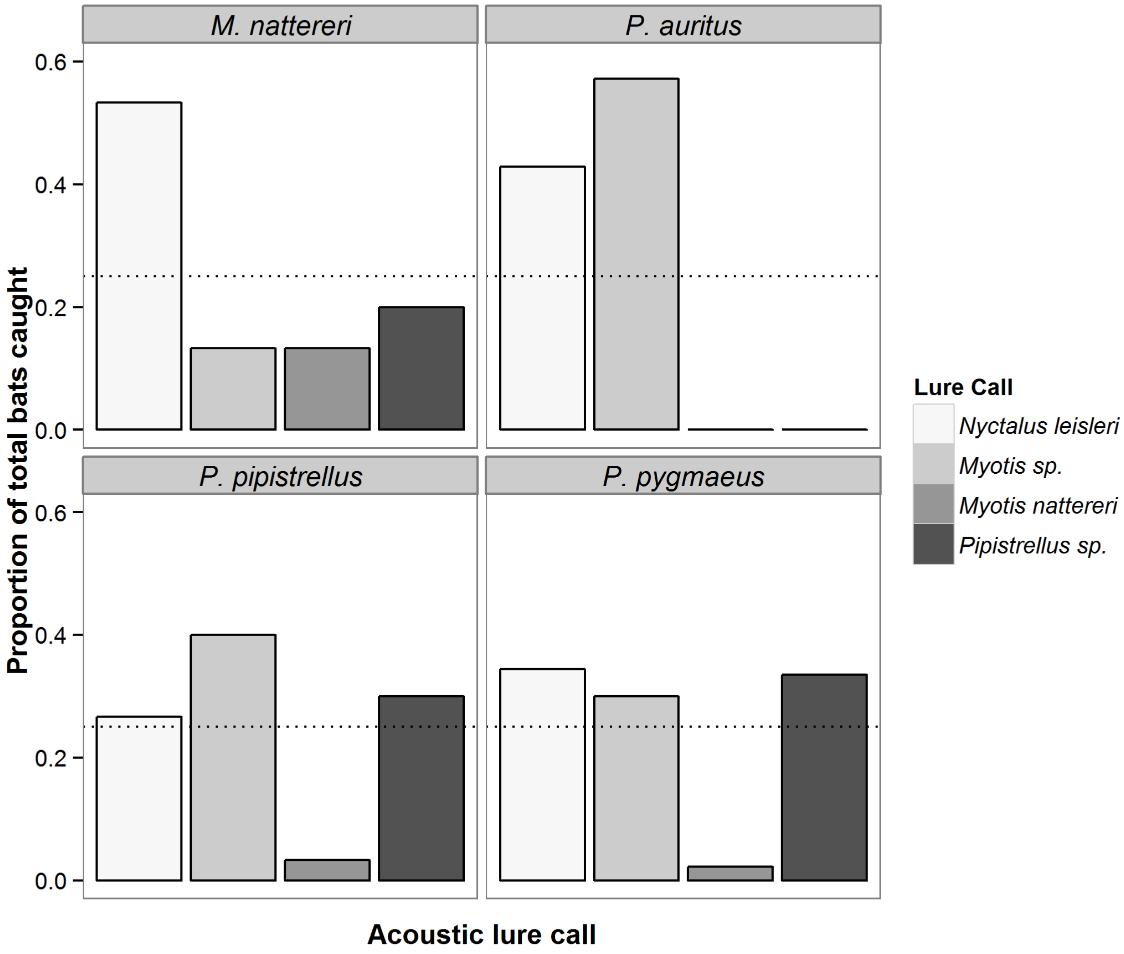


Figure 2.3 The effectiveness of different call sequence types broadcast by the acoustic lure in capturing bats. Bats caught without the acoustic lure were not included within this analysis. The dashed line signifies the expected proportion of bats caught for each call type. The expected value was calculated using a chi-square test and represents the expected proportion of total bats caught if all lure calls were of equal effectiveness.

2.4.6 Effect of sex, age and seasonality on trapping success of *P. pygmaeus* with an acoustic lure

The acoustic lure significantly increased the capture rate of both male (*n* = 51, *v* = 1316, *P* = 0.001), and female (*n* = 39, *v* = 702, *P* = 0.001) *P. pygmaeus*. Broadcasting synthesised bat calls also significantly increased the capture rate of both juvenile (*n* = 23, *v* = 273, *P* = 0.001) and adult (*n* = 54, *v* = 1482, *P* = 0.002) *P. pygmaeus.* The effectiveness of the acoustic lure for female *P. pygmaeus* did not vary across the active season ($F_{1,55}$ = 1.04, P = 0.321), whereas males responded more strongly to the lure later in the summer than in the spring ($F_{1,48}$ = 20.3, P = 0.001, r^2 = 0.3; Figure 2.4).

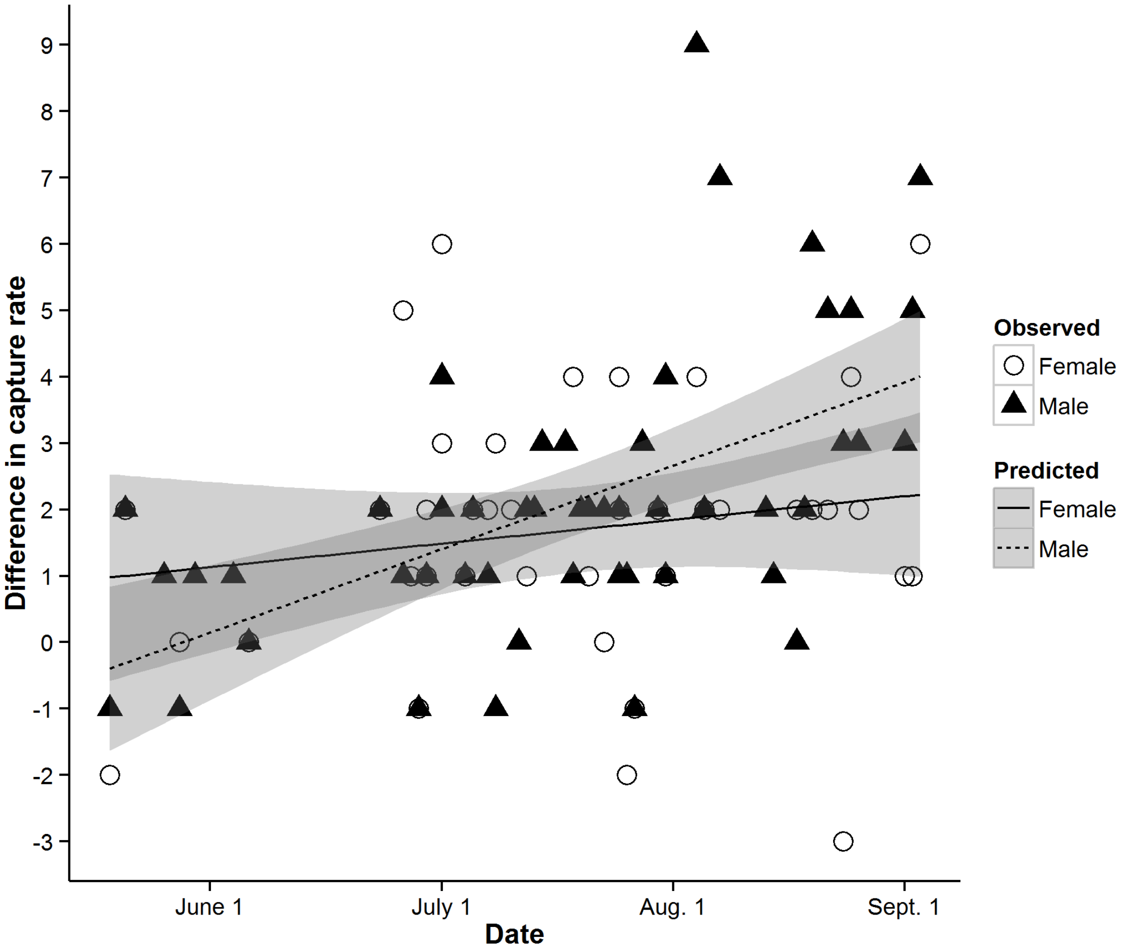


Figure 2.4 Relationship between survey date and the difference in capture rate between *P. pygmaeus* bats caught with and without the acoustic lure for both sexes. The shaded area represents 95% confidence intervals for either sex. No trapping was conducted in late June to avoid capturing heavily pregnant females. Male *P. pygmaeus* responded more strongly to the lure later in the summer than in the spring (P = 0.001, r^2 = 0.3).

2.5 Discussion

2.5.1 Using acoustic surveys as a surrogate for relative bat abundance

Acoustic surveys are widely used in field studies to act as an index of relative abundance; however, the relationship between these two indices is rarely tested (e.g. Kalko et al. 2008). Trapping can be a costly and time-consuming process requiring expertise, whereas acoustic surveys are non-intrusive and comparatively simple. Here, I showed that, in the case of *P. pygmaeus* and *P. pipistrellus*, activity levels vary positively with relative abundance and could be used a surrogate for abundance to increase surveying efficiency. This provides additional support that surveys monitoring population change over time (e.g. Bat Conservation Trust's Field Survey, part of a suite of surveys in the National Bat Monitoring Program run by Bat Conservation Trust 2013) are reflecting relative changes in bat populations, despite using only acoustic surveys. Additionally, acoustic surveys may be an effective method of quantifying the relative conservation value of a habitat type on the basis of the extent to which bats use it. *P. pygmaeus* capture rates also increased later on in the summer, possibly because of a heightened response to the acoustic lure at this time of year, as discussed below. There was no significant relationship between *Myotis* spp. activity and capture rate. This is unsurprising, given that each species within this group is likely to have varying levels of detection by acoustic surveys (e.g. flight height) and capture rates (e.g. differing responses to an acoustic lure). Combining the data into a larger species group will therefore mask any species-specific relationship between activity and capture rate from being observed.

2.5.2 Effectiveness of surveying methods at determining species presence

Although using multiple surveying methods can maximise species detection efficiency (MacSwiney et al. 2008; Meyer et al. 2011), it is often impractical. I found only a marginal benefit of undertaking both acoustic surveys and trapping for *P. pipistrellus* and *P. pygmaeus*. Given that bat detectors are cost effective, can be automated to run for long time periods, and are non-intrusive (Hourigan et al. 2008), acoustic surveys alone are a satisfactory method for surveys that focus on a specific conspicuous species. In comparison, accurately determining bat community composition or the occurrence of quiet species such as *P. auritus* would likely benefit from a complementary approach. This supports the work by Flaquer et al. (2007) who found that rarer species are often detected only by one method, which suggests they could be easily overlooked if only one sampling technique is used. In addition, the effectiveness of each surveying method may differ depending on the habitat type that they are used in (e.g. between open and closed habitat). It should be noted that the present study was conducted in an area of relatively low bat diversity; in locations with high species richness, identifying bat calls to species level may be more difficult and this may provide additional incentives for using trapping alongside acoustic methods.

2.5.3 Effect of an acoustic lure on capture rate

The acoustic lure greatly increased bat-capture rate, with between a 2- and 12-fold increase in trapping success across species. Bats are known to respond to conspecific and heterospecific calls (Fenton 2003b; Dechmann et al. 2009; Knörnschild et al. 2012) and the acoustic lure appeared to invoke a response similar to that to the synthesised calls that were played. The ecological mechanism through which the lure works, however, remains unknown. A response may have occurred as a result of bats eavesdropping on surrounding calls to locate food sources (Gillam 2007), or acting aggressively to a perceived competitor (Hill and Greenaway 2005). Additionally, it is plausible that the lure may be impairing the ability of the bats to echolocate, thereby masking the position or presence of the trap. Mist nets and harp traps are conspicuous acoustic targets to bats (Berry et al. 2004); detection rates may therefore be reduced by an increased external sensory input. Bats exhibit high rates of trap avoidance (Larsen et al. 2007), which the use of an acoustic lure appears to reduce. It is likely that I have underestimated the effectiveness of the acoustic lure, given that some bats respond to the lure but do not make a close approach (Hill, D.A., pers. comm.). This may have increased capture rate at traps without the acoustic lure because of heightened activity in the immediate vicinity. Trapping enables confirmation of species identity, detailed information of populations/individuals (e.g. sex ratios and body condition) and more accurate abundance estimates. The use of an acoustic lure can improve surveying efficiency by maximising bat-capture rates, which will reduce the money, time and effort required while trapping. Our research therefore supports the findings of Hill and Greenaway (2005) and Goiti et al. (2007) in demonstrating that an acoustic lure is an effective method of increasing bat-capture rates across a range of species. However, further research on whether some species avoid certain call types and how this may vary between the sexes and throughout the season would be useful in understanding any disruptive effect on bat populations the acoustic lure could be having. We, therefore, support the recommendations of Hill and Greenaway (2005) that call playback times should be brief and avoid frequent repetition within the same location.

2.5.4 Effect of broadcasting different types of synthesised bat calls on capture rate

Although the acoustic lure increased total trapping success, there were significant differences in the effectiveness of each type of synthesised bat-call broadcast. All species responded strongly to at least some heterospecific calls. This finding supports the work of Schöner et al. (2010) who found that *P. auritus* showed responsiveness to *Myotis* calls, but contrasts with Ruczyński et al. (2009) who found little response of *P. auritus* to any broadcast calls. The lack of responsiveness to broadcast *M. nattereri* calls by both *Pipistrellus* species and *P. auritus* demonstrated that bats perceived call types differently rather than exhibiting a generic response to the acoustic lure regardless of call type. The amplitude, frequency and duty cycle differ between the synthesised bat calls that are broadcast by the acoustic lure. Differences in trapping efficiency between synthesised calls may reflect that certain calls are able to mask the presence of a trap better than others.

If a specific bat species is the focus of trapping then knowledge of which playback calls attract this species will be valuable in maximising its capture rate while minimising by-catch of alternate species. For example, a study with the aim of trapping only *P. pygmaeus* should consider broadcasting *Pipistrellus* spp. calls because of their relative ineffectiveness in attracting other species, thereby minimising secondary disturbance. Likewise, the same study should consider avoiding the broadcasting of *N. leisleri* social calls because of their attractiveness across species. The development of new calls and a call library for the acoustic lure will further increase capture rates as knowledge of which calls are most effective increases.

2.5.5 Effect of sex, age and seasonality on trapping success of *P. pygmaeus* with an acoustic lure

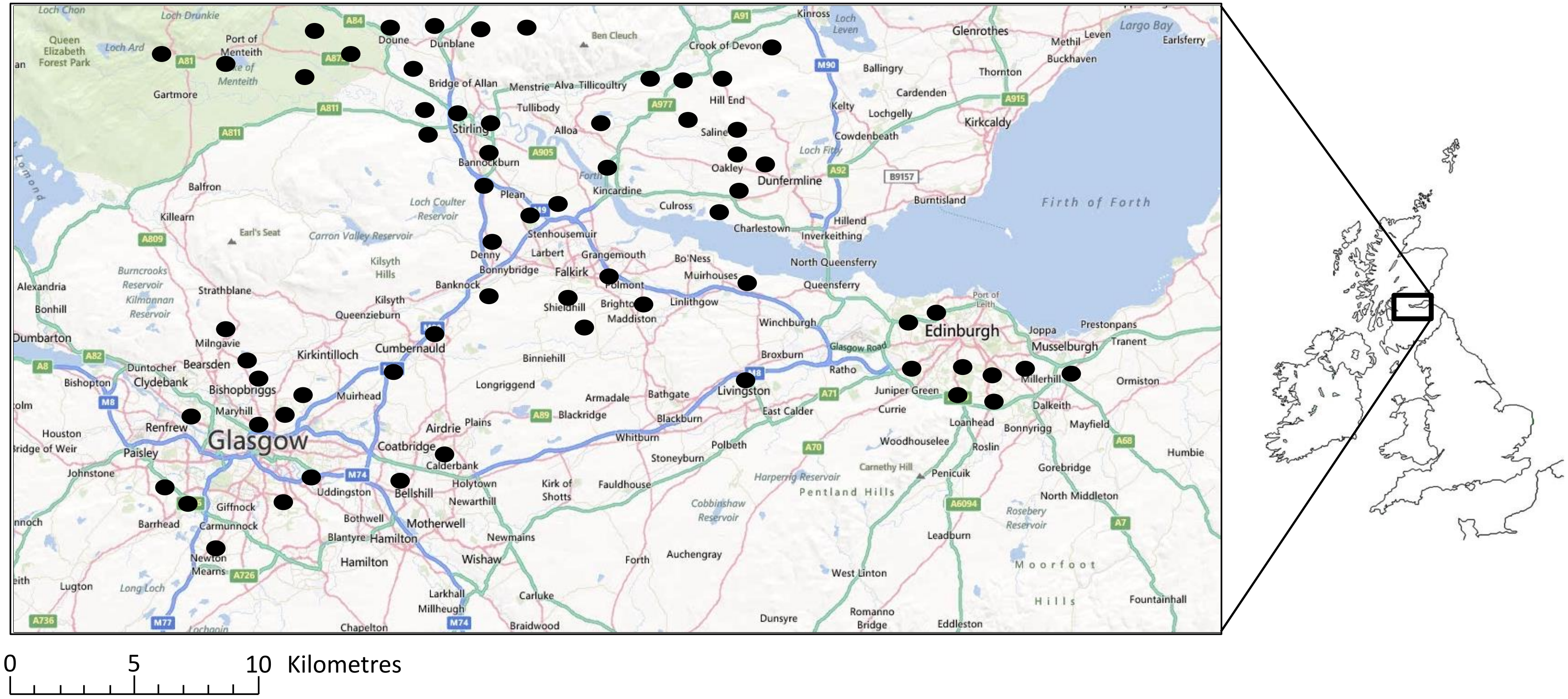
Determining the sex ratio and age structure of population is important, both for ecological studies and conservation purposes; for example, the presence of a lactating female in early summer can indicate that a maternity roost is close (Henry et al. 2002). The present study found that the acoustic lure increased *P. pygmaeus* trapping success for both sexes and for adults and juveniles alike, supporting its use in estimating overall population sizes for this species. The increase in trapping efficiency of the acoustic lure as the summer progresses for male *P. pygmaeus* may reflect a heightened responsiveness to surrounding bat calls as the peak breeding season (i.e. autumn) approaches. The increase in male-capture rate may be a result of increased aggression to a perceived competitor; Sachteleben and von Helversen (2006) found that *P. pipistrellus* chases intruders out of its territory during courtship displays, which may suggest that *P. pygmaeus* is behaving similarly while reacting to the acoustic lure. That bats may alter their responsiveness to the lure highlights the need to survey throughout the active season.

2.6 Conclusions

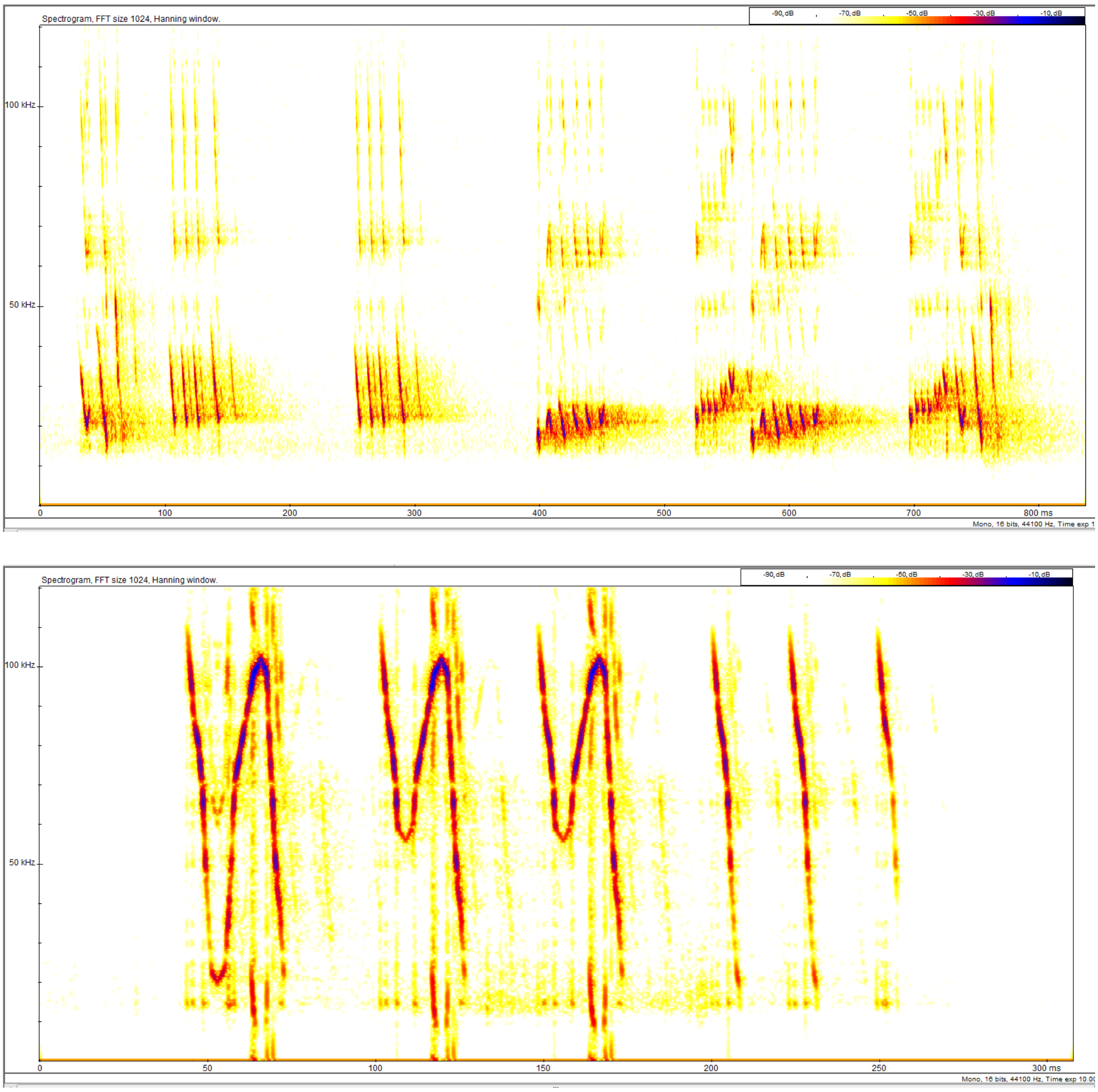
By optimising surveying procedures, it is possible to provide more informative insights into biodiversity of an area, minimise disturbance to wildlife, and make surveying more cost and time effective. I have shown, for certain species, that acoustic surveys are a suitable surrogate for relative abundance. However, in woodlands the widespread presence of quiet species means they may be better suited to a complementary approach that includes trapping. The use of an acoustic lure increases the effectiveness of trapping and I have demonstrated that species respond differently to the broadcasting of different call types; this will allow the future use of targeted calls to minimise disturbance to non-target species.

2.7 Acknowledgements

This project was supported by the Glasgow Natural Historian Society, People's Trust for Endangered Species, British Ecological Society and Nuffield Foundation. I thank Liam Cavin, Rebekah Mayhew, Lena Olley, Jenny Wallace, and the numerous volunteers who contributed to the data collection. I also thank Kate Barlow, David Hill, Frank Greenaway and two anonymous reviewers for their valuable comments on the manuscript.



Appendix 2.1 Map of central Scotland showing approximate locations of woodland patches (black dots) surveyed between 2009 - 2011



Appendix 2.2 Spectogram of sample calls that were played by the acoustic lure, mixed *pipistrelle* spp. calls (top) and *Myotis nattereri* calls (bottom).

Chapter 3

Differential responses to woodland character and landscape context by cryptic bats in urban environments

An adapted version of this chapter has been published as:

Lintott, P.R., Bunnefeld, N., Minderman, J., Fuentes-Montemayor, E., Mayhew, R., Olley, L., & Park, K.J. Differential responses to woodland character and landscape context by cryptic bats in urban environments. *PLOS ONE*, e0126850

3.1 *Summary*

Urbanisation is one of the most dramatic forms of land use change that relatively few species can adapt to. Determining how and why species respond differently to urban habitats is important in predicting future biodiversity loss as urban areas rapidly expand. Understanding how morphological or behavioural traits can influence species adaptability to the built environment may enable us to improve the effectiveness of conservation efforts. Although many bat species are able to exploit human resources, bat species richness generally declines with increasing urbanisation and there is considerable variation in the responses of different bat species to urbanisation. Here, I use acoustic recordings from two cryptic, and largely sympatric European bat species to assess differential responses in their use of fragmented urban woodland and the surrounding urban matrix. There was a high probability of *P. pygmaeus* activity relative to *P. pipistrellus* in woodlands with low clutter and understory cover which were surrounded by low levels of built environment. Additionally, the probability of recording *P. pygmaeus* relative to *P. pipistrellus* was considerably higher in urban woodland interior or edge habitat in contrast to urban grey or non-wooded green space. These results show differential habitat use occurring between two morphologically similar species; whilst the underlying mechanism for this partitioning is unknown it may be driven by competition avoidance over foraging resources. Their differing response to urbanisation indicates the difficulties involved when attempting to assess how adaptable a species is to urbanisation for conservation purposes.

3.2 Introduction

Urbanisation is one of the most dramatic forms of land use change. By 2050 it is expected that 70% of the world's population will live in urban areas, this expansion will require rapid urban growth which can fragment, destroy or degrade existing natural ecosystems (Zipperer & Pickett 2012). This can lead to reductions in species richness, diversity, and changes in community composition within the urban landscape (e.g. McKinney 2008; Grimm et al. 2008). We know relatively little about the underlying mechanisms that make certain species adept at adapting to urbanisation, which makes the development of management plans to conserve native biodiversity difficult to formulate (Magle et al. 2012). Morphological or behavioural factors influence how species respond to the urban landscape, and these traits have been used to classify species as 'urban avoiders', 'urban utilizers' or 'urban dwellers' (Fischer et al. 2015), although in reality there is likely to be a continuous spectrum of adaptability. Understanding where along this spectrum a species lies will help determine the extent of conservation action required.

The prevalence of many species within the urban environment depends on their ability to survive and adapt to heavily modified landscapes and anthropogenic disturbances. In this regard, Chiroptera are one of the few orders of animals in which many species have formed strong associations with human-modified habitats. Human habitations provide roosts, while adaptations of the environment provide food sources, such as 'light-attracted' bat species exploiting insect congregations that form at artificial light sources (Mathews et al. 2015). However, whilst many species have adapted to exploit the urban landscape, the general pattern is of lower bat activity and species richness with increasing levels of urbanisation (e.g. Gaisler et al. 1998, Lane et al. 2006, but see Gehrt & Chelsvig 2003). Adaptation to the built environment is highly species-specific, for example species with high mobility (e.g. those with fast, high flight) are often able to utilise habitat patches of high foraging potential in an otherwise unsuitable landscape as their movement is relatively independent from structural features. In contrast, slow flying bats may respond more strongly to small-scale features (e.g. road networks) and therefore their ranging ecology and habitat selection may be more heavily impacted (Russo & Ancillotto 2014). For example, in the Eastern pipistrelle (*Pipistrellus subflavus),* the location of foraging sites is influenced more strongly by the distance to hibernacula than the level of urbanisation or degree of woodland fragmentation (Johnson et al. 2008).

Woodland is widely regarded as primary foraging habitat for a range of bat species (Lacki et al. 2007), however urban woodland is of variable quality, subject to invasive species encroachment and often consists of small, fragmented patches (Alvey 2006). Although management strategies for the conservation of urban woodland are being developed in many countries due to the benefits for human health (Matsuoka & Kaplan 2008) and biodiversity conservation (Cornelis & Hermy 2004; Croci et al. 2008), their effectiveness for the latter is unknown as basic ecological data is lacking for many taxa in urban landscapes. Grouping the conservation requirements of morphologically similar species together would increase the efficiency and effectiveness of management strategies as a greater number of species would benefit from any single conservation action. However, this is problematic if morphologically similar species differ substantially and unpredictably in their response to changes or pressures associated with urbanisation due to factors including differences in dietary preferences or inter-specific competition.

In this paper I examine whether closely related species can respond differently to urbanisation. I use two, often sympatric, cryptic species of pipistrelle bat *P. pygmaeus* and *P. pipistrellus* which are widespread throughout Europe to investigate how habitat selection within the built environment varies among species. These two species have very similar flight morphologies (Jones & Van Parijs 1993), although they show a small but significant difference in their body size (Barlow & Jones 1999) and echolocation call frequencies. Little is known of the response of these cryptic species to the urban landscape although Hale et al. (2012) found that *P. pipistrellus* activity at urban ponds peaked with moderate levels of adjacent urban grey space. Morphological traits are often linked to habitat specialisation and from this the risk of exclusion from highly modified landscapes can be inferred (Safi & Kerth 2004). Consequently, the morphological similarities between *P. pipistrellus* and *P. pygmaeus* suggest that both species will respond similarly to the urban matrix. Specifically, I address the following three questions:

1) Do *P. pipistrellus* and *P. pygmaeus* respond similarly to urban woodland vegetation character (e.g. tree density) and patch configuration (woodland size and shape)?

2) Do *P. pipistrellus* and *P. pygmaeus* respond similarly to the composition, spatial configuration, and heterogeneity of the surrounding landscape and, if so, at what spatial extent?

3) Do *P. pipistrellus* and *P. pygmaeus* exhibit similar habitat selection within the urban matrix?

4) What are the conservation implications of these findings?

3.3. Materials and methods

3.3.1 Site selection

A total of 31 urban woodlands in central Scotland, Great Britain (Figure 3.1) were identified using Ordnance Survey digital maps (EDINA Digimap Ordnance Survey Service 2014) and surveyed between May 19th and September 1st 2011. Urban areas were designated as those where urban cover was the dominant land use within a 1 km grid square as categorised by the Centre for Ecology and Hydrology Land Cover Map 2000. Sites were selected by size, longitude, and degree of urbanisation in the surrounding 1 km using a stratified random sampling method. Selected woodlands were a minimum of 50 years old, and were either broadleaved or consisted of a mixture of conifer and broadleaved trees. Sites were surveyed in random order through the field season to avoid any spatial or temporal bias.

3.3.2 Vegetation surveys

Vegetation surveys were conducted within a week of the bat survey to ensure that appropriate vegetative conditions were recorded. Four circular plots with radii of 20m were randomly located within each woodland patch. At each of the four plots, all trees were counted, identified to at least genus level, and tree basal area measured. Vegetation clutter was measured from 0 – 4 metres in height at 18 evenly spaced points within each plot to determine vertical forest structure; adopting a similar

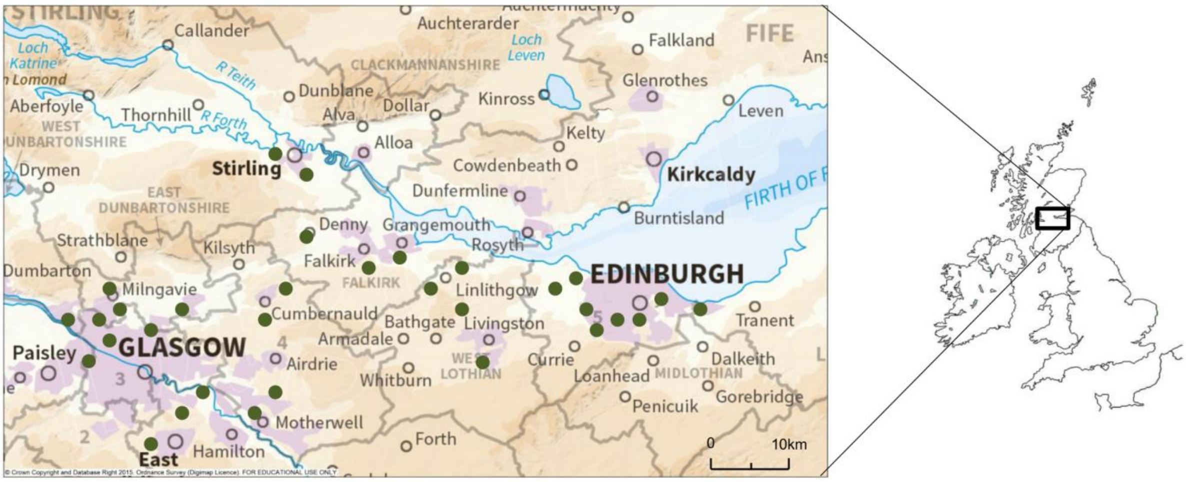


Figure 3.1 Map of central Scotland showing approximate locations of woodland sites (dark green dots) surveyed in 2011. Map produced using EDINA Digimap Ordnance Survey Service.

approach to Smith & Gehrt (2010), a four metre pole with sixteen 0.25 subsections marked upon it was placed at each point within the plot. Any foliage, branches, or stems touching a subsection was counted and summed to provide a measure of clutter (100% clutter occurred when foliage touched all points on the pole in each of the 18 points within the plot). Within each plot canopy cover (%) was assessed at 18 points in each plot using a sighting tube with an internal crosshair; if the crosshair intersected canopy vegetation, presence of canopy was recorded. Data for the four vegetation plots were combined to provide a description of each woodland patch. Additionally, the remaining woodland was visually assessed to ensure that the vegetation surveys were representative of the entire woodland patch.

3.3.3 Bat surveys

3.3.3.1 Woodland stand survey

Acoustic surveys were used to determine species presence and a measure of relative activity within each woodland patch. Acoustic surveys were undertaken to quantify foraging activity of bats; these are widely used in studies to determine species presence and habitat use for bats (e.g. Roche et al. 2011; Fuentes-Montemayor et al. 2014), and there is evidence that pipistrelle spp. activity correlates positively with density estimates within woodland (Lintott et al. 2014a; Chapter 2). Bat activity was quantified using a frequency division bat detector (Anabat SD1, Titley Electronics) fixed on a 1 m high pole with the microphone pointing upwards. The bat detector was placed within the centre of one of the four plots (see section 3.3.2) and rotated between plots every 30 minutes for four hours in total (the length of the shortest night in the study area). Plot locations were ≥ 20 m from the woodland edge, and ≥ 40 m from each other and positioned to avoid paths. All bat recordings were analysed using Analook W (Corben 2006). One bat pass was defined as at least two echolocation calls within one second of each other (Fenton 1970; Walsh & Harris 1996). Both *P. pipistrellus* and *P. pygmaeus* can be determined by the characteristic frequency (Fc = the frequency at the right hand end of the flattest portion of a call; Corben 2006) of their search-phase echolocation calls (following Russ 1999). Bat passes with a Fc of between 49 and 51 kHz were classed as unknown *Pipistrellus* species.

3.3.3.2 Urban matrix survey

Acoustic recording point counts (8 minute duration) were conducted at different locations within and around each woodland patch using a frequency division bat detector (Anabat SD2, Titley Electronics) to compare differences in *P. pipistrellus* and *P. pygmaeus* activity at the woodland interior, edge, surrounding green space, and grey space. Grey space was categorised as land that is sealed, impermeable ‘hard’ surfaces such as tarmac or concrete (e.g. car parks, urban housing), whilst unsealed, permeable ‘soft’ surfaces such as soil and grass were classed as non-wooded green space (e.g. parkland, amenity grassland; following James et al. 2009). Three point counts were conducted within each habitat (a total of 12 point counts per night). These were conducted simultaneously to the woodland stand survey (Section 3.3.3.1) and recordings were analysed in the same manner.

3.3.4 Landscape analysis

Bat detector locations were plotted using ArcGIS 10 (ESRI Inc 2014) and the centre point of the four plots within each site determined. Buffers of 250 m, 500 m, 1000 m, 1500 m, 2000 m, 2500 m and 3000m radius were created around the central point. I selected these different scales because the smallest represents site-specific characteristics, the intermediate scales have previously been found to be important predictors of pipistrelle spp. activity within human-disturbed landscapes (Fuentes-Montemayor et al. 2011), and the largest scale reflects the upper limit of home range size for *P. pygmaeus* and *P. pipistrellus* (Nicholls & Racey 2006). Data from the OS MasterMap Topography Layer (EDINA Digimap Ordnance Survey Service 2014) was used to reclassify the landscape within each buffer into a set of discrete biotope types. These were (i) grey space (buildings, structures, roads, and paths); (ii) green space (gardens, parkland, managed grassland, rough grassland, and farmland); (iii) inland fresh water and (iv) woodland (coniferous, deciduous and mixed woodland). Woodland Euclidean nearest neighbour distance (ENN, the mean value of ENN distances between all woodland patches within the landscape) and the Shannon diversity index (SHDI, a measure of landscape heterogeneity) were calculated as previous studies have found these variables to influence bat foraging activity (Fuentes-Montemayor et al. 2013). The proportion of land covered by each biotope, woodland ENN, and SHDI were calculated for each buffer scale using Fragstats v4.0 (McGarigal et al. 2002).

3.3.5 Data analysis

Statistical analyses were undertaken using R version 2.14 (R Core Team 2012) using the lme4 (Bates et al. 2013) and effects package (Fox 2003).

3.3.5.1 Woodland stand survey

I performed a Generalised Linear Mixed-Effects model (GLMMs; Zuur et al. 2009) with binomial error distribution and a logit link to quantify the influence of woodland characteristics and landscape metrics on *P. pipistrellus* and *P. pygmaeus* activity. In order to assess the relative effects of these variables on *P. pygmaeus* in comparison to *P. pipistrellus*, the model was run with the proportion of *P. pygmaeus* to *P. pipistrellus* passes per plot (n=124) as the response variable, with ‘site’ (woodland) included as a random (grouping) factor (n= 31) to account for pseudoreplication of multiple recordings per site (Zuur et al. 2009; Pinheiro & Bates 2000). Based upon the scientific literature on the ecology of woodland bats (e.g. Fuentes-Montemayor et al. 2013) the following predictor variables were included in the model: (i) woodland vegetation characteristics: tree species richness, average tree basal area, woodland clutter and woodland canopy cover (covariates) and woodland type as a fixed factor; (ii) patch configuration: woodland size, woodland shape (covariates), and the interaction between size and shape. Woodland shape is the perimeter divided by the minimum perimeter possible for a maximally compact patch of the same area. This equals 1 when the patch is maximally compact and increases as shape becomes irregular (McGarigal et al. 2002); (iii) landscape metrics (covariates). Temperature and date were also included in all models as covariates. Given the high collinearity found among landscape metrics (i.e. between the proportions of different biotope types or the same biotope type at a variety of spatial scales) preliminary analyses were conducted to determine which landscape metrics should be included in the model. I used GLMMs to assess how the proportion of *P. pygmaeus* to *P. pipistrellus* passes per plot with single landscape parameters (at each spatial scale) as a preliminary assessment of which key landscape predictors should be included in the final model (i.e. highest R^2 value). If several landscape parameters were of equal importance (i.e. <5% difference between the highest R^2 value) they were all selected, providing they were not strongly correlated.

I present the result of the full model including standardised parameters and confidence intervals for all explanatory variables. Inferences on the effect of each parameter were made by (i) comparing its standardized estimate with other predictor variables to determine relative importance, (ii) the upper and lower 95% quantiles of each parameter distribution obtained from N=2000 simulated draws from the estimated distribution (Gelman & Hill 2007), and (iii) a comparison of models excluding each parameter in turn using Likelihood Ratio Tests (LRTs) (Faraway 2005). LRTs of main effect parameters also involved in interactions were performed by comparing a model excluding the main effect term to a model including all main effects (but not interactions) only. Prediction plots were constructed by undertaking simulated draws (n = 2000) from the estimated distribution of one explanatory variable whilst maintaining all other parameters in the model at their median observed values.

3.3.5.2 Urban matrix survey

Generalised Linear Mixed-effects Models with a binomial distribution were conducted to assess differences in bat activity between habitats within the urban matrix (n=93 per habitat); woodland interior, woodland edge, urban green space, and urban grey space. The probability of recording *P. pygmaeus* (relative to recording *P. pipistrellus*) within each point count location was included as the response variable. Habitat (e.g. woodland interior) was included in the model as a fixed factor, whereas 'site' was used as a random factor (to account for pseudoreplication within sites). Date and temperature were included as covariates.

3.4 Results

3.4.1 Woodland stand survey

I recorded a total of 2,364 bat passes during a total of 124 hours of surveys. Bats were recorded within all but one of the 31 woodlands surveyed. I recorded a total of 1,584 *P. pygmaeus* passes (67% of all bat passes) in 28 of the woodlands, and 642 (27%) *P. pipistrellus* passes in 23 woodlands. A further 68 pipistrelle passes were recorded however these could not be classified to species level. Additionally, I recorded 69 *Myotis* spp. bat passes within seven woodlands and one *P. nathusii* pass. Both of these taxa were found in an insufficient number of sites for robust statistical analysis and were therefore excluded from further analysis.

In the results described below it should be noted that significant variables derived from the bat GLMMs indicate a differential response between the species to site or landscape characteristics; variables which are similarly influential for both species will not therefore be statistically significant in these models. Preliminary landscape analysis identified the proportion of grey space in the surrounding 3 km as the key landscape predictor (i.e. highest R^2 value; Figure 3.2) which was then incorporated into the final model.

The importance of woodland vegetation characteristics and the surrounding landscape differed between *P. pygmaeus* and *P. pipistrellus* (Table 3.2). The proportion of grey space in the surrounding 3 km had the largest effect size and a negative influence on the probability of recording *P. pygmaeus* relative to *P. pipistrellus.* Based on the estimated coefficients in Table 3.2, the predicted probability of recording *P. pygmaeus* was 0.93 (0.91-0.95) in woodlands surrounded by only a low proportion (10%) of grey space, whilst there was an equal probability of recording either *P. pygmaeus* or *P. pipistrellus* in woodlands surrounded by moderate levels of grey space (30%; Figure 3.3A). In woodlands surrounded by high levels of grey space (45%), the predicted probability of recording *P. pygmaeus* relative to *P. pipistrellus* was 0.17 (0.12 – 0.25). Woodland clutter had the largest effect size of the vegetation characteristics I assessed. There was a high probability of recording *P. pygmaeus* in woodlands with low (10%) clutter (0.86; 0.82-0.89), whilst in densely cluttered woodlands (40%) the probability of recording *P. pygmaeus* relative to recording *P. pipistrellus* fell to 0.37 (0.26-0.50; Figure 3.3B). Similarly, the probability of recording *P. pygmaeus* in woodlands with low understory cover (20%) was 0.89 (0.85-0.92), whilst in woodlands with continuous understory cover (100%) there was a similar probability of recording either *P. pygmaeus* (0.55; 0.49-0.61) or *P. pipistrellus* (0.45; 0.39–0.51; Figure 3.3C). Additionally the probability of *P. pygmaeus* decreased in woodlands with a high average tree basal area, however the effect size was relatively small (Table 3.2).

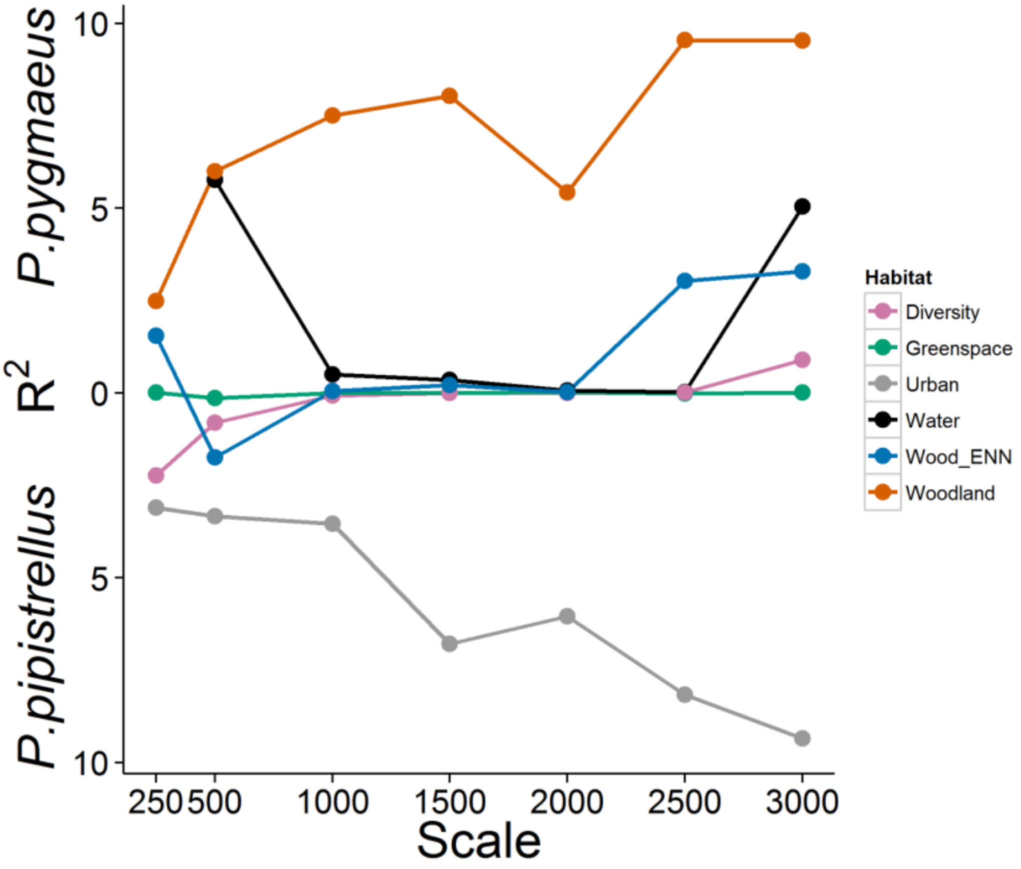


Figure 3.2 R^2 values obtained from GLMM models with binomial error distribution comparing the percentage of landscape covered by each biotype type at a variety of spatial scales to the probability of recording *P. pygmaeus* relative to *P. pipistrellus* in fragmented urban woodland. The position of the R^2 values along the y-axis reflect the direction of the parameter estimates; hence R^2 values in the upper half of the graph refer to a landscape metric that is associated with an increased probability of detecting *P. pygmaeus,* whilst R^2 values in the lower half of the graph refer to a landscape metric that is associated with an increased probability of detecting *P. pipistrellus*.

Table 3.2 Parameter estimates and likelihood ratio tests of the GLMM for the relative proportion of *P. pygmaeus* passes to *P.pipistrellus* passes in urban woodland. The model was run to calculate the probability of recording a *P. pygmaeus* pass relative to *P.pipistrellus*; hence positive estimates indicate an increased probability of detecting *P. pygmaeus* and negative estimates indicate an increased probability of detecting *P. pipistrellus* with a given explanatory variable. Test statistics were derived from the deletion of each term from the full model (for the 2-way interaction) and from the model with main effects only (main effect terms).

Fixed effects	**Estimate (± SE)**	**Log Likelihood**	**χ2**	**df**	***p***
Intercept	1.53 ± 0.57				
Date	-0.35 ± 0.44	-165.99	0.58	1	0.45
Temperature	0.28 ± 0.46	-165.87	0.35	1	0.56
Tree basal area	-0.26 ± 0.09	-170.86	10.3	1	0.001**
Tree species richness	0.02 ± 0.14	-165.71	0.02	1	0.90
Proportion grey space (3km)	-1.05 ± 0.41	-168.71	6.01		0.01*
Woodland canopy cover	-0.13 ± 0.14	-166.15	0.90	1	0.34
Woodland clutter	-0.73 ± 0.16	-176.11	20.8	1	<0.001***
Woodland shape	-0.63 ± 0.45	-166.62	1.84	1	0.17
Woodland size	0.07 ± 0.43	-165.71	0.03	1	0.85
Woodland type	-0.92 ± 0.86	-166.29	1.18	1	0.28
Woodland understory	-0.69 ± 0.14	-178.74	26.1		<0.001***
Shape * Size	0.11 ± 0.75	-166.82	2.28	2	0.52

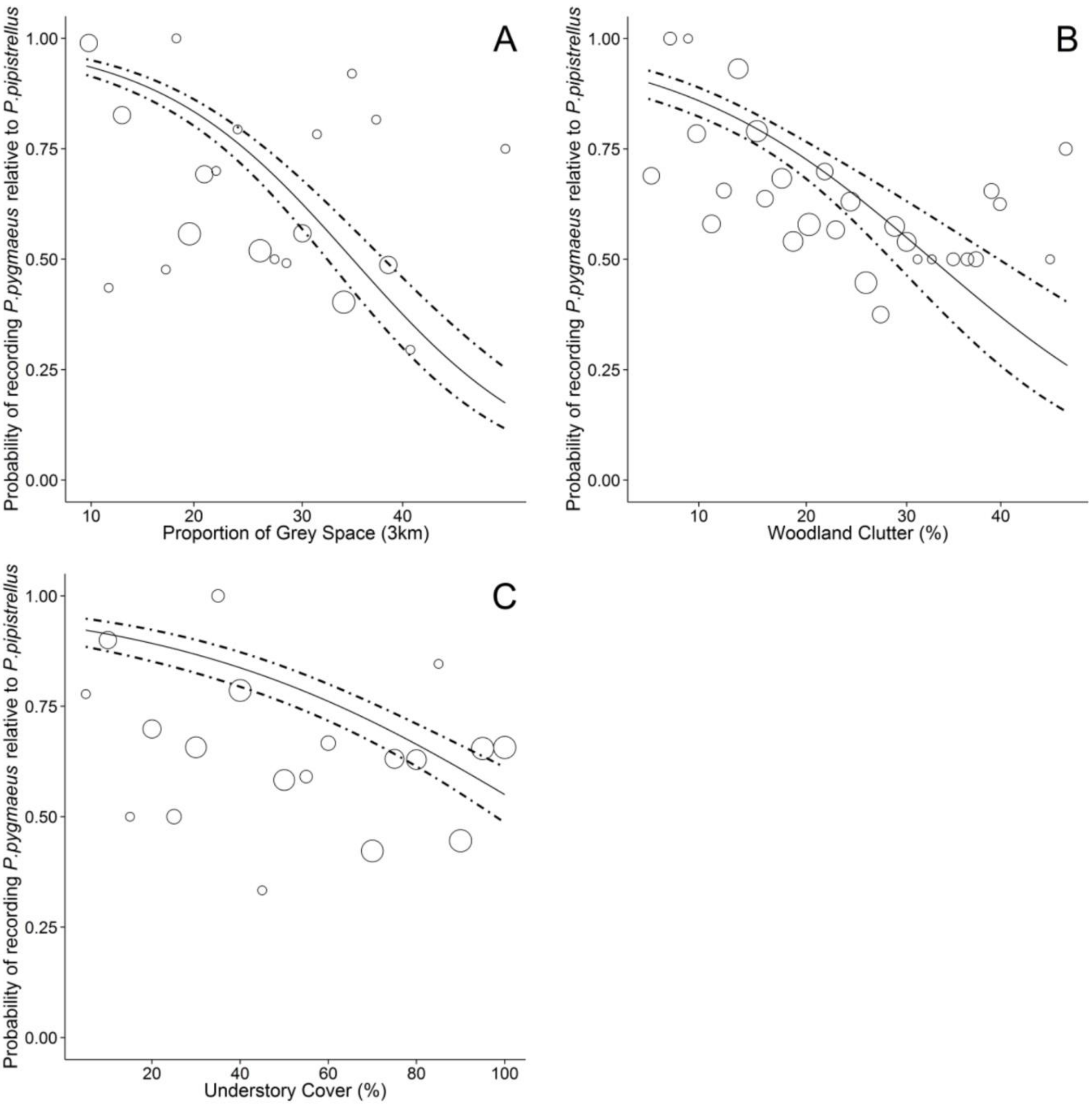


Figure 3.3 Estimated probability of recording *P. pygmaeus* relative to *P. pipistrellus* in fragmented urban woodland. Dashed lines indicate 95% confidence intervals. Original data on the proportion of *P. pygmaeus* passes are superimposed as grey circles with diameter proportion to the total number of *P. pygmaeus* passes recorded.

3.4.2 Urban matrix survey

I recorded a total of 260 *P. pipistrellus* passes and 701 *P. pygmaeus* passes within the four habitat types. The probability of recording *P. pygmaeus* relative to recording *P. pipistrellus* was significantly associated with habitat type (χ^2=20.57, df=3, p<0.001), and was substantially higher in woodland (interior and edge) than the surrounding urban matrix (Figure 3.4). There was no substantial difference in the probability of recording *P. pygmaeus* (relative to *P. pipistrellus*) between urban green space and non-wooded grey space (Figure 3.4).

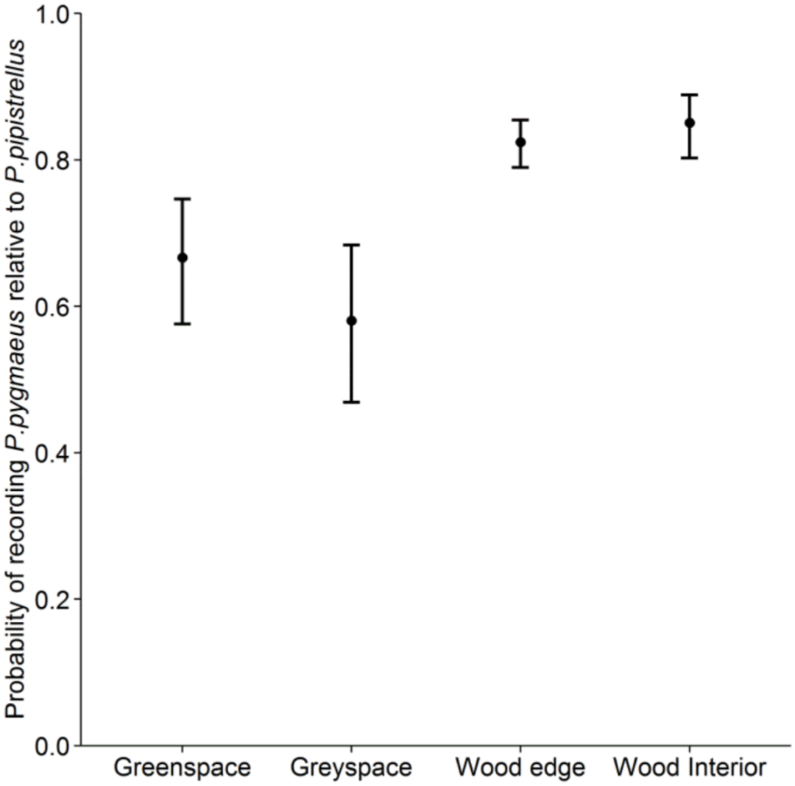


Figure 3.4 Boxplot showing the estimated probability of recording *P. pygmaeus* relative to recording *P. pipistrellus* in the urban matrix. The upper and lower whiskers show 95% confidence limits. Fitted values by GLMMs are used. Woodland interiors

were relatively open and contained low levels of woodland clutter within the urban matrix survey.

3.5 Discussion

Determining the ecological and behavioural mechanisms driving habitat use within the urban matrix is the key to understanding the adaptability of species to urbanisation. In this study I show that even two morphologically similar species can have widely differing responses to fragmented urban woodland and the surrounding urban matrix.

3.5.1 The response of *P. pipistrellus* and *P. pygmaeus* to urban woodland vegetation character and patch configuration

Although habitat partitioning between *P. pipistrellus* and *P. pygmaeus* is known from radio tracking studies (e.g. Nicholls & Racey 2006), these studies have involved relatively small sample sizes and were conducted in non-urban habitats. Whilst previous studies have indicated that habitat partitioning between the two species occurs between habitat types (e.g. Davidson-Watts & Jones 2006), here I show that similar behaviour occurs within habitat types, at a fine spatial scale.

Our results indicate that *P. pygmaeus* appear to be using woodlands with low clutter and understory growth relatively more intensely than *P. pipistrellus,* despite both species having similar wing shapes and echolocation calls which make them well adapted to foraging along woodland edges and relatively open habitats (Kalko & Schnitzler 1993). These findings support Davidson-Watts & Jones (2006) who found that *P. pygmaeus* spend less time flying, make fewer foraging bouts but travel greater distances, suggesting that this species has more selective foraging habitats.

Conversely, *P. pipistrellus* is commonly regarded as a generalist forager (Davidson-Watts & Jones 2006; Russ & Montgomery 2002), and therefore would be expected to be found in a wider range of habitat types. Although it is surprising that *P. pipistrellus* are not also using less cluttered habitats, Nicholls and Racey (2006) suggested that *P. pipistrellus* actively avoid *P. pygmaeus* foraging sites (but see Barlow & Jones 1997). Coexisting species must differ in at least one niche dimension to avoid excessive competition such as using different foraging locations (Li et al. 2014). It is therefore possible that the use of woodlands with high clutter and understory by *P. pipistrellus* may reflect the wider, non-selective, use of woodland habitats within the urban matrix to avoid competition. In contrast, *P. pygmaeus* may be preferentially selecting those woodlands which offer optimal foraging locations. *Pipistrellus* species are known to also forage above the canopy of closed mature woodland stands (Müller et al. 2013) which although not recorded in this study, may provide additional or alternative foraging resources for either or both *Pipistrellus* species. Differences in habitat use may also reflect that the diets of the two species differ as *P. pipistrellus* feed mostly on insects that occur in a wide range of habitats, whereas *P. pygmaeus* feed mainly on insects in riparian woodland (Barlow 1997). Assessing which woodland characteristics determine prey availability may also help explain differential habitat use.

3.5.2 The response of *P. pipistrellus* and *P. pygmaeus* to the composition, spatial configuration, and heterogeneity of the surrounding landscape

Regardless of the spatial scale surrounding the woodland (250 m to 3 km) I found that the probability of recording *P. pygmaeus* relative to *P. pipistrellus* was greater when the landscape contained a high proportion of woodland and a low proportion of urban grey space. This supports previous studies identifying *P. pipistrellus* as a generalist species (Nicholls & Racey 2006; Vaughan et al. 1997) which can tolerate moderate levels of urbanisation (Hale et al. 2012). Similarly, the proportion of grey space in the surrounding 3 km was the strongest predictor of which of the two species would be recorded. The underlying cause as to why *P. pipistrellus* is better able to adapt to the urban landscape is unknown although the lower frequency of its echolocation call may aid adaptability to cities as species with lower calls are better able to use open habitats and access a wider spectrum of habitats (Threlfall et al. 2012). Alternatively, *P. pipistrellus* may have the greater behavioural capacity to adapt to exploit the urban landscape, for example using buildings and planted tree lines as paths for courtship flights and territory boundaries (Sachteleben & von Helversen 2006). It is surprising given the strong association between *P. pygmaeus* habitat preferences and waterbodies (Russ & Montgomery 2002) that the composition of water in the landscape was not a significant predictor of differences in habitat use between the two species. However, urban waterways are frequently used by both species (Lintott et al. 2015a; chapter 6) and it is likely that the continuous nature of urban waterways is facilitating the movement of both species through the urban matrix. Additionally, in contrast to alternative biotope types (e.g. green space or grey space) there was relatively little variability among sites in the composition of freshwater in the surrounding landscape (Appendix 3.8.1), which may have masked any differing habitat use as consequence of freshwater.

3.5.3 Differences between *P. pipistrellus* and *P. pygmaeus* in habitat selection within the urban matrix

The higher adaptability to the built landscape by *P. pipistrellus* relative to *P. pygmaeus* is further supported by the extent to which this species was recorded in a variety of habitat types contained within the urban matrix. In contrast, *P. pygmaeus,* relative to *P. pipistrellus,* predominantly used woodland edge and interior habitats; foraging locations that both species are well adapted for. This strengthens Nicholls and Racey's (2006) findings that *P. pipistrellus* appear to actively avoid *P. pygmaeus* foraging sites resulting in differential habitat use. Within the urban matrix, this may transpire as *P. pipistrellus* appearing to using a wider range of habitats, thereby giving the impression that it is a generalist. Similarly *P. pipistrellus* may be commuting further to use those woodlands which offer suitable foraging resources but are surrounded by sufficient grey space to deter *P. pygmaeus*.

3.5.4 Conservation implications

Understanding how species respond to urbanisation is critical in identifying priority species which may require conservation effort. Categorising species as either 'urban avoiders', 'urban utilizers' or 'urban dwellers' appears a convenient way of achieving this (Fischer et al. 2015). Bats are often categorised in this manner based upon their morphological traits (e.g. Threlfall et al. 2012; Jung & Kalko 2011), however our results show that habitat use differs between species which are morphologically very similar (Barlow et al. 1997; Häussler et al. 1999) suggesting that such differences may be a weak indication of ecological differences between taxa (Nicholls & Racey 2006; Davidson-Watts et al. 2006). Similarly, using species presence as an indication of adaptability to the built landscape should be treated cautiously prior to assessing if adaptability to urbanisation is sex-dependent (Lintott et al. 2014b; Chapter 4), or if species in urban landscapes largely consist of sink populations. If *P. pipistrellus* are using the urban ecosystem as a means of avoiding competition with *P. pygmaeus* it may be that they are not so much exploiting the urban landscape but using it out of necessity.

3.6 Conclusions

The complexity of understanding species-specific responses to urbanisation makes identifying priority species for conservation action difficult. Here, I show that attempts to use morphological traits as a means of categorising species into the likelihood of them adapting to urban locations are problematic, as even two sympatric and cryptic species can respond differently. *P. pygmaeus* appear to be using less cluttered woodlands whilst *P. pipistrellus* appear to be adapting a generalist foraging behaviour using, often cluttered, woodlands surrounded by relatively high levels of urban grey space; this may be a result of differential habitat use to avoid competition.

3.7 Acknowledgements

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3.8 Appendix

Appendix 3.8.1 The composition of the landscape surrounding the 31 urban woodlands surveyed throughout central Scotland in 2011.

Scale (m)	% of habitat type within landscape (Mean ± SD)			
	Woodland	Greenspace	Grey space	Freshwater
250	26 ± 16	47 ± 14	24 ± 12	1 ± 1
500	14 ± 9	51 ± 11	29 ± 9	1 ± 1
1000	10 ± 6	50 ± 8	30 ± 8	1 ± 1
1500	10 ± 5	48 ± 7	30 ± 8	1 ± 1
2000	10 ± 5	45 ± 8	29 ± 8	1 ± 1
2500	10 ± 4	45 ± 8	27 ± 8	1 ± 1
3000	10 ± 4	45 ± 9	26 ± 9	1 ± 1

Chapter 4

City life makes females fussy: sex differences in habitat use of temperate bats in urban areas

This chapter has been published as:

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4.1 Summary

Urbanization is a major driver of the global loss of biodiversity; to mitigate its adverse effects, it is essential to understand what drives species' patterns of habitat use within the urban matrix. While many animal species are known to exhibit sex differences in habitat use, adaptability to the urban landscape is commonly examined at the species level, without consideration of intraspecific differences. The high energetic demands of pregnancy and lactation in female mammals can lead to sexual differences in habitat use, but little is known of how this might affect their response to urbanization. I predicted that female *Pipistrellus pygmaeus* would show greater selectivity of forging locations within urban woodland in comparison to males at both a local and landscape scale. In line with these predictions, I found there was a lower probability of finding females within woodlands that were poorly connected, highly cluttered, with a higher edge: interior ratio and fewer mature trees. By contrast, habitat quality and the composition of the surrounding landscape were less of a limiting factor in determining male distributions. These results indicate strong sexual differences in the habitat use of fragmented urban woodland, and this has important implications for our understanding of the adaptability of bats, and mammals more generally, to urbanization.

4.2 Introduction

Urbanization is driving the fragmentation of landscapes at an unprecedented rate and is therefore a significant contributing factor to the current biodiversity crisis (Grimm et al. 2008). Understanding patterns of habitat use and its drivers within the urban matrix is crucial to minimize urbanisations adverse effect on biodiversity (Aronson et al. 2014) taking into account the impact of urbanization at a variety of spatial scales (Goddard et al. 2010). While many studies of urban biodiversity have focused on species-level responses, there has been relatively little consideration of the potential importance of intraspecific differences.

Sexual differences in animal behaviour and habitat use is taxonomically widespread and one of the most commonly studied concepts in biology, identified and investigated as far back as Darwin (1871). Habitat segregation between sexes can occur because of differences in antipredation behaviour during the breeding period (e.g. Eurasian wild sheep; Singh et al. 2010), differences in social motivation to interact that may lead to behavioural incompatibility (e.g. *Cervus elaphus* (red deer); Alves et al. 2013), physiological differences (e.g. pelagic shark; Sims 2005), or to decrease intraspecific resource competition (e.g. *Phocarctos hookeri* (New Zealand sea lion); Leung et al. 2012). These behaviours often result in segregation between distinct habitat types; however, we have relatively little information about whether similar patterns occur within urban landscapes.

There are few other orders of animals that are as strongly associated with people as bats. Human habitations provide roosts, while adaptations of the environment supply food sources, such as insects at artificial light sources (Fenton 2003a). However, while many species have adapted to exploit the urban landscape, the general pattern is of declining bat activity and bat species richness with increasing levels of urbanization (Gaisler et al. 1998; Lane et al. 2006).

The species diversity, variety of social systems and tendency among some species to segregate during the maternity season make bats an ideal taxon for studying sex differences in habitat use; however, relatively little attention has been paid to this subject (Altringham & Senior 2005). Sexual segregation may occur within the roost (Altringham & Senior 2005), while foraging (Levin et al. 2013), and during migration (Fleming & Eby 2003). The energetic demands of pregnancy and lactation can limit females to foraging only within the highest quality habitats; thereby excluding them from marginal upland habitat (Senior et al. 2005) and arable land (Mackie & Racey 2007). Conversely, habitat quality is less of a limiting factor for males and non-breeding females as they have lower energy demands and are able to use torpor more frequently during the summer to maximize energy savings (Altringham & Senior 2005). Woodland is widely regarded as a primary habitat for bats (Lacki et al. 2007), however, within the urban matrix it is of variable quality, subject to invasive species encroachment and often consists of small, fragmented patches (Alvey 2006). Consequently, the vegetation characteristics of urban woodland influence bat species presence and community composition (Smith & Gehrt 2010). Differences in habitat requirements between males and females may further limit the distribution of a species within the urban matrix but there is little known about the potential for sexual differences as most studies of bats in urban environments are conducted using acoustic detectors that are unable to distinguish between sexes.

I hypothesize that at the local scale, the variable quality of urban woodland may limit females as they are frequently restricted to foraging within high-quality habitats. Additionally, the necessity of females to commute between foraging and roosting locations owing to the demands of lactation will make the composition, spatial configuration and heterogeneity of the landscape surrounding woodland relatively more important for females than males. Thus, I predict that female *Pipistrellus pygmaeus* will show greater selectivity of foraging locations within fragmented urban woodland in comparison to males, and that this difference will be expressed at both a local and landscape level.

In this paper, I therefore use 128 h of trapping data to test whether male and female *P. pygmaeus* differ in their use of fragmented urban woodland. Although *P. pygmaeus* is relatively widespread across Europe it is thought to have experienced historic population declines (Stebbings 1988 but see Barlow et al. 2015), and is negatively impacted upon by urbanisation (Lintott et al. 2015; chapter 3). Rather than examining broad-scale differences in use between urban and non-urban habitat, I am testing how differences in habitat characteristics at a fine spatial scale, and the composition of the surrounding matrix, may lead to sex differences in habitat use within the urban landscape.

4.3 Material and methods

4.3.1 Study sites

I identified 32 urban woodland study sites in central Scotland (appendix 4.7.1) using Ordnance Survey digital maps (EDINA 2014), which I surveyed between 19 May 2011 and 1 September 2011. Urban areas were designated as those where urban cover was the dominant land use within a 1 km grid square (i.e. the proportion of the grid square containing urban grey space was greater than all alternative habitat types) as categorized by the Centre for Ecology and Hydrology Land Cover Map 2000 (LCM2000). Sites were selected by size, longitude and degree of urbanization in the surrounding 1km using a stratified random sampling method. Selected woodlands were a minimum of 50 years old and were either broadleaved or consisted of a mixture of conifer and broadleaved trees. I surveyed sites in random order through the field season to avoid any spatial or temporal bias.

4.3.2 Vegetation surveys

I conducted vegetation surveys within a week of the bat survey to ensure that appropriate vegetative conditions were recorded. Four circular plots with radii of 20mwere randomly located within each woodland patch. At each of the four plots, all trees were counted, identified to at least genus level and tree basal area measured. Vegetation clutter was measured from 0 to 4m in height at 18 evenly spaced points within each plot to determine vertical forest structure; adopting a similar approach to Smith & Gehrt (2010), a 4m pole with sixteen 0.25 subsections marked upon it was placed at each point within the plot. Any foliage, branches or stems touching a subsection was counted and summed to provide a measure of clutter (100% clutter occurred when foliage touched all points on the pole at every point within the plot). Within each plot, canopy cover (%) was assessed at 18 points in each plot using a sighting tube with an internal crosshair; if the crosshair intersected canopy vegetation, presence of canopy was recorded (Jennings et al. 1999). Data for the four vegetation plots were combined to provide a description of each woodland patch. Additionally, I visually assessed the remaining woodland to ensure that the vegetation surveys were representative of the entire woodland patch.

4.3.3 Bat surveys

I used one Austbat harp trap (2.4 × 1.8m) and three Ecotone mist nets (2.4 × 6m each) within each woodland to provide an estimate of the relative abundance of male and female *P. pygmaeus*. A trap was placed in each of the plots that had previously been surveyed for vegetation. An acoustic lure was used to increase trapping rate (as described by Lintott et al. 2014a; Chapter 2). I commenced trapping 30 min after sunset to avoid the peak emergence and commuting time for *P. pygmaeus*. Traps were checked every 15 min to extract any captured bats, which were then identified to species, aged, sexed, measured, weighed and marked temporarily by fur clipping. Breeding females were identified by either signs of pregnancy or nipples that showed the expected characteristics of previous suckling (following Racey 1974).

4.3.4 Landscape analysis

I plotted bat trap locations using ARCGIS 10 (ESRI Inc 2013) and determined the centre point of the four traps within each site. Buffers of 250, 500, 1000, 1500 and 2000m radius were created around the central point reflecting the upper limit of home range size for *P. pygmaeus* (Nicholls & Racey 2006). Data from the OS MasterMap Topography Layer (EDINA 2014) were used to reclassify the landscape within each buffer into a set of discrete biotope types. These were: (i) grey space (buildings, structures, roads and paths); (ii) green space (gardens, parkland, managed grassland, rough grassland and farmland); (iii) inland fresh water; and (iv) woodland (coniferous, deciduous and mixed woodland). Woodland Euclidean nearest neighbour distance (ENN, the mean value of ENN distances among all woodland patches within the landscape) and the Shannon diversity index (SHDI, a measure of landscape heterogeneity) were calculated as previous studies have found these landscape variables to be important (Fuentes-Montemayor et al. 2013). The proportion of land covered by each biotope, woodland ENN and SHDI were calculated for each buffer scale using FRAGSTATS v. 4.0 (McGarigal et al. 2002).

4.3.5 Data analysis

I undertook statistical analyses using R v. 2.14 (R Core Team 2012) using the lme4 (Bates et al. 2012) and effects package (Fox 2003). I performed a general linear mixed-effects model (GLMMs) with binomial error distribution and a logit link to quantify the influence of woodland characteristics and landscape metrics on male and female abundance. In order to assess the relative effects of these variables on males in comparison to females, the model was run with the proportion of females to males per trap (n=128) as the response variable, with 'site' included as a random (grouping) factor. Based upon the scientific literature on the ecology of woodland bats (Fuentes-Montemayor et al. 2013) the following predictor variables were included in the model: (i) woodland vegetation characteristics: tree species richness, average tree basal area, woodland clutter and woodland canopy cover (covariates) and woodland type as a fixed factor; (ii) patch configuration: woodland size, woodland shape (covariates) and the interaction between size and shape. Woodland shape is the perimeter divided by the minimum perimeter possible for a maximally compact patch of the same area. This equals 1 when the patch is maximally compact and increases as shape becomes irregular (McGarigal et al. 2002); and (iii) landscape metrics (covariates). Temperature and date were also included in all models as covariates. I assessed landscape metrics for issues of multicollinearity, and used GLMMs for abundance with single landscape parameters (at each spatial scale) as a preliminary assessment of which key landscape predictors should be included in the final model.

All resulting predictor variables were tested for collinearity, however, none was considered to be strongly correlated based upon a Pearson correlation coefficient of greater than or equal to 0.6 and $p \leq 0.05$. Continuous predictor variables were centred and standardized following Schielzeth (2010) to allow direct comparison of the size of estimated coefficients. I present the result of the full model including standardized parameters and confidence intervals for all explanatory variables. Inferences on the effect of each parameter were made by: (i) comparing its standardized estimate with other predictor variables to determine relative importance; (ii) the upper and lower 95% quantiles of each parameter distribution obtained from n=2000 simulated draws from the estimated distribution (Gelman & Hill 2007); and (iii) a comparison of models excluding each parameter in turn using likelihood ratio tests (LRTs; Faraway 2005). LRTs of main effect parameters also involved in interactions were performed by comparing the model excluding the main effect term to the model including all main effects (but not interactions) only. Prediction plots were constructed by undertaking simulated draws (n=2000) from the estimated distribution of one explanatory variable while maintaining all other parameters in the model at their mean observed values.

4.4 Results

I captured 162 *P. pygmaeus* within 27 of the 32 woodlands. The sample population comprised 67 adult males (41%) within 25 woodlands and 55 adult females (34%), 52 of which were classified as breeding females, within 19 woodlands. I caught the first juvenile on 10 July and from this date onwards, 40 juveniles (25%) were captured in 12 of the 23 woodlands surveyed. Juveniles were found in an insufficient number of sites and for only a relatively short period of the season and were therefore excluded from further analysis.

The importance of woodland vegetation characteristics, patch configuration and the surrounding landscape differed between the sexes (Table 4.1). Woodland isolation (ENN) in the surrounding 1km had the largest effect size and a negative influence on the probability of capturing a female. Based on the estimated coefficients in table 4.1, the predicted probability of capturing a female was 0.03 (0.002–0.36) in isolated woodland, 0.24 (0.14–0.39) in moderately connected woodland, while there was little difference in the probability of finding either males (0.52; 0.28–0.75) or females (0.48; 0.25–0.72) in well-connected woodland (Figure 4.1A). Similarly, while there was a similar likelihood of capturing either males (0.42; 0.22–0.64) or females (0.58; 0.36–0.78) in woodlands with low (5%) woodland clutter, females avoided highly cluttered locations; the probability of finding a female in woodland containing 45% clutter was 0.08 (0.02–0.32; Figure 4.1B). Woodland shape and average tree basal area were both marginally significant predictors of sex differences in habitat use. There were similar

Table 4.1 Parameter estimates and likelihood ratio tests of the General Linear Mixed-Effects Model for the relative proportion of the number of trapped female *P. pygmaeus* to males in urban woodland . The model was run to calculate the probability of finding a female relative to a male; hence positive estimates refer to an explanatory variable that relates to an increased probability of finding a female. The most important landscape parameters at the most important spatial scale for either sex were included in the model. Test statistics derived from the deletion of each term from the full model (for the 2-way interaction) and from the model with main effects only (main effect terms).

Fixed effects	**Estimate (± SE)**	**Log Likelihood**	**χ2**	**χ2 df**	***p***
Intercept	-0.58 ± 0.40				
Date	0.07 ± 0.30	-31.49	0.05	1	0.83
Temperature	0.14 ± 0.32	-31.54	0.16	1	0.69
Tree basal area	0.50 ± 0.31	-33.11	3.30	1	0.07^
Tree species richness	0.42 ± 0.28	-32.67	2.42	1	0.12
Woodland canopy cover	-0.39 ± 0.29	-32.35	1.78	1	0.18
Woodland clutter	-0.64 ± 0.26	-34.95	6.97	1	0.01**
Woodland shape	-0.50 ± 0.30	-32.97	3.02	1	0.08^
Woodland size	-0.13 ± 0.26	-31.57	0.21	1	0.65
Woodland type	-0.84 ± 0.67	-32.28	1.63	1	0.2
Water connectivity (1km)	-0.13 ± 0.22	-33.26	3.60	1	0.06
Woodland connectivity (1km)	-0.87 ± 0.44	-33.77	4.61	1	0.03*
Shape * Size	0.13 ± 0.44	-33.03	3.22	2	0.36

probabilities of capturing either females (0.42; 0.24–0.63) or males (0.58; 0.37–0.76) in compact woodland, however, this contrasted with average tree basal area were both marginally significant predictors of sex differences in habitat use. There were similar probabilities of capturing either females (0.42; 0.24–0.63) or males (0.58; 0.37–0.76) in compact woodland, however, this contrasted with complex woodland with a high edge to interior ratio where the probability of capturing a female was much lower at 0.14 (0.03–0.46). The probability of capturing a female increased in woodland with a high tree basal area. An increase in average tree basal area from 10 to 40 cm2 led to an increase in the probability of capturing a female from 0.39 (0.26–0.55) to 0.8 (0.24–0.98), while declining for males from 0.61 (0.45–0.74) to 0.2 (0.02–0.76). Additionally, the probability of capturing a female was increased in woodlands with well-connected urban waterways in the surrounding 1 km, however, the effect size was relatively small (Table 4.1).

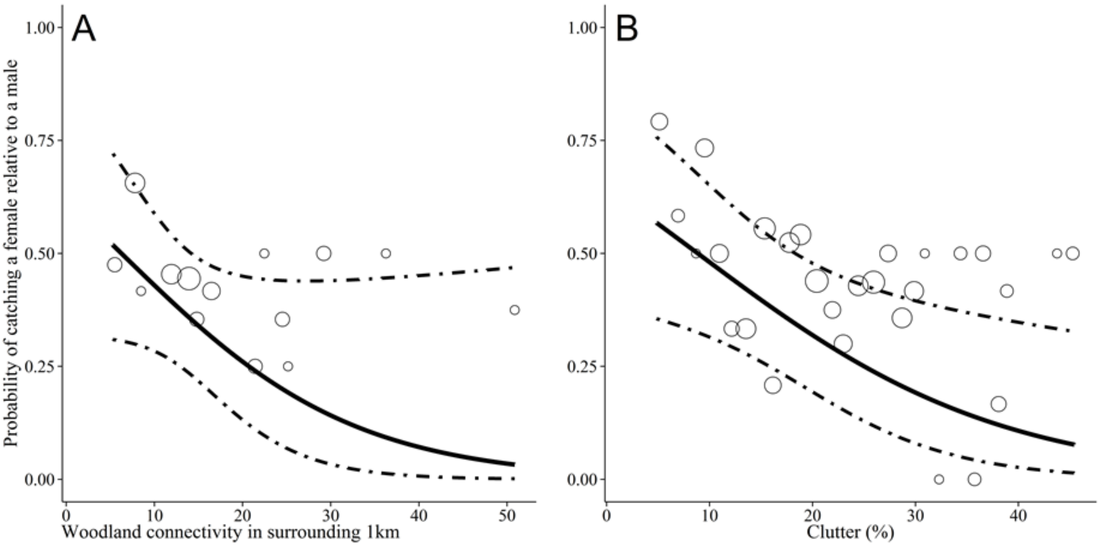

Figure 4.1 Estimated probability of finding a female relative to a male *P. pygmaeus* in fragmented urban woodland. Dashed lines indicate 95% confidence intervals. Original data on the proportion of females are superimposed as grey circles with diameter proportion to the total number of females. Woodland connectivity (a) is measured using the Euclidean nearest neighbour distance (ENN, the mean value of ENN distances between all woodland patches within the landscape). A landscape containing highly connected woodlands would have a low ENN value, while poorly connected woodlands would have a high ENN value.

4.5 Discussion

This study demonstrates the importance of habitat quality and connectivity to breeding female bats in the built-up landscape and has important implications for our understanding of the adaptability of this species to human disturbed landscapes. Lower abundance of *P. pygmaeus* females within poorly connected woodland patches of complex shapes with high clutter levels and small average tree basal areas suggests that differences in habitat use between the sexes occur not only at a broad, between-habitat scale (Senior et al. 2005) but also within habitats, at a fine spatial scale. Male and female *P. pygmaeus* demonstrated marked differences in their response to the character of fragmented urban woodland. The lack of selectivity exhibited by males suggests that they are able to use a wider range of conditions as they have lower energy demands than reproductive females (Barclay 1991). Females face higher energetic demands during pregnancy and lactation, and have a relatively shorter time period to accumulate sufficient fat for the following hibernation period (Levin et al. 2013). Additionally, reproductive females use torpor less frequently than males as it can reduce fetal growth rates (Racey & Entwistle 2000). Female response to the vegetation characteristics and patch configuration of urban woodland is therefore likely to reflect selective foraging in optimum habitats. The wing shape and echolocation call of *P. pygmaeus* makes it well adapted for foraging in open habitats (Kalko & Schnitzler 1993), which appears to be demonstrated in female preference for woodlands containing reduced woodland clutter. The association between female abundance and large average tree basal areas, a trait associated with mature woodlands and low levels of woodland clutter (Fuentes-Montemayor et al. 2012), may occur as woodlands containing larger trees can provide a larger number of microhabitats and therefore more foraging opportunities, a greater availability of night roosts (Evelyn et al. 2004), and reduced predation risk (Regnery et al. 2013). Higher female abundance within compact woodland suggests a preference for woodland patches which expose proportionally less edge to the surrounding urban matrix. Woodland edges in the urban matrix are often adjacent to habitats under high anthropogenic pressure and can often comprise only those tree species and invertebrate populations that are able to tolerate such conditions (Lehvävirta et al. 2006). It may be that the combination of anthropogenic disturbance (i.e. noise or light pollution) and reduced prey availability provide poorer foraging habitat for females in contrast to woodland interior.

The relative importance of the landscape surrounding urban woodland for females may reflect the differences in roosting strategies between the sexes. The importance of woodland connectivity for females is probably driven by the necessity of lactating females to return frequently to the roost. Radio tracking of lactating *P. pygmaeus* females shows that, on average, they return to their roost 3.7 times per night (Bartonicka et al. 2008). While the roost sites of females captured during this study are unknown, the use of well-connected woodlands will reduce the necessity to commute across the urban matrix. This will decrease the perceived predation risk of commuting across open habitats alongside reducing the extent of anthropogenic disturbances (e.g. noise and light pollution or the risk of vehicle collisions; Medinas et al. 2013; Threlfall et al. 2013). The daily energy expenditure of reproductive females can double by peak lactation (Kurta et al. 1989); making it imperative that foraging flights are of optimal efficiency. Conversely, males are not constrained by the requirement to return to a particular roost during the night, often roosting either alone or in small groups in separate roosts (Altringham & Senior 2005).

I found no evidence of spatially separated habitat use between sexes, as males were just as likely to be found in those habitats preferentially selected by females. However our results suggest that intramale segregation may be occurring; with males in poorer habitat potentially suffering reduced foraging efficiency which may have subsequent consequences for reproductive fitness or survival over winter (Speakman & Rowland 1999). The mechanism behind segregation is unknown, although suggestions from past studies have included females (and the males that share their roost) excluding other males from their home range (Altringham & Senior 2005) to differences in physiological and social needs (Levin et al. 2013). Here I show that habitat quality appears to be less of a limiting factor for males who appear to make wider use of the urban matrix (i.e. poorly connected woodland) and can tolerate higher anthropogenic pressure (i.e. complex woodlands with more pronounced edge effects), which may be driving sex differences in habitat use. Late summer and autumnal activities such as mating behaviour may change habitat use in both sexes given that there will be a stronger pressure for males to frequent similar localities as females, and that females will be less restricted in habitat choice by not having to return to a maternity roost. Although I accounted for date in our model, the extent to which the differential habitat selection between the sexes continues into the mating period is unknown and future research on this would be of value.

The vulnerability of bat species to human disturbed landscapes is often assessed through use of acoustic surveys (Jung & Kalko 2011), which allow researchers to quantify relative levels of bat activity among habitats. For example, in urban environments foraging activity of *P. pygmaeus* is higher within the woodland interior than along woodland edge habitat, urban grey space and non-wooded green space (Lintott et al. 2015b; Chapter 3). There is evidence, at least for some species (including *P. pygmaeus*), that foraging activity recorded via acoustic surveys can be used as a surrogate for abundance without the need to trap, which can be a costly and time-consuming process that requires expertise (Lintott et al. 2014a; Chapter 2). However, our results highlight the value of trapping data which enables differences in habitat selection between males and females to be assessed, something which is not possible using acoustic monitoring. Acoustic surveys using bat detectors may therefore distort our perception of how tolerant bats are to anthropogenic disturbance. While trapping is a more intensive and intrusive survey technique, and necessarily limited to smaller geographical regions, studies such as these are important in complementing large-scale, long-term acoustic monitoring (e.g. National Bat Monitoring Programme; Bat Conservation Trust 2013) in identifying key habitats for breeding females and how to optimize their management. As urbanization continues to contribute to the global loss of biodiversity it is imperative that monitoring strategies are optimized to ensure that a true understanding of the scale of loss is gained. This study shows that determining species presence may not be a satisfactory indicator of adaptability or tolerance to the urban matrix if there are sexual differences in habitat selection.

4.6 Acknowledgements

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4.7 Appendices

Appendix 4.7.1 Map of central Scotland showing approximate locations of woodland sites (black dots) surveyed in 2011.

Chapter 5

Moth species richness, abundance and diversity in fragmented urban woodlands: implications for conservation and management strategies

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5.1 Summary

Urban expansion threatens global biodiversity through the destruction of natural and semi-natural habitats and increased levels of disturbance. Whilst woodlands in urban areas may reduce the impact of urbanisation on biodiversity, they are often subject to under or over-management and consist of small, fragmented patches which may be isolated. Effective management strategies for urban woodland require an understanding of the ecology and habitat requirements of all relevant taxa. Yet, little is known of how invertebrate, and in particular moth, assemblages utilise urban woodland despite being commonly found within the urban landscape. Here I show that the abundance, species richness, and species diversity of moth assemblages found within urban woodlands are determined by woodland vegetation character, patch configuration and the surrounding landscape. In general, mature broadleaved woodlands supported the highest abundance and diversity of moths. Large compact woodlands with proportionally less edge exposed to the surrounding matrix were associated with higher moth abundance than small complex woodlands. Woodland vegetation characteristics were more important than the surrounding landscape, suggesting that management at a local scale to ensure provision of good quality habitat may be relatively more important for moth populations than improving habitat connectivity across the urban matrix. Our results show that the planting of broadleaved woodlands, retaining mature trees and minimising woodland fragmentation will be beneficial for moth assemblages.

5.2 Introduction

Urban expansion threatens global biodiversity through the destruction of natural and semi-natural habitats and increased levels of disturbance (Grimm et al. 2008). Projections for 2030 estimate that urban land cover will have tripled compared to 2000 (Seto et al. 2012), so understanding how urbanisation affects different taxa, and what actions may reduce detrimental effects, is essential for biodiversity conservation.

Urban areas are one of the most dramatic forms of habitat conversions (McKinney 2006). However, green spaces within urban areas can be important for mitigating the impacts of urbanisation on biodiversity, and can hold relatively rich wildlife communities. Woodlands are the most important semi-natural habitat within European urban landscapes and have the capacity to accommodate a large number of species (Croci et al. 2008). For instance, bird species richness is often higher in urban compared to rural woodland due to greater food resources and more favourable microclimatic conditions in urban woodlands (Atchison & Rodewald 2006). Although site characteristics are important in determining species presence, the fragmented nature of urban woodland patches means that the surrounding landscape can be of similar importance. Woodland isolation, the proximity of buildings, and the extent of urbanisation in the surrounding landscape are known to influence the species richness of well-studied taxa such as birds and small mammals (Croci et al. 2008; Morimoto et al. 2006; Sadler et al. 2006). Management strategies for urban woodland are being developed in many countries as they are beneficial for human health (Matsuoka & Kaplan 2008; Takano et al. 2002) and biodiversity conservation (Cornelis & Hermy

2004; Croci et al. 2008). However, information is scarce or absent for many taxa and as a consequence there is a lack of consideration of these taxa in management plans.

Moths (Lepidoptera) are an important component of terrestrial ecosystems due to their role as food resources for birds (Wilson et al. 1999) and small mammals (Vaughan 1997), as pollinators (Proctor et al. 1996; Devoto et al. 2011), and nutrient recyclers (Merckx et al. 2013). There have been substantial population declines in many moth species, including two-thirds of analysed common macromoth species in the UK (Conrad et al. 2006; Fox et al. 2013). The main drivers of decline are expected to include climate change (Fox et al. 2013), agricultural intensification (Merckx et al. 2012a) and afforestation with non-native trees and a decline in traditional management regimes for woodlands (Warren & Bourn 2011).

Although considerable efforts have been made to identify key drivers of moth abundance and diversity in agricultural landscapes (e.g. Fuentes-Montemayor et al. 2011; Merckx et al. 2012a; Jonason et al. 2013), the effects of urbanisation on moth populations remain poorly understood (Fox 2013). Despite the suggestion by Summerville & Crist (2008) that future research on forest Lepidoptera should include an understanding of the importance of urban woodland in retaining viable and diverse moth communities, research is lacking on this topic. In St Petersburg, Kozlov (1996) found that habitat fragmentation of urban woodland was the main driver of population declines in micromoths due to a reduction in colonization rates. Bates et al. (2014) found that species richness and abundance within urban gardens was negatively affected by urbanisation, although certain species did respond positively to the urban matrix. In contrast, in the San Francisco Bay Area, Rickman & Connor (2003) found that the extent of urbanization was not associated with species richness or total abundance of leaf-miner moth communities.

In agricultural woodlands, moth abundance and richness are positively related to a high diversity of tree species, a high proportion of native trees (Fuentes-Montemayor et al. 2012), and herbaceous plant species richness (Usher & Keiller 1998). However, the composition of urban woodlands is often quite different to that of rural woodlands. For example, understory vegetation in urban woodland tends to be dominated by short life-span (annual) species (Vallet et al. 2010), which may have negative consequences for moth species dependent on specific food plants. Additionally, stress factors including restrictive soil volume, high salinity, and trampling can restrict the tree species that are capable of successfully growing in urban environments (Alvey 2006). The response of moths to fragmented urban woodlands may therefore differ considerably from the response within agricultural landscapes. Woodland patch configuration (shape and size) is often a strong determinant of moth abundance in non-urban landscapes (Merckx et al. 2012b; Slade et al. 2013), and at the landscape scale, the presence of isolated trees, hedgerow trees and small woodland patches can function as ‘stepping stones’ for macromoths (Slade et al. 2013). In urban landscapes, reductions in garden size, switching from vegetated to hard surfaces, and the expansion of urban developments is expected to reduce resource availability for moths, but this has rarely been studied (Fox 2013; but see Bates et al. 2014).

Effective management strategies for the conservation of biodiversity in urban woodlands require comprehensive data on the ecology and habitat requirements of all relevant taxa (Lindenmayer et al. 2006). Minimal management of urban woodland can lead to changes in vegetation structure (e.g. increased tree and shrub density, denser canopy cover) which may have contrasting species-specific effects (e.g. Smith & Gehrt 2010). Conversely, over-management, such as the removal of understory to enhance the recreational value of the woodland, can negatively affect a range of taxa (e.g. birds; Heyman 2010). It is not clear how moths may respond to urban woodland management, and, the limited management advice available focuses on macromoths, with little attention given to the habitat requirements of micromoths (Blakesley et al. 2010; Bland & Young 1996).

In this paper I investigate how woodland vegetation characteristics (e.g. tree species richness), patch configuration (e.g. woodland size), and the surrounding landscape (e.g. proportion of urban areas) influence moth assemblages. I aim to use this information to build an evidence base so that conserving moth diversity can be incorporated into management plans. Specifically, I address the following questions:

1. How are moth assemblages determined by local woodland characteristics (vegetation structure and patch configuration) and the composition, spatial configuration and heterogeneity of the surrounding landscape?

2. Are woodland site characteristics more important than the characteristics of the surrounding landscape in determining moth abundance, species richness and species diversity?

3. What practical applications do our findings have for the management of urban woodland for moth assemblages?

5.3 Materials & methods

5.3.1 Site selection

A total of 32 urban woodland sites in central Scotland (Figure 5.1) were identified using Ordnance Survey digital maps (EDINA Digimap Ordnance Survey Service 2013). Urban areas were designated as those where urban cover was the dominant land use within a 1km grid square as categorised by the Centre for Ecology and Hydrology Land Cover Map 2000. Sites were selected by size, longitude, and degree of urbanisation in the surrounding 1 km using a stratified random sampling method. Selected woodlands were a minimum of 50 years old, were either broadleaved or consisted of a mixture of conifer and broadleaved trees (mixed woodland was defined as a habitat with between 10% and 90% of conifers contained within it), and were surveyed once between May 19th to September 1st 2011. Sites were surveyed in random order through the field season to avoid any spatial or temporal bias. I recognise that a single visit to each site provides only a coarse description of local moth assemblages, but I adopted this approach in order to maximise the number of sites and cover a wider range of characteristics when attempting to determine the factors influencing moths in urban woodlands.

5.3.2 Vegetation surveys

Vegetation surveys were conducted within a week of each moth survey. Four circular plots with radii of 20m were randomly located within each woodland patch (each within 50m of a corresponding moth trap). At each of the four plots, all trees were counted, identified to at least genus level, and tree basal area measured (only trees

≥7cm in diameter at breast height were measured). Dominant ground cover type (‘grass’, ‘ferns’, ‘moss’, ‘herbs’ or ‘bare ground’) and understory cover (%) using the Domin scale (Rodwell 2006) was visually estimated at 20 evenly spaced points within each plot. Results of the four vegetation plots were combined using the mean to provide a description of each woodland patch. Visual assessment of the remaining woodland showed that vegetation surveys were representative of the entire woodland patch.

5.3.3 Moth surveys

Moths were captured using portable 6W heath light traps using E7586 9" actinic tube lights which were run on 12V batteries. A total of four traps were placed within each woodland; two traps were placed along woodland edge and two within the woodland interior (≥ 20m from the woodland edge). Traps were selectively positioned to ensure that similar light levels were emitted (i.e. ensuring that vegetation located around the trap did not obscure its range). When possible, traps were placed a minimum of 100 metres apart to ensure independence (Dodd et al. 2008). The attraction radii of heath light traps are commonly between 10-30m depending on moth family (Truxa & Fiedler 2012; Merckx & Slade 2014), so it is unlikely that even in smaller woodlands, where it was not possible to maintain a full 100 metres separation, that distance between traps was an issue. Additionally, careful placement ensured that vegetation provided an additional physical and light-impermeable barrier between traps. Positioning traps in the vicinity of streetlights was avoided along the woodland edge. Lights were activated 30 minutes after sunset and remained on for the following four hours (the length of

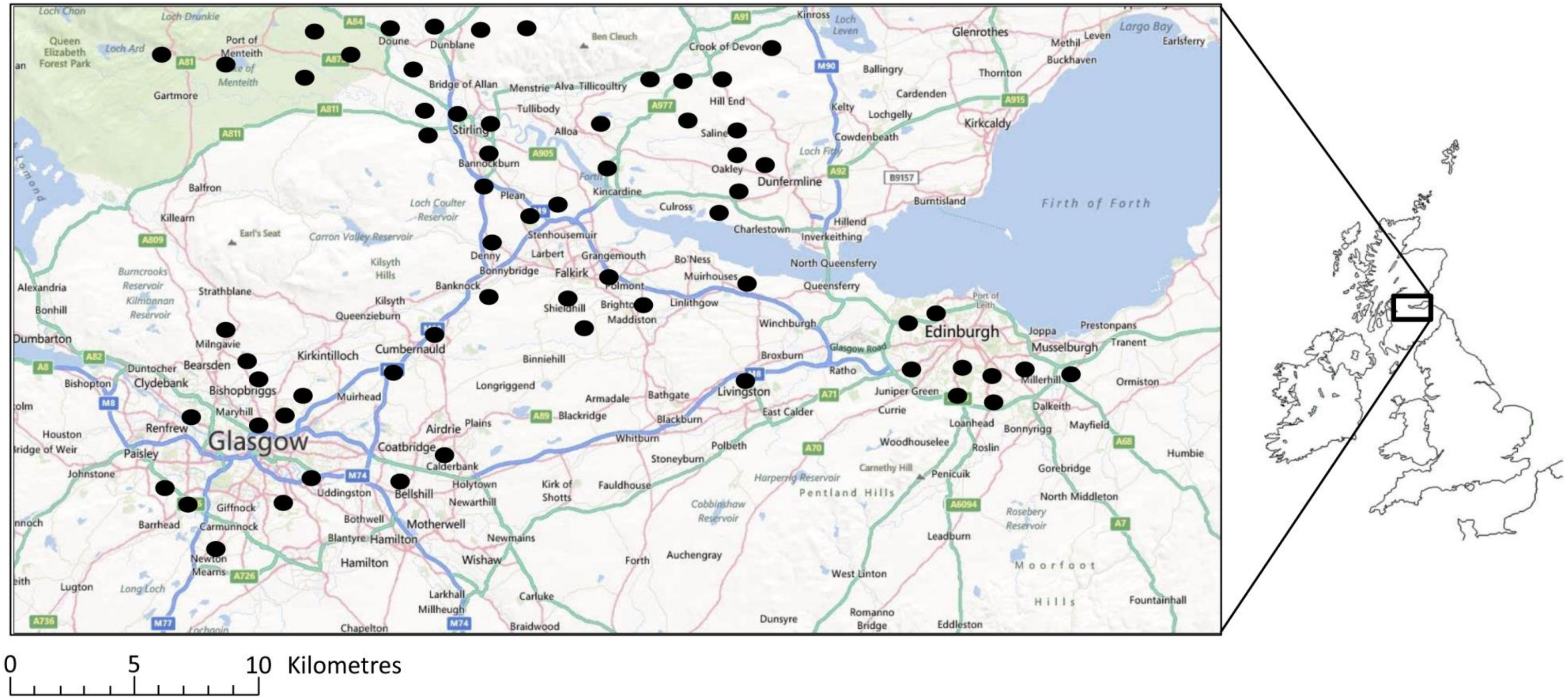

Figure 5.1 Map of central Scotland showing approximate locations of woodland sites (black dots) surveyed in 2011.

the shortest night in the study area). Captured insects were euthanized and stored for later identification. Surveys were only conducted in dry weather, when temperature was ≥ 10°C and wind force ≤ Beaufort scale 4. Moths were divided into macrolepidoptera (a group of moth families containing mostly large species or “macromoths”, plus all butterfly families) and microlepidoptera (a group of moth families comprising mostly smaller species or “micromoths”), of which *ca.*900 and 1700 species occur in the UK, respectively (using Chinery 1993 and Waring & Townsend 2003).

5.3.4 Landscape analysis

Moth trap locations were plotted using ArcGIS 10 (ESRI Inc 2013) and the centre point of the four traps within each site determined. Buffers of 250m, 500m, 1000m, 1500m, 2000m, 2500m, and 3000m radius were created around this central point reflecting the range of spatial scales associated with non-migrating moth species (Merckx et al. 2009; Merckx et al. 2010a; Nieminen et al. 1999; Slade et al. 2013). Data from the OS MasterMap Topography Layer (EDINA Digimap Ordnance Survey Service 2013) were used to classify the landscape within each buffer into a set of discrete biotope types. These were (i) grey space (buildings, structures, roads, and paths); (ii) green space (gardens, parkland, managed grassland, rough grassland, and scrubland); (iii) inland fresh water and (iv) woodland (coniferous, deciduous and mixed woodland). Woodland Euclidean nearest neighbour distance (ENN, the mean value of ENN distances between all woodland patches within the landscape) and the Shannon diversity index (SHDI, a measure of landscape heterogeneity incorporating the relative abundance of the four biotype types) were calculated as previous studies have found these variables to be important (Fuentes-Montemayor et al. 2012). The proportion of land covered by each biotope, woodland ENN, and SHDI were calculated for each buffer scale using Fragstats v4.0 (McGarigal et al. 2012).

5.3.5 Data analysis

Statistical analyses were undertaken using R version 2.14 (R Core Team 2012). The lme4 package (Bates et al. 2013) was used for statistical analysis, whilst ggplot2 (Wickham 2009) and the effects package (Fox 2003) were used for graphics. The software package PAST (Hammer et al. 2001) was used to calculate diversity indices for macro- and micromoths. I selected Margalef diversity because it can deal with occasions where number of individuals in a trap is equal to number of species (a frequent occurrence), is commonly used as a measure of spatial species diversity, and because its biological interpretation is straightforward (Magurran 1988).

I performed a series of Generalised Linear Mixed-Effects Models (GLMMs; Zuur 2009) to incorporate both within and between-site variance. This allowed us to account for confounding factors which may cause within stand variance in sampling efficiency (i.e. background ambient light from the urban landscape). Using GLMMs I was able to quantify the influence of woodland characteristics and landscape metrics on moth abundance, richness, and diversity. I ran models using moths per trap (n=128) as the response variable, with ‘site’ included in all models as a random (grouping) factor. Based upon the scientific literature on the ecology of woodland moths and typical management regimes undertaken in urban woodland the following predictor variables were included in the starting model: (i) woodland vegetation characteristics: tree species richness, percentage of native trees, average tree basal area and understory cover (covariates), and woodland type (fixed factor); (ii) patch configuration: woodland size and woodland shape (patch perimeter divided by the minimum perimeter possible for a maximally compact patch of the same areas; equals 1 when the patch is maximally compact and increases as shape becomes more irregular; McGarigal et al. 2002), both as covariates, trap location (woodland edge vs. woodland interior; fixed factor); (iii) landscape metrics. Temperature (nightly average) and date were included in all models as covariates to account for any potential temporal bias in the results. Given the high collinearity among landscape metrics (i.e. between the proportions of different biotope types or the same biotope type at a variety of spatial scales) preliminary analyses were conducted to determine which landscape metrics should be included in each model. Individual GLMM models (one for each landscape parameter at each spatial scale) were constructed and marginal R^2 values (determined following Nakagawa & Schielzeth (2012)) calculated to quantify the amount of variation in the data explained by each landscape parameter. For each model I used moth abundance, richness, or diversity (n=128) as the response variable, a landscape parameter at a specific scale as a covariate, and ‘site’ as a random factor. I selected the landscape parameter which explained the most variation (i.e. highest marginal R^2 value) and included it in the relevant model.

I also included interactions between woodland size and shape, woodland size and trap location, and woodland shape and trap location as these have previously been identified as important predictors of moth distributions (Fuentes-Montemayor et al. 2012). All predictor variables were tested for collinearity, however none were considered to be strongly correlated based upon a Pearson correlation coefficient of ≥

0.6 and $P \leq 0.05$. Continuous predictor variables were centred and standardized following Schielzeth (2010). Models containing response variables using count data (e.g. moth abundance or richness) were fitted with a Poisson distribution. Models containing continuous response variables (e.g. moth diversity) were fitted with a Gaussian distribution. All models were validated by visual examination of residuals (e.g. plotting residuals vs. fitted values to check for constant variance; Crawley, 2012). Models were checked and found to be not spatially auto-correlated using the Mantel test in the ade4 package within R (Dray and Dufour 2007).

I present the results of each full model including standardised parameters and confidence intervals for all explanatory variables. Inferences on the effect of each parameter were made by (i) comparing its standardized estimate with other predictor variables to determine relative importance, (ii) the upper and lower 95% quantiles of each parameter distribution obtained from N = 2000 simulated draws from the estimated distribution (Gellman & Hill 2007), and (iii) a comparison of models excluding each parameter in turn using Likelihood Ratio Tests (LRTs) (Faraway 2005). LRTs of main effect parameters also involved in interactions were performed by comparing a model excluding the main effect term to a model including all main effects (but not interactions) only. Prediction plots were constructed by undertaking simulated draws (n = 2000) from the estimated distribution of one explanatory variable whilst maintaining all other parameters in the model at their median observed values. This allowed the percentage increase (or decrease) and 95% confidence intervals to be calculated for a predicted change in moth abundance, diversity, or species richness relative to changing one parameter.

5.4 Results

I recorded a total of 33 tree species/genera within our survey (Appendix 5.8.1), 23 of which are thought native to the British Isles. Tree species richness ranged from 2 to 13 species per site, whilst tree density varied from 207 to 1,766 trees per ha. Mixed woodland was composed of, on average, 24% coniferous trees and 76% broadleaved trees. Dominant ground cover was grouped into two categories ('bare ground' and 'vegetated') for analysis purposes; the dominant ground cover of 18 of the 34 sites was 'bare ground' whilst each descriptive subcategory of 'vegetation' (grass, ferns, moss, herbs) was dominant in fewer than 5 sites each .

I collected a total of 1,198 micromoths belonging to 72 species and 16 families and 1,656 macromoths from 103 species and 8 families. A mean of 49 (±8) macromoths comprising 14 (±1) species were collected per woodland site. A mean of 34 (±14) micromoths of 6 (±0.5) species were collected per woodland site. I recorded three species of micromoth which are noted as nationally scarce (Davis 2012; Appendix 5.8.2) and seven species of macromoth which are classified as of conservation concern (Fox et al. 2006; Appendix 5.8.3).

5.4.1 The importance of landscape for macro and micromoths

There was considerable variety in the composition of the landscape surrounding each woodland; urban grey space ranged from 17 to 49% coverage in the surrounding 1km, whilst green space (including urban gardens) varied from 36 to 71%. In general, the small effect size of the landscape parameters indicated that the composition of the surrounding urban matrix was a poor predictor of moth abundance, species richness, or diversity (Figure 5.2). Macromoth populations showed the strongest relations to landscape parameters at a relatively small scale (250m) whilst micromoths were influenced at larger scales (>1000m; Figure 5.2). On average, the relative importance of the landscape for micromoths was double that of macromoths (Tables 5.1 & 5.2).

5.4.2 Macromoth abundance

The inclusion of temperature, average tree basal area, woodland type, trap location, and interactions between woodland size and shape, trap location and shape, and trap location and woodland size all significantly improved the fit of the macromoth abundance model (Table 5.1). Woodland type was the most important predictor within the model; moth abundance was 69% (68-70%) higher in broadleaved woodlands compared to mixed woodlands (Appendix 5.8.4). A change in average tree basal area from 20cm^2 to 40cm^2 within broadleaved woodlands is associated with an increase in the abundance of macromoths from 14 to 24 individuals (65%, 95% CI 56-74%; Figure 5.3a). The interaction between woodland size and shape indicated that as woodland patch size increases, macromoth abundance increases in complex woodlands, but remains relatively constant in compact woodlands. Additionally, the model was significantly improved by the interaction between trap location and woodland shape, indicating that macromoth abundance in the woodland interior increased with woodland shape but was lower at woodland edges. However, the effect size was marginal (Table 5.1; Appendix 5.8.5). In contrast, the interaction between trap location and woodland size was a relatively important predictor; macromoth abundance at the woodland edge marginally decreased as woodland size increased, whilst there was a considerable increase in abundance within the woodland interior with woodland size (Appendix 5.8.5).

5.4.3 Macromoth diversity

The inclusion of temperature, average tree basal area and woodland type all significantly improved the fit of the macromoth diversity model (Table 5.1). Macromoth diversity was 39% (38-41%) greater in broadleaved woodlands in comparison to mixed woodland (Appendix 5D), and an increase in tree basal area within broadleaved woodlands from 20cm^2 to 40cm^2 is associated with an increase the species diversity of macromoths by 23% (15-29%; Figure 5.3b).

Table 5.1 Parameter estimates and likelihood ratio tests of the GLMM’s for macromoth abundance, species diversity, and species richness in fragmented urban woodland. The most important landscape parameter at the most important spatial scale was included for each model; the % of water in the surrounding 250m of the woodland was included in the macromoth abundance model, the % of green space in the surrounding 1.5km included for species diversity, and the % of woodland in the surrounding 250 m included for macromoth species richness. Significance codes: ‘***’ p ≤0.001, ‘**’ p≤0.01, ‘*’ p≤0.05, ‘^’ p≤0.1.

	Macromoth Abundance				**Macromoth Species Diversity**				**Macromoth Species Richness**			
Fixed effects	Estimate (± SE)	AIC	χ2	*p*	Estimate (± SE)	AIC	χ2	*p*	Estimate (± SE)	AIC	χ2	*p*
Intercept	1.5 ± 0.2				2.6 ± 0.2				2 ± 0.2			
Temperature	0.4 ± 0.1	548.8	4.9	0.03*	0.3 ± 0.1	371.8	5.6	0.02*	0.3 ± 0.08	236.9	7.9	0.005**
Date	-0.01 ± 0.1	544.3	0.3	0.6	-0.02 ± 0.1	366.2	0.0	1	0.01 ± 0.08	229.2	0.2	0.6
Tree Species Richness ^{1}	-0.03 ± 0.2	544.1	0.1	0.7	-0.07 ± 0.1	366.3	0.2	0.7	-0.02 ± 0.1	229.0	0.0	0.8
Understory Cover ^{1}	-0.1 ± 0.1	544.0	0.1	0.8	-0.1 ± 0.1	366.8	0.6	0.4	-0.07 ± 0.08	229.2	0.2	0.7
Tree Basal Area ^{1}	0.3 ± 0.2	549.7	5.8	0.02*	0.3 ± 0.2	371.0	4.8	0.03*	0.2 ± 0.1	234.2	5.2	0.02*
Native Trees ^{1}	-0.04 ± 0.1	544.0	0.1	0.8	-0.2 ± 0.1	368.8	2.6	0.1	-0.1 ± 0.09	230.9	1.9	0.2
Woodland Type ^{14}	1 ± 0.3	554.3	10.4	0.001**	1 ± 0.3	378.3	12.2	<0.0001***	0.7 ± 0.2	240.7	11.7	0.0006***
Trap location ^{25}	0.3 ± 0.05	579.2	35.2	<0.0001***	0.01 ± 0.2	366.2	0.0	1	0.06 ± 0.08	229.8	0.8	0.4
Shape ^{2}	0.03 ± 0.1	544.3	0.3	0.6	0.1 ± 0.2	366.3	0.2	0.7	0.07 ± 0.1	229.0	0.0	0.9
Size ^{2}	-0.03 ± 0.1	545.5	1.6	0.2	-0.09 ± 0.2	366.2	0.0	0.9	-0.01 ± 0.1	229.9	0.9	0.3
% Water (250m) ^{3}	-0.1 ± 0.1	545.4	1.4	0.2	n/a	n/a	n/a	n/a	-0.09 ± 0.09	234.4	5.4	0.02*
% Green (1500m) ^{3}	n/a	n/a	n/a	n/a	0.05 ± 0.1	366.4	0.3	0.6	n/a	n/a	n/a	n/a
Shape x Size ^{2}	0.4 ± 0.2	536.1	4.2	0.04*	0.08 ± 0.2	367.9	0.3	0.6	0.2 ± 0.1	233.2	1.8	0.2
Shape x Trap location ^{2}	-0.04 ± 0.06	560.7	32.9	<0.0001***	-0.3 ± 0.2	367.9	4.2	0.2	-0.09 ± 0.08	229.2	1.9	0.6
Size x Trap location ^{2}	0.2 ± 0.06	577.2	49.4	<0.0001***	0.2 ± 0.2	364.9	1.3	0.7	0.1 ± 0.08	230.1	2.7	0.4

Explanatory variables: ‘^{1}’ Vegetation structure, ‘^{2}’ Patch configuration, ‘^{3}’ Composition, spatial configuration, and heterogeneity of surrounding landscape.

^{4} Positive values indicate a positive effect of ‘broadleaved’ woodland (with respect to ‘mixed’ woodland).

^{5} Positive values indicate a positive effect of woodland interior (with respect to woodland edge).

Table 5.2 Parameter estimates and likelihood ratio tests of the GLMM's for micromoth abundance, species diversity, and species richness in fragmented urban woodland. The most important landscape parameter at the most important spatial scale was included for each model; the % of woodland in the surrounding 2000m of the woodland was included in the micromoth abundance model, the % of woodland in the surrounding 1.5km included for species diversity, and the % of woodland in the surrounding 2000m included for micromoth species richness. Significance codes: '***' p ≤0.001, '**' p≤0.01, '*' p≤0.05, '^' p≤0.1.

	Micromoth Abundance				**Micromoth Species Diversity**				**Micromoth Species Richness**			
Fixed effects	Estimate (± SE)	AIC	χ2	*p*	Estimate (± SE)	AIC	χ2	*p*	Estimate (± SE)	AIC	χ2	*p*
Intercept	0.2 ± 0.3				1.2 ± 0.2				0.9 ± 0.3			
Temperature	0.9 ± 0.2	513.7	16.4	<0.0001***	0.3 ± 0.1	314.4	7.3	0.007**	0.5 ± 0.1	222.2	10.1	0.001**
Date	-0.2 ± 0.2	497.6	0.4	0.5	0.08 ± 0.1	307.7	0.6	0.5	-0.1 ± 0.2	212.3	0.2	0.6
Tree Species Richness [1]	-0.2 ± 0.2	497.7	0.5	0.5	-0.2 ± 0.1	309.8	2.7	0.1	-0.2 ± 0.2	212	0.9	0.3
Understory Cover [1]	-0.2 ± 0.2	498	0.8	0.4	-0.01 ± 0.1	307.1	0.01	1	0.08 ± 0.1	212	0.8	0.4
Tree Basal Area [1]	0.4 ± 0.3	500.1	2.9	0.09^	0.08 ± 0.1	307.7	0.5	0.5	0.2 ± 0.2	213.6	1.6	0.2
Native Trees [1]	-0.3 ± 0.23	498.4	1.2	0.3	-0.1 ± 0.1	308.8	1.7	0.2	-0.2 ± 0.2	213.6	1.6	0.2
Woodland Type [14]	1.8 ± 0.5	508	10.8	0.001**	0.7 ± 0.2	314.7	7.6	0.006**	1 ± 0.3	219.2	7.2	0.007**
Trap location [25]	0.06 ± 0.07	497.4	0.1	0.7	0.01 ± 0.1	307.1	0.01	1	0.09 ± 0.1	212.1	0.01	0.9
Shape [2]	0.05 ± 0.2	497.3	0.1	0.7	0.2 ± 0.1	307.8	0.7	0.4	-0.2 ± 0.2	212.3	0.2	0.7
Size [2]	0.1 ± 0.2	497.8	0.6	0.5	-0.01 ± 0.1	307.2	0.08	0.8	0.05 ± 0.2	212.1	0.01	1
% Wood (2000m)[3]	-0.2 ± 0.2	498.7	1.5	0.2	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
% Wood (1500m)[3]	n/a	n/a	n/a	n/a	-0.1 ± 0.09	309.6	2.4	0.1	n/a	n/a	n/a	n/a
% Wood (2000m)[3]	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	-0.2 ± 0.1	215.4	3.3	0.07^
Shape x Size[2]	0.1 ± 0.3	498.6	0.2	0.68	0.01 ± 0.2	311.7	0.01	1	0.2 ± 0.2	213.6	0.8	0.4
Shape x Trap location [2]	-0.2 ± 0.1	499.2	4.7	0.2	-0.2 ± 0.1	309.7	1.9	0.6	0.3 ± 0.2	213.2	4.5	0.2
Size x Trap location [2]	0.07 ± 0.1	495.9	1.5	0.7	-0.04 ± 0.1	307.9	0.2	1	-0.1 ± 0.2	210.1	1.4	0.7

Explanatory variables: '[1]' Vegetation structure, '[2]' Patch configuration, '[3]' Composition, spatial configuration, and heterogeneity of surrounding landscape.

[4] Positive values indicate a positive effect of 'broadleaved' woodland (with respect to 'mixed' woodland).

[5] Positive values indicate a positive effect of woodland interior (with respect to woodland edge).

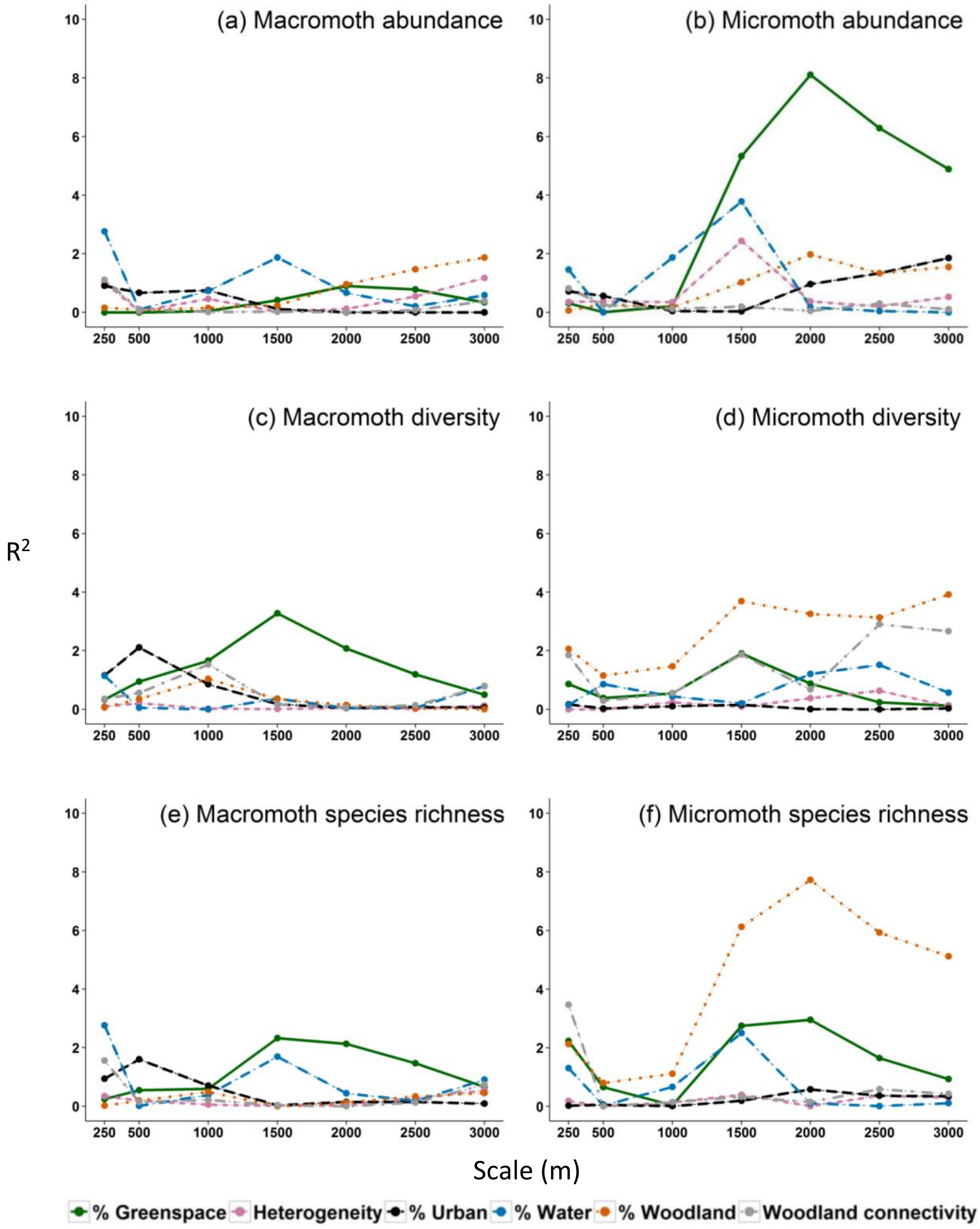

Figure 5.2 R^2 values obtained from poisson GLMM models comparing the percentage of landscape covered by each biotope type at a variety of spatial scales and; (a) macromoth abundance, (b) micromoth abundance, (c) macromoth diversity, (d) micromoth diversity, (e) macromoth richness, (f) micromoth richness. I calculated marginal R^2 values for mixed effect models (a) to (f) using moths per trap as the response variable.

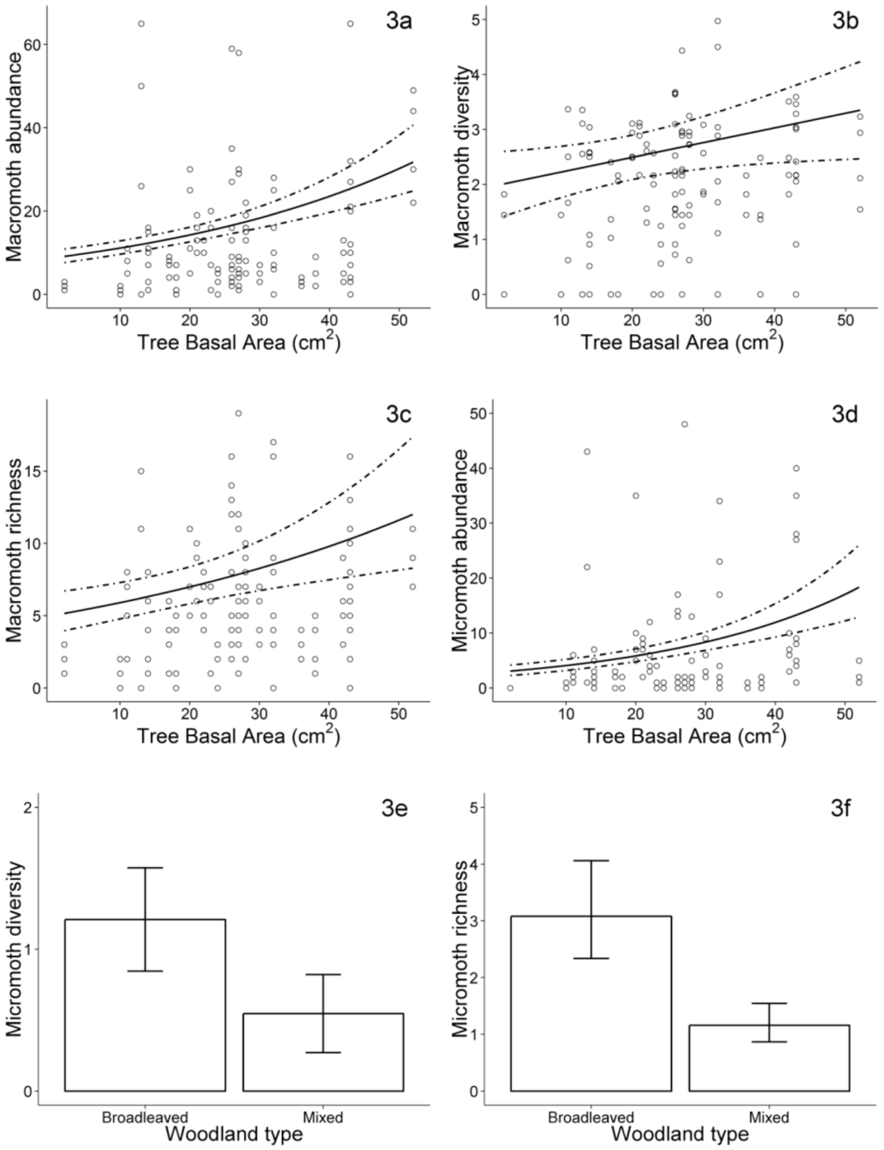

Figure 5.3 Measurements of moth assemblages plotted against the strongest continuous predictor in each model. Dots are observed data whilst the lines are predictions of moth abundance, diversity and richness with varying levels of the continuous predictor. Dashed lines represent 95% confidence intervals around the predictions. All prediction plots are calculated for broadleaved woodland and by setting all continuous parameters at their median observed values in the model. In models where there are no significant continuous predictor variables, the strongest categorical predictor is shown. Error bars represent 95% confidence intervals around the predictions.

5.4.4 Macromoth richness

As with diversity, the model of macromoth species richness was significantly improved by the inclusion of temperature, average tree basal area, and woodland type (Table 5.1). The inclusion of the percentage of water in the surrounding 250m of the woodland patch was also a significant predictor however had little predictive power due to a low effect size. Woodland type was the most important predictor within the model; moth species richness was 37% (30-45%) greater in broadleaved woodlands as compared to mixed woodland (Appendix 5D). Average tree basal area was also influential; an increase in average tree basal area within broadleaved woodlands from 20cm^2 to 40cm^2 is associated with an increase in macromoth richness from 7 to 10 species, an increase of 39% (28-52%; Figure 5.3c).

5.4.5 Micromoth abundance

The inclusion of temperature and woodland type significantly improved the fit of the micromoth abundance model (Table 5.2). The standardized effect size of woodland type was almost double that of any other predictor variable; micromoth abundance was 795% (550-1040%) greater in broadleaved woodlands compared to mixed woodland (Appendix 5D). Average tree basal area was a marginally significant predictor of micromoth abundance (Table 5.2); an increase in average tree basal area within broadleaved woodlands from 20cm^2 to 40cm^2 increases the abundance of micromoths from 6 to 12 individuals (102%, 95% CI 91-114%; Figure 5.3d).

5.4.6 Micromoth diversity

The inclusion of temperature and woodland type were the only significant variables within the micromoth diversity model (Table 5.2), with diversity found to be 57% (45-64%) greater in broadleaved woodlands than mixed woodland (Figure 5.3e).

5.4.7 Micromoth richness

The model of micromoth richness was significantly improved by the inclusion of temperature and woodland type, and marginally improved by the addition of the percentage of woodland in the surrounding 2km (Table 5.2). Micromoth richness was 104% (88-120%) greater in broadleaved woodlands compared to mixed woodland (Figure 5.3f). The inclusion of percentage woodland in the surrounding 2km was marginally significant in improving model fit; an increase in woodland cover from 10 to 20% in the surrounding 2km is associated with a decrease in micromoth richness by 41% (26-53%).

5.5 Discussion

Understanding the impact of urbanisation on global biodiversity is vital as the rate of urban expansion continues to accelerate (Aronson et al. 2014). Urban spread is often cited as a contributory factor in the population decline and range contraction of many moth species, despite relatively little research having being conducted within the urban matrix (Fox 2013). Here, I show how moths in fragmented urban woodland respond to vegetation characteristics, patch configuration, and the surrounding landscape. Our results contribute to a greater understanding of how management of urban woodland can incorporate the needs of often neglected taxa such as moths.

The number of macromoths captured per woodland in this study was approximately half of that captured in a study conducted in the same region, in similar environmental conditions, and using the same methods, but within agricultural woodlands (Fuentes-Montemayor et al. 2012). Urban woodlands contained, on average, a third fewer macromoth species than agricultural woodlands. Similarly, abundance of micromoths was approximately a third higher in agricultural woodlands, but for this group, a similar number of species were recorded. This suggests that urban woodlands are of poorer quality than those on farmland, although the underlying cause(s) are unclear. A caveat to this is that the two studies were conducted in different years, which is likely to introduce temporal differences, although the environmental conditions (e.g. temperature) were similar.

The strongest predictor of moth assemblages for all models was woodland type; woodland comprising only of broadleaved trees contained a higher abundance, species richness, and diversity of moths than mixed woodland. A preference for broadleaved woodlands, in comparison to mixed woodlands, has also been found to be important for moth communities in agricultural landscapes (Fuentes-Montemayor et al. 2012). We might have expected species richness to be higher in mixed woodland given that species adapted to benefit from human activity, such as those feeding on exotic conifer species introduced into gardens, are showing population increases (Conrad et al. 2004; Fox et al. 2013). It may be that the relative scarcity of conifer species within urban woodlands (24% of all trees identified in this survey) means that fragmented mixed woodlands are unable to support viable populations of conifer moth specialists. In addition, the presence of conifer species will reduce the availability and quality of broadleaved habitat available.

The abundance, species richness and diversity of macromoth assemblages and the abundance of micromoths were higher in woodlands with large average tree basal areas, a trait associated with mature woodlands (Fuentes-Montemayor et al. 2012). Younger woodlands may contain smaller and more species-poor moth assemblages because colonisation rates may be slower within a fragmented landscape. Although the permeability of the surrounding matrix and dispersal ability will determine colonisation rates of individual moth species, it is likely that mature woodlands will have remained relatively undisturbed during the process of urbanisation. Similar trends between patch age and colonisation rates explain plant species distribution in urban vegetation fragments (Bastin & Thomas 1999). Additionally, woodlands containing larger trees may provide more niches and therefore more foraging opportunities (Summerville & Crist 2008).

The differences between moth assemblages at the woodland edge and woodland interior were accentuated by woodland size and shape. Macromoth abundance was greater within the woodland interior of larger woodlands indicating an edge effect within smaller woodlands that reduces abundance. Edge effects often strongly influence insect communities in fragmented landscapes (McGeoch & Gaston 2000). Slade et al. (2013) found that forest fragments need to be larger than five hectares and require interior woodland habitat a minimum of 100 m from the woodland edge to sustain populations of forest specialist macromoth species, whilst Usher & Keiller (1998) suggest that woodlands of less than 1ha fail to support characteristic woodland moth communities. Similarly, the shape of the woodland patch in our study appears to determine the extent of impact that the edge effect with moth assemblages in the woodland interior negatively affected as woodland shape complexity increased. These findings support Usher & Keiller (1998), Fuentes-Montemayor et al. (2012) and Merckx et al. (2012b) who suggest that compact woodland patches that expose proportionally less edge to the surrounding matrix can support larger and more diverse moth communities. Woodland edges in the urban matrix are often adjacent to habitats under high anthropogenic pressure which may determine the tree species and invertebrate populations that are able to tolerate such conditions (Lehvävirta et al. 2006). Edge effects may also explain the interaction between shape and size; macromoth abundance is highest in large complex woodlands demonstrating that woodlands of sufficient size can maintain core woodland habitat despite being irregular or elongated. Micromoth species richness was the only descriptor of moth assemblages which was influenced by the surrounding landscape. Micromoth species richness was negatively influenced by woodland cover at a variety of spatial scales, with the strongest effect at 2000m. These findings contrast with those of Ricketts et al. (2001), Summerville & Crist (2004), and Fuentes-Montemayor et al. (2012) who found a strong positive influence between woodland cover in the surrounding landscape and moth presence.

Woodland site characteristics were consistently more important than the surrounding landscape in determining the abundance, species richness and diversity of moths. Our findings are in accordance with those of Wood & Pullin (2002) who found that some butterfly species within the urban landscape were limited more by the availability of suitable habitat than their ability to move among habitat patches. Similarly, Angold et al. (2006) demonstrated the importance of local habitat variables over landscape variables within the urban matrix in determining carabid species distribution. Additionally, Bates et al. (2014) found that distance to woodland did not significantly influence moth species richness or abundance within urban gardens. However, our findings contrast with patterns seen in moth communities within fragmented woodland in an agricultural setting which are strongly influenced by the landscape (Fuentes-Montemayor et al. 2012). It may be that fragmented agricultural woodlands are pockets of suitable habitat within an ecologically poor landscape, whilst the widespread presence of urban gardens and green space in urban landscapes may facilitate dispersal. Urban gardens can maintain relatively high levels of invertebrate species richness (Smith et al. 2006) and therefore may minimise patch isolation by providing additional habitat for moth species outside of the fragmented woodland (Bates et al. 2014). The marked difference in the abundance and diversity of moths in agricultural woodlands may reflect that although the urban landscape is more permeable for moths, urban woodland is of poorer quality which restricts the abundance and diversity of moths. Although habitat quality was an important factor in determining the distribution of moths throughout the urban landscape, we found that moths were relatively widespread throughout the city environment. Bat species such as *Plecotus auritus* forage almost exclusively on Lepidoptera (Vaughan 1997), yet this species was rarely found within my studies (e.g. chapters 3, 6, 7). This indicates that there are other limiting factors restricting the distribution of *P. auritus* within the urban matrix other than availability of prey items.

5.5.1 Practical implications for the management of urban woodland for moth assemblages

Although rarer species (i.e. nationally scarce or of conservation concern) may require specific management plans to enhance their populations (but see Merckx et al. 2010b), the management of fragmented urban woodland patches to increase moth abundance, species richness, and species diversity should take into consideration the following general points:

1. Maintaining broadleaved woodlands will support high moth abundance, species richness, and species diversity. Habitat action plans exist for the management of some urban woodland (e.g. London Borough of Richmond upon Thames 2013) which emphasise the role of planting and supporting the natural regeneration of native broadleaved species. I found no significant relationship between moth assemblages and native species which may reflect that naturalised species such as *Acer pseudoplatanus* (the most frequently recorded tree species during this study) are providing a suitable habitat for many species. Although *A. pseudoplatanus* is negatively perceived from a management perspective as it is a non-native, our findings support those of Peterken (2001) who found little evidence that it reduces native biodiversity.

2. Management strategies to retain the presence of mature trees and stands are important not only for macromoth assemblages, but also provide preferred habitats for many other taxa (e.g. bats; Perry et al. 2007), in addition to meeting the needs of the public's perception of aesthetically pleasing woodland (Ode & Fry 2002). Old trees in urban woodlands are often perceived as a public danger due to the risk of falling

branches, however minimising the removal of deadwood or retaining it within the woodland once it has fallen may prove beneficial for both macromoth assemblages and other invertebrate species (e.g. saproxylic beetles; Carpaneto et al. 2010).

3. Differences in the abundance of macromoths between the woodland edge and woodland interior may result from high anthropogenic pressure in the surrounding urban matrix. Light intensity was higher at the woodland edge than within the woodland interior (Lintott *unpublished data*), which can have a detrimental impact on moth populations (Conrad et al. 2006). Integrating public safety concerns such as the preference for lit pathways through urban green space into biodiversity management plans (Luymes & Tamminga 1995) requires care as 'edge effects' can unintentionally be created within the woodland interior. Although not addressed in this paper, future work investigating the direct impact of anthropogenic disturbance (i.e. extent of recreational use within woodland, noise/light intensity) on urban moth assemblages would be of value.

5.5.2 Limitations

(i) *Temporal variations*: Each site was surveyed only once, which provides only a coarse description of local moth assemblages within urban areas. However, I ensured that weather conditions were relatively similar during surveys and that surveying order was randomised to ensure that woodland patches with different characteristics (i.e. size or shape) were evenly surveyed throughout the season. In addition, previous studies have shown that patterns of moth community composition in relation to, for example, patch area effects remain consistent despite seasonal species turnover (Summerville and Crist 2003). Therefore, temporal variations are unlikely to have influenced the patterns detected during our study and the conclusions drawn from them. Similar techniques have provided insights into how moths respond to agricultural woodland (Fuentes-Montemayor et al. 2012); this paper uses the same methodology to give, for the first time, an indication of the species richness, abundance, and diversity of moth populations within fragmented urban woodland. (ii) Trapping effects: Even though light trapping is the most effective technique for general moth recording (in terms of the wide spectrum of species it attracts relative to the sampling effort; Waring & Townsend 2003), many moth species are not attracted to light. However, our trapping method allowed us to detect general patterns in moth abundance/richness associated with urban woodland, even if this does not reflect the habitat preferences of all moth species. Higher background ambient light along the woodland edges may have a direct impact on moth populations, however it may also impair sampling efficiency (i.e. Yela & Holyoak 1997). As trap location (edge versus interior) was not influential on all measures of moth assemblages, it is likely that where an edge effect was observed (i.e. macromoth abundance) this was a true trend rather than simply existing as an artefact of the sampling method. Determining the extent to which the surrounding ambient urban light may be impacting moth populations within urban woodland is, however, beyond the scope of this paper.

5.6 Conclusions

In summary, woodland vegetation character, woodland patch configuration and the surrounding landscape all influence moth populations in urban woodland to different extents. The creation and maintenance of large, compact, mature, broadleaved woodland patches will enhance moth populations within the urban landscape. The importance of the surrounding landscape in determining moth distributions is less pronounced in urban landscapes than in alternative landscapes under intense human land-use including agricultural areas. The urban matrix may not be limiting the dispersal of moths, with the exception of micromoths in scarcely wooded landscapes. The detrimental impacts of edge effects make moth populations in small fragmented urban woodland vulnerable.

5.7 Acknowledgements

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5.8 Appendices

Appendix 5.8.1 The relative abundance of tree species recorded within all 32 urban woodland patches.

Scientific name	**Common name**	**Native to Britain**	**Relative abundance (%)**
Acer pseudoplatanus	Sycamore	No	14.56
Fraxinus excelsior	Common ash	Yes	11.76
Betula pendula	Silver birch	Yes	11.12
Crataegus monogyna	Common hawthorn	Yes	7.99
Pinus slyvestris	Scots pine	Yes	7.77
Ulmus glabra	Wych elm	Yes	7.26
Fagus sylvatica	Common beech	Yes	6.40
Sorbus aucuparia	Common rowan	Yes	3.69
Prunus avium	Wild cherry	Yes	3.61
Quercus petraea	Sessile Oak	Yes	3.43
Ilex aquifolium	Common holly	Yes	3.22
Larix decidua	European larch	No	2.92
Alnus glutinosa	Common alder	Yes	2.88
Picea sitchensis	Sitka spruce	No	2.83
Sambucus nigra	Elder	Yes	1.80
Salix caprea	Goat willow	Yes	1.67
Populus tremula	European aspen	Yes	1.12
Betula pubescens	Downy birch	Yes	0.99
Ulmus procera	English Elm	Yes	0.86
Tilia x europaea	Common lime	Yes	0.64
Taxus baccata	Yew	Yes	0.47
Quercus robur	English Oak	Yes	0.43
Carpinus betulus	European hornbeam	Yes	0.43
Cupressaceae spp.	Cypress spp.	No	0.43
Laurus nobilis	Bay laurel	No	0.39
Aesculus hippocastanum	Horse chestnut	No	0.39
Corylus avellana	Common hazel	Yes	0.26
Acer platanoides	Norway maple	No	0.21
Hamamelis spp.	Witch hazel	No	0.17
Salix phylicifolia	Tea leaved willow	Yes	0.13
Salix cinerea	Grey willow	Yes	0.09
Buddleja davidii	Buddleja	No	0.04
Pseudotsuga menziesii	Douglas fir	No	0.04

Appendix 5.8.2 List of micromoths collected

Scientific name	**Common name (and Family)**	**Abundance per site (mean ± SE)**	**Abundance per trap (edge) (mean ± SE)**	**Abundance per trap (interior) (mean ± SE)**
Scoparia ambigualis	(Crambidae)	12.24 ± 4.11	3.93 ± 3.97	2.19 ± 0.63
Yponomeuta evonymella [b]	Bird-cherry ermine (Yponomeutidae)	11.68 ± 11.68	2.81 ± 3.38	3.03 ± 2.59
Chrysoteuchia culmella	Garden Grass-veneer (Crambidae)	1.15 ± 0.85	0.07 ± 0.09	0.50 ± 0.26
Zeiraphera isertana [b]	(Tortricidae)	0.79 ± 0.59	0.04 ± 0.05	0.35 ± 0.28
Agriphila tristella	(Crambidae)	0.68 ± 0.29	0.04 ± 0.05	0.29 ± 0.11
Aphomia sociella	Bee moth (Pyralidae)	0.68 ± 0.27	0.21 ± 0.22	0.13 ± 0.04
Agriphila straminella	Pearl veneer (Crambidae)	0.56 ± 0.28	0.07 ± 0.08	0.21 ± 0.11
Eudonia mercurella	(Crambidae)	0.53 ± 0.21	0.10 ± 0.11	0.16 ± 0.06
Hedya nubiferana [b]	Marbled orchard tortrix (Tortricidae)	0.50 ± 0.29	0.15 ± 0.17	0.10 ± 0.05
Pleuroptya ruralis	Mother of pearl (Crambidae)	0.41 ± 0.18	0.15 ± 0.16	0.06 ± 0.03
Blastobasis decolorella	(Blastobasidae)	0.35 ± 0.19	0.12 ± 0.14	0.06 ± 0.04
Pandemis cerasana [b]	Barred fruit-tree tortrix (Tortricidae)	0.35 ± 0.18	0.10 ± 0.12	0.07 ± 0.05
Celypha lacunana	(Tortricidae)	0.29 ± 0.12	0.07 ± 0.08	0.07 ± 0.04
Dipleurina lacustrata	(Crambidae)	0.29 ± 0.21	0.06 ± 0.07	0.09 ± 0.06
Mompha conturbatella [b]	(Momphidae)	0.29 ± 0.27	0.07 ± 0.09	0.07 ± 0.06
Notocelia uddmanniana	Bramble shoot moth (Tortricidae)	0.24 ± 0.13	0.09 ± 0.10	0.03 ± 0.03
Pandemis heparana [b]	Dark fruit-tree tortrix (Tortricidae)	0.24 ± 0.09	0.10 ± 0.11	0.01 ± 0.01
Blastobasis lignea	(Blastobasidae)	0.18 ± 0.15	0.01 ± 0.02	0.07 ± 0.06
Crambus nemorella	Crambidae	0.18 ± 0.13	0.03 ± 0.04	0.06 ± 0.04
Udea olivalis [b]	(Crambidae)	0.18 ± 0.09	0.06 ± 0.07	0.03 ± 0.02
Apotomis betuletana [b]	(Tortricidae)	0.15 ± 0.10	0.07 ± 0.09	–
Endrosis sarcitrella	(Oecophoridae)	0.15 ± 0.07	0.06 ± 0.07	0.01 ± 0.01
Eudonia murana	(Crambidae)	0.15 ± 0.12	0.06 ± 0.07	0.01 ± 0.01
Numonia advenella [b]	(Pyralidae)	0.15 ± 0.10	0.06 ± 0.06	0.01 ± 0.01
Udea lutealis	(Crambidae)	0.15 ± 0.07	0.01 ± 0.02	0.06 ± 0.03

Latin Name	**Common name (and Family)**	**Abundance per site (mean ± SE)**	**Abundance per trap (edge) (mean ± SE)**	**Abundance per trap (interior) (mean ± SE)**
Cnephasia asseclana	Flax tortrix (Tortricidae)	0.09 ± 0.06	–	0.04 ± 0.03
Epiblema cynosbatella	(Tortricidae)	0.09 ± 0.09	0.04 ± 0.06	–
Eucosma cana	(Tortricidae)	0.09 ± 0.06	–	0.04 ± 0.03
Hofmannophila pseudospretella	Brown house moth (Oecophoridae)	0.09 ± 0.05	0.03 ± 0.04	0.01 ± 0.01
Mompha lacteella/propinquella [c]	(Momphidae)	0.09 ± 0.06	–	0.04 ± 0.03
Plodia interpunctella	Indian meal moth (Pyralidae)	0.09 ± 0.06	0.01 ± 0.02	0.03 ± 0.03
Blastodacna atra [c]	Apple pith moth (Cosmopterigidae)	0.06 ± 0.04	0.01 ± 0.02	0.01 ± 0.01
Clepsis spectrana	Cyclamen tortrix (Tortricidae)	0.06 ± 0.06	–	0.03 ± 0.03
Coleophora alticolella	(Coleophridae)	0.06 ± 0.06	–	0.03 ± 0.03
Coleophora serratella	(Coleophridae)	0.06 ± 0.06	0.03 ± 0.04	–
Epinotia solandriana [b]	(Tortricidae)	0.06 ± 0.06	0.01 ± 0.02	0.01 ± 0.01
Epinotia subocellana [b]	(Tortricidae)	0.06 ± 0.06	0.03 ± 0.04	–
Epinotia tenerana [b]	Nut bud moth (Tortricidae)	0.06 ± 0.04	–	0.01 ± 0.01
Eucosma hohenwartiana	(Tortricidae)	0.06 ± 0.04	0.01 ± 0.02	0.01 ± 0.01
Eurrhypara hortulata	Small magpie (Crambidae)	0.06 ± 0.04	0.03 ± 0.04	–
Nemapogon cloacella [b]	Cork moth (Tineidae)	0.06 ± 0.04	0.03 ± 0.04	–
Spuleria flavicaput [b]	(Cosmopterigidae)	0.06 ± 0.04	0.03 ± 0.04	–
Ypsolopha ustella [b]	(Yponomeutidae)	0.06 ± 0.06	0.01 ± 0.02	0.01 ± 0.01
Acleris bergmanniana [b]	(Tortricidae)	0.03 ± 0.03	0.01 ± 0.02	–
Acleris forsskaleana [b]	(Tortricidae)	0.03 ± 0.03	–	0.01 ± 0.01
Acleris variegana	Garden rose tortrix (Tortricidae)	0.03 ± 0.03	–	0.01 ± 0.01
Agonopterix conterminella [b]	(Oecophoridae)	0.03 ± 0.03	–	0.01 ± 0.01
Agonopterix nervosa	(Oecophoridae)	0.03 ± 0.03	0.01 ± 0.02	–
Aleimma loeflingiana [b]	(Tortricidae)	0.03 ± 0.03	0.00 ± 0.00	0.01 ± 0.01
Argyresthia bonnetella	(Yponomeutidae)	0.03 ± 0.03	0.01 ± 0.02	–
Blastodacna hellerella [b]	(Cosmopterigidae)	0.03 ± 0.03	0.01 ± 0.02	0.00 ± 0.00

Latin Name	**Common name (and Family)**	**Abundance per site (mean ± SE)**	**Abundance per trap (edge) (mean ± SE)**	**Abundance per trap (interior) (mean ± SE)**
Borkhausenia fuscescens	(Oecophoridae)	0.03 ± 0.03	–	0.01 ± 0.01
Bryotropha terrella	(Gelechiidae)	0.03 ± 0.03	0.01 ± 0.02	–
Carpatolechia notatella[b]	Sallow-leaf groundling (Gelechiidae)	0.03 ± 0.03	–	0.03 ± 0.01
Carcina quercana[b]	(Oecophoridae)	0.03 ± 0.03	0.03 ± 0.03	–
Cnephasia incertana	Light Grey Tortrix (Tortricidae)	0.03 ± 0.03	–	0.01 ± 0.01
Cydia fagiglandana [b]	(Tortricidae)	0.03 ± 0.03	–	0.01 ± 0.01
Elophila nymphaeata	Brown China-mark (Crambidae)	0.03 ± 0.03	0.01 ± 0.02	–
Epiblema mercurella	(Pyralidae)	0.03 ± 0.03	–	0.01 ± 0.01
Epinotia abbreviana [b]	(Tortricidae)	0.03 ± 0.03	–	0.01 ± 0.01
Epinotia fraternana [bc]	(Tortricidae)	0.03 ± 0.03	0.01 ± 0.02	–
Esperia sulphurella	(Oecophoridae)	0.03 ± 0.03	0.01 ± 0.02	–
Gypsonoma sociana [b]	(Tortricidae)	0.03 ± 0.03	0.01 ± 0.02	0.00 ± 0.00
Metendothenia atropunctana [b]	(Tortricidae)	0.03 ± 0.03	0.01 ± 0.02	–
Notocelia aquana	(Tortricidae)	0.03 ± 0.03	–	0.01 ± 0.01
Platyptilia pallidactyla	(Pterophoridae)	0.03 ± 0.03	–	0.01 ± 0.01
Scoparia subfusca	(Crambidae)	0.03 ± 0.03	–	0.01 ± 0.01
Stigmella salicis	(Nepticulidae)	0.03 ± 0.03	0.01 ± 0.02	–
Syndemis musculana [b]	(Tortricidae)	0.03 ± 0.03	0.01 ± 0.02	–
Tachystola acroxantha	(Oecophoridae)	0.03 ± 0.03	0.01 ± 0.02	–
Tortrix viridana [b]	Green oak tortrix (Tortricidae)	0.03 ± 0.03	–	0.01 ± 0.01
Udea prunalis [b]	(Crambidae)	0.03 ± 0.03	–	0.01 ± 0.01
Zeiraphera griseana [b]	(Tortricidae)	0.03 ± 0.03	–	0.01 ± 0.01

[b] Species classified as 'woodland species' as they are known to use woodland as their main habitat or to have a woody plant as their larval food (using Emmet and Heath 1991; Waring and Townsend 2003). [c] Species which are listed as nationally scarce (Davis 2002).

Appendix 5.8.3 List of macromoths collected

Scientific Name	Common name (and Family)	Abundance per site (mean ± SE)	Abundance per trap (edge) (mean ± SE)	Abundance per trap (interior) (mean ± SE)
Alcis repandata[b]	Mottled beauty (G)	5.82 ± 1.86	1.59 ± 0.22	4.24 ± 0.54
Apamea monoglypha	Dark arches (N)	4.76 ± 1.51	1.44 ± 0.19	3.32 ± 0.42
Noctua pronuba	Large yellow underwing (N)	4.24 ± 1.06	3.12 ± 0.32	1.12 ± 0.14
Campaea margaritata[b]	Light emerald (G)	4.15 ± 1.80	0.91 ± 0.17	3.24 ± 0.54
Xestia triangulum	Double square-spot (N)	2.38 ± 0.69	0.94 ± 0.14	1.44 ± 0.16
Hydriomena furcate [b]	July highflyer (G)	1.88 ± 0.66	0.65 ± 0.12	1.24 ± 0.17
Cosmia trapezina [b]	Dun-bar (N)	1.59 ± 0.61	0.71 ± 0.13	0.88 ± 0.16
Noctua janthina	Lesser broad-bordered yellow underwing (N)	1.59 ± 0.71	0.71 ± 0.12	0.85 ± 0.17
Noctua comes	Lesser yellow underwing (N)	1.41 ± 0.54	0.65 ± 0.07	0.76 ± 0.16
Hepialus fusconebulosa	Map-winged swift (H)	1.18 ± 0.56	0.59 ± 0.14	0.59 ± 0.11
Xanthorhoe montanata	Silver-ground carpet (G)	1.09 ± 0.40	0.44 ± 0.09	0.65 ± 0.10
Xestia baja	Dotted clay (N)	0.94 ± 0.47	0.68 ± 0.13	0.26 ± 0.08
Chloroclysta truncata	Common marbled marpet (G)	0.79 ± 0.42	0.29 ± 0.09	0.50 ± 0.12
Ochropacha duplaris [b]	Common lutestring (T)	0.79 ± 0.30	0.29 ± 0.06	0.50 ± 0.10
Colostygia pectinataria	Green carpet (G)	0.71 ± 0.36	0.32 ± 0.07	0.41 ± 0.09
Cabera pusaria[b]	Common white wave (G)	0.68 ± 0.21	0.26 ± 0.05	0.41 ± 0.06
Mythimna impura	Smoky wainscot (N)	0.65 ± 0.36	0.59 ± 0.18	0.06 ± 0.02
Graphiphora augur [b c]	Double dart (N)	0.62 ± 0.36	0.21 ± 0.04	0.41 ± 0.12
Perizoma alchemillata	Small rivulet (G)	0.62 ± 0.31	0.26 ± 0.07	0.35 ± 0.08
Cerapteryx graminis	Antler moth (N)	0.59 ± 0.18	0.44 ± 0.08	0.15 ± 0.03
Idaea biselata [b]	Small fan-footed wave (G)	0.59 ± 0.18	0.24 ± 0.05	0.35 ± 0.07
Bupalus piniaria[b]	Bordered white (G)	0.53 ± 0.50	0.44 ± 0.16	0.09 ± 0.03
Ptilodon capucina [b]	Coxcomb prominent (No)	0.53 ± 0.36	0.24 ± 0.07	0.29 ± 0.07
Ecliptopera silaceata	Small phoenix (G)	0.50 ± 0.22	0.29 ± 0.08	0.21 ± 0.04
Idaea aversata	Riband wave (G)	0.47 ± 0.25	0.24 ± 0.07	0.24 ± 0.04

Latin Name	Common name (and Family)	Abundance per site (mean ± SE)	Abundance per trap (edge) (mean ± SE)	Abundance per trap (interior) (mean ± SE)
Diarsia brunnea[b]	Purple clay (N)	0.32 ± 0.15	0.06 ± 0.02	0.26 ± 0.06
Diarsia mendica[b]	Ingrailed clay (G)	0.32 ± 0.14	0.15 ± 0.03	0.18 ± 0.05
Hypena proboscidalis	Snout (N)	0.32 ± 0.12	0.12 ± 0.03	0.21 ± 0.04
Cabera exanthemata[b]	Common wave (G)	0.29 ± 0.19	0.09 ± 0.03	0.21 ± 0.06
Eupithecia vulgata	Common pug (G)	0.29 ± 0.16	0.15 ± 0.05	0.15 ± 0.04
Scotopteryx chenopodiata	Shaded broad-bar (G)	0.24 ± 0.13	0.18 ± 0.05	0.06 ± 0.02
Crocallis elinguaria[b]	Scalloped oak (G)	0.21 ± 0.13	0.09 ± 0.03	0.12 ± 0.03
Epirrhoe alternata	Common carpet (G)	0.21 ± 0.10	0.12 ± 0.03	0.09 ± 0.04
Naenia typical[c]	Gothic (N)	0.21 ± 0.13	0.15 ± 0.05	0.06 ± 0.02
Odontopera bidentata[b]	Scalloped hazel (G)	0.21 ± 0.13	0.06 ± 0.02	0.15 ± 0.05
Oligia fasciuncula	Middle-barred minor (N)	0.21 ± 0.13	0.12 ± 0.03	0.09 ± 0.03
Opisthograptis luteolata[b]	Brimstone moth (G)	0.21 ± 0.08	0.06 ± 0.02	0.15 ± 0.04
Thera Britannica[b]	Spruce carpet (G)	0.21 ± 0.10	0.06 ± 0.02	0.15 ± 0.04
Xanthorhoe designata	Flame carpet (G)	0.21 ± 0.08	0.12 ± 0.03	0.09 ± 0.03
Diarsia rubi[c]	Small square-spot (N)	0.18 ± 0.09	0.06 ± 0.03	0.12 ± 0.04
Eulithis pyraliata	Barred straw (G)	0.18 ± 0.15	0.18 ± 0.06	–
Lampropteryx suffumata[b]	Water carpet (G)	0.18 ± 0.11	0.09 ± 0.03	0.09 ± 0.03
Lomaspilis marginata[b]	Clouded border (G)	0.18 ± 0.11	–	0.18 ± 0.05
Xanthorhoe fluctuate[c]	Garden carpet (G)	0.18 ± 0.07	0.09 ± 0.03	0.09 ± 0.03
Xestia sexstrigata	Six-striped rustic (N)	0.18 ± 0.18	0.18 ± 0.07	–
Zanclognatha tarsipennalis	Fan-foot (N)	0.18 ± 0.08	0.12 ± 0.03	0.06 ± 0.02
Eulithis prunata	Phoenix (G)	0.15 ± 0.06	0.03 ± 0.01	0.12 ± 0.03
Herminia grisealis[b]	Small fan-foot (N)	0.15 ± 0.07	0.09 ± 0.03	0.09 ± 0.03
Mesapamea secalis	Common/Remm's/Lesser common rustic (N)	0.15 ± 0.07	0.15 ± 0.03	–
Ochropleura plecta	Flame shoulder (N)	0.15 ± 0.10	0.09 ± 0.03	0.06 ± 0.02
Ourapteryx sambucaria[b]	Swallow-tailed moth (G)	0.15 ± 0.10	0.09 ± 0.03	0.06 ± 0.02

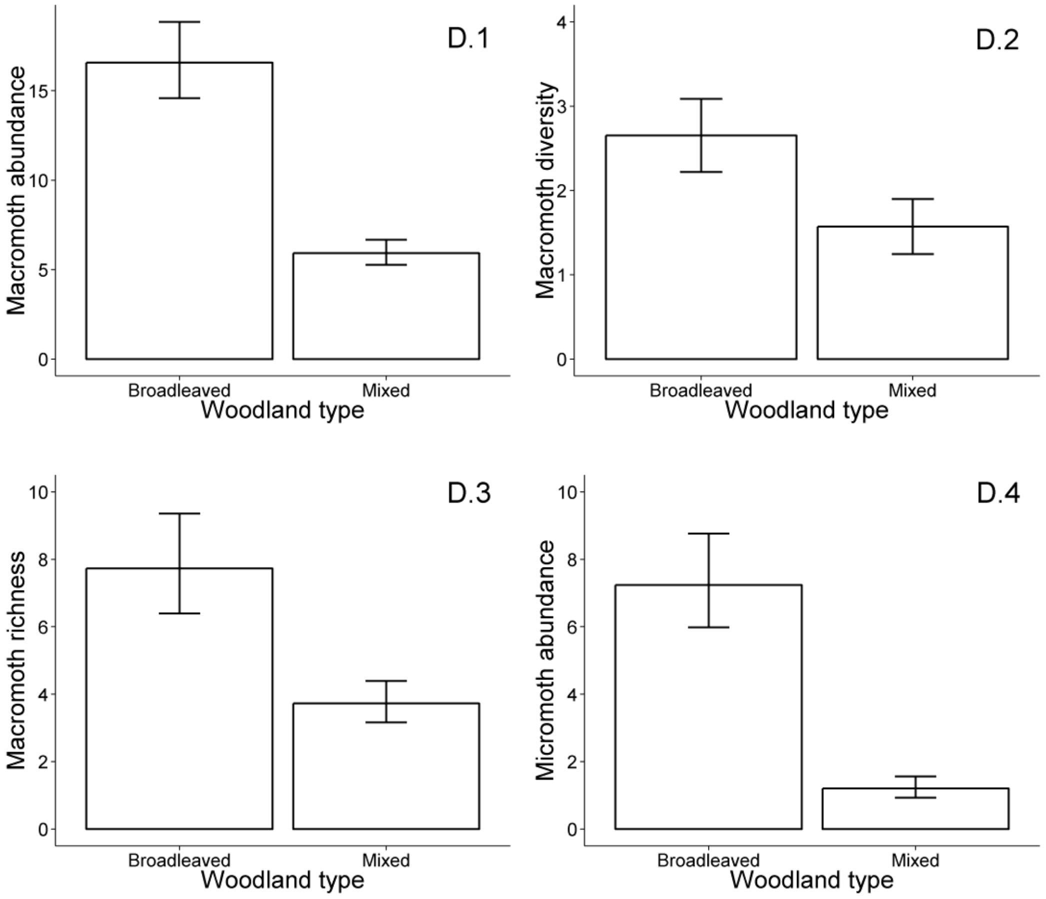
Latin Name	**Common name (and Family)**	**Abundance per site (mean ± SE)**	**Abundance per trap (edge) (mean ± SE)**	**Abundance per trap (interior) (mean ± SE)**
Laothoe populi [b]	Poplar hawk-moth (S)	0.12 ± 0.07	0.09 ± 0.03	0.03 ± 0.01
Noctua fimbriata [b]	Broad-bordered yellow underwing (N)	0.12 ± 0.07	0.06 ± 0.02	0.06 ± 0.02
Amphipyra berbera[b]	Svensson's copper underwing (N)	0.09 ± 0.06	0.06 ± 0.02	0.06 ± 0.02
Apamea crenata	Clouded-bordered brindle (N)	0.09 ± 0.05	0.03 ± 0.01	0.06 ± 0.02
Autographa pulchrina	Beautiful golden Y (N)	0.09 ± 0.05	0.03 ± 0.01	0.06 ± 0.02
Cidaria fulvata [b]	Barred yellow (G)	0.09 ± 0.05	0.03 ± 0.01	0.12 ± 0.03
Deileptenia ribeata [b]	Satin beauty (G)	0.09 ± 0.06	0.06 ± 0.03	0.03 ± 0.01
Diachrysia chrysitis	Burnished brass (N)	0.09 ± 0.05	0.09 ± 0.03	–
Eupithecia assimilata	Currant pug (G)	0.09 ± 0.09	0.03 ± 0.01	0.06 ± 0.03
Geometra papilionaria [b]	Large emerald (G)	0.09 ± 0.06	0.03 ± 0.01	0.06 ± 0.03
Hylaea fasciaria [b]	Barred red (G)	0.09 ± 0.05	0.06 ± 0.02	0.03 ± 0.01
Anaplectoides prasina [b]	Green arches (N)	0.06 ± 0.04	0.03 ± 0.01	0.03 ± 0.01
Arctia caja	Garden tiger (A)	0.06 ± 0.06	0.06 ± 0.02	–
Axylia putris	Flame (N)	0.06 ± 0.04	0.03 ± 0.01	0.03 ± 0.01
Chloroclysta citrate [b]	Dark marbled carpet (G)	0.06 ± 0.04	0.09 ± 0.03	0.03 ± 0.01
Eupithecia tantillaria [b]	Dwarf pug (G)	0.06 ± 0.04	–	0.06 ± 0.02
Lacanobia thalassina [b]	Pale-shouldered brocade (N)	0.06 ± 0.04	–	0.06 ± 0.02
Pasiphila rectangulata [b]	Green pug (G)	0.06 ± 0.04	–	0.06 ± 0.02
Perizoma didymata	Twin-spot carpet (G)	0.06 ± 0.04	0.03 ± 0.01	0.03 ± 0.01
Photedes minima	Small dotted buff (N)	0.06 ± 0.04	0.06 ± 0.02	–
Plemyria rubiginata	Blue-borded carpet (G)	0.06 ± 0.06	–	0.06 ± 0.02
Selenia dentaria [b]	Early thorn (G)	0.06 ± 0.06	–	0.06 ± 0.02
Thyatira batis [b]	Peach blossom (T)	0.06 ± 0.04	0.03 ± 0.01	0.03 ± 0.01
Venusia cambric [b]	Welsh wave (G)	0.06 ± 0.04	0.03 ± 0.01	0.03 ± 0.01
Abrostola tripartita	Spectacle (N)	0.03 ± 0.03	0 – 0	0.03 ± 0.01
Amphipyra tragopoginis [c]	Mouse moth (N)	0.03 ± 0.03	0.03 ± 0.01	–
Autographa bractea	Gold spangle (N)	0.03 ± 0.03	0.03 ± 0.01	–

Latin Name	Common name (and Family)	Abundance per site (mean ± SE)	Abundance per trap (edge) (mean ± SE)	Abundance per trap (interior) (mean ± SE)
Camptogramma bilineata[b]	Yellow shell (G)	0.03 ± 0.03	–	0.03 ± 0.01
Euchoeca nebulata [b]	Dingy shell (G)	0.03 ± 0.03	–	0.03 ± 0.01
Eulithis populata	Northern spinach (G)	0.03 ± 0.03	0.03 ± 0.01	–
Eupithecia absinthiata	Wormwood pug (G)	0.03 ± 0.03	0.06 ± 0.02	0.03 ± 0.01
Eupithecia pusillata	Juniper pug (G)	0.03 ± 0.03	0.03 ± 0.01	–
Eupithecia subfuscata	Grey pug (G)	0.03 ± 0.03	–	0.03 ± 0.01
Hadena bicruris	Lychnis (N)	0.03 ± 0.03	0.03 ± 0.01	–
Hepialus hecta [b]	Gold swift (H)	0.03 ± 0.03	0.03 ± 0.01	–
Hepialus humuli	Ghost moth (H)	0.03 ± 0.03	–	0.03 ± 0.01
Luperina testacea	Flounced rustic (N)	0.03 ± 0.03	–	0.03 ± 0.01
Oligia versicolor	Marbled minor / Tawny marbled minor (N)	0.03 ± 0.03	0.03 ± 0.01	–
Petrophora chlorosata [b]	Brown silver-line (G)	0.03 ± 0.03	0.03 ± 0.01	–
Phalera bucephala [b]	Buff-tip (No)	0.03 ± 0.03	0.03 ± 0.01	–
Plusia festucae	Gold spot / Lempke's gold spot (N)	0.03 ± 0.03	0.03 ± 0.01	–
Schrankia costaestrigalis	Pinion-streaked snout (N)	0.03 ± 0.03	–	0.03 ± 0.01
Xanthia icteritia [c]	Sallow (N)	0.03 ± 0.03	0.03 ± 0.01	–
Xestia sexstrigata	Six-striped rustic (N)	0.03 ± 0.03	0.03 ± 0.01	–

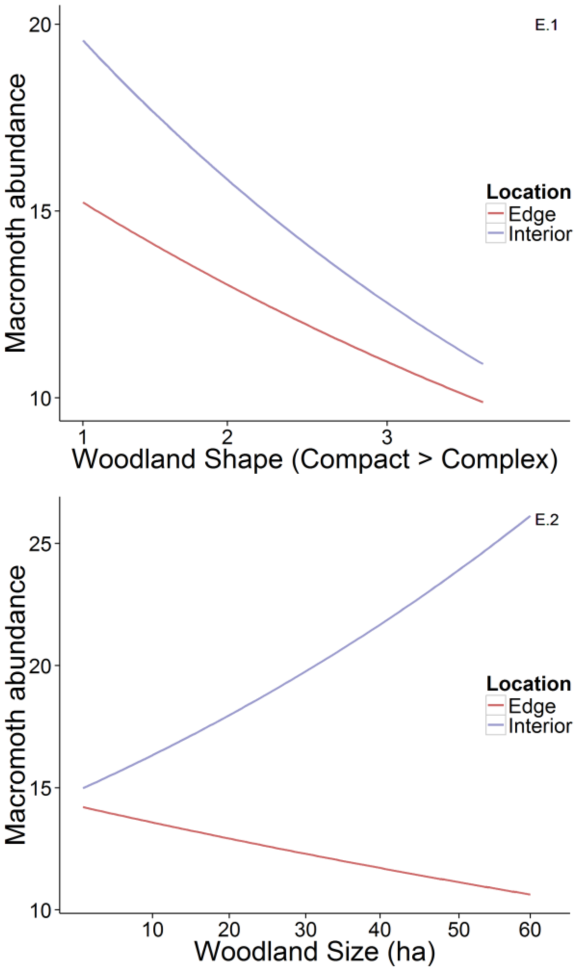
[a] List of family codes: Arctiidae (A), Geometridae (G), Gelechiidae (GE), Hepialidae (H), Noctuidae (N), Notodontidae (NO), Sphingidae (S) and Thyatiridae (T)

[b] Species classified as 'woodland species' as they are known to use woodland as their main habitat or to have a woody plant as their larval food (using Emmet and Heath 1991; Waring and Townsend 2003). [c] Species which are classified as of conservation concern after declining by 75% or more between 1968 and 2007 (Fox et al. 2013).

Appendix 5.8.4 Predicted measurements of moth assemblages plotted against woodland type; the strongest categorical predictor in each model. Error bars represent 95% confidence intervals around the predictions. The prediction plot is calculated by setting all other parameters at their median observed values in the model.



Appendix 5.8.5 Interaction plots of moth abundance for patch configuration variables.



Chapter 6

Opportunities for improving the foraging potential of urban waterways for bats

An adapted version of this chapter is in press as:

Lintott, P. R., Bunnefeld, N. & Park, K. J. (2015) Opportunities for improving the foraging potential of urban waterways for bats. *Biological Conservation*. *In press*

6.1 Summary

The rapid rate of urbanisation over the past century has occurred over a relatively small proportion of the earth’s surface, yet it has had considerable ecological impact at a global scale. Urban waterways have historically been regarded as a disposable resource for human benefit which has had severe biological consequences. River rehabilitation schemes are attempting to address this; however restoration is frequently undertaken with minimal scientific input and fails to improve biodiversity. Many bat species are strongly associated with aquatic or adjacent riparian habitats but respond negatively to the built environment; however, we know little about the utilisation of urban waterways by bats. I therefore conducted a large scale, multi-species study that examined how local habitat characteristics and the composition and heterogeneity of the surrounding landscape influence bat presence and activity along urban waterways. I recorded a total of 19,689 bat passes of seven species/genera from 30 urban waterways throughout Britain. I show that the built environment can negatively affect a variety of species from the riparian zone up to 3km from a waterway. Additionally, *Myotis* spp. activity was greater in waterways bounded by steep banksides and clear of invasive plant species. I also found differences in the response of two cryptic pipistrelle species to the built environment at multiple spatial scales indicating the difficulties of assessing how adaptable even morphologically similar species are to urbanisation. Beneficial urban waterway rehabilitation schemes for bats require management at multiple spatial scales. At a local scale, retaining a vegetated riparian zone, with a reduction in invasive aquatic plant species, is likely to benefit a variety of taxa. At a landscape scale, our results show that the influence of

the built environment can stretch a considerable distance highlighting the necessity for conservation funding to be spent on the implementation of landscape scale environmental improvement schemes that encompass the entire urban matrix.

6.2 Introduction

The unprecedented rate of urbanisation over the past century has occurred on a small proportion of the earth’s terrestrial surface (<3%), yet its ecological footprint is widespread and its impact global (Grimm et al. 2008). Urbanisation can fragment and dramatically modify large parcels of land, often permanently with little chance for recovery (McKinney 2006). As urban landscapes expand, they influence an increasing proportion of regional, national and global biodiversity (Dearborn & Kark 2010). Understanding how species respond to the built environment is therefore essential for mitigating and managing urban ecosystems.

Urban waterways have historically been regarded as a disposable resource for human benefit including their modification for flood mitigation, water supply, and use as sinks for pollution (Paul & Meyer 2001). These alterations have had severe biological consequences creating disturbed ecological systems with water quality problems, highly variable flow regimes and an extremely modified physical habitat (Beavan et al. 2001). However in recent decades, increasing recognition of the importance of urban green space (including urban waterways) for its environmental and human wellbeing benefits has led to efforts to rehabilitate urban waterways (Matsuoka & Kaplan 2008). Supported by legislation and policy frameworks (e.g. the EU Water Framework Directive, the Australian Commonwealth Wetlands Policy 1997), pollution problems and habitat degradation are being addressed for urban waterways and associated surrounding riparian habitat. Despite the fact that urban waterways are frequently recorded as key habitats within the built environment for maintaining biodiversity (e.g. Gaisler et al. 1998), restoration efforts in these habitats have often failed to increase native biodiversity for taxa including fish and benthic macroinvertebrates (Stranko et al. 2012). Many river restoration projects are undertaken with minimal scientific input (Wohl et al. 2005), indicating the need for a greater understanding of species requirements to inform management strategies.

Within fragmented and disturbed landscapes, urban waterways may function as corridors linking fragmented greenspace patches (i.e. woodland, parkland; Bryant 2006) and connect the urban landscape with surrounding rural habitat. Waterways can therefore improve gene flow between populations, act as migration routes out of urban areas, and facilitate movement throughout the urban matrix whilst avoiding areas of high anthropogenic disturbance (Baschak & Brown 1995). However, waterways can also increase the dispersal of invasive species. For example, Dallimer et al. (2012) found that neophyte richness increased in the direction of water flow along urban rivers. Understanding which local factors (e.g. riparian vegetation characteristics) influence the use of waterways by species is essential in ensuring that native species are able to utilise these ecological corridors to travel within the urban environment. Additionally, there is an increasing emphasis being placed on understanding species distributions within urban areas at a landscape scale (Ignatieva et al. 2011), for example by determining how the surrounding built environment may influence which species are able to access waterways. Examining how best to restore biodiversity in urban rivers and canals therefore requires assessment at multiple spatial scales to examine how species respond to modified waterways and the complexity of the surrounding urban matrix.

The prevalence of species within the urban matrix depends on their capacity to survive and adapt to heavily modified landscapes and anthropogenic disturbances. In this regard, although many species of bats (Chiroptera) have adapted to exploit human resources (e.g. insects at artificial light sources; Mathews et al. 2015), the majority of bat species are negatively impacted by urbanisation (Russo & Ancillotto 2014). The highest rates of bat foraging activity within the urban matrix are often found by waterways due to drinking opportunities and high insect prey concentrations (Li & Wilkins 2014). Although a substantial volume of work has been conducted in non-urban environments, investigating how vegetation characteristics and habitat composition at multiple spatial scales influence bat use of waterways (e.g. Akasaka et al. 2009), relatively little is known about the factors that influence foraging bats along urban waterways.

Within our study area of Britain there are 17 bat species, a few of which are strongly associated with aquatic environments. *M. daubentonii* is widespread throughout Europe and parts of Asia and is classified as a species of ‘Least Concern’ by the IUCN Red List of Threatened Species (2008), however its strong association with riverine habitats makes this species particularly vulnerable to changes in river management which may isolate populations or have a severe effect on available foraging habitat (Warren et al. 2000). Langton et al. (2010) found that *M. daubentonii* activity was negatively associated with the percentage of built land in the surrounding 1 km indicating that this species may be negatively impacted by urbanisation.

The two most common species of pipistrelle bat found within the study area, *P. pygmaeus* and *P. pipistrellus*, are cryptic species with very similar flight morphologies (Jones & Van Parijs 1993) but different foraging behaviours. In a non-urban setting, Davidson-Watts et al. (2006) found that *P. pygmaeus* preferentially selected riparian habitats over all other habitat types in its core foraging areas, whereas *P. pipistrellus* was more of a generalist, foraging in a wider range of habitats. Scott et al. (2009) found that significantly more *P. pygmaeus* and *P. pipistrellus* feeding buzzes were recorded in sites with better quality riparian zones. Little is known of the response of these species to the built environment although Hale et al. (2012) found that *P. pipistrellus* activity at urban ponds peaked with moderate levels of adjacent urban grey space.

This paper addresses how waterway and bank vegetation characteristics and the composition of the riparian zone influence activity levels for a range of bat species/genera. Given their relatively high mobility, I also assess how the wider landscape influences bat activity. Additionally, I examine if two morphologically similar species respond differently to the extent of urban grey space. I use these results to recommend management strategies to protect and improve urban waterways for the benefit of bats.

6.3 Materials & methods

6.3.1 Site selection

A total of 30 stretches of urban waterways within Britain were identified using digital maps (EDINA 2013). Stretches of waterway measuring at least 8km in length, where a minimum of a third of the watercourse was contained within an urban area, were selected (Figure 6.1). Urban areas were designated as those where urban cover was the dominant land use within a 1km grid square as categorised by the UK Land Cover Map 2000. Waterways were selected by latitude, longitude, safety issues (e.g. avoiding stretches of river containing weirs), and degree of urbanisation in the surrounding 1km using a stratified random sampling method. Sites surveyed on consecutive nights were a minimum of 50km apart to minimise any bias. Starting points were randomised among sites to ensure there was no spatial bias towards urban or rural areas. Each waterway was surveyed once by a single surveyor. I recognise that a single visit to each waterway provides only a coarse description of local bat activity but here we are interested in the relative influence of waterway characteristics on bat activity which requires that the number of replicates is maximised.

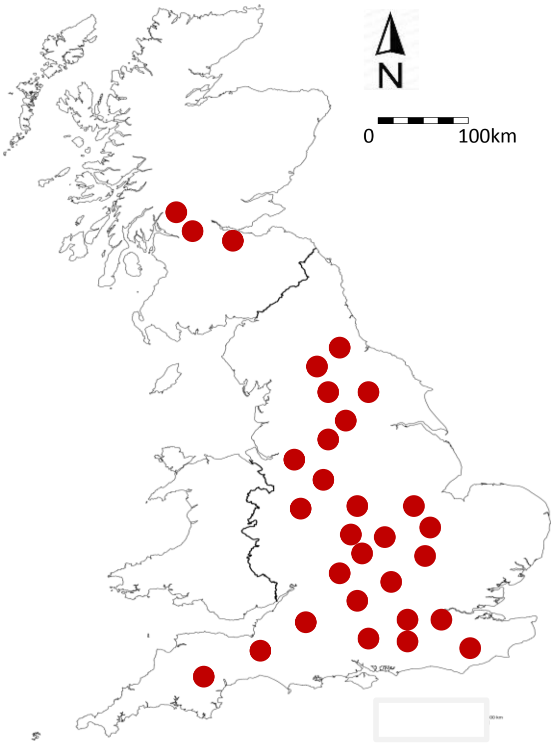


Figure 6.1 Surveyed urban waterways across Britian. Reproduced from Ordnance Survey map data by permission of the Ordnance Survey © Crown copyright 2001.

6.3.2 Vegetation surveys

Vegetation surveys were conducted on the same day as the bat survey to ensure that appropriate vegetative conditions were recorded. A total of 16 point count locations were designated along each waterway, a minimum of 400m apart. Vegetation characteristics, based upon the Environment Agency's River Habitat Survey (Raven et al. 1998), were recorded at each location (listed in section 6.3.6.1).

6.3.3 Bat surveys

Determining how bats respond to waterway quality and characteristics is difficult given that the vast majority of waterway surveys (e.g. Langton et al. 2010) are conducted bankside, which limits surveying to those locations where the bankside is accessible (i.e. missing heavily vegetated areas or stretches of river bounded by private land). I therefore used the technique of surveying by kayak to enable us to record bat activity along entire stretches of waterway through contrasting landscapes.

Bat activity was quantified using a frequency division bat detector (Anabat SD2, Titley Electronics) with the detector microphone mounted on a helmet. The helmet was worn by the surveyor who paddled the waterway stopping for 8 minute point counts at each of the 16 locations surveyed for vegetation. During surveying the microphone was approximately 1m above the river surface and pointed in the direction of travel. Each transect section between point counts was paddled at approximately 5km/h. Wherever possible, the transect sections and point counts were undertaken 4 metres from the right hand bank to minimise differences in non-aquatic habitat surveyed between point counts. Artificial lighting was recorded at each point count using a light meter (Kewtech KEWLM1 Light Meter). Surveying was conducted between May and August in 2012. Each survey commenced 30 minutes after sunset, and was conducted in dry weather, when the temperature was ≥ 10°C, and wind speed ≤ 4 on the Beaufort scale.

6.3.4 Sound analysis

All bat recordings were analysed using Analook W (Corben 2006). One bat pass was defined as a continuous sequence of at least two echolocation calls from a passing bat (Walsh & Harris 1996). All seven bat genera present within the study area can be identified from detector recordings based upon the search-phase of their echolocation call. However, it can often be difficult to distinguish between the echolocation calls of species within the same bat genus due to similarities in call structure (Schnitzler & Kalko 2001). As a consequence, recordings of *Myotis*, *Nyctalus*, and *Plecotus* were identified to genus level and were grouped together within genera-wide categories. The three *Pipistrellus* species in this area (*P. pipistrellus*, *P. pygmaeus* and *P. nathusii*) can be determined by the characteristic frequency (Fc = the frequency at the right hand end of the flattest portion of a call; Corben 2006) of their search-phase echolocation calls. Bat passes with a Fc of between 49 and 51 kHz were classed as *Pipistrellus* spp..

6.3.5 Landscape analysis

Point count locations and transect route were recorded using the BatNav GPS unit (Wildwood Ecology) and plotted using ArcGIS 10 (ESRI Inc 2013). Buffers of 200m were placed around each point count location covering the waterway and the surrounding riparian landscape. Bats may perceive the landscape at different scales (e.g. Fabianek et al. 2011; Dixon 2012), therefore buffers of 1 and 3km were placed around each transect to calculate the composition of the wider landscape. I used data from the OS MasterMap Topography Layer (EDINA 2013) to reclassify the landscape within each buffer into a set of discrete biotope types. These were (i) grey space (e.g. buildings, roads); (ii) green space (gardens, parkland, managed grassland, farmland); (iii) inland freshwater and (iv) woodland. The Shannon diversity index (SHDI, a measure of landscape heterogeneity) was calculated as previous studies have found that this influences bat foraging activity in human-disturbed landscapes (Fuentes-Montemayor et al. 2013). The proportion of land covered by each biotope, and SHDI were calculated for each buffer using Fragstats v4.0 (McGarigal et al. 2012).

6.3.6 Data analysis

Statistical analysis was conducted at two spatial scales; the local scale (using point count data), and the landscape scale (using all calls recorded on the waterway i.e. point count and transects combined). Data analysis was undertaken using R version 2.14 (R Core Team 2012) using the lme4 (Bates et al. 2013), effects (Fox 2003), and ggplot2 packages (Wickham 2009).

6.3.6.1 Local vegetation and habitat characteristics

I performed a series of Generalised Linear Mixed-Effects models (GLMMs) with binomial error distribution and a logit link to quantify the influence of vegetation and riparian habitat type on bats. A binomial model was run for each species/genera using presence/absence at each point count (n=480) as the response variable to account for highly skewed count data whilst losing relatively little information. Waterway was included as a random (grouping) factor (n=30) to account for pseudoreplication of multiple point counts along each waterway. Based upon vegetation characteristics commonly recorded during river habitat surveys and scientific literature on the ecology of urban bats (e.g. Langton et al. 2010) the following predictor variables were included in the model: (i) waterway and bankside vegetation characteristics: bank profile, bank vegetation type (categorised as either manmade, uniform vegetation structure (1 vegetation type), simple vegetation structure (2-3 vegetation types), or complex (≥ 4 vegetation types) where vegetation types were classified into bryophytes, grasses, tall herbs/grasses, scrub or shrubs, and samplings and trees following Raven et al. 1998), extent of waterway overhung by vegetation, and a visual estimation of invasive aquatic species coverage within the waterway (e.g. Floating Pennywort, *Hydrocotyle ranunculoides*) ; (ii) local habitat characteristics: the extent of freshwater, grey space and landscape heterogeneity in the surrounding 200m of the point count. Quadratic terms were fitted if their addition significantly improved model fit. As temperature and date were positively correlated, only date was included as a covariate as it explained a higher amount of variation in the response variable. Artificial lighting was strongly positively correlated with the extent of grey space in the surrounding 200m of the point count. I therefore only included the extent of localised grey space in our models as this gave a better indication of the extent of anthropogenic pressure facing bats particularly at low light levels (i.e. rural locations) where the light meter was not sensitive enough to distinguish slight differences in surrounding artificial lighting. I present the result of the full model including standardised parameters and confidence intervals for all explanatory variables.

Prediction plots were constructed by undertaking simulated draws (n = 2000) from the estimated distribution of one explanatory variable whilst maintaining all other parameters in the model at their median observed values. Spatial auto-correlation was assessed using a spline correlogram of the model residuals (Zuur et al. 2009) and Moran's I test (Paradis et al. 2004). On the one occasion where spatial auto-correlation was observed (*Nyctalus* spp. model), the easting and northing Cartesian coordinates and their interaction were added to the model as explanatory variables.

6.3.6.2 Landscape characteristics

Generalised linear models (GLMs) with a negative binomial distribution were conducted for each species/genera to assess differences in bat activity between waterways surrounded by contrasting landscapes. Given the high collinearity found among landscape metrics (i.e. between the proportions of different biotope types or the same biotope type at differing spatial scales) preliminary analyses were conducted to determine which landscape metrics should be included in the final model. The approach I followed is outlined by Zuur et al. (2009) and is frequently used to determine the most important landscape predictors to include in the full model (e.g. Fuentes-Montemayor et al. 2013). I used individual GLMs, one per biotope per spatial scale, with the total number of passes recorded per waterway, selecting those metrics with the lowest Akaike Information Criterion (AIC). The full model was run with the landscape metric and date included as explanatory variables and offset by the time taken to complete each full transect to account for differences in transect length between waterways. I used the same approach to determine influential explanatory variables as used in the local vegetation and habitat characteristics models (see section 6.3.6.1).

6.3.6.3 Differences between species in their response to urbanisation

I assessed the differences between cryptic species *P. pipistrellus* and *P. pygmaeus* in their response to urbanisation at both a 1 and 3km scale. As the proportion of grey space is highly correlated between these two scales, I present only the results for the spatial scale which had the largest effect size. In order to assess the relative effects of grey space, the model was run with the proportion of point counts containing *P. pygmaeus* to *P. pipistrellus* passes (n=480) as the response variable, with waterway included as a random (grouping) factor (n=30). I used the same approach as section 6.3.6.1 to determine if there was a significant difference between species in their response to urbanisation at the landscape scale. Differential responses to urbanisation were only assessed for pipistrelle species as there is ecological interest in understanding if cryptic species respond differently in their habitat selection.

6.4 Results

I recorded a total of 19,689 bat passes from 30 urban waterways across the U.K (Table 6.1). Of these, 8,825 passes (45%) were of *P. pipistrellus*, 5,649 passes (29%) of *P. pygmaeus*, 3,846 (20%) *Myotis* spp. passes, 505 (3%) *Nyctalus* spp. passes, and 43 *Eptesicus serotinus* (< 1%) passes, 40 *Plecotus auritus* passes (< 1%), and 18 *P. nathusii* passes (< 1%).

Table 6.1 Summary table of the species recorded from 30 urban waterways across Britain.

Species	Total passes recorded	% of bat calls	Waterways recorded (%)	Point counts recorded (%)
Pipistrellus pipistrellus	8825	45	100	58
Pipistrellus pygmaeus	5649	29	90	45
Myotis spp.	3846	20	97	54
Nyctalus spp.	505	3	63	11
Eptesicus serotinus	43	< 1%	17	1
Plecotus auritus	40	< 1%	30	1
Pipistrellus nathusii	18	< 1%	27	1

6.4.1 *Myotis* spp.

The probability of recording *Myotis* spp. was strongly negatively related to the extent of grey space in the riparian zone surrounding urban waterways, negatively related to the presence of invasive plant species and positively associated with bank profile (Table 6.2). At locations where the surrounding habitat contained a low proportion of grey space (10%) there was a 68% probability of recording *Myotis* spp. whilst in locations surrounded by highly urban areas (80% grey space) this was reduced to 32% (Figure 6.2a). In locations with little or no invasive plant species there was a 59-65% probability of recording *Myotis* spp., whereas this declined to to 2% in locations where 30% of the river was covered (Figure 6.2b). Where there was a shallow bank profile (40°) there was a 31% probability of recording *Myotis* spp. whilst in locations with vertical bank sides this increased to a 64% probability (Figure 6.2c).

Myotis spp. activity was negatively related to the proportion of grey space in the surrounding 3km (Appendix 6.7.1). Based on estimated coefficients in Table 6.2, the predicted activity rate of *Myotis* spp. was 188 (95% confidence interval (CI): 94-373) passes in landscapes containing a low proportion of urban grey space (10%). In highly urban areas (40% grey space) the predicted activity rate was only a third of this (predicted 59 passes CI: 26-133) (Figure 6.2d).

6.4.2 *Nyctalus* spp.

The probability of recording Nyctalus *spp.* was greatest at locations with approximately 25% freshwater coverage in the nearby (200m) landscape (Figure 6.3), dropping to < 1% in locations containing either no water or high levels of water (40%). Both the extent of urban grey space and extent of overhanging vegetation were statistically significant but had a low effect size and so little biological significance. There were no significant landscape predictors of *Nyctalus spp.* activity (Table 6.2).

6.4.3 *Pipistrellus pipistrellus*

The proportion of freshwater was the strongest predictor of *P. pipistrellus* presence; where the surrounding habitat was comprised of a low proportion of water (10%), the probability of recording *P. pipistrellus* was 60%, but reduced to 31% in locations where water was a prominent habitat within the local landscape (40%) (Figure 6.4a). The extent of the built environment adjacent to the waterway was also important; in locations where the surrounding habitat contained a low proportion of grey space (10%) there was a 66% probability of recording *P. pipistrellus,* whereas in highly urban areas (80% grey space) this was reduced to 44% (Figure 6.4b). The extent of overhanging vegetation was positively related to *P. pipistrellus* activity; however this was of only marginal significance. There were no significant landscape predictors of *P. pipistrellus* activity (Table 6.3).

Table 6.2 Parameter estimates and likelihood ratio tests of the GLMM for the probability of recording either *Myotis* spp. or *Nyctalus* spp. along an urban waterway. Additionally, the parameter estimate and likelihood ratio test of the GLM for the most important landscape parameter at the most important spatial scale is included.

Species	Scale	Fixed effects	Estimate (± SE)	Log Likelihood	χ2	p
Myotis spp.		Intercept	0.38 ± 0.39			
Myotis spp.	Local	**Bank profile**	**0.23 ± 0.12**	**-288.55**	**3.93**	**0.04**
Myotis spp.	Local	Bank vegetation	0.14 ± 0.37	-287.06	0.94	0.82
Myotis spp.	Local	Date	0.02 ± 0.22	-286.59	0.01	0.92
Myotis spp.	Local	**Invasive species (quadratic)**	**-0.26 ± 0.13**	**-289.73**	**6.28**	**0.01**
Myotis spp.	Local	Overhanging vegetation	0.16 ± 0.12	-287.44	1.7	0.19
Myotis spp.	Local	Freshwater (200m)	-0.01 ± 0.12	-286.59	0.01	0.96
Myotis spp.	Local	**Grey space (200m)**	**-0.46 ± 0.15**	**-291.57**	**10**	**0.002**
Myotis spp.	Local	Landscape heterogeneity (200m)	-0.04 ± 0.13	-286.66	0.15	0.69
Myotis spp.	Landscape	Intercept	-0.50 ± 0.17			
Myotis spp.	Landscape	Date	-0.06 ± 0.17	-343.26	0.11	0.74
Myotis spp.	Landscape	**Proportion of grey space (3km)**	**-0.44 ± 0.17**	**-347.14**	**3.99**	**0.04**
Nyctalus spp.		Intercept	-3.52 ± 0.80			
Nyctalus spp.	Local	Bank profile	0.33 ± 0.19	-141.25	2.17	0.14
Nyctalus spp.	Local	Bank vegetation	1.45 ± 0.83	-142.92	5.51	0.14
Nyctalus spp.	Local	Date	-0.02 ± 0.19	-140.19	0.05	0.82
Nyctalus spp.	Local	Invasive species	0.04 ± 0.20	-140.26	0.19	0.66
Nyctalus spp.	Local	**Overhanging vegetation**	**-0.42 ± 0.29**	**-142.19**	**4.05**	**0.04**
Nyctalus spp.	Local	**Freshwater (200m) quadratic**	**-0.41 ± 0.14**	**-140.16**	**11.52**	**<0.001**
Nyctalus spp.	Local	**Grey space (200m)**	**-0.37 ± 0.25**	**-142.29**	**4.25**	**0.04**
Nyctalus spp.	Local	Landscape heterogeneity (200m)	-0.06 ± 0.18	-140.17	0.01	0.94
Nyctalus spp.	Landscape	Intercept	-2.86 ± 0.30			
Nyctalus spp.	Landscape	Date	0.58 ± 0.31	-196.61	4.03	0.44
Nyctalus spp.	Landscape	Proportion of woodland (1km)	-0.81 ± 0.33	-195.13	2.56	0.11

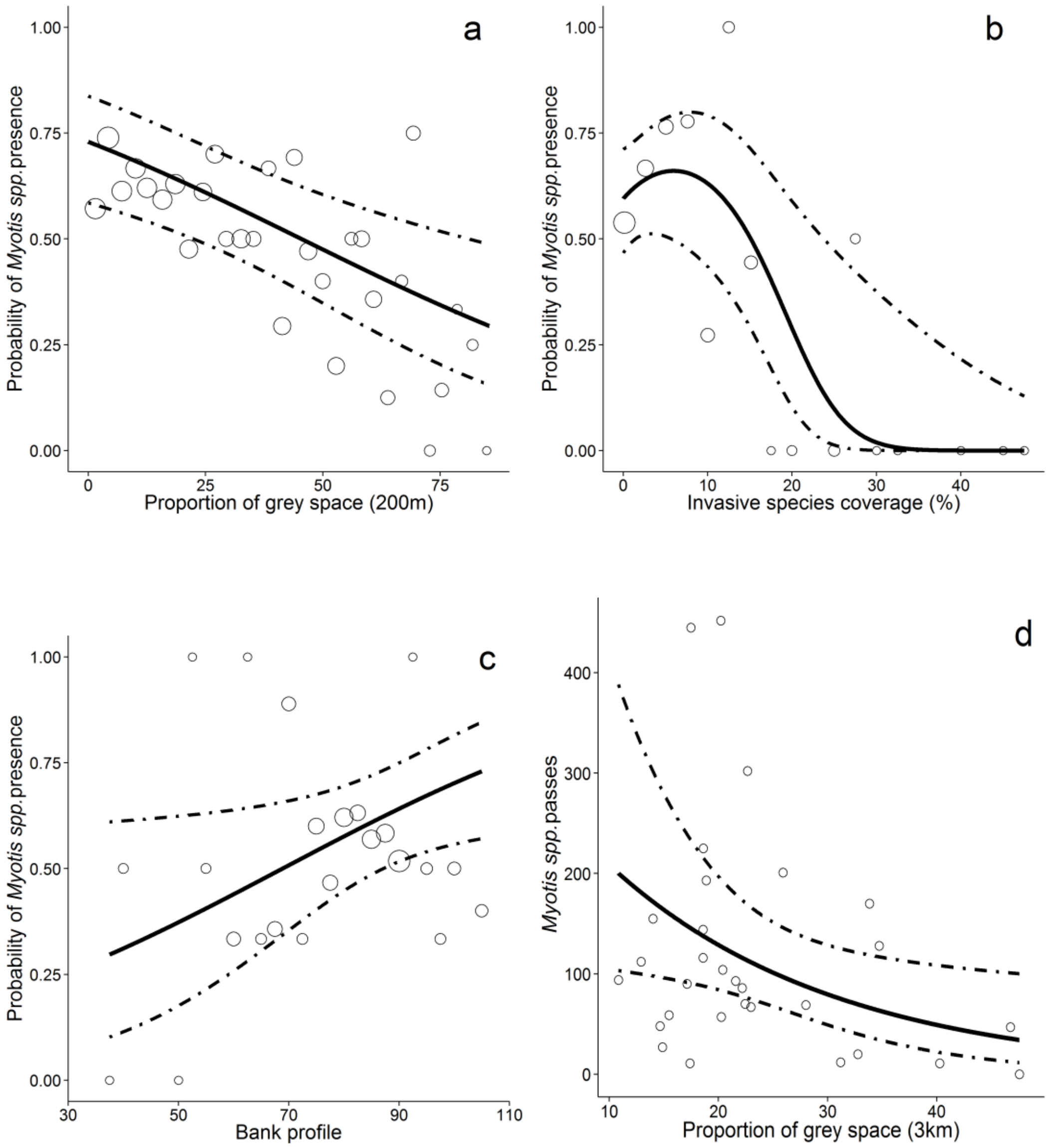


Figure 6.2 Estimated probability of recording *Myotis* spp. against (a) the proportion of grey space in the surrounding 200m of a waterway, (b) the percentage of invasive plant species found within the waterway, and (c) average profile of both banksides. Figure 6.2d, the number of *Myotis* spp. passes in relation to (d) the proportion of grey space in the surrounding 3km. Original data on the presence of *Myotis* spp. are superimposed as circles with diameter proportional to the number of point counts where *Myotis* spp. was recorded. Dashed lines represent 95% confidence intervals around the predictions.

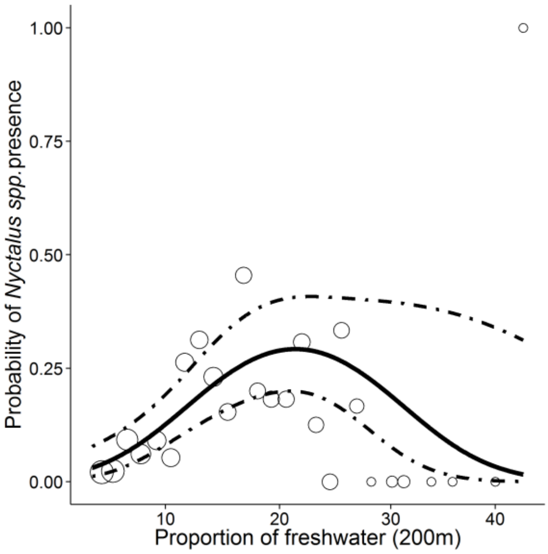


Figure 6.3 The estimated probability of recording *Nyctalus* spp. in relation to the proportion of freshwater in the surrounding 200m of a waterway. Original data on the presence of *Nyctalus* spp. are superimposed as circles with diameter proportional to the number of point counts where *Nyctalus* spp. was recorded. Dashed lines represent 95% confidence intervals around the predictions.

6.4.4 *Pipistrellus pygmaeus*

The probability of recording *P. pygmaeus* was negatively related to the extent of grey space and positively related to the extent of overhanging vegetation on a waterway; however both these were of only marginal significance (Table 6.3). *P. pygmaeus* activity was negatively related to the proportion of water in the surrounding 3km. Based on estimated coefficients in Table 6.3, the predicted activity rate of *P. pygmaeus* was 192 (95% CI: 75-494) passes in landscapes containing a relatively low level of water (1%). In landscapes containing relatively high levels of water (5%) the predicted activity rate was a tenth of this (21: 4-119) passes (Figure 6.5). *P. pygmaeus* activity was also positively related to the proportion of woodland in the surrounding 1km however this was of only marginal significance.

Table 6.3 Parameter estimates and likelihood ratio tests of the GLMM for the probability of recording either *P. pipistrellus* or *P. pygmaeus* along an urban waterway. Additionally, the parameter estimate and likelihood ratio test of the GLM for the most important landscape parameter at the most important spatial scale is included.

Species	Scale	Fixed effects	Estimate (± SE)	Log Likelihood	χ2	p
P. pipistrellus		Intercept	0.27 ± 0.39			
P. pipistrellus	Local	Bank profile	0.02 ± 0.12	-288.11	0.03	0.87
P. pipistrellus	Local	Bank vegetation	0.39 ± 0.37	-289.14	2.1	0.55
P. pipistrellus	Local	Date	-0.22 ± 0.24	-288.5	0.81	0.37
P. pipistrellus	Local	Invasive species	0.05 ± 0.11	-288.21	0.24	0.63
P. pipistrellus	Local	Overhanging vegetation	0.22 ± 0.13	-289.62	3.05	0.08
P. pipistrellus	Local	**Freshwater (200m)**	**0.29 ± 0.12**	**-290.92**	**5.66**	**0.02**
P. pipistrellus	Local	**Grey space (200m)**	**0.28 ± 0.14**	**-289.98**	**3.79**	**0.05**
P. pipistrellus	Local	Landscape heterogeneity (200m)	0.10 ± 0.13	-288.39	0.61	0.44
P. pipistrellus	Landscape	Intercept	-0.25 ± 0.21			
P. pipistrellus	Landscape	**Date**	**-0.46 ± 0.18**	**-395.53**	**4.87**	**0.03**
P. pipistrellus	Landscape	Proportion of freshwater (3km)	-0.03 ± 0.21	-390.7	0.04	0.84
P. pygmaeus		Intercept	-0.75 ± 0.49			
P. pygmaeus	Local	Bank profile	0.10 ± 0.12	-259.18	0.71	0.40
P. pygmaeus	Local	Bank vegetation	0.25 ± 0.43	-259.45	1.23	0.75
P. pygmaeus	Local	Date	-0.18 ± 0.34	-258.96	0.26	0.61
P. pygmaeus	Local	Invasive species	0.04 ± 0.12	-258.88	0.09	0.77
P. pygmaeus	Local	Overhanging vegetation	0.24 ± 0.13	-260.56	3.46	0.06
P. pygmaeus	Local	Freshwater (200m)	0.01 ± 0.14	-258.83	0.01	0.99
P. pygmaeus	Local	Grey space (200m)	-0.31 ± 0.16	-260.61	3.53	0.06
P. pygmaeus	Local	Landscape heterogeneity (200m)	0.12 ± 0.13	-259.19	0.71	0.40
P. pygmaeus	Landscape	Intercept	-0.22 ± 0.27			
P. pygmaeus	Landscape	Date	-0.25 ± 0.28	-346.58	0.88	0.35
P. pygmaeus	Landscape	**Proportion of freshwater (3km)**	**-0.77 ± 0.28**	**-350.22**	**4.53**	**0.03***

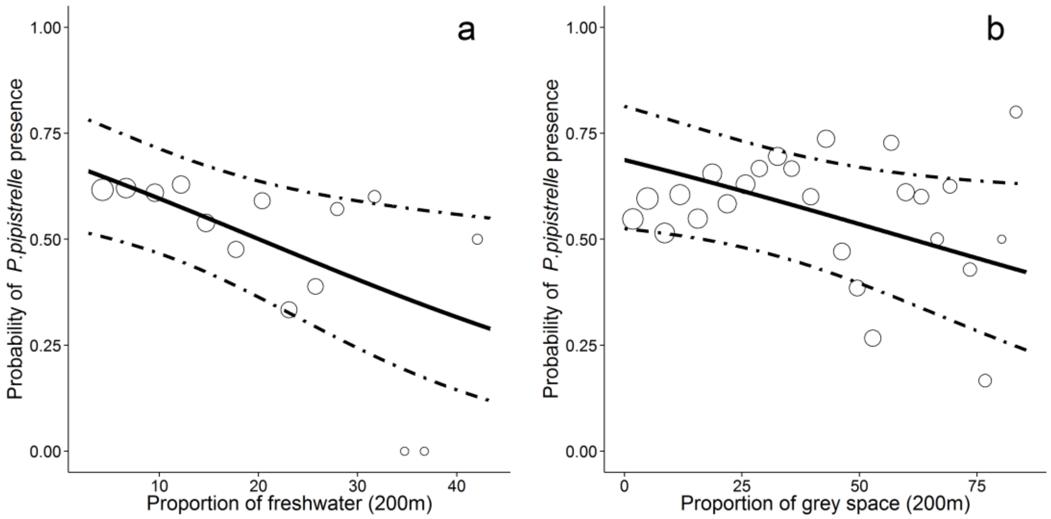


Figure 6.4 Estimated probability of recording *P. pipistrellus* in relation to (a) the proportion of freshwater and (b) the proportion of grey space in the surrounding 200m of a waterway. Original data on the presence of *P. pipistrellus* are superimposed as grey circles with diameter proportional to the number of point counts where *P. pipistrellus* was recorded. Dashed lines represent 95% confidence intervals around the predictions.

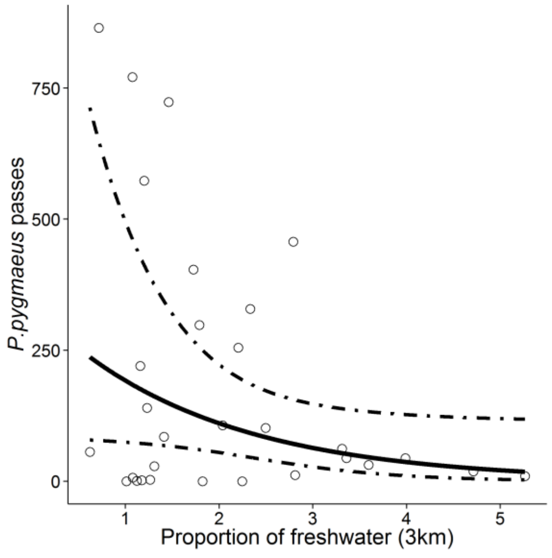


Figure 6.5 Estimated activity rate of *P. pygmaeus* in relation to the proportion of freshwater in the surrounding 3km of a waterway. Original data on the presence of *P. pygmaeus* are superimposed as grey circles with diameter proportional to the number

of point counts where *P. pygmaeus* was recorded. Dashed lines represent 95% confidence intervals around the predictions.

6.4.5 Differences between species in their response to urbanisation

P. pygmaeus responded more negatively to urbanisation than *P. pipistrellus;* as the proportion of grey space in the surrounding 3km increased, the probability of recording *P. pygmaeus* relative to *P. pipistrellus* declined. Based on the estimated coefficients in Table 6.4 the probability of recording *P. pygmaeus* or *P. pipistrellus* in waterways surrounded by low levels of grey space (20%; Figure 6.6) was approximately equal. However, in waterways surrounded by high levels of grey space (50%), the probability of recording *P. pygmaeus* relative to *P. pipistrellus* was 0.15 (95% CI: 0.09-0.25).

Table 6.4 Parameter estimates and likelihood ratio tests of the GLMM for the probability of recording *P. pygmaeus* relative to *P. pipistrellus* along urban waterways. The model was run to calculate the probability of recording *P. pygmaeus* relative to *P. pipistrellus*; hence positive estimates indicate an increased probability of detecting *P. pygmaeus* and negative estimates indicate a decreased probability of detecting *P. pygmaeus* for a given explanatory variable.

Fixed effects	Estimate (± SE)	Log Likelihood	χ2	p
Intercept	-0.66 ± 0.29			
Date	0.04 ± 0.19	-217.07	0.05	0.82
Proportion of grey space (3km)	**-0.76 ± 0.23**	**-222.41**	**10.73**	**0.001**

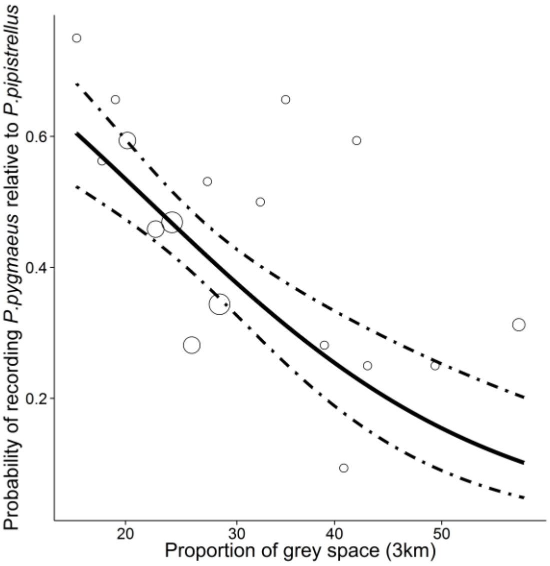


Figure 6.6 Estimated probability of recording *P. pygmaeus* relative to *P. pipistrellus* along urban waterways. Dashed lines indicate 95% confidence intervals. Original data on the proportion of *P. pygmaeus* passes are superimposed as grey circles with diameter proportion to the total number of *P. pygmaeus* passes recorded.

6.5 Discussion

Expanding urbanisation is increasing the extent to which wildlife comes into contact with the built environment and anthropogenic disturbances. Understanding how species respond to the urban landscape is essential for designing effective conservation strategies. To our knowledge this is the first study that shows that whilst a range of bat species/genera are able to utilise urban waterways, their use can be limited by vegetation cover in riparian zones and both local and landscape habitat composition.

6.5.1 Effects of local waterway characteristics

The proportion of grey space in the immediate vicinity of a waterway negatively impacted the foraging activity of all species/genera studied with the exception of

Nyctalus spp. P. pipistrellus is commonly regarded as a generalist species (Nicholls & Racey 2006) and therefore is often perceived to be more adaptable to habitat change and degradation than specialist species (Berthinussen & Altringham 2012). However, I show that even *P. pipistrellus* foraging activity is negatively affected by highly urban surroundings. The continuous nature of urban waterways is thought to facilitate the movement of species through the urban matrix (e.g. Rouqette et al. 2013). Our results show that highly urbanised waterways may have similar barrier effects as roads or artificial lighting (e.g. Kerth & Melber 2009), thus making the urban matrix increasingly fragmented and reducing connectivity between green space patches.

Although I only identified *Myotis* passes down to genus, it is likely that the majority of our calls were of *M. daubentonii* given that this species is widespread throughout Britain and strongly associated with riverine habitats (Warren et al. 2000). *Myotis* spp. activity was higher in locations with vertical bank sides, which suggests that *Myotis* spp. are frequently using channelised river stretches and canals. Channelised waterways are associated with steep banksides and reduced macroinvertebrate diversity (Horsák et al. 2009), and would not be expected to support high foraging opportunities. However canals, by design, are locations where water movement is either stationary or minimal. Sections of smooth water are favoured by *M. daubentonii* as broken water may interfere with a bats' echolocation or make prey detection and capture more difficult (Warren et al. 2000). Similarly, the presence of invasive aquatic plant species may interfere with the echolocation calls of bats, particularly the trawling action of *M. daubentonii*, and also reduce invertebrate abundance (Stiers et al. 2011), which may reduce foraging efficiency for *M. daubentonii*.

The response of *Nyctalus* spp. to the extent of freshwater at the local scale supports Gaisler et al. (1998) who found that riverine habitat was preferred by *N. noctula* in the urban landscape. However, in contrast to the linear response Gaisler et al. (1998) found, in our study *Nyctalus* spp. presence peaked at moderate levels of freshwater and declined at higher proportions. The reason for this is unclear, but may correspond to *Nyctalus* spp. utilising a wide range of foraging habitats including open woodland, parkland, and streetlights (Mackie & Racey 2007) which are reduced in extent by a high proportion of freshwater. Moderate levels of freshwater may allow *Nyctalus* spp. to commute through the urban matrix while providing a sufficient range of additional foraging resources and habitats. In contrast to Boughey (2010), I found that *Nyctalus* spp. was affected by the landscape at a relatively local scale (200m). In non-urban locations *Nyctalus* spp. are relatively fast fliers with large home ranges and as such as are unlikely to be constrained by local habitat features. However, in urban areas it appears that local habitat type is important, possibly as commuting and foraging is restricted to fewer locations.

6.5.2 Effects of the surrounding landscape

The wider landscape was important in determining the use of waterways by both *P. pygmaeus* and *Myotis* spp. Both taxa had the strongest response to the built environment at a 3km scale indicating that the effect of urban grey space is wide reaching (Appendix 6.1). Although *P. pygmaeus* are strongly associated with water and riparian woodland (Nicholls & Racey 2006), our results show that the proportion of freshwater was negatively related to *P. pygmaeus* activity. This might reflect an intensive use of freshwater in landscapes where this habitat is limited. Similar findings that highlight the more intensive use of isolated key habitats within human-disturbed landscapes are known for taxa including bats (Fuentes-Montemayor et al. 2013) and birds (Vanhinsbergh et al. 2002).

Our findings for *Myotis* spp. support those of Langton et al. (2010) who found a negative association between *M. daubentonii* activity and built land in the surrounding 1km of a river. Biological water quality declines with increasing urbanisation (Walsh et al. 2001) and is the primary limiting factor of invertebrate diversity (Beavan et al. 2001). Lower prey abundance is therefore likely to reduce *Myotis* spp. foraging efficiency and activity in urbanised waterways. Similarly, the extent of grey space was inversely related to woodland coverage in the surrounding landscape. Many *Myotis* species including *M. daubentonii* forage and roost within woodland (Parsons & Jones 2003) and preferentially select woodland over the built environment to forage within (Sparks et al. 2005). The absence of this habitat within the built landscape is therefore likely to contribute to reduced *Myotis* spp. activity.

6.5.3 Differences between species in their response to urbanisation

P. auritus was rarely detected which is not surprising given that it is a woodland species, although it may also have been under-recorded due to its low intensity echolocation calls (Parsons & Jones 2000). *Nyctalus* spp. were recorded at almost two-thirds of the waterways surveyed which would be expected given that they are open – adapted bats which are associated with a tolerance of urban areas (Threlfall et al. 2011). However, *Nyctalus* spp. were only found at 11% of point count locations indicating a patchy distribution within urban landscapes which may be explained by their consistent use of specific foraging locations rather than foraging speculatively over larger areas (Mackie & Racey 2007).

Species with similar morphological traits are often inferred to respond similarly to highly modified landscapes (Safi & Kerth 2004). I show that two cryptic, and largely sympatric European bat species, *P. pygmaeus* and *P. pipistrellus* respond differently in their response to the urban matrix. Despite *P. pipistrellus* showing a stronger negative response to grey space in the immediate vicinity of a waterway, the probability of recording *P. pipistrellus* relative to *P. pygmaeus* was greater when the landscape contained a high proportion of grey space. This supports previous studies identifying *P. pipistrellus* as a generalist species (Nicholls & Racey 2006) which can tolerate moderate levels of urbanisation relative to *P. pygmaeus* (Hale et al. 2012). It also supports my findings in chapter 3 of this thesis which found that there was higher *P. pygmaeus* activity in woodlands surrounded by lower levels of built environment.

It may be that *P. pygmaeus* can exploit local areas of anthropogenic disturbance for foraging purposes (i.e. foraging around street lamps) but is less tolerant of wide-scale urbanisation than *P. pipistrellus*.

6.5.4 Conservation implications

Species are frequently classed as either urban 'avoiders', 'adaptors' or 'exploiters' (McKinney 2006 but see Fischer et al. 2015) in order to determine the extent of conservation action required. Our results show the difficulties associated with categorising species, for example *P. pipistrellus* has been classified as an 'urban adaptor' (Hale et al. 2012) yet appears to show a strong negative response to localised pockets of grey space. Caution should also be taken when inferring high population density within urban areas as adaptation to the built environment, as urban biotopes can act as ecological traps for bats (Russo & Ancillotto 2014). Similarly, there are strong sexual differences in habitat use within the urban matrix which may distort our understanding of the adaptability of a species to urbanisation (Lintott et al. 2014b; Chapter 4).

Historically, urban waterways have been regarded as biologically poor and as sinks for pollution, however legislation and policy frameworks (e.g. the EU Water Framework Directive) are attempting to readdress this. However, the present risk is that if the management actions used by practitioners or decision-makers are not informed by evidence then biodiversity conservation may be negatively impacted (Shwartz et al. 2014). The majority of research, and therefore conservation effort, regarding urban conservation is focused on large, public, green spaces (e.g. parks) whilst relatively little is known of the importance of the wider matrix (Shwartz et al. 2014). In this study I show that a range of bat species (e.g. *M. daubentonii*), respond to both local attributes (e.g. bank profile) and to the composition of the urban matrix and therefore require a more cohesive landscape approach to their conservation. Whilst this study focussed on waterways throughout Britain, these findings are of relevance to urban waterways elsewhere due to the strong connection between bats and riparian habitats (e.g. Walsh & Harris 1996). Additionally, the consideration of bats as bioindicator species (Jones et al. 2009), and the adoption of bats in the UK Government's *Biodiversity Indicators* (DEFRA 2014) highlights the potential utility of this taxa to inform on the responses of other taxa similarly affected by urbanisation. Recent biodiversity strategies (e.g. Biodiversity 2020) implementing international and EU legislation aim to establish coherent ecological networks for the benefit of wildlife and people, and I show that at the local scale preventing urbanised riparian zones will benefit many bat species by facilitating movement through the urban matrix. Additionally, the retention of vegetated riparian zones will benefit biodiversity across a range of taxa (e.g. birds and butterflies, Dallimer et al. 2012). Similarly the removal of invasive plant species may increase the suitability of waterways for foraging *Myotis* spp. but also have wider biodiversity benefits (e.g. recovery of native biodiversity; Zavaleta et al. 2001). The importance of local scale factors in determining bat presence in our study suggests that small scale management strategies (e.g. volunteer canal clean-ups or local urban greening schemes) which are generally more cost effective and feasible than citywide conservation strategies (e.g. Barthel et al. 2005) are important in retaining and restoring urban waterway biodiversity. At a landscape scale, I show that extensive urbanisation has a similar negative effect on many bat species as is found across all major taxonomic groups (Olden et al. 2006). The importance of maintaining waterways in good ecological conditions within highly urbanised landscapes is highlighted by the increased use of waterways by *P. pygmaeus* in locations where this resource is scarce. *P. pygmaeus* appear to be using nearby resources more intensively rather than travelling further across the urban matrix to alternative foraging resources. Although conservation strategies will not prevent urban expansion, they can help guide suitable mitigation measures such as highlighting the value of maintaining isolated water bodies in good ecological condition (e.g. removing invasive plant species) in contrast to focusing the majority of effort on the establishment, restoration and maintenance of protected areas (Hoffman et al. 2011). Our results therefore support Inger et al. (2015) in their call for an increasing proportion of conservation funds to be spent on the implementation of landscape scale environmental improvement schemes which will encompass the entire urban matrix and be beneficial for relatively common species such as *P. pygmaeus*.

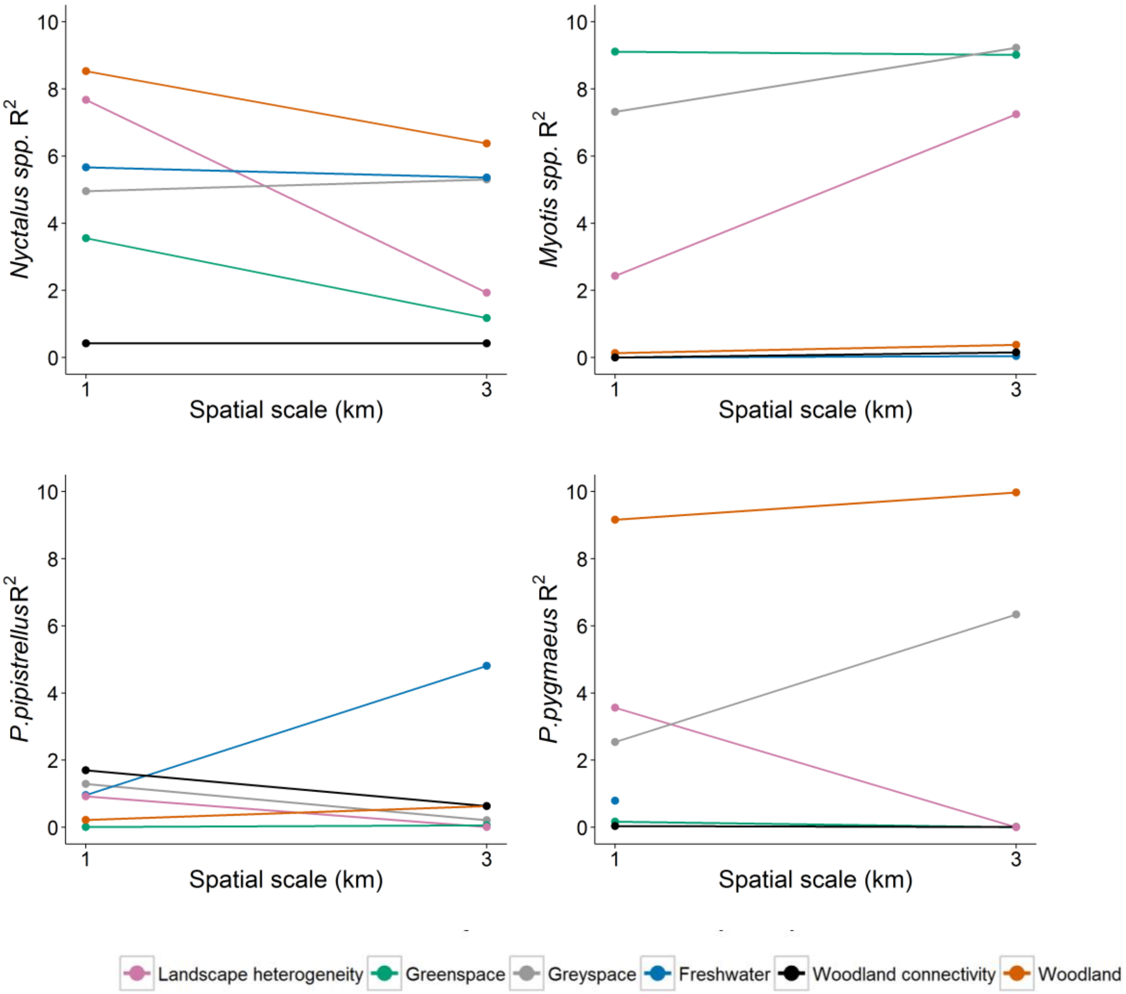
There has been increasing policy interest in promoting the use of semi-natural urban habitats to benefit human health and well-being (Irvine et al. (2013), alongside using urban wildlife encounters to reconnect the public with nature to increase ecological awareness (Prévot-Julliard et al. 2011). Yet, waterways are rarely considered when assessing how green space contributes to public health or their engagement with nature (Völker & Kistemann 2011). Well managed waterways therefore have the potential to be important settings for recreational activities such as swimming or canoeing, for human health and wellbeing, and for supporting a range of wildlife species. Town developers and urban planners frequently prioritise the development of waterfronts as cities historically developed on riversides and property/land prices are highest in these locations (Völker & Kistemann 2011); I show that awareness of wildlife requirements and the implementation of relatively simple solutions (e.g. retaining a vegetated riparian zone) can have a considerable impact on what species will be found along our urban rivers and canals.

6.6 Acknowledgements

I wish to thank those kayaking clubs who provided advice on the suitability of waterways for surveying. I also thank Bob Firmin and Wildwood Ecology for providing surveying equipment.

6.7 Appendices

Appendix 6.7.1. R2 values obtained from negative binomial GLM models comparing the percentage of landscape covered by each biotype type at a variety of spatial scales and waterway activity rates for a variety of bat species/genera.



Chapter 7

The influence of vegetation characteristics, anthropogenic disturbance and the surrounding landscape in determining use of urban gardens by bats

An adapted version of this chapter is in review as:

Lintott, P.R., Bunnefeld, N., Daly,H., Christie, M. & Park, K.J. *In review,* The influence of vegetation characteristics, anthropogenic disturbances and the surrounding landscape in determining use of urban gardens by bats. *Mammal Research*

*The fieldwork and GIS analysis for this chapter were completed by Stirling Undergraduate students Helen Daly and Michael Christie under my supervision.

7.1 Summary

The fragmentation and loss of semi-natural habitats as a consequence of urbanisation has reduced species diversity and estranged people from nature. Domestic gardens comprise a substantial proportion of the urban matrix and have the potential to support a variety of wildlife whilst providing a stimulating environment for people. Despite the prevalence of bats within the urban landscape, little is known of how garden characteristics and the surrounding matrix influence their use of gardens. We investigated how vegetation and environmental characteristics of gardens and the composition of the surrounding landscape influence bat presence within urban gardens. We surveyed 45 gardens in Edinburgh, a large conurbation in the UK; bat activity was generally very low, with only 228 bat passes from two species recorded. We show that these species respond negatively to urbanisation at both the local and landscape level. The presence of *Pipistrellus pipistrellus* was negatively related to the extent of garden comprised of artificial ground cover. The probability of recording *P. pygmaeus* was negatively related to noise pollution and positively associated with woodland connectivity in the surrounding 2km.

Although *P. pipistrellus* is widespread within urban areas, it may be vulnerable to localised habitat modification. In contrast, *P. pygmaeus* was more strongly influenced by landscape scale factors, indicating this species may be vulnerable to increased urban expansion and habitat fragmentation. Counteracting the negative impacts of urbanisation on bats therefore requires management at multiple scales.

7.2 Introduction

The impact of urbanisation can be dramatic. Consequences of urban development include the loss and degradation of habitat, increased pollution and reduced species diversity, yet our understanding of the mechanisms underlying these processes is rudimentary (Chace & Walsh 2006). The fragmentation and loss of semi-natural habitats as a consequence of urbanisation has resulted in biotic homogenisation including reductions in species richness and a high prevalence of invasive species (Goddard et al. 2010). Declines in biodiversity have also led to the estrangement of people from nature, with the consequences that expenditure on green space is one of the first items to be eliminated from municipal budgets as they are viewed as a luxury in comparison to more pressing socioeconomic concerns (Miller 2005). Determining how species use the urban matrix can improve our understanding of how species respond to the built environment and how to improve the opportunities for people to encounter and enjoy wildlife in their backyard.

There is increasing recognition of the importance of urban green space in improving the mental and physical well-being of humans (van den Berg et al. 2010), and as wildlife habitats (e.g. Rudd et al. 2002). Domestic gardens, small enclosed areas of land adjoining dwellings, form a substantial proportion of urban green infrastructure, yet their contribution to ecosystem services and urban biodiversity are seldom assessed (Cameron et al. 2012; but see Baker & Harris 2007). Local authorities rarely consider gardens as green space given their limited control over existing domestic gardens. However, the effectiveness of public space (e.g. woodland) for retaining biodiversity is often reliant on urban gardens in the surrounding landscape (Gaston et al. 2005).

Determining how species are using gardens can therefore enable the creation of more coherent management plans for the urban matrix as a whole, coupled with recommendations of how individual gardens can be managed beneficially for wildlife at the local scale.

As semi-natural habitats become increasingly fragmented, urban gardens may offer foraging opportunities for bats (Chiroptera). Gardens containing mature vegetation and trees hold the highest abundance of invertebrates (Smith et al. 2006a). Additionally, gardens may function as corridors linking fragmented green space patches (e.g. woodland) within the urban matrix and connecting urban landscapes with surrounding rural habitat (Goddard et al. 2010). Given the strong association between bat foraging activity and water and woodland (Walsh & Harris 1996), gardens should be an important habitat for bats because collectively they contain 2.5-3.5 million ponds and 28.7 million trees across the UK (Davies et al. 2009). However, changes in urban planning and householder attitudes have resulted in smaller gardens and an increase in gardens that are largely or wholly covered by hard surfaces (i.e. decking or gravel driveways). Between 1998 and 2008, an area of vegetated garden approximately 21 times the size of Hyde Park (3,000 ha) was lost in London due to lifestyle trends (London Wildlife Trust 2011). Furthermore, those households participating in wildlife gardening primarily focus on feeding wild birds with little consideration for other taxa (Gaston et al. 2007). Investigating how a wider range of taxa use urban gardens, and the local and landscape factors that determine their frequency of use is essential in understanding the role of gardens in maintaining biodiversity within the urban matrix.

Despite their prevalence within the urban landscape, the use of gardens by bats has not been assessed to the extent that the use of gardens by birds (e.g. Daniels & Kirkpatrick 2006; Paker et al. 2014) and invertebrates (e.g. Smith et al. 2006a; Smith et al. 2006b) has been. Although many bat species have adapted to exploit human resources (e.g. insects at artificial light sources; Fenton 2003), the majority of species are negatively impacted by urbanisation (e.g. Gaisler et al. 1998; Mathews et al. 2015). In a study of British urban mammals, Baker and Harris (2007) found garden use by bats was greater in gardens surrounded by low levels of urban grey space (e.g. buildings, structures, roads, and paths) and closer to key habitats outside the garden (e.g. woodland patches), but did not investigate differences among bat species. As bat species vary in their response to urbanisation (Hale et al. 2012; Lintott et al. 2015; chapter 3) it is important to investigate how different species are utilising urban gardens. Here, I investigate the use of domestic gardens by bats in Edinburgh, one of the UK's largest cities. I determined how garden characteristics and the composition and heterogeneity of the surrounding landscape influence bat presence within urban gardens. Additionally, I contrast the results obtained from gardens with comparable data from urban woodland and waterways to qualitatively assess the relative importance of urban gardens for bats.

7.3 Materials & methods

7.3.1 Site selection

Edinburgh is a large city in central Scotland with an area of 110 square km and a population in 2014 of 492,680 (National Records of Scotland 2014). Private gardens comprise 27% of the total land area of Edinburgh (City of Edinburgh Council 2014). We identified a total of 45 urban gardens within the city of Edinburgh using satellite imagery (Google Earth 2013) that were surveyed between June 18th and August 25th 2013 (Appendix 7.7.1). We classified gardens as urban if the dominant land use in the surrounding 1km grid square was categorised as urban cover (Centre for Ecology and Hydrology 2007). To ensure that we could directly relate bat activity to the vegetation characteristics and environmental variables of a particular garden (thereby discounting the influence of adjacent gardens to which we did not have access), we only surveyed gardens that were a minimum of 20m away from adjacent green space (including other gardens). Surveyed gardens were a minimum of 500m apart with an average distance of 843m (2SE ± 98m) between sites and were selected by size, location, and degree of urbanisation in the surrounding 1 km using a stratified random sampling method. Given the size of Edinburgh the distances between surveyed gardens was considered suitable as a compromise between ensuring independence and obtaining a sufficient sample size. We surveyed a maximum of three sites per night, each a minimum of 1km apart.

7.3.2. Vegetation surveys

I conducted vegetation surveys within a week of the bat survey. Within each garden, tree species richness, extent of canopy cover (% of total garden) and total tree abundance were calculated. I visually estimated the percentage of artificial ground cover, the percentage of garden enclosed by surrounding infrastructure, and building height. Garden size was calculated using ArcGIS 10 (*section 7.3.5*).

7.3.3 Bat Surveys

I used acoustic surveys to determine species presence and a measure of relative activity within each garden. I quantified bat activity by holding a frequency division bat detector (Anabat SD1, Titley Electronics) at chest height whilst walking slowly around the garden, ensuring I covered the whole area during the surveying period. I surveyed each garden for a 30 minute period between 30 minutes and 3 hours after sunset. Although the sampling period was relatively short within each garden, here I am interested in comparing relative bat activity between gardens and this sampling approach enabled us to maximise the number of gardens that could be surveyed during the field season.

I analysed all bat recordings using Analook W (Corben 2006). One bat pass was defined as at least two echolocation calls within one second of each other (Fenton 1970; Walsh & Harris 1996). All four bat genera present within the study area can be identified from detector recordings based upon the search-phase of their echolocation calls. The three *Pipistrellus* species in this area (*P. pipistrellus, P. pygmaeus* and *P. nathusii*) can be distinguished by the characteristic frequency (Fc = the frequency at the right hand end of the flattest portion of a call; Corben 2006) of their search-phase echolocation calls. Bat passes with a Fc of between 49 and 51 kHz were classed as unknown *Pipistrellus* spp..

7.3.4 Environmental variables

I measured a range of environmental variables at the same time as the bat survey. Average noise levels (decibels) were calculated using a sound level meter (Compact Sound Level Meter with a range between 30 and 130 dB) from repeated measurements every ten minutes from different locations within the garden to account for variance within the surveying period (i.e. fluctuating traffic levels). The extent of light pollution within each garden was determined by estimating the percentage of the garden that was floodlit.

7.3.5 Landscape Analysis

I determined and plotted the centre point of each of the gardens using ArcGIS 10 (ESRI Inc 2013). I created buffers of 250m, 500m, 1000m, 1500m and 2000m around the centre point reflecting the home range size of *Pipistrellus* species (i.e. Nicholls & Racey 2006). I used data from the OS MasterMap Topography Layer (EDINA Digimap Ordnance Survey Service 2013) to reclassify the landscape within each buffer into a set of discrete biotope types for which the proportion of cover was calculated. These were (i) grey space (buildings, structures, roads, and paths); (ii) green space (gardens, parkland, managed grassland, rough grassland, and farmland); (iii) inland fresh water and (iv) woodland (coniferous, deciduous and mixed woodland). Woodland Euclidean nearest neighbour distance (ENN, the mean value of ENN distances between all woodland patches within the landscape) and the Shannon diversity index (SHDI, a measure of landscape heterogeneity) were calculated, as previous studies have found that these variables influence bat foraging activity (Lintott et al. 2014b; Chapter 4). I calculated the proportion of land covered by each biotope, woodland ENN, and SHDI for each buffer scale using Fragstats v4.0 (McGarigal et al. 2002).

7.3.6 Data analysis

We performed statistical analyses using R version 2.14 (R Core Team 2012) using the effects (Fox 2003), and ggplot2 packages (Wickham 2009). We performed Generalised

Linear models (GLMs) with binomial error distribution to quantify the influence of garden characteristics and the composition of the surrounding landscape in determining how bat species use urban gardens. We ran a binomial model using presence/absence data to account for the relatively low but highly skewed activity data whilst losing little information. Spatial auto-correlation was assessed using Moran's I test (Paradis et al. 2004), however there was no significant relationship between the latitude and longitude of the gardens and the presence of *P. pygmaeus* or *P. pipistrellus*. Each model was run with the presence or absence of the species within each garden (n=49) as the response variable. Based upon the scientific literature of urban bats (e.g. Gaisler et al. 1998), we included the following predictor variables (all covariates) in the model : (i) garden characteristics: artificial ground cover (%), extent of garden enclosed by buildings (%), the extent of tree canopy cover (%), garden size (ha), noise pollution (dB), proportion of the garden floodlit, and tree species richness; (ii) landscape metrics (see section 7.3.5); (iii) environmental variables: date, temperature and time from sunset. All garden characteristic predictor variables were tested for collinearity, however none were considered to be strongly correlated based upon a Pearson correlation coefficient of ≥0.6 and p ≤ 0.05. Given the high collinearity found among landscape metrics (i.e. between the proportions of different biotope types or the same biotope type at a variety of spatial scales) we conducted preliminary analyses to determine which landscape metrics should be included in the model: we used binomial GLMs for the presence of each species with single landscape parameters (at each spatial scale) and selected the scale-landscape predictor with the highest R2 value (Appendix 7.7.2).

We present the result of the full model including standardised parameters and confidence intervals for all explanatory variables. Inferences on the effect of each parameter were made by (i) comparing its standardized estimate with other predictor variables to determine relative importance, (ii) the upper and lower 95% quantiles of each parameter distribution obtained from N=2000 simulated draws from the estimated distribution (Gelman & Hill 2007), and (iii) a comparison of models excluding each parameter in turn using Likelihood Ratio Tests (LRTs) (Faraway 2005). Prediction plots were constructed by undertaking simulated draws (n = 2000) from the estimated distribution of one explanatory variable whilst maintaining all other parameters in the model at their median observed values.

7.4 Results

I recorded a total of 228 bat passes in 21 of the 49 gardens that I sampled. Of these passes, 161 (71%) were *P. pipistrellus* in 19 of the gardens and 65 (29%) were *P. pygmaeus* in 13 gardens. A further two *Pipistrellus* passes were recorded which could not be classified to species level.

7.4.1 *Pipistrellus pipistrellus*

The probability of recording *P. pipistrellus* was negatively related to the extent of garden comprised of artificial ground cover. Based on estimated coefficients in Table 7.1, in gardens with 0% artificial ground cover there was a 76% (CI: 37-95%) probability of recording *P. pipistrellus* while in gardens containing a high percentage of artificial ground cover (80%) this was reduced to 8% (CI: 0.9-45%; Figure 7.1).

7.4.2 *Pipistrellus pygmaeus*

The probability of recording *P. pygmaeus* was negatively related to noise levels within the gardens and positively associated with woodland ENN (a measure of woodland connectivity) in the surrounding 2km^2. Woodland ENN was the strongest predictor of *P. pygmaeus* presence; based on estimate coefficients in Table 7.2, the probability of recording *P. pygmaeus* in gardens surrounded by highly connected woodland was 71% (95% confidence interval (CI): 24-95%; Figure 7.2a). In contrast, in gardens surrounded by poorly connected woodlands the probability of recording *P. pygmaeus* was 0.1% (CI: 0-19%). The probability of recording *P. pygmaeus* in gardens with relatively low noise level (40 dB) was 72% (20-96%) in contrast with noisier gardens (60dB) where this was reduced to 0.6% (0-40%; Figure 7.2b). Garden size was positively related to the presence of *P. pygmaeus* however this was of only marginal significance.

Table 7.1 Parameter estimates, and residual deviance tests of the GLM for the probability of recording *P. pipistrellus* within urban gardens. Percentage green space within 500m was determined as the most influential landscape scale variable from preliminary analyses and is included here. Significant response variables are highlighted in bold.

Fixed effects	Estimate (± SE)	log likelihood	χ2	p
Intercept	-1.14 ± 0.47			
Artificial ground cover	**-1.34 ± 0.62**	**-26.38**	**6.09**	**0.01***
Date	0.87 ± 0.56	-24.7	2.73	0.09
Extent of enclosed garden	0.90 ± 0.66	-24.75	2.84	0.09
Garden canopy cover	0.07 ± 0.41	-23.34	0.02	0.88
Garden size	-0.01 ± 0.49	-23.33	0.01	0.98
Noise	-0.74 ± 0.57	-24.22	1.77	0.18
Proportion of garden floodlit	-0.90 ± 0.60	-24.74	2.81	0.09
Temperature	-0.48 ± 0.44	-23.94	1.21	0.27
Time from sunset	-0.42 ± 0.53	-23.65	0.64	0.42
Tree species richness	-0.12 ± 0.44	-23.49	0.31	0.58
% Green space (500m)	-0.38 ± 0.57	-23.56	0.44	0.51

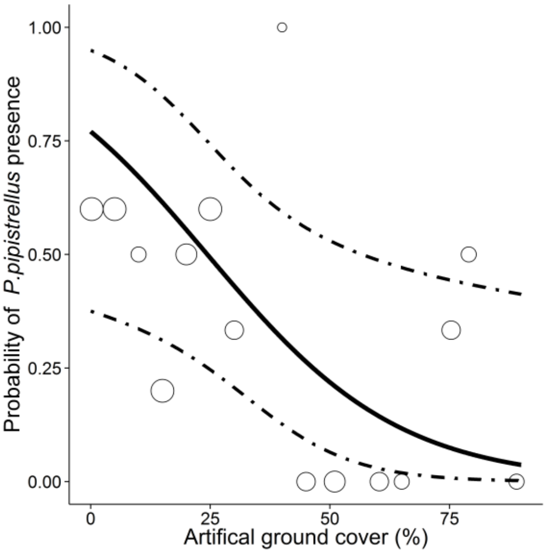


Figure 7.1 Estimated probability of recording *P. pipistrellus* in relation to the extent of artificial ground cover within the garden. The size of the circles is proportional to the number of point count locations where *P. pipistrellus* was recorded. Dashed lines represent 95% confidence intervals around the predictions.

Table 7.2. Parameter estimates, and residual deviance tests of the GLM for the probability of recording *P. pygmaeus* within urban gardens. Woodland connected within 2km was determined as the most influential landscape scale variable from preliminary analyses and is included here. Significant response variables are highlighted in bold.

Fixed effects	Estimate (± SE)	log likelihood	χ2	p
Intercept	-1.94 ± 0.72			
Artificial ground cover	-0.28 ± 0.58	-18.21	0.01	0.94
Date	-0.70 ± 0.79	-18.73	1.04	0.31
Extent of enclosed garden	0.12 ± 0.49	-18.21	0.01	0.96
Garden canopy cover	-0.04 ± 0.53	-18.28	0.14	0.71
Garden size	0.61 ± 0.55	-19.69	2.92	0.09
Noise	**-1.34 ± 0.83**	**-20.73**	**5.05**	**0.02***
Proportion of garden floodlit	-0.78 ± 0.74	-19.34	2.27	0.13
Temperature	0.63 ± 0.53	-18.71	1.01	0.32
Time from sunset	0.91 ± 0.67	-18.96	1.50	0.22
Tree species richness	-0.85 ± 0.60	-19.23	2.04	0.15
Woodland connectivity (2km)	**-1.91 ± 0.87**	**-22.16**	**7.90**	**0.01****

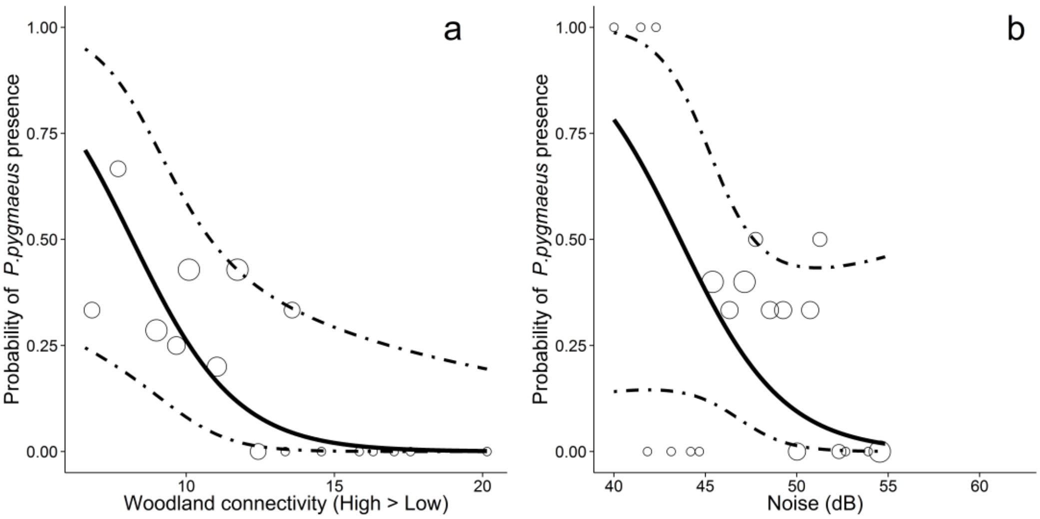


Figure 7.2 Estimated probability of recording *P. pygmaeus* in relation to (a) woodland connectivity in the surrounding 2km of an urban garden and (b) noise level. The size of the circles is proportional to the number of point count locations where *P. pygmaeus* was recorded. Dashed lines represent 95% confidence intervals around the predictions.

7.5 Discussion

Urbanisation leads to the loss and fragmentation of semi-natural habitats, so remaining areas of green space, including urban gardens, may be of increasing importance to retaining biodiversity. Despite their small size, cumulatively gardens account for 19 to 27% of land area in a range of British cities (Gaston et al. 2005). In this study, we show that the vegetation characteristics, anthropogenic disturbances and the surrounding landscape are important in determining bat presence within urban gardens.

7.5.1 Limitations

Each site was surveyed only once and for a relatively brief recording period, which provides only a coarse description of how bats are using urban gardens. This methodology was designed to maximise the number of sites that could be surveyed. Similar surveying lengths (30 minutes per site) have previously been used in studies of bat habitat use (e.g. Vaughan et al. 1997). Additionally, an important caveat is that we deliberately only surveyed relatively isolated gardens to ensure we could identify the garden characteristics that were influencing bat presence (see section 7.3.1). This is likely to have reduced recorded activity levels given that bats would have to cross at least 20m of non-green space to access the garden. However given the complexity of the urban matrix the vast majority of gardens (or groups of adjacent gardens) are isolated to a similar extent and so our results are equally applicable across the majority of urban gardens.

7.5.2 Effects of garden characteristics and the surrounding landscape

Although *P. pipistrellus* is frequently found within the urban landscape (Hale et al. 2012), we found there was a strong negative response of this species to the extent of artificial ground cover within gardens. Gardens containing a higher percentage of artificial ground have reduced structural complexity (i.e. reduced floral diversity) which can impact invertebrate abundance and diversity (Smith et al. 2006a; Smith et al. 2006b).

The negative response of *P. pygmaeus* to noise levels is likely to relate to the extent of traffic in the matrix immediately surrounding a garden. Urban areas frequently have such high levels of traffic that roads can act as either filters or barriers to bat movement and restrict access to critical foraging habitat (Bennett et al. 2013). In the countryside, *P. pygmaeus* activity decreases with distance to busy roads (Berthinussen & Altringham 2012), and this finding suggests a similar trend in the built environment.

The wider landscape was more influential in determining the presence of *P. pygmaeus* within urban gardens than *P. pipistrellus*. This supports previous studies identifying *P. pipistrellus* as a generalist species that can tolerate moderate levels of urban grey space in the landscape (Hale et al. 2012). In contrast, *P. pygmaeus* is strongly associated with water and woodland (Nicholls & Racey 2006) and is less tolerant of wide-scale urbanisation (Hale et al. 2012). In this study *P. pygmaeus* was more likely to be found in gardens surrounded by well-connected woodlands, indicating that gardens may support woodland patches in enhancing connectivity across the urban matrix. Our results are in agreement with those of Baker and Harris (2007) who found that the presence of bats within a garden was positively related to the presence of key semi-natural habitats in the surrounding landscape.

7.5.3 Conservation implications

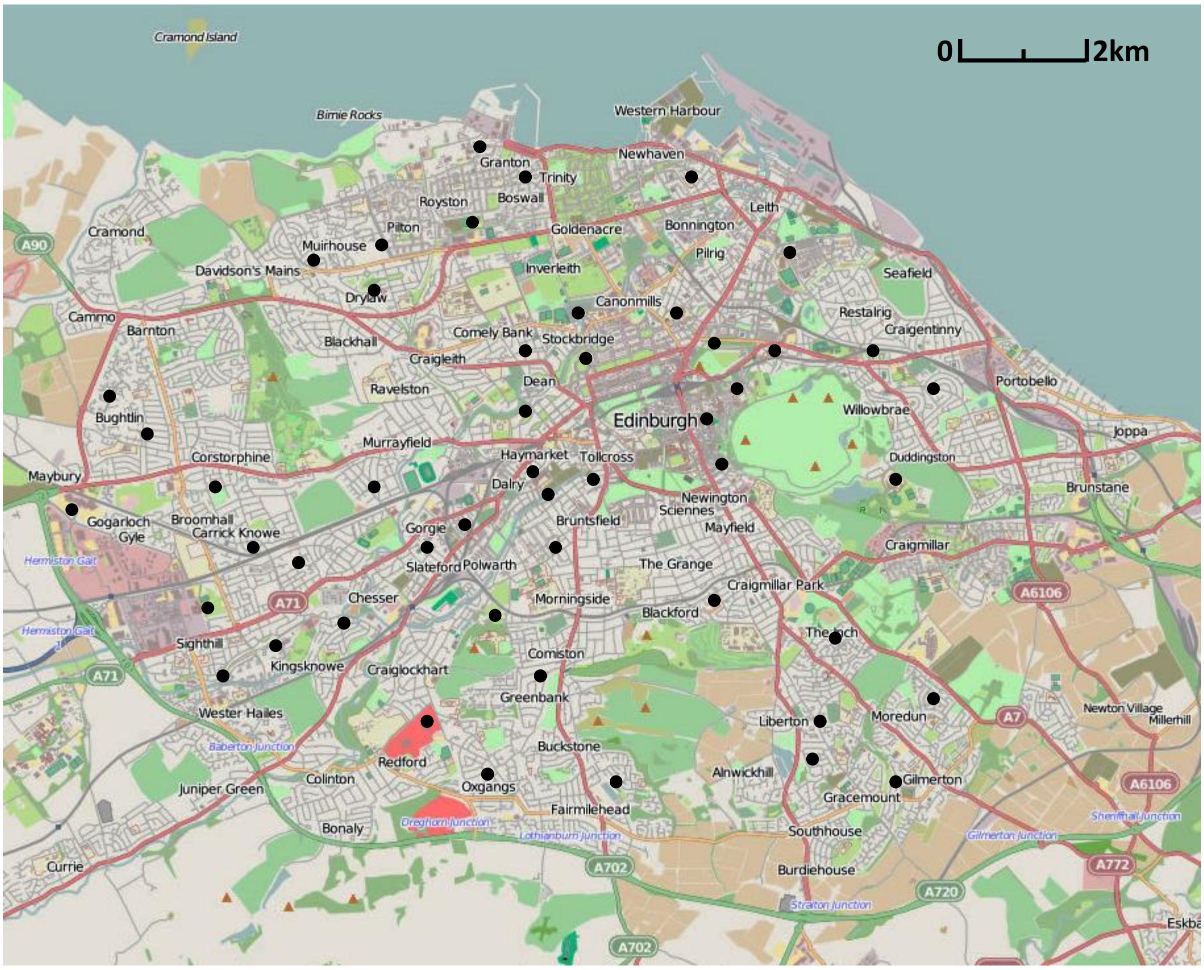
In urban ecology studies, species are commonly classified as either ‘urban exploiters’, ‘urban adapters’ or ‘urban avoiders’ to broadly classify the extent of conservation effort a species may require (Blair 2001). *P. pipistrellus* has previously been classified as an ‘urban adaptor’ (Hale et al. 2012) or ‘urban exploiter’ (Lintott et al. 2015; chapter 3), yet in this study I found that *P. pipistrellus* exhibits a strong negative response to gardens containing high artificial ground cover. Although *P. pipistrellus* is thought to be relatively well adapted to the urban landscape (Hale et al. 2012), our results indicate a negative response to metrics associated with localised urbanisation supporting the findings of Lintott et al. (2015; chapter 6). Although *P. pipistrellus* is widespread within the urban landscape it may be more vulnerable to localised habitat modification. *P. pygmaeus* has previously been classified as an ‘urban avoider’ (Hale et al. 2012) but despite its relative scarcity relative to *P. pipistrellus* in the current study it was still found in a quarter of urban gardens. This contrasts with many other species (e.g. *Myotis nattereri*, *Plecotus auritus*) that occur within the Central Scotland region but were not recorded within this survey. Based on our recordings I therefore suggest that *P. pygmaeus* is better categorised as an 'urban adaptor', supporting the findings of Lintott et al. (2015; chapter 3). The presence of *P. pygmaeus* within urban gardens appears to be more influenced by the wider landscape than within-garden characteristics, indicating that this species may be more vulnerable to town planning decisions (i.e. the loss of woodland patches or the expansion of road networks). Our results therefore support Inger et al. (2015) in their call for the implementation of landscape scale environmental improvement schemes which encompass the entire urban matrix.

Ensuring the accessibility and quality of urban gardens will not only increase their use by wildlife but may also aid public engagement. Urban encounters with wildlife often form the basis of attitudes and motivation for urban inhabitants to become involved in wider conservation and environmental issues (Randler et al. 2007). Bjurlin & Cypher (2005) found a positive relationship between exposure to, and appreciation of, foxes (*Vulpes vulpes*) by residents in California indicating the potential to garner support for wider conservation action and protection of species. Bats are commonly negatively perceived by the public (e.g. Fenton 2003); given the relatively frequent occurrence of bats within urban gardens the opportunity therefore exists to use these encounters as a beneficial mechanism for bat conservation.

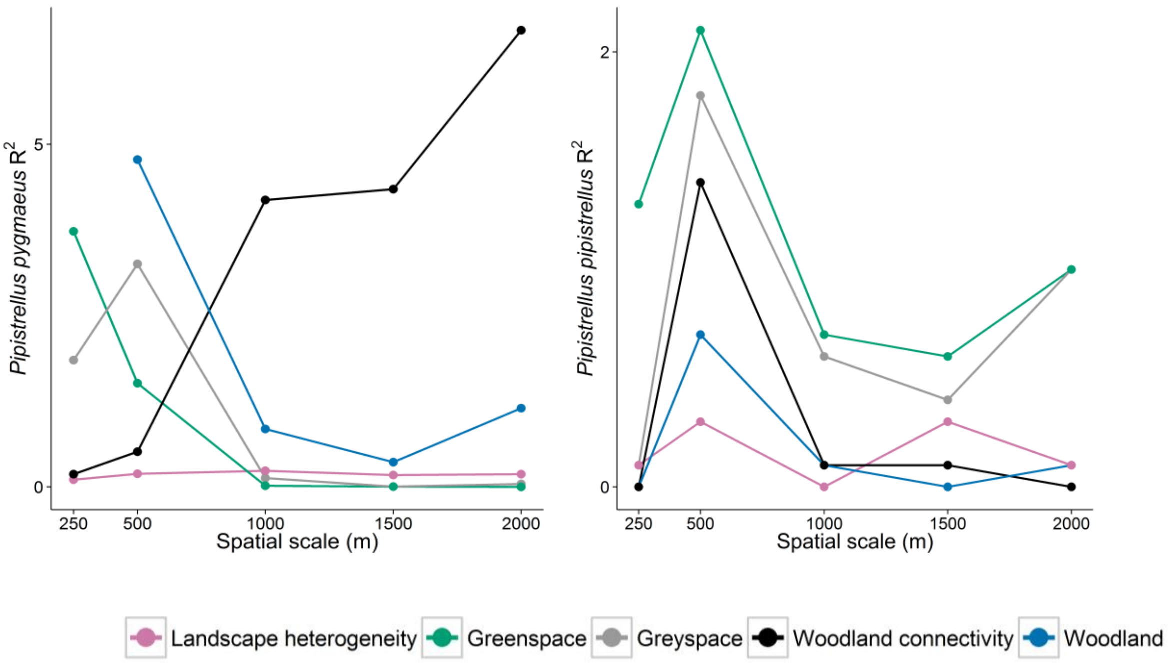
7.6 Acknowledgements

I wish to thank the residents of Edinburgh who granted access to their gardens for this study. I would also like to thank Joe Taylor for his help with surveying.

7.7 Appendices



Appendix 7.7.1 Location of urban gardens surveyed in Edinburgh, Great Britain.



Appendix 7.7.2 R2 values obtained from binomial GLM models comparing the percentage of landscape covered by each biotype at a variety of spatial scales and the probability of recording either *P. pygmaeus* or *P. pipistrellus* within urban gardens.

Chapter 8

Differential responses of cryptic bat species to the urban landscape

An adapted version of this chapter is currently in review as:

Lintott, P.R., Barlow, K., Bunnefeld, N., Briggs,P., Gajas Roig, C. & Park, K.J. *In review,* Differential responses of cryptic bat species to the urban landscape. *Diversity & Distributions*

8.1 Summary

The impact of urbanisation on wildlife can be severe. Urbanisation, alongside agricultural intensification, is a key global driver in the modification of land use and has been linked to population declines even in widespread and relatively common species. Many species are unable to adapt to the loss, fragmentation and degradation of semi-natural habitat prevalent within urban landscapes. Cities comprise a complex assortment of habitat types yet relatively little is known of how their composition and spatial configuration influences species presence. Although many bat species are able to exploit human resources, the majority of species are negatively impacted by urbanisation. Here, I use data from the National Bat Monitoring Programme, a long-running citizen science scheme, to assess how two cryptic and largely sympatric European bat species respond to the urban landscape at a national level (n=124 sites throughout Britain). The morphological similarities between *Pipistrellus pygmaeus* and *P. pipistrellus* suggest that both species should respond similarly to the urban matrix. However I found that the relative prevalence of *P. pygmaeus* compared to *P. pipistrellus* was greater in urban landscapes with a higher density of rivers and lakes, whereas *P. pipistrellus* were frequently detected in landscapes comprising a high proportion of green space (e.g. gardens or parklands). Although *P. pipistrellus* is thought to be well adapted to the urban landscape, I found a strong negative response to urbanisation at a relatively local scale (1km), whilst *P. pygmaeus* was detected more regularly in wooded urban landscapes containing freshwater. These results show differential habitat use at a landscape scale of two morphologically similar species, highlighting that cryptic species may respond differently to anthropogenic disturbance. I found that even those species considered relatively common and well-

adapted to the urban landscape respond negatively to the built environment indicating the future challenges involved in maintaining biodiversity within an increasingly urbanised world.

8.2 Introduction

Over the past two centuries rapid urban expansion has become a dominant driving force within global environmental change (Wu et al. 2013). Urban areas represent unique combinations of disturbances, stresses, structures and functions in ecological systems (Pickett et al. 1997), and relatively little is known of how to maintain or manage wildlife within urban ecosystems (Shwartz et al. 2014). Understanding how connectivity within the urban landscape (the degree to which a landscape can facilitate or restrain movement of organisms amongst resource patches) influences species distribution is critical given its influence on dispersal rates, home range movements, colonisation rates, and extinction risk (Tischendorf & Fahrig 2000). A landscape-scale approach is therefore needed to understand how the composition, configuration and spatial heterogeneity of the urban landscape impacts upon species persistence within the built environment.

Urbanisation imposes stresses that few species are able to adapt to (Ditchkoff et al. 2006). Understanding how species respond to urbanisation enables us to identify those species which may require most conservation effort to cope with anthropogenic disturbances. Morphological or behavioural factors can influence how adept certain species are at adapting to urbanisation. These traits have therefore been used to classify species as ‘urban avoiders’, ‘urban utilizers’ or ‘urban dwellers’ (Fischer et al. 2015), although in reality there is likely to be a continuous spectrum of adaptability.

Given the scarcity of information on species-specific responses to urbanisation, the likely response of an individual species to the urban landscape is often predicted from their morphological traits (e.g. Jung & Kalko 2011; Threlfall et al. 2012). Such congruence in response to urbanisation would suggest that species-specific conservation strategies would also benefit morphologically similar species, but this has rarely been tested.

Although many species of Chiroptera (bats) have formed strong associations with people (e.g. roosting in buildings; Jenkins et al. 1998), the general pattern is of lower bat activity and species richness with increasing levels of urbanisation (e.g. Gaisler et al. 1998; Lane et al. 2006). The loss and fragmentation of natural and semi-natural habitats within the urban landscape has reduced the availability of foraging grounds for bats (Russo & Ancillotto 2015). Additionally, movement within the built environment will frequently involve flying over busy roads which can be a major source of bat mortality and anthropogenic disturbances (e.g. noise and light pollution) which can exclude bats from foraging resources (Stone et al. 2009; Lesiński et al. 2011; Berthinussen & Altringham 2012).

The majority of conservation effort is focused on already vulnerable species, however there is increasing evidence that some widespread species are also declining rapidly, and that changes in land-use are the primary driver for this (Shreeve & Dennis 2011). Here, I study two, often sympatric, cryptic species of pipistrelle *Pipistrellus pygmaeus* and *P. pipistrellus* which, although relatively widespread across Europe, have experienced historic population declines (Stebbings 1988 but see Barlow et al. 2015). Only formally recognised as different species as recently as 1999 (Jones & Barratt

1999), these two species are morphological similar and adopt comparable foraging strategies (Barlow & Jones 1997, Nicholls & Racey 2006a). Relatively little is known of the response of these cryptic species to the urban landscape although Hale et al. (2012) found that *P. pipistrellus* activity at urban ponds in a large conurbation peaked with moderate levels of adjacent urban grey space (i.e. built-up areas), whilst Lintott et al. (2015; Chapter 3) found greater *P. pygmaeus* activity relative to *P. pipistrellus* in woodlands with low clutter and understory cover which were surrounded by low levels of built environment. However, these studies have been conducted at the regional level (e.g. the West Midlands, Britain - Hale et al. 2012; central Scotland – Lintott et al. 2015; Chapter 3); here I use data generated from the National Bat Monitoring Programme (NBMP), a long-running citizen science scheme (see http://www.bats.org.uk/pages/nbmp.html; Barlow et al. 2015) to determine how these two species respond to urban landscapes in towns and cities across Great Britain. Specifically, I address the following questions:

1) Do two cryptic, morphologically similar species respond to the composition and spatial configuration of urban landscape in a similar manner?

2) How do the composition, configuration, and heterogeneity of the urban landscape influence the distribution of two widespread and relatively common species of bat; *P. pipistrellus* and *P. pygmaeus*?

8.3 Materials & Methods

8.3.1 Site selection

This study focuses on the response of species to the built environment, therefore only sites classified as urban were included, although the % cover of grey space (e.g. buildings and roads) within a radius of 1km varied widely from 1 – 67%) . Urban areas were designated as those where urban cover was the dominant land use within a 1km grid square as categorised by Boughey et al. (2011). Sites were selected which had been surveyed for at least two years between 2007 and 2012 (surveys conducted prior to 2007 were discounted given the rapid land use change that occurs in cities) and were a minimum of 5 km apart to minimise the possibility of sampling the same population of bats. This resulted in a total of 124 urban sites surrounded by a wide diversity of landscapes (Figure 8.1; Appendix 8.7.1).

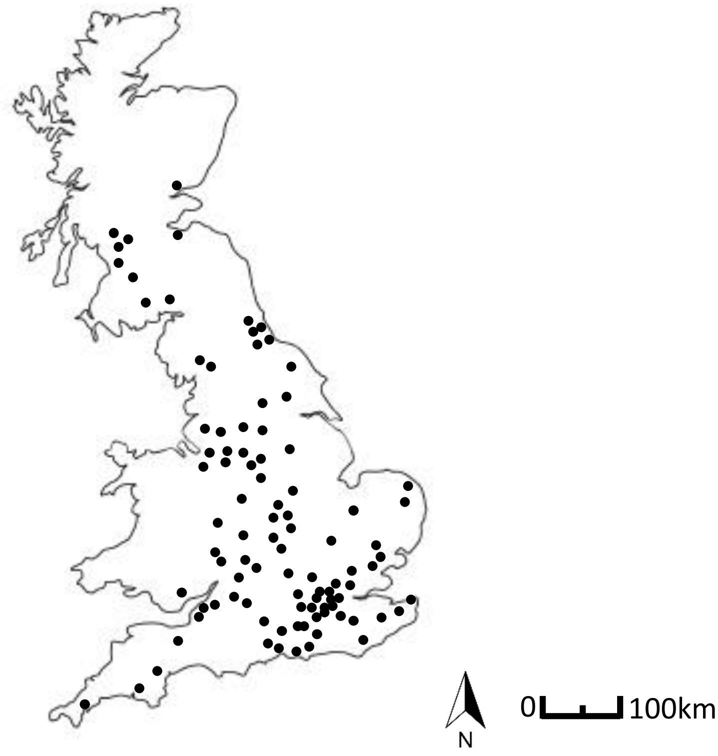


Figure 8.1. The location of the 124 urban transects undertaken as part of the Bat Conservation Trust's National Bat Monitoring Programme.

Field surveys were conducted annually by trained volunteer surveyors in suitable weather conditions (avoiding heavy rain, high winds and temperatures at sunset below 7˚C; Barlow et al. 2015). Surveyors conducted two surveys (a minimum of five days apart) in July following an approximately triangular transect (3 km in length) within a randomly allocated 1 km grid square. Surveyors undertook 2-minute point counts at 12 evenly spaced locations where a heterodyne bat detector was tuned to 50 kHz and the number of bat passes (a continuous sequence of echolocation calls) of *P. pipistrellus* and *P. pygmaeus* was counted. Volunteers were provided with the option of including an 'Unsure pipistrelle' count for those bat calls which they heard but were unable to identify to species level with any certainty (for full details of the survey methods see Barlow et al. 2015).

8.3.2 Landscape analysis

Transects were plotted using ArcGIS 10 (ESRI Inc 2013) and the centre point of the 12 point counts within each site determined. Buffers of 1 km, 2 km, and 3 km were created around the central point reflecting the upper limit of home range size for *P. pygmaeus* and *P. pipistrellus* (Nicholls & Racey 2006b). Data from the OS MasterMap Topography Layer (EDINA Digimap Ordnance Survey Service 2013) was used to reclassify the landscape within each buffer into a set of discrete biotope types. These were (i) grey space (buildings, structures, roads, and paths); (ii) green space (gardens, parkland, managed grassland, rough grassland, and farmland); (iii) inland fresh water and (iv) woodland (coniferous, deciduous and mixed woodland). Woodland Euclidean nearest neighbour distance (ENN, the mean value of ENN distances among all woodland patches within the landscape) and the Shannon diversity index (SHDI, a measure of landscape heterogeneity) were calculated as previous studies have found these variables to influence bat foraging activity (e.g. Lintott et al. 2014b; Chapter 4). The proportion of land covered by each biotope, woodland ENN, and SHDI were calculated for each buffer scale using Fragstats v4.0 (McGarigal et al. 2002).

8.3.3 Data analysis

Statistical analyses were undertaken using R version 2.14 (R Core Team 2012) using the lme4 (Bates et al. 2013) and effects package (Fox 2003).

8.3.3.1 Differences in the response to the urban environment by two cryptic bat species

I performed a Generalised Linear model (GLM) with binomial error distribution and a logit link to quantify the influence of the urban matrix on the presence of *P. pipistrellus* and *P. pygmaeus*. In order to assess the relative effect of the surrounding landscape on *P. pygmaeus* in comparison to *P. pipistrellus*, the model was run with the response variable expressed as the proportion of the number of point counts per transect where *P. pygmaeus* was recorded versus the number of point counts per transect where *P. pipistrellus* was recorded. Given the high collinearity found among landscape metrics (i.e. between the proportions of different biotope types or the same biotope type at a variety of spatial scales) preliminary GLMs were conducted to determine which metrics at which spatial scale should be included in the model; metrics with the highest R^2 value were selected for inclusion in the final model (Appendix 8.7.2). When several landscape parameters seemed equally important (i.e. <5% difference from the highest R^2 value) they were all selected providing they were not strongly correlated

(Pearson correlation coefficient <0.4 and p>0.05 used as thresholds). I also included the easting and northing Cartesian coordinates of each transect into the model to account for spatial auto-correlation and that the population densities of the two species vary across Britain (Altringham 2014).

I present the result of the full model including standardised parameters and confidence intervals for all explanatory variables. Inferences on the effect of each parameter were made by (i) comparing its standardized estimate with other predictor variables to determine relative importance, (ii) the upper and lower 95% quantiles of each parameter distribution obtained from N=2000 simulated draws from the estimated distribution (Gelman & Hill 2007), and (iii) a comparison of models excluding each parameter in turn using Likelihood Ratio Tests (LRTs) (Faraway 2005). Prediction plots were constructed by undertaking simulated draws (n = 2000) from the estimated distribution of one explanatory variable whilst maintaining all other parameters in the model at their median observed values.

8.3.3.2 The impact of urbanisation on common bat species

In addition to directly contrasting how *P. pipistrellus* and *P. pygmaeus* respond differently to the urban landscape (section 8.3.3.1), I was interested in assessing what landscape factors were important in influencing the distributions of *P. pipistrellus* and *P. pygmaeus*. I therefore undertook two Generalised Linear models with negative binomial distributions, one for *P. pipistrellus* and the other for *P. pygmaeus* to determine how the urban landscape influences each of their distributions. The percentage of point counts per transect where either *P. pipistrellus* or *P. pygmaeus* were recorded was used as a measure of the relative prevalence of that species at that site. I used the same approach to determine influential explanatory variables as described in section 8.3.3.1.

8.4 Results

The presence of *P. pipistrellus* was recorded in 117 of the 124 sites (94%) and within 27% of all point counts, while *P. pygmaeus* was recorded in 79 of the sites (63%) and within 12% of the point counts.

8.4.1 Differences in the response to the urban environment by two cryptic bat species

Based on the estimated coefficients in Table 8.1, in locations with very few rivers or lakes in the surrounding 3km, there was a 0.17 (95% CI: 0.14 – 0.22) probability of recording *P. pygmaeus* relative to *P. pipistrellus*; conversely *P. pygmaeus* was more likely to be recorded (0.72; 0.53 – 0.86) in locations containing relatively high proportions (8%) of fresh water (Figure 8.2a). *P. pygmaeus* and *P. pipistrellus* were equally likely to recorded in urban areas with low levels of green space in the surrounding 1km (20%), whilst the probability of recording *P. pygmaeus* relative to *P. pipistrellus* reduced to 0.23 (0.19 – 0.27) in urban areas comprising of a high proportion of green space (80%; Figure 8.2b). *P. pygmaeus* were also more likely to be recorded in landscapes with higher woodland connectivity in the surrounding 3km (Table 8.1), however the relationship was strongly influenced by one outlier which, when excluded, substantially reduced the effect of this variable.

Table 8.1. Parameter estimates and likelihood ratio tests of GLM for the probability of detecting *P. pygmaeus* relative to *P. pipistrellus* in urban landscapes. The model was run to calculate the probability of recording *P. pygmaeus* presence relative to *P. pipistrellus*; hence positive estimates indicate an increased probability of detecting *P. pygmaeus* and negative estimates indicate an increased probability of detecting *P. pipistrellus* with a given explanatory variable. Significant explanatory variables are highlighted in bold.

Explanatory variable	Estimate (± SE)	log likelihood	χ2	p
Intercept	-1.01 ± 0.10			
Proportion of freshwater (3km)	**0.52 ± 0.10**	**-163.47**	**23.05**	**<0.001**
Proportion of green space (1km)	**-0.34 ± 0.10**	**-156.91**	**9.93**	**0.002**
Woodland connectivity (3km)	**0.31 ± 0.18**	**-154.14**	**4.4**	**0.036**
Easting	-0.19 ± 0.11	-153.16	2.43	0.12
Northing	0.17 ± 0.10	-152.94	1.2	0.16

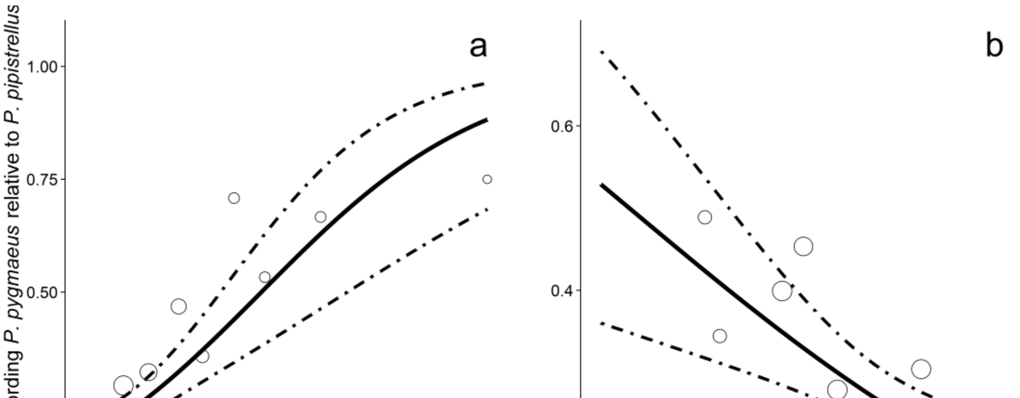


Figure 8.2. Estimated probability of recording *P. pygmaeus* relative to *P. pipistrellus* within urban landscapes. Dashed lines indicate 95% confidence intervals. Raw data on the probability of recording *P. pygmaeus* relative to *P. pipistrellus* are superimposed as grey circles with diameter proportional to the total number of sites where either species was recorded.

8.4.2 The impact of urbanisation on common bat species

The number of point counts per survey where *P. pygmaeus* was recorded was positively related to the percentage of freshwater and woodland in the surrounding 3 km. In urban areas containing a relatively high percentage of fresh water (10%) the likelihood of recording *P. pygmaeus* was 0.32 (0.15 – 0.67) which decreased to 0.06 (0.06 – 0.08) in areas containing no freshwater (Figure 8.3a). In locations containing no woodland there was a low likelihood of detecting *P. pygmaeus* (0.07; 0.5-0.1) whereas the probability increased to 0.18 (0.11 – 0.30) in relatively wooded areas (30%; Table 8.2; Figure 8.3b).

Table 8.2. Parameter estimates and likelihood ratio tests of GLM's for the probability of detecting either *P. pygmaeus* or *P. pipistrellus* in urban landscapes for the most important landscape parameter at the most important spatial scale. Significant explanatory variables are highlighted in bold.

Species	Explanatory variable	Estimate (± SE)	log likelihood	χ2	p
P. pygmaeus	Intercept	0.19 ± 0.10			
P. pygmaeus	**Proportion of freshwater (3km)**	**0.27 ± 0.06**	**-370.10**	**14.59**	**<0.001**
P. pygmaeus	**Proportion of woodland (3km)**	**0.21 ± 0.08**	**-361.46**	**5.95**	**0.01**
P. pygmaeus	Easting	-0.11 ± 0.10	-357.43	1.10	0.30
P. pygmaeus	Northing	0.13 ± 0.10	-372.19	1.92	0.17
P. pipistrellus	Intercept	1.17 ± 0.05			
P. pipistrellus	Landscape heterogeneity (3km)	0.05 ± 0.07	-495.93	3.39	0.18
P. pipistrellus	**Proportion of grey space (1km)**	**-0.28 ± 0.08**	**-505.81**	**13.26**	**<0.001**
P. pipistrellus	**Proportion of freshwater(3km)**	**-0.20 ± 0.07**	**-502.96**	**10.42**	**0.001**
P. pipistrellus	Easting	0.01 ± 0.06	-492.55	0.01	0.98
P. pipistrellus	Northing	0.01 ± 0.06	-492.55	0.01	0.95

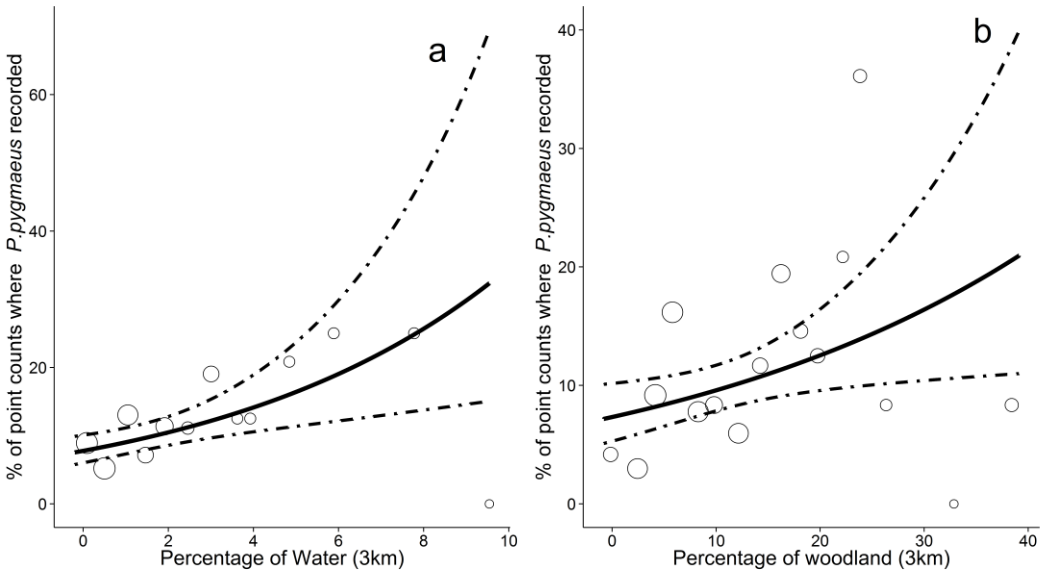


Figure 8.3. The estimated probability of recording *P. pygmaeus* in relation to the percentage of water (a) and woodland (b) in the surrounding 3 km. The size of the circles is proportional to the number of locations where *P. pygmaeus* was recorded. Dashed lines represent 95% confidence intervals around the predictions.

In landscapes containing low levels of grey space (5%) there was a 0.35 (0.3-0.4) probability of recording *P. pipistrellus* however this was reduced to 0.14 (0.9 – 0.22) in highly urbanised landscapes (60%; Figure 8.4a). In urban areas containing no fresh water in the surrounding 3km the likelihood of recording *P. pipistrellus* was 0.35 (0.3-0.42) which decreased to 0.11 (0.05 – 0.23) in areas containing a relatively high proportion of fresh water (10%; Figure 8.4b).

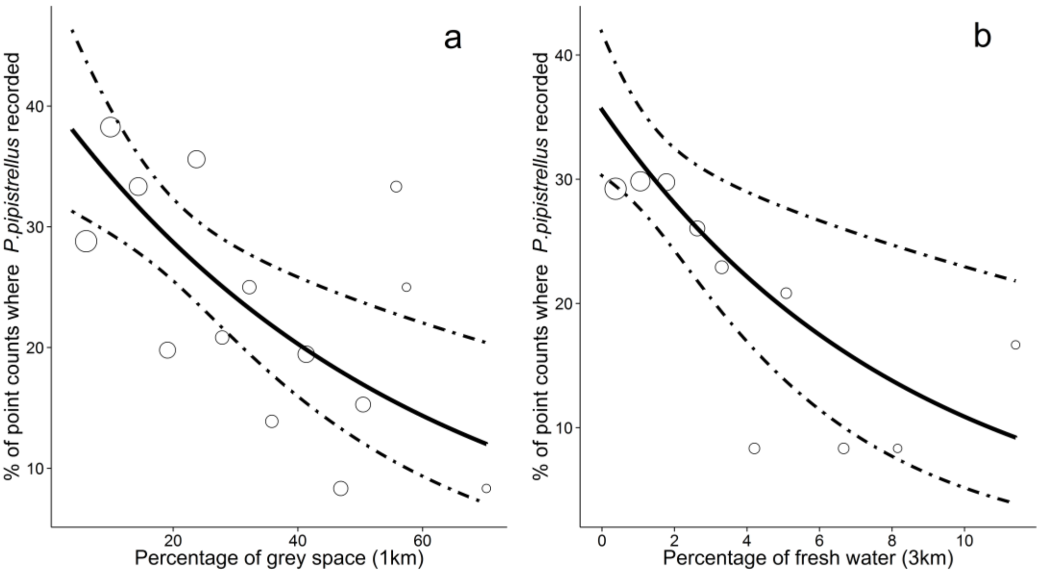


Figure 8.4. The estimated probability of recording *P. pipistrellus* in relation to the percentage of grey space in the surrounding 1 km (a) and the percentage of fresh water in the surrounding 3 km (b). The size of the circles is in proportion to the number of locations where *P. pipistrellus* was recorded. Dashed lines represent 95% confidence intervals around the predictions.

8.5 Discussion

The sensitivity of bats to habitat fragmentation and changes in land use is one of many factors which have led to the recognition of bats as ideal bioindicators (Russo & Jones 2015). European bat populations are showing signs of recovery, as threats such as water pollution and deliberate persecution have become less influential because of EU wide nature conservation protection measures (Van der Meij et al. 2014). However, as urbanisation across Europe is projected to increase up until at least 2050 (United Nations 2014), I show that even species perceived to be relatively common and tolerant of the urban landscape respond negatively to the built environment indicating the challenges involved in maintaining biodiversity within an increasingly urbanised world.

8.5.1 Differences in habitat use between *P. pipistrellus* and *P. pygmaeus*

Understanding the factors influencing the distribution of species within the built environment is critical in identifying how adaptable species are to urbanisation. Species with similar morphological traits are frequently inferred to respond similarly in their response to anthropogenic environments (Safi & Kerth 2004). Our results, however, show differences in responses to the urban landscape between species which are morphologically very similar. I found that the relative prevalence of *P. pygmaeus* compared to *P. pipistrellus* was greater in landscapes with higher amounts of fresh water within the urban matrix. This supports previous studies strongly associating *P. pygmaeus* with water and riparian woodland (Nicholls & Racey 2006b), whilst *P. pipistrellus* is regarded as a generalist which can tolerate moderate levels of urbanisation (Hale et al. 2012). Urban waterways facilitate the movement of species through the urban matrix (e.g. Rouqette et al. 2013); therefore as *P. pygmaeus* is perceived to be less tolerant of the built environment (e.g. Hale et al. 2012) it is likely that waterways are one of the few habitat types that this species is using as either a foraging resource or for commuting through the urban matrix.

I found that *P. pipistrellus* was less likely to be found in locations with relatively high amounts of fresh water in the surrounding landscape. Previous studies have suggested that *P. pipistrellus* appear to actively avoid *P. pygmaeus* foraging sites resulting in differential habitat use (Nicholls & Racey 2006b; Lintott et al. 2015b; Chapter 3). Coexisting species frequently use different foraging locations to avoid excessive competition (Li et al. 2014). The low prevalence of *P. pipistrellus* in locations containing a high proportion of water may reflect that this species is avoiding competition, and as a habitat generalist, is able to use a wide variety of habitat types compared to *P. pygmaeus*. Similarly, *P. pipistrellus* was frequently recorded in urban landscapes containing a high proportion of green space (e.g. gardens, parkland and rough grassland), supporting previous findings that *P. pipistrellus* appears to be a habitat generalist (e.g. Davidson-Watts et al. 2006; Nicholls & Racey 2006b).

My findings suggest that differences in habitat use can occur between sympatic bat species despite having virtually identical flight morphology. Both species are aerial insectivores but they do differ in the frequency of maximum energy in their echolocation calls by around 10kHz (Davidson-Watts et al. 2006). This difference in call frequency could influence differences in prey size and therefore habitat selection, however Jones and van Parijs (1993) found that differences in target strengths from prey species were too small to be of importance in determining differences in prey size selection between the species. Therefore my results appear to support that of Davidson-Watts et al. (2006) who show that species may exploit quite different niches despite showing considerable morphological overlap

8.5.2 The impact of urbanisation on common bat species

Although *P. pipistrellus* is thought to be relatively well adapted to the urban landscape (Hale et al. 2012), our results indicate that it shows a strong negative response to relatively local (1km) areas of grey space. As the rate of housing projects and developments continue to accelerate within cities, the remaining green space is becoming increasingly threatened. Our results indicate that even one of the most adaptable of European bat species may not be able to tolerate highly urbanised locations. The strong association of *P. pygmaeus* to woodland and freshwater is unsurprising as *P. pygmaeus* are well adapted to foraging along waterways, woodland edges and within open woodland (Kalko & Schnitzler 1993). However, caution should be taken in drawing the conclusion that maintaining urban woodland will support *P. pygmaeus* populations given that female *P. pygmaeus* show greater selectivity of foraging locations within this habitat (Lintott et al. 2014b; Chapter 4).

The conservation needs of common species are frequently overlooked given their abundance and widespread distribution (Gaston 2011). However, common species are vital as they contribute strongly to the structure, biomass and energy turnover of the majority of terrestrial and marine ecosystems (Gaston 2011). Here I show that bat species previously regarded as relatively common and adaptable to anthropogenic disturbances are still negatively affected by urbanisation. Populations of *P. pygmaeus* and *P. pipistrellus* appear to have stabilised (Barlow et al. 2015) after historical declines (e.g. Stebbings 1988), probably as a consequence of increased legal protection, raised awareness of bat conservation, and changes in climate (Barlow et al. 2015). However, our results indicate that increasing urbanisation is likely to have a negative effect on both pipistrelle species, and therefore support Inger et al. (2015) in their call for an increasing proportion of conservation funds to be spent in ensuring the survival of our common species through the implementation of landscape scale environmental improvement programs, such as the creation of effective urban green space schemes. Focusing conservation effort on our commoner species such as *P. pygmaeus* and *P. pipistrellus* will ensure that they avoid a similar fate to the rocky mountain grasshopper (*Melanoplus spretus*) and the passenger pigeon (*Ectopistes migratorius*); common species that were rapidly driven to extinction through anthropogenic activities (Gaston 2011). Additionally, ensuring common species remain with urban landscapes represents one of the best opportunities for the public to encounter and engage with wildlife (Shwartz et al. 2014). In this study I show that whilst both pipistrelle species are relatively widespread within the urban matrix, landscape scale environmental programmes are still required to ensure that the negative effects of the built environment are minimised.

In contrast to those chapters where the fieldwork was undertaken in Central Scotland (chapters 2,3, 7) we found that *P. pipistrellus* was generally much more common in urban landscapes than *P. pygmaeus* across Britain. This supports my previous findings that *P. pygmaeus* has a stronger negative response to urbanisation than *P. pipistrellus*. It is known that *P. pygmaeus* and *P. pipistrellus* have a patchy distribution throughout Britain. In Central Scotland, it is *P. pygmaeus* that is the more commonly detected species. It is therefore unsurprising that I recorded P. *pygmaeus* more often in my Scottish surveys; nevertheless even in these studies *P. pygmaeus* displayed a stronger negative response to urbanisation than *P. pipistrellus*.

8.53. Limitations of the NBMP

The bat detector surveys in the NBMP use tuneable, heterodyne bat detectors that can be used to determine difference echolocation calls produced by different bat species. Identification is carried out in the field and it is therefore important that surveyors taking part are accurately able to distinguish between different species. Although it has been shown that accurate species identification is possible for a wide range of European bat species using this method, some error in bat identification is likely (Barlow et al. 2015). However, given the large sample size of this study, the option for surveyors to record bat calls they could not classify down to species level as ‘unsure pipistrelle’, and that our findings reflect similar patterns in response to urbanisation as my other chapters (e.g. chapters 3,6,7), it is unlikely that error in bat identification will have significantly altered these results.

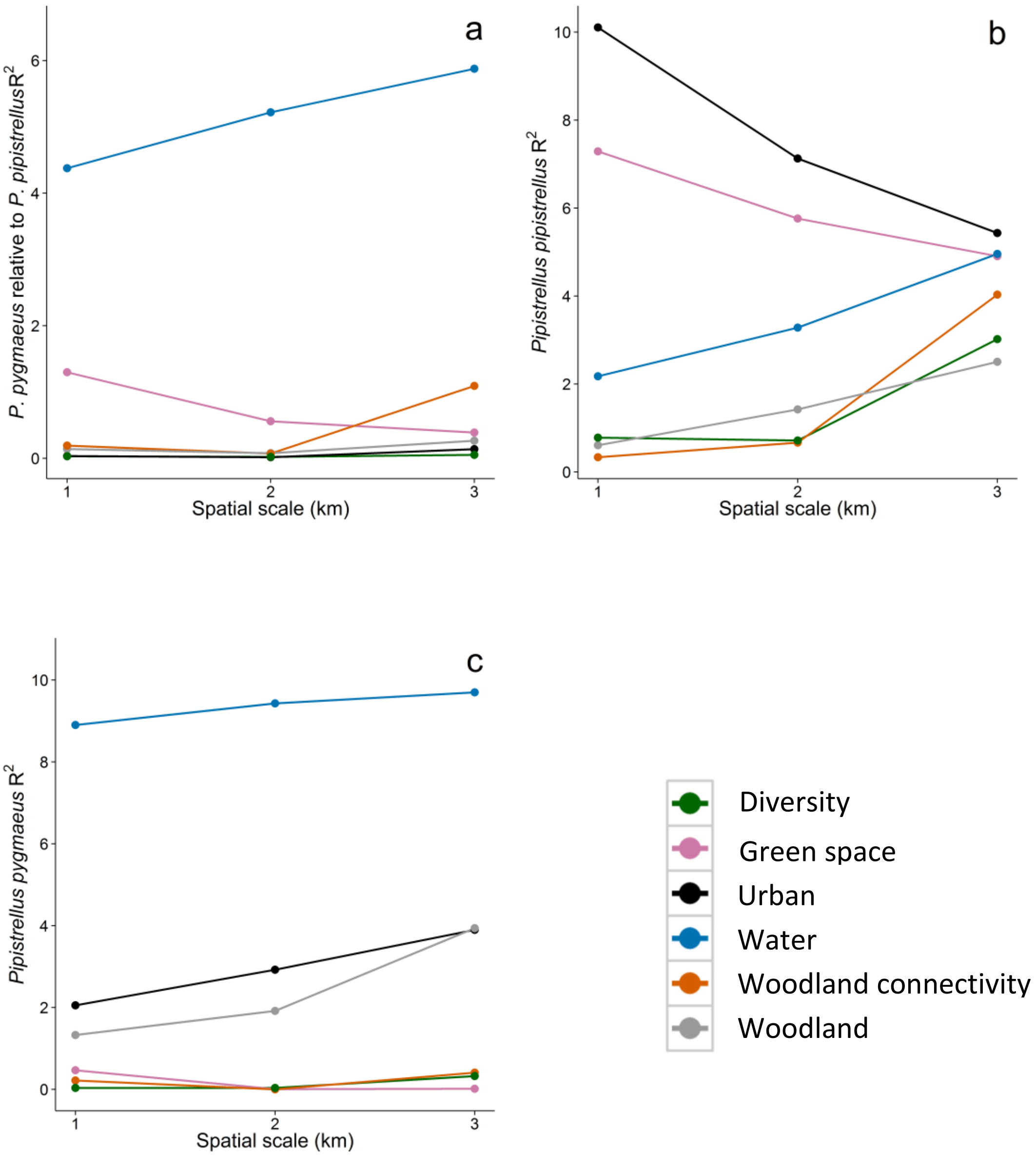
8.6 Acknowledgements

I would like to thank all the Bat Conservation Trust volunteers who have taken part in the NBMP and contributed to these results. I thank Katherine Boughey for her advice and support with handling the NBMP database. The NBMP is run by Bat Conservation Trust, in partnership with the Joint Nature Conservation Committee, and supported and steered by Natural England, Natural Resources Wales, Northern Ireland Environment Agency, and Scottish Natural Heritage.

8.7 Appendices

Appendix 8.7.1 The variation in the composition of the landscape of the 124 urban sites that were surveyed.

Biotope type	Scale (km)	Average % composition	Minimum % composition	Maximum % composition
Grey space	1	16	1	67
Green space	1	68	11	97
Inland fresh water	1	1	0	35
Woodland	1	13	0	85
Grey space	2	16	2	60
Green space	2	70	30	96
Inland fresh water	2	1	0	21
Woodland	2	11	0	59
Grey space	3	16	2	55
Green space	3	70	28	94
Inland fresh water	3	1	0	11
Woodland	3	11	0	39



Appendix 8.7.2 R2 values obtained from GLM models comparing the percentage of landscape covered by each biotope at a variety of spatial scales to a) the proportion of point counts per transect where *P. pygmaeus* was recorded versus where *P. pipistrellus* was recorded; the percentage of point counts per transect where either b) *P. pipistrellus* or c) *P. pygmaeus* were recorded.

Chapter 9

General discussion

Urbanisation is widely regarded as one of the major causes of declines in species richness and diversity, in this thesis I have shown that the behaviour, habitat preferences and distribution of bats are strongly influenced by the built environment at both a local and landscape scale. As ecological interest in biodiversity within the urban ecosystem rapidly increases (Niemelä 1999), the results and recommendations presented here will contribute to a greater understanding of how bat populations can be managed effectively within the urban landscape.

9.1 Relative importance of habitats within the urban matrix

Through the course of this thesis I have undertaken analysis within, arguably, three of the most important habitat types for wildlife within the urban matrix (woodland, waterways, green space). Each of these habitat types has previously been found to support a wide variety of taxa (e.g Leston & Rodewald 2006; Goddard et al. 2010), however there was little known about how bats used these habitats within urban areas. In contrast to alternate human-modified landscapes (e.g. agriculture; Fuentes-Montemayor 2013) I found a relatively low diversity of bat species, with *P. pygmaeus* and *P. pipistrellus* comprising the vast majority of the acoustic calls recorded and the bats trapped. In contrast, there were many species known to occur in the wider study areas (e.g. *Myotis nattereri* or *Plecotus auritus)* that were rarely recorded regardless of local habitat quality. There was also considerable variation in the extent that each of the main habitats was used. Although a direct comparison is impossible given the differences in surveying methodology, by comparing the studies conducted in the same geographical region (Central Scotland), the relative frequency of use between habitats is clear to see. Only nine passes per surveying hour were recorded within urban gardens in contrast to 19 and 308 passes per surveying hour in urban woodland and waterways. It was unsurprising that the greatest bat activity was recorded along urban waterways given the potential of waterways to facilitate movement throughout the urban matrix whilst avoiding areas of high anthropogenic disturbance (Baschak & Brown 1995). The relative importance of rivers and canals support the findings in chapter 6 which suggests that the urbanisation of riparian zones (with associated increases in anthropogenic disturbances) should be avoided.

9.2 Managing the built environment at a local scale

Habitat loss as a result of urbanisation is often permanent and holds little chance for recovery (McKinney 2006) which, when coupled with the complexity of managing large numbers of stakeholders within the city environment, makes landscape-scale conservation projects particularly difficult. In contrast, local scale management actions and conservation strategies can be effective in improving urban biodiversity, are cost and time effective and can be undertaken by local conservation groups or volunteers. This bottom-up approach has the potential to increase public participation in, and awareness of, environmental issues as these are activities that anyone can undertake (Madre et al. 2014). Throughout this thesis I have shown that the presence of both bat and moth populations within the urban landscape are determined by habitat attributes at the local scale. Anthropogenic disturbances such as light pollution (chapter 6) and artificial ground cover (chapter 7) may be reducing connectivity within the urban habitat even for those species commonly regarded as well adapted to survive within the urban matrix. As a conservation strategy it is considerably more efficient to invest in ensuring connectivity between existing patches of green space (e.g. automatic streetlights which switch on/off according to human presence; Mrazovac et al. 2014) than restoring or creating new patches of greenspace. Similarly, it is much easier to manage woodland more effectively (e.g. ensuring patches of open habitat to support female *P. pygmaeus* foraging activity) than to plant new woodland to recreate similar conditions. It is therefore clear that whilst small scale adaptions to the urban matrix cannot recreate the resources or primary habitats found within the rural setting, there is considerable potential to improve the connectivity of the urban landscape and foraging opportunities for wildlife.

In this thesis I show that species respond differently to the urban woodland, with particular attention being paid to the differential responses of *P. pipistrellus* and *P. pygmaeus*, however woodland managers should consider the species present in the landscape (e.g. regions with greater bat species diversity such as southern England) before management plans are drawn up. For example, whilst the removal of woodland clutter may benefit *P. pygmaeus* it may impact species such as *Barbastella barbastellus* which preferentially select dense woodland (Zeale et al. 2012). However, given that *B. barbastellus* are rarely found within urban habitats (Zeale et al. 2012) this may not be a large concern. The urban ecologist therefore has the difficult decision to make on whether to focus on managing habitats for those, albeit relatively common, species we know are able to use the urban matrix to some extent (e.g. *Pipistrellus* spp.) or to improve urban habitats with the aim of increasing the prevalence of rarer species (see section 9.4).

9.3 Managing the built environment at a landscape scale

Within cities, the remaining areas of semi-natural habitats are frequently found within small and isolated patches dispersed between built-up areas. Therefore, to fully understand the processes influencing biodiversity patterns, investigating the impact of habitat composition, configuration and heterogeneity at a landscape-wide scale is required (Turrini & Knop 2015). Improving connectivity between semi-natural habitats is difficult in long established cities which have existed for centuries offer relatively little flexibility in improving connectivity between semi-natural habitat types (although Hamburg's plan to construct a green roof over its motorway which runs through the city hints at future possibilities; European Union 2011). However the creation of relatively new garden cities (e.g. Bicester in Britain) provides opportunities for integrating conservation strategy into urban planning. However, even the limited breadth of taxa studied in this thesis demonstrates the difficulties associated with conserving biodiversity within the urban landscape given that every species, including cryptic species, will differ in the extent of their response.

It is important to consider that maintaining or even attempting to increase the amount of green space to enhance biodiversity may have a considerable impact on how cities are constructed. By 2050 it is projected that over two-thirds of the global population will be living within urban areas (United Nations 2014); managing the landscape therefore becomes even more complex. There are two broad methods in which to cope with ever increasing urbanisation, either (i) minimising urban sprawl by focusing on creating a compact city so that ecological impact is locally intense but constrained within a relatively small area, or (ii) minimising the intensity of urbanisation so that ecological impact is lessened; however it is spread over a more extensive area (Dallimer et al. 2011; Sushinsky et al. 2013). Throughout this thesis I have shown that extensive grey space can negatively impact all bat species including those commonly found within city environments. Attempts to minimise urban sprawl by compacting the city may therefore have a considerable impact on the abundance and diversity of wildlife able to utilise the urban environment. In chapters 3, 6 and 8, which compare habitat differences between morphometrically similar species, I found that *P. pipistrellus* appear to actively avoid areas favoured by *P. pygmaeus* resulting in differential habitat use, supporting previous findings by Nicholls & Racey (2006b). For example, *P. pipistrellus* appears to utilise a wider range of urban habitats including woodlands which offer suitable foraging resources but which are surrounded by sufficient grey space to deter *P. pygmaeus.* However, even *P. pipistrellus* are negatively affected by the built environment suggesting that further urbanisation may restrict the distribution of *P. pipistrellus* and lead to additional competition for resources between the two species.

9.4 Conservation focus in urban areas

With the exception of chapter 6 which included consideration of *Myotis* spp. and *Nyctalus* spp., this thesis has focused primarily on how the two commonest species of pipistrelle in the UK (*P. pygmaeus* and *P. pipistrellus*) respond to urban landscape. This was primarily a consequence of the relatively low diversity of bat species found within the built environment; however it also presented the opportunity to examine the behaviour of our commonest species in greater depth from sex differences in foraging activity to examining how morphometrically similar species respond to urbanisation.

Additionally, it presented the opportunity to question where the focus of conservation management in the built environment should be placed and if the focus should differ from conventional, non-urban conservation goals.

The primary aim of conservation biology revolves around minimising and moderating the impact of human actions on habitat and its wildlife. Urbanisation is often grouped together with other destructive human actions such as logging in the Amazon, the collapse of fish stocks, and the increase in carbon emission as a threat to biodiversity. However whilst it is fairly logical that as conservationists we should aim to protect the Amazon, understanding how and what to conserve within the urban ecosystem is considerably more complex. Whilst we may be able to reduce or even ban logging in the Amazon with resultant positive effects on biodiversity in the region, it is inconceivable that we will prevent urban growth or reduce anthropogenic pressures to the extent that cities regain a similar level of diversity to many rural areas. Throughout this thesis I have shown that species regarded as either ‘urban exploiters’ or ‘urban adapters’ due to their frequent occurrence within the built environment (e.g. *P. pipistrellus;* Chapter 3; Hale et al. 2012) can still be negatively influenced by urbanisation. Urban conservation strategies should therefore start by ensuring the survival of these commoner species within the city landscape not only to maintain the important ecosystem functions that they may be contributing to but also for their role in inspiring and improving the lifestyle of human urban inhabitants.

The abundance and widespread nature of common species frequently means they are overlooked in conservation strategies despite contributing much of the structure, biomass, and energy turnover of the majority of terrestrial and marine systems

(Gaston 2010). Even relatively small population declines in common species can frequently result in the loss of large numbers of individuals which can have severe ecosystem consequences (Inger et al. 2014). Conservation management is frequently focused on efforts to increase the abundance of rare species, often through the establishment, restoration and maintenance of protected areas, however these offer little protection for more common and widespread species (Inger et al. 2015). It is rarely possible to create protected areas for wildlife within the built environment given the pressure on managing green space for recreational activities and public enjoyment (Hoffman et al. 2010). Instead, Inger et al. (2014) argue that an increasing proportion of conservation funding should be afforded to wider scale environmental improvement programmes (e.g. the implementation of urban green space schemes) which will be beneficial for common species. This thesis supports these findings; I found that *Pipistrellus* species were prevalent throughout the urban landscape from waterways to private gardens. Focusing effort on a limited few protected areas is unlikely to benefit these species as much as conservation strategies such as encouraging the re-greening of urban gardens (chapter 7) or reducing light pollution along riparian zones (chapter 6) to ensure greater connectivity within the urban landscape. Efforts to improve green space across the urban matrix will not only benefit common species but ensure a higher percentage of urban residents will have access to high quality green space.

Accessing urban green space is well known to be beneficial for both the mental and physical health of the public (e.g. Tzoulas & Greening 2011) and will also increase wildlife spotting opportunities. Encounters with wildlife may strongly influence attitudes towards conservation, although the majority of studies which validate this hypothesis are primarily descriptive (Shwartz et al. 2014). However, Bjurlin & Cypher (2005) did show that positive relationship between citizen exposure to and appreciation of urbanised kit foxes (*Vulpes macrotis*) in California indicating the potential to garner support for wider conservation action and protection of species. As interest in urban ecology grows, the frequency of interactions between those observing or studying urban wildlife and members of the public will increase. One or a few bystanders watching or feeding wildlife can stimulate observable responses towards wildlife by others (Dick & Hendee 1986). This provides the urban ecologist with the opportunity to inform, educate, and inspire the public about both the diverse range of wildlife in their backyard and wider conservation issues.

Just as zoos frequently justify their existence by their commitment to environmental education and thus inform the public about wider biodiversity and conservation issues (Stoinski et al. 2002), reassessing the goals of urban conservation to focus predominantly on the conservation of relatively common species and ensuring public engagement and education may be key. The city ecosystem can be biodiverse; adjusting expectations to appreciate and secure the future of wildlife that is currently able to exist in areas of relatively high anthropogenic disturbance may be more important than attempting to increase the accessibility of the city for rarer species. One of the key messages from this thesis is that even common bat species are negatively affected by urbanisation and much greater attention should be paid to securing their future. As Murphy (1988) comments:

“Our urban centres can be viewed as bellwethers of our global environmental fate. Our success at meeting the challenges of protecting biological diversity in urban areas is a good measure of our commitment to protect functioning ecosystems worldwide. If we cannot act as responsible stewards in our own backyards, the long-term prospects for biological diversity in the rest of this planet are grim indeed”

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