Multiscale habitat preferences and selectivity in bats across urban to rural landscapes

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Table of Contents

1. ABSTRACT

Human dominated landscapes are increasingly putting pressure on the ability of many bat species to survive, due to their sensitivity to environmental change. Thus, there is an increasing need to understand the habitat preferences of bats across urban landscapes important to their survival. This study used acoustic call data to investigate bat habitat selectivity and multiscale habitat preferences throughout North and West Yorkshire. Across 15 1x1km transect sites, overall abundance was found to decrease with increasing urban cover, and increase in suburban and rural areas. Different habitat variables were extracted from each site and manipulated in ArcGIS to see which were the most significant in determining bat presence and selectivity. Kruskal-Wallis tests revealed that *Nyctalus noctula, Pipistrellus pipistrellus* and *Pipistrellus pygmaeus* were significantly selective of woodland edge, inland water, buildings and road habitat features. The strongest habitat preference for all species was for percentage cover of water and forest, particularly at smaller scales. Interspecies comparisons revealed *P. pipistrellus* showed strong associations with percentage of building cover at both scales, whilst *P. pygmaeus* revealed significant preferences for water. Spearman correlation tests measuring the strength of association between bats and percentage cover of habitat variables showed strong correlations at larger scales for water and forest cover. Conservation management should therefore focus on preserving natural habitat features in rural and urban areas.

2. INTRODUCTION

2.1. Urban Growth

The rapid global urban population growth seen in the last 65 years, from 746 million to 3.9 billion in 2014, has had significant impacts on bat species richness and abundance (UN, 2014; Kunz *et al.,* 2012). This is primarily due to habitat loss, fragmentation, degradation (Altringham, 2011), chemical pollution, barrier effects, introduction of invasive species and a decline in prey species (Wickramasinghe *et al.*, 2004; Lentini *et al.*, 2012; Berthinussen & Altringham, 2012a). Many studies are currently looking into the possibility of using bats as bioindicators of environmental change (Wordley *et al.,* 2014; Russo & Ancillotto*,* 2014), as their widespread distribution and sensitivity to even minute perturbations could reflect the status or possible risk of such changes in other species (Jones*,* 1995). Some of the responses to change can be seen with declines in abundance, population size, range distributions and behaviour (Altringham, 2011). This may be due to the absence of specific habitat features and suitable microclimates that limit the distribution of many species. Therefore information regarding the abundance of bats in urban areas has vital applications for conservation, as 82% of the UK is urbanised and steadily increasing (UN, 2014). In addition, research on specific habitat preferences, the ability of certain bat species to adapt to urban environments and what features make others more vulnerable could be used in management in order to reduce the impacts (Altringham, 2011; Russo *&* Ancillotto, 2014).

2.2. Value of bats

Apart from justifying the value of bats in terms of their diverse nature and unique evolutionary history (Fenton *et al.,* 1998), bats provide a range of ecosystem services and benefits to both the environment and humans (Altringham, 2011; Millennium Ecosystem Assessment, 2005). The Brazilian-free tailed bat forages on and maintains populations of the cotton bollworm insect pest, saving the US economy over $23 billion dollars in terms of preventative damage to cotton and reduced pesticide use (Cleveland *et al.,* 2006). In Asian markets, over 70% of the fruit sold is pollinated or seed dispersed by bats, in particular the Durian fruit which is worth $2 billion annually (Kunz *et al*., 2012; Altringham, 2011). Guano is a source of high phosphorus and nitrogen, and one of the primary limiting nutrients of plant life. Duchamp *et al.* (2010) studied the potential benefits of the 'pepper shaker-effect,' a hypothesis where bats flying from nutrient-rich regions to nutrient-poor habitats redistribute the guano and act as mobile fertilisers.

Ecotourism also boosts the economy, as seen in Congress Avenue, Texas, generating $12 million annually (Pennisi *et al*., 2004). Medicine is also derived from the Vampire bat's salivary enzyme, desmoteplase, which acts as an anticoagulant for post-ischemic stroke patients (Furlan *et al*., 2006). It has been found to extend the time required to administer tissue plasminogen activator during the post-stroke period from 3 to 9 hours (Schleuning, 2000). Other aspects of bat biology providing benefits to humans include the development of the ©UltraCane, a device that enables the blind to detect oncoming objects. Developed by researchers at the University of Leeds, it was based on the echolocation calls of bats and has helped thousands of visually impaired people (Scheggi *et al*., 2014).

2.3. Importance and impacts of an urban landscape on bats

Urban foraging

Each bat is perfectly adapted to each habitat in terms of wing morphology, diet, ecological niche, echolocation call, hibernacula and behaviour (Altringham, 2011; Threfall *et al.,* 2008). The effects of particular habitat features on bats differs, as each specie uses the landscape differently (Altringham, 2011; Coleman & Barclay, 2011). Some exhibit behavioural plasticity and can adapt to urban environments, enabling them to effectively exploit their habitat without the disruption of roads, light pollution or buildings (Russo & Ancillotto, 2014; Stone *et al*., 2009). They are known as urban adaptors or synurbic species (Kerth & Melber, 2009; Russo & Ancillotto, 2014). This has frequently been seen in bats with long, narrow wing morphology with a high wing loading, as open air foragers are largely unaffected by urbanisation (Norbeg & Rayner, 1987). The ability of synanthropic bats to dominate urban foraging areas can be problematic for the less well adapted species (Silvis *et al*., 2014, Russo & Ancillotto, 2014), and may result in competition. Populations of *Rhinolophus hipposideros* in Wales may be in decline be due to the expansion of *Pipistrellus pipistrellus,* which have increased as a result of greater feeding efficiency provided by artificial lights normally avoided by the lesser horseshoe bat (Warren *et al*., 2000; Lacoeuilhe *et al.,* 2014; Arlettaz *et al*., 2000).

Water in urban areas

Bats are vulnerable to evaporative water loss as a consequence of their morphology and large surface area to volume ratio (Razgour *et al.,* 2010). Within urban areas, open artificial sources such as ponds, ditches and swimming pools provide bats with fundamental opportunities to drink and forage. Certain species show preferences over these larger, less cluttered and open bodies of water (Siemers & Schaub, 2011). The reduction in pulse-echo overlap, ability to detect spectral shift and high insect abundance over still water sources can attract large numbers of bats to urban and modified sites (Altringham, 2011). Such examples can be seen in North Carolina, where studies looking at the importance of managed water bodies over natural wetlands revealed significantly higher bat activity by heliponds, despite equal densities of insects at both sites (Vindigni *et al.*, 2009). Similarly, studies on Greek islands have shown that bats will also use artificial water sources such as swimming pools due to the lack of natural sources in such arid habitats, with minimal annual rainfall (Davy *et al.,* 2007).

Urban threats and barriers

The impact of roads on bats was largely overlooked until a hypothesized extinction model was proposed by Forman *et al.,* (2003). Habitat destruction by their construction reduces foraging and roosting habitat; vital resources key to a bats survival (Bellamy *et al.,* 2013). This can lead to a reduction in habitat quality due to the addition of chemical, acoustic and light pollution (Altringham, 2011). This has been known to alter and negatively impact the foraging ability of *Myotis myotis* via acoustic pollution from incoming traffic, where the bat is unable to detect spectral shifts in its ground dwelling arthropod prey (Siemers & Schaub, 2011). A large number of collisions occur with low flying species (<0-4m), and studies investigating the effectiveness of mitigation strategies (bat gantries), revealed that 84% of the bats acoustically surveyed were at risk crossing the roads at unsafe heights (Altringham, 2011), despite their manoeuvrability (Berthinussen & Altringham, 2012b).

The barrier effect is also problematic, as the disruption of connected core habitats reduces the range and size of a bats habitat (Altringham, 2011). When landscape connectivity no longer facilitates the movement and passage of bats, this can lead to reduced survival of smaller, genetically isolated populations restricted to patches. This is due to their habitat-specific preferences and flight and echolocation abilities (Jackson & Fahrig, 2011). Higher flying species such as Noctule bats are less affected by the expansion of roads, due to their fast open air foraging and greater commuting distances (Jung & Kalko, 2012), whereas slower, gleaning species are more sensitive to such barriers (Berthinussen & Altringham, 2012a). The vagility and mobile flying capabilities of bats was thought to enable them to avoid such threats (Stanley *et al.*, 2003). However, research has revealed a significant relationship between the decrease in bat activity and diversity with closer proximity to roads, providing the first conclusive evidence of their effect on bats in the UK (Berthinussen & Altringham, 2012a).

2.4. Other anthropogenic threats facing bats

The threat of turbines has been little studied and understood in bats (Altringham, 2011; Cryan & Barclay, 2009). One recent study manipulating wind turbines and using thermal imaging cameras concluded that blade rotation speed did not influence the way in which the bats interacted with the structure (Cryan *et al.,* 2014). The best studies have included more rigorous empirical data and methodology, revealing that 75% of tree roosting species in North America were among those bats affected and killed by turbines (Altringham, 2011). Other threat to bats include anthropogenic climate change, as global temperatures continue to rise with possible increases of 5.0-6.4˚C by 2081-2100 (IPCC, 2014). Despite their ability to fly, migrate and possibly expand their ranges to higher latitudes, their survival ultimately depends on their adaptability (Altringham, 2011) and state of the environment they are driven to (La Val, 2004). If the habitat is fragmented and lacking specific habitat features, specialist species will be more at risk from extinction (Lopez-Roig & Serra-Cobo, 2014; Altringham, 2011). Evidence for northerly shifts in species distribution has been recorded from bat captures between 1973-1999 in Monteverde, Costa Rica (La Val (2004). Rebello (2010) used IPCC climate change scenarios to predict the future biogeographical distribution of 28 European bat species, where Boreal species are predicted to be most likely at risk from extinction and incapable of shifting its distribution northwards.

Cave and mine closures also threaten the survival of many bat species worldwide (Cardiff *et al.,* 2012). This is problematic for bats as many synurbic species depend on them for survival and winter roosting (Altringham, 2011; Speakman *et al.,* 1991). Tourism also brings its own problems in terms of noise and light pollution which may disrupt torpid bats (McCracken, 1989). In Ankarana National Park, Madagascar, different measures of visitor disturbance was investigated in *Rousettus madagascariensis,* revealing that direct light and close proximity led to higher levels of activity (Cardiff *et al.,* 2012).

2.5. The importance of species-habitat associations and Habitat Suitability Modelling

As habitat fragmentation increases due agricultural and urbanisation land-use change, the value of understanding the relationship between bats and their habitat is more vital than ever to their conservation worldwide (Bellamy *et al.,* 2013). Habitat Suitability Models can be powerful statistical tools in informing and increasing the effectiveness of conservation management. This is done by studying habitat suitability relationships at multiple scales, by creating predictive models and investigating which environmental geographic variables (EGVs) determine their biogeographic distribution. Such maps are considered ecologically informative, and this relationship can be explained by their morphological and behavioural characteristics that allow them to adapt and persist in those habitats (Mayle, 1990).

The advancement in technology and developments in statistical packages have provided researchers with the ability to create accurate HS maps that use presence-only data. This data can then be extrapolated and projected to a much larger sample area, conserving resources and effort (Bellamy *et al.*, 2013). The simplicity and readability of HSM maps allows conservation policy makers to prioritize efforts towards biodiversity ‘hotspots’ and species rich areas (Razgour *et al.,* 2011). This is in contrast to the informed guesswork which previously dominated policy with a substantial lack of evidence (Altringham, 2011), efficient methodologies, or data on species-habitat relationships (Miller *et al.*, 2003). Such studies have been predominantly conducted in rural sites and national parks, thus the importance of understanding specie-habitat relationships in urban areas is now required.

2.6. Aims and predictions

Few studies have looked into the particular effects of urbanisation on bats, in terms of abundance, distribution and habitat preferences at different spatial scales. This study **aims** to i) assess the relative abundance and distribution of bats across urban to rural landscapes, as well as ii) investigate whether bats are being selective of particular enviro-geographic variables (EGVs) at 15 different sites. Finally, iii) examine whether bat presence is determined by percentage cover of water, forest or buildings, and compare interspecies preferences at two different spatial scales (100m and 1000m). The significance of this study is to establish what the most important habitat features different species of bats select and show preferences for, in both rural and urban areas. This information on species-habitat associations could be of value for urban conservation strategies across North and West Yorkshire.

Prediction: That the overall species abundance and diversity of British bats will decrease in urban areas and overall increase in rural and suburban habitats. Forest and inland water cover within rural and urban areas are expected to be the most important habitat features in determining bat presence. *P. pygmaeus* is expected to have strong associations with water habitat features. Certain species will be better adapted to urban environments, such as *P. pipistrellus,* showing stronger associations between roads and buildings in urban areas due to their generalist and adaptable nature.

3. METHODS

3.1. Area of study

The study was conducted across North and West Yorkshire (see Figure 1), beginning in Leeds and ending in the rural town of Addingham. Locations of each transect can be seen in the Appendix, Table 1. All locations encompassed a variety of habitat types including meadow, wetlands, heathland, agricultural fields, woodland patches, as well as the urbanised structures and settlements, particularly in Leeds. The areas selected were to incorporate a broad range of habitats to be able to better interpret how patterns of species presence may be explained by the urbanisation of previously natural habitats. Equally, to observe whether certain species are able to overcome and adapt to changing landscapes.

Figure 1. Map of study area across North and West Yorkshire downloaded from Digimap Edina (http://digimap.edina.ac.uk/), with 15 3-4km transects GPS trails marked in red.

3.2. Collection of species data

The 15 1X1 km transect study field sites were selected across a 1:50000 scale Ordnance Survey map of Leeds and Bradford, Harrogate and Ilkley. It encompassed five urban, suburban and rural sites each (see Table 1, Appendix), as classified by percentage cover of buildings. The study was carried out from June to August 2014, where broadband acoustic surveys were conducted to collect presence-only data for different bat species. Each site was separated by 5km in order to reduce the occurrence of residual spatial autocorrelation (rSAC). Each transect was repeated and the reversal of each transect starting point was done in order to reduce bias. This is due to the possible influence of time on the levels of bat activity (Bellamy *et al.*, 2013). One site had to be redone and another shifted due to accessibility issues.

Each of the site routes and pathways were looked at using Edina (http://digimap.edina.ac.uk/) and Google earth maps before being conducted, in order to assess accessibility and ensure safety. Trail drive runs of the transect areas were also performed 30 minutes before each survey. At each site, 3-4km transects were conducted to collect the data, on the premise of suitable weather conditions (no rain) during dusk. This included dry nights with temperatures above 10 ˚C, and low wind speeds below 20km/h which was measured and noted using an anemometer (Technoline EA 3000 anemometer, www.technoline.eu). One survey was stopped mid-way due to heavy rainfall. Each transect was walked at speeds of 2.5-3.5km/h, and bat calls between 10-60 kHz were detected using the Pettersson D240x ultrasonic bat detector (www.batsound.com). The output sound was recorded as a WAV file by an Edirol R-09 recorder (www.edirol.com). A Garmin eTrex 10 GPS device measured and recorded speed, elevation, distance and direction (British National Grid coordinates), as well as precise geographic positions every 20 seconds which was used to geo-reference with the bats calls recorded during the transect (www.garmin.com). Both GPS and recorder were time synchronised.

3.3. Data conversion

Bat Classify software was used to split individual time-expansion WAV bat calls, and then run an automatic analysis on them in order to determine which British bat specie was present. Once processed, the final results were readable as a CSV file, whereby an evaluated list of the probability of occurrence for 12 different UK bats species was listed (https://bitbucket.org/chrisscott/batclassify). Sonograms in Bat sound Pro 3.2 (www.batsound.som) were used to determine the presence of the less abundant species such as *Myotis brandtii/mystacinus*. Analysis was conducted using calls identified at a species level of >90% confidence. In Excel, cells containing calls at >90 confidence were sorted and kept, and the Department of Natural Resources GPS software (DNR GPS) was then used to extract the time stamps recorded from the GPS to match with the bat call timings for each transect (http://www.dnr.state.mn.us/mis/gis/DNRGPS/DNRGPS.html). Any repeated calls of the same species recorded within the 20 seconds by the GPS were removed, as this was most likely to be the same bat and thus not a unique data point.

Repeated transect data was the collated together with the first set of 15 transects, according to location and species, in separate CSV files. The X and Y coordinates were then batch converted (http://www.ordnancesurvey.co.uk/gps/transformation/batch#) to British National Grid coordinates for use in ArcGIS (10.1). The classifications for urban, suburban and rural areas was calculated by creating buffer zones 1000m along the transect routes (with a polygon line shapefile) and calculating percentage cover of buildings; 75% building cover- urban, 25-75% building cover- suburban and <25% building cover- classed as rural. The size of the buffer was chosen to encompass the average core home range of a British bat between 1-1.5km, however certain species have larger foraging ranges (Kronwitter, 1988; Altringham, 2011). Figure 1, the map of the study site, was created by downloading 'miniscale' map data of the North and West Yorkshire region from Digimap Edina (http://digimap.edina.ac.uk/), and importing the transect paths from the GPS device.

3.4. Environmental geographic variables and ArcGIS

ArcGIS (10.1) was used to create different habitat layers (EGVs) in preparation to analyse the data. Topography, building height and vector data was downloaded from Digimap Edina in the areas of each survey. This was then used to form the base map (as vector data). The British National Grid GPS coordinate points of each bat were then imported and saved as a unique bat layer, and then placed on the corresponding topography layer that it was recorded on as a separate species. Then, seven different habitat layers were extracted and saved separately in order to conduct the proximity and buffer analysis (see Table 1). Such variables were selected due to the increasing evidence of their value in several bat species, and their ecological requirements (Brown, 2013). Urban features were also selected in order to assess their influence on bat selectivity. The large number of EGVs used in Bellamy *et al*., (2013) study of multiscale HSMs in the Lake District National Park would not be suitable in this smaller study, as the area has a largely heterogeneous landscape, with much variation in elevation and other topographical features. By comparison the transect sites in this study encompassed a more urbanised, homogeneous landscape.

This study used two scales for the buffer analysis; 100m and 1000m to encompass broad, common home ranges of European bats. Proximity data (distance to woodland edge, inland water, roads and buildings in metres) was calculated in ArcGIS using the 'Near' function, from the bat point to the closest edge of the 'polygon' habitat feature class. To calculate percentage cover of woodland, buildings and water; 100m and 1000m buffers were created around each bat point using the geoprocessing tool. Then the 'Tabulate intersection' tool was used to calculate the percentage cover of each habitat variable within the buffers at the two different scales. For each given bat species with a distance or percentage cover to a habitat feature (representing presence-only data) at each transect location, random points were generated using the random points generator. This performed within 1000m of the transect boundaries of the path walked during the survey (see Figure 2). Proximity and buffer analysis was then also conducted on the random points. This was to compare and see whether a particular species was, on average, found closer to that feature than the random points were, in order to determine whether bats were being selective of their habitat.

GIS habitat layer	Data description	Source of data
Cover of water (%)	Calculate percentage cover (tabulate intersection) at different spatial scales (100m or 1000m)	OS MasterMap© Topography Layer
Distance to inland water (m)	Near distance from input bat layer source to nearest water source	OS MasterMap© Topography Layer

Cover of buildings (%)	Calculate percentage cover of buildings (tabulate intersection) at different spatial scales (100m or 1000m)	OS MasterMap© Topography Layer
Distance to buildings (m)	Near distance from input bat layer source to nearest building edge	OS MasterMap© Topography Layer
Distance to roads (m)	Near distance from input bat layer source to nearest road	OS MasterMap© Topography Layer
Cover of forest (%)	Calculate percentage cover (tabulate intersection) of forest (mixed) at different spatial scales (100m or 1000m)	OS MasterMap© Topography Layer
Distance to woodland edge (m)	Near distance from input bat layer source to nearest woodland edge	OS MasterMap© Topography Layer

Table 1. The seven different habitat layers created in ArcGIS which were used for analysis. The variables calculating percentage cover were conducted at two different spatial scales (100 and 1000m) using buffers, whereas the non-scalar variables where distance was calculated were not.

Figure 2. Image of vector map data of the Swinsty transect area downloaded from Digimaps, for use in ArcGIS. Used to calculate proximity data and conduct buffer analysis. Bat layer includes random points generated in yellow, occurrence points in red. The transect path was drawn in accordingly with the polyline tool, which matched the precise GPS location.

3.5. Statistical analysis of data

The data were then exported as CSV files for use in Excel and SPSS to compare the medians and variance of all the distances of the presence points to those for random points using a Kruskal-Wallis non-parametric test. This was chosen rather than an ANOVA, as the data was non-normally distributed, as determined by conducting a Shapiro-Wilk Test (descriptive statistics). Transformations did not normalize the data. This was to investigate whether *N. noctula, P. pipistrellus, P. pygmaeus* were being selective of the different habitat features, (distances to woodland edge, roads, inland water and buildings). Data from all 15 transects study sites were pooled together, because each separate transect was only used to select a wide range of habitats for practical expediency. The same was done for the percentage cover analysis at the two different scales (100m and 1000m). The critical significance value (α) was 5% (0.05). Boxplots were used to graphically represent the distance and percentage cover data showing the medians with upper and lower quartiles. They provide effective summaries for large amounts of data and allowed for the comparison between the bat occurrences and random points.

To investigate whether bat presence was being driven by percentage cover of forest, buildings or water at different scales, buffer analysis was conducted in ArcGIS. The percentage cover of water, forest and buildings was calculated within a 100m and 1000m buffer scales around each individual bat. Bat occurrence data was then tested against randomly generated points using a Kruskal-Wallis. In order to compare *N. noctula, P. pipistrellus, P. pygmaeus* with each other to look for interspecies habitat preference differences, pairwise comparisons were made and boxplots to visually display any differences between the medians. All bat occurrence distance data was pooled from all the sites, including random points. The same was done for percentage cover at the two spatial scales. A Spearman's Rank correlation test was then conducted to assess the relationship between the total number of bat passes (as an index measure of abundance, not actual abundance), and the percentage cover of water, buildings and forest for all three species. This was to see whether these variables covary in a linear fashion, and measure the strength of association between total number of bat passes and percentage cover of the EGVs. Significant results are shown in scatter plots. The critical significance value (α) was 5% (0.05). Species abundance was displayed in tables and bar charts in order to show their distributions in rural, suburban and urban areas (according to calculated percentage cover of buildings), to give a general profile of the bat species recorded across the region at different sites.

4. RESULTS

The acoustic surveys across 15 sites in West and North Yorkshire recorded four species of bat; *Nyctalus noctula, Pipistrellus pipistrellus, Pipistrellus pygmaeus* and *Myotis brandtii/mystacinus* (Table 2). Certain species could not be separated, such as *Nyctalus leisleri* and *N. noctula. N. leisleri* however is not frequently seen in the region and so it was presumed that such calls were made by *N. noctula.* Again the software was unable to distinguish between *M. brandtii* and *M. mystacinus* calls, and so were grouped together. *M. brandtii/mystacinus.* Their abundance (index measure of abundance), and distribution across all the sites is shown in Table 2 and Figures 3 and 4.

4.1. Abundance and distribution

A profile of the bats across the region with abundance, distribution (according to rural, suburban and urban classification, calculated by percentage cover of buildings) are displayed in Table 2 and Figures 3 and 4.

	Index of abundance				
Species	Urban	Suburban	Rural	Total species abundance	Total % abundance
Nyctalus noctula	33	18	64	115	16.22002821
Pipistrellus pipistrellus	75	164	180	419	59.09732017
Pipistrellus pygmaeus	2	55	116	173	24.40056417
Myotis brandtii/mystacinus	0	0	2	2	0.282087447

Table 2. Total number of bats and percentage of abundance of each specie recorded in urban, suburban and rural transects across West and North Yorkshire. Overall *P. pipistrellus* was the most abundant bat species across all habitats, with a total of 419 recorded presences. *M. brandtii/mystacinus* was the least abundant compared to all other species. *P. pipistrellus* abundance increased further away from urban areas, as well as in *P. pygmaeus,* which were far less abundant than *P. pipistrellus* in urban areas. *N. noctula* was partially more abundant in urban areas, than in suburban or rural.

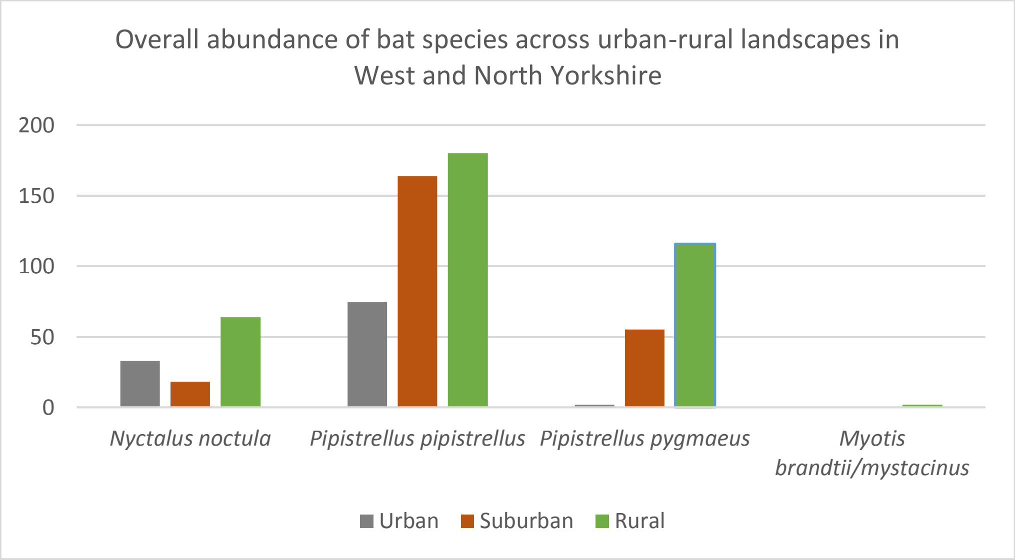


Figure 3. Bar chart illustrating the abundance (index of abundance, not actual abundance) of the 4 bat species recorded across the study sites according to habitat type (urban, suburban and rural). A majority of bats were present in rural areas, as well as substantial bat occurrences in suburban sites. There was little presence of *M. brandtii/mystacinus. P. pipistrellus* and *P. pygmaeus* were the most abundant of all species.

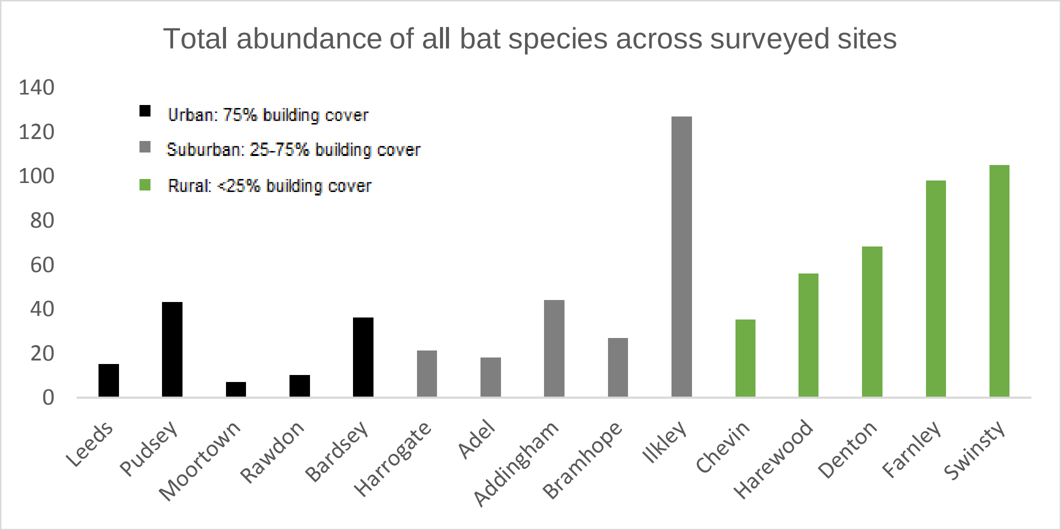


Figure 4. Bar chart illustrating the abundance of the four recorded species of bat within each transect area**.** From the most urbanised (Leeds) to the most rural (Swinsty) area according to percentage cover of buildings within a 1000m polygon buffer around the linear transect walked. 75% building cover- urban, 25-75% building cover- suburban and <25% building cover- classed as rural. Overall increase in bat abundance recorded at sites with lower percentage cover of buildings.

4.2. Distance to habitat features (EGVs)

To investigate whether *N. noctula, P. pipistrellus, P. pygmaeus* were being selective about the different habitat features, (distances to woodland edge, roads, inland water and buildings), the difference between the medians of bat occurrences and random points were compared using a Kruskal-Wallis test. Data from all the transects were pooled together. X^2 values, *P* values and sample sizes (*n*) are displayed in Table 3, and see boxplots in Figures 1, 2 and 3 in the Appendix. Analysis was not conducted on *M. brandtii/mystacinus* as there were too few data points.

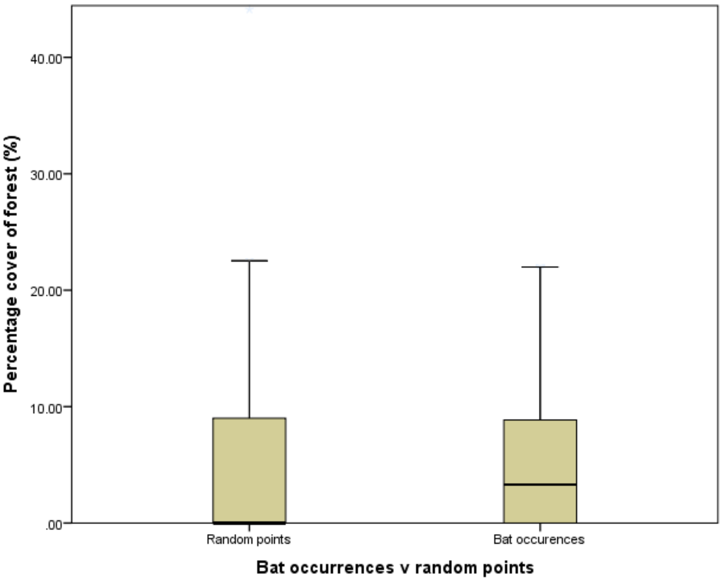
EGV	Species	X^2 value	n_1	n_2	n_3	P value
Distance to woodland edge (m)	*P. pipistrellus*	26.004	410	387	797	0.0001
	P. pygmaeus	6.846	146	173	319	0.009
	N. noctula	32.39	115	115	230	0.0001
Distance to inland water (m)	*P. pipistrellus*	24.045	410	387	797	0.0001
	P. pygmaeus	15.537	146	173	319	0.0001
	N. noctula	11.16	146	173	319	0.001
Distance to buildings (m)	*P. pipistrellus*	19.403	410	387	797	0.0001
	P. pygmaeus	7.384	146	173	319	0.007
	N. noctula	15.485	146	173	319	0.0001
Distance to roads (m)	*P. pipistrellus*	18.36	410	387	797	0.0001
	P. pygmaeus	100.093	146	173	319	0.0001
	N. noctula	99.929	146	173	319	0.0001

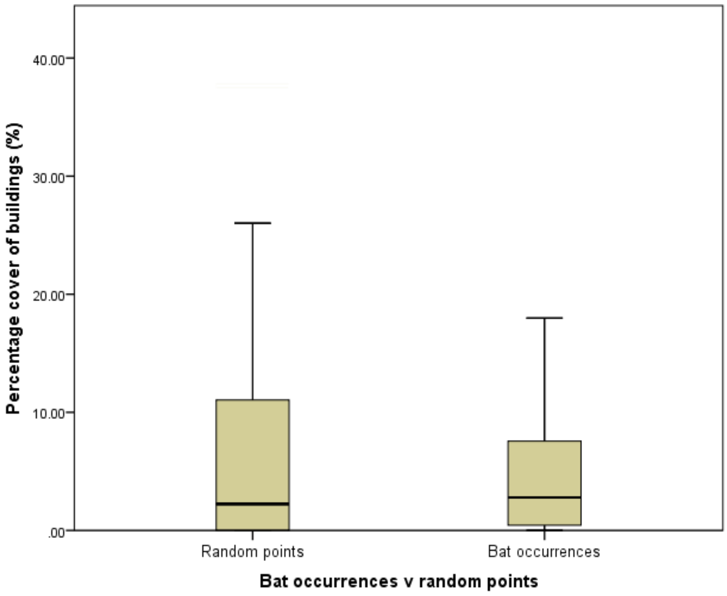
Table 3. The X^2 values, *P* values and sample size results from a non-parametric Kruskal-Wallis test for the differences between bat occurrences and random points along the range of distances to the four EGVs measured across the region. Results for 3 species; *P. pipistrellus, P. pygmaeus* and *N. noctula*. There were significant differences between all the bat occurrences and random point distances to each habitat feature.

4.3. Percentage cover of habitat features (EGVs) at two spatial scales

The percentage cover of water, forest or buildings was calculated within 100m and 1000m buffer scales around each individual bat. Bat occurrence data was then tested against randomly generated points using a Kruskal-Wallis to see if bats were being selective (see Figures 5, 6, 7, 8, 9 and 10).

Results for 100m





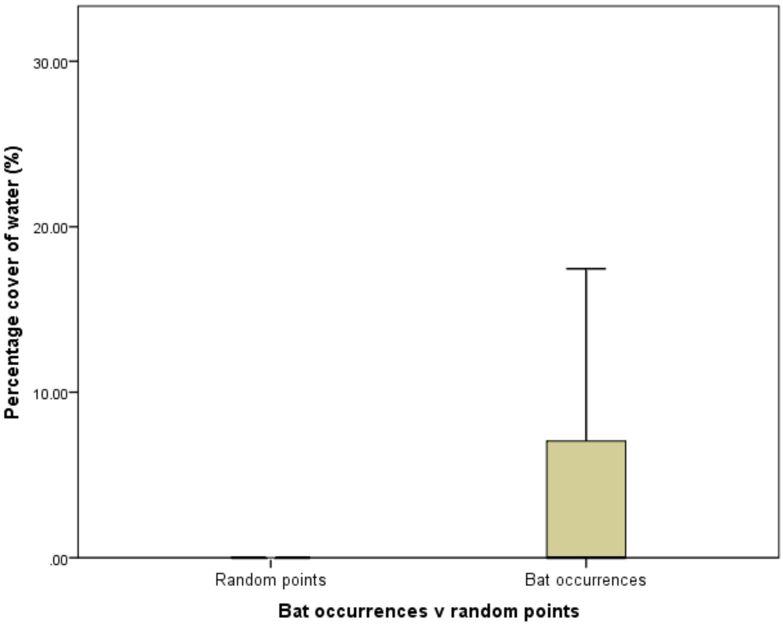


Figure 5. Boxplots showing the occurrence of *P. pipistrellus* versus random points at different percentage covers of forest (top right), buildings (above) and water (bottom left) at a 100m scale. Medians with upper and lower quartile ranges. There was a significant difference for the percentage cover of forest: X^2=11.434, n_1=364, n_2=365, n_3=729, P=0.001. Although the overlapping of error bars suggest no difference, the medians differ and the Kruskal-Wallis confirmed the significance. No significance was found with percentage cover of buildings: X^2=1.309, n_1=364, n_2=365, n_3=729, P=0. 253. Significance was seen with percentage cover of water: X^2=65.092, n_1=364, n_2=365, n_3=729, P=0.0001.

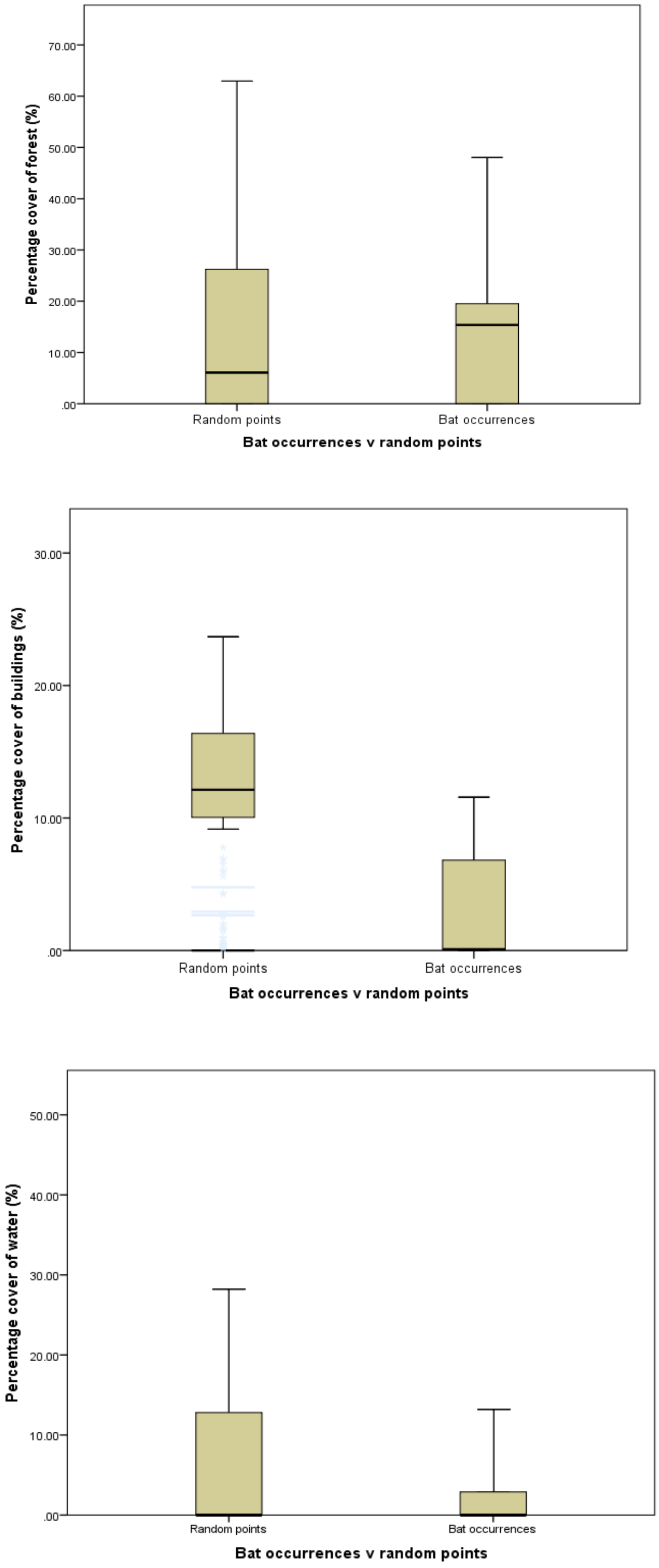


Figure 6. Boxplots showing the occurrence of *P. Pygmaeus* versus random points at different percentage covers of forest, buildings and water at a 100m scale. Medians with upper and lower quartile ranges. There was no significant difference for either natural habitat variables; the percentage cover of forest: X^2=0.0001, n_1=211, n_2=153, n_3=364, *P*=0.995 or percentage cover of water: X^2=2.511, n_1=211, n_2=153, n_3=364, *P*=0.113. Only the percentage cover of buildings had significance: X^2=24.523, n_1=211, n_2=153, n_3=364, P=0.0001.

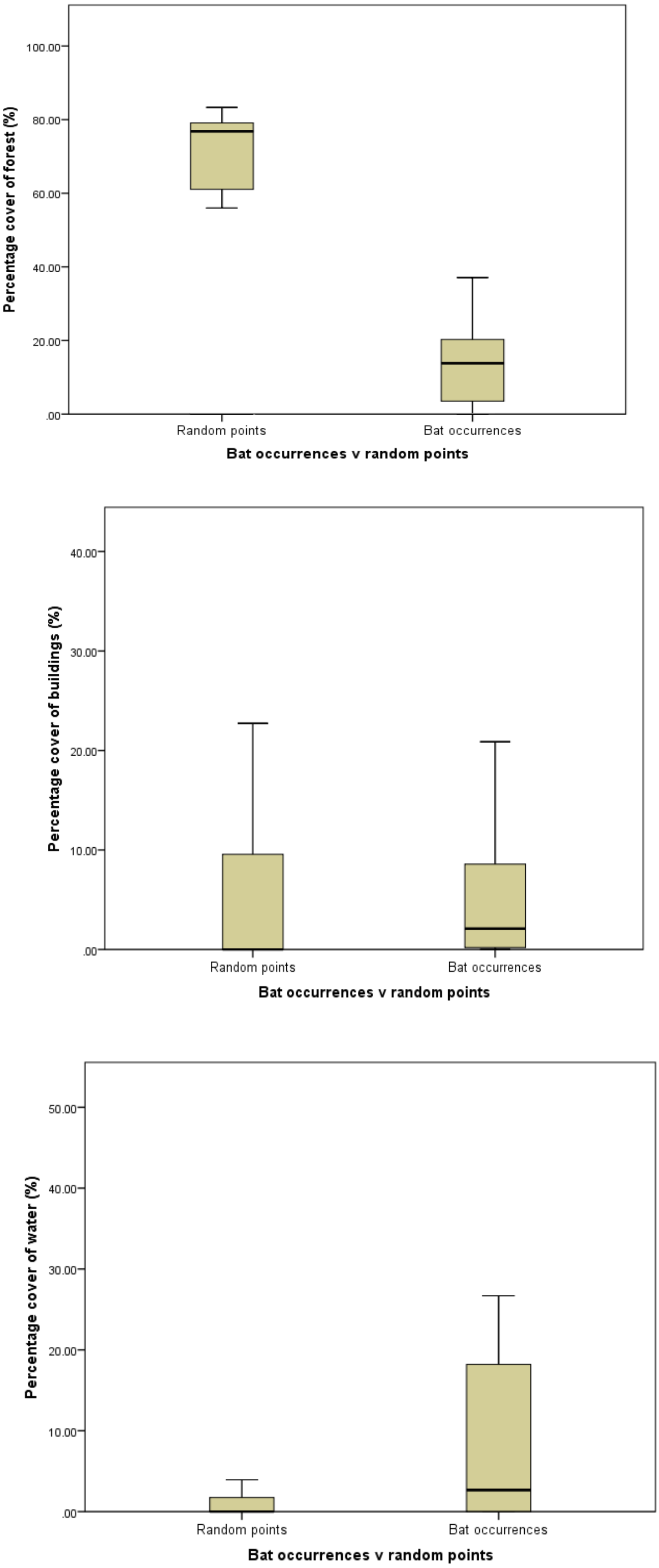
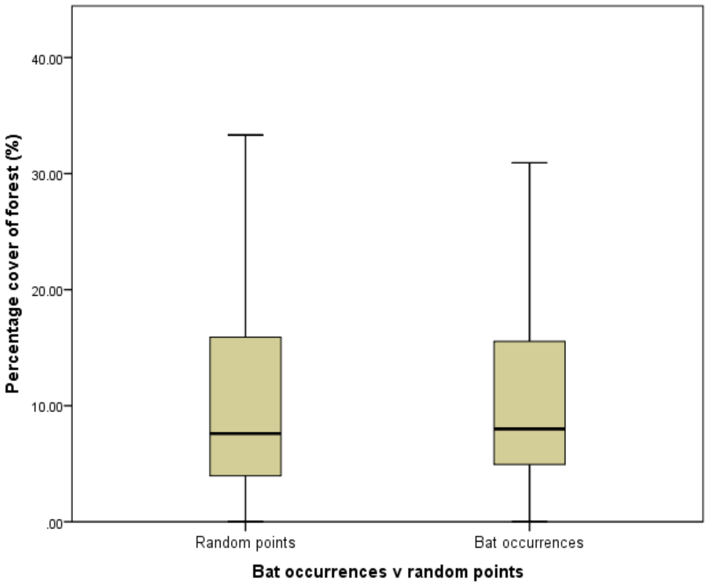
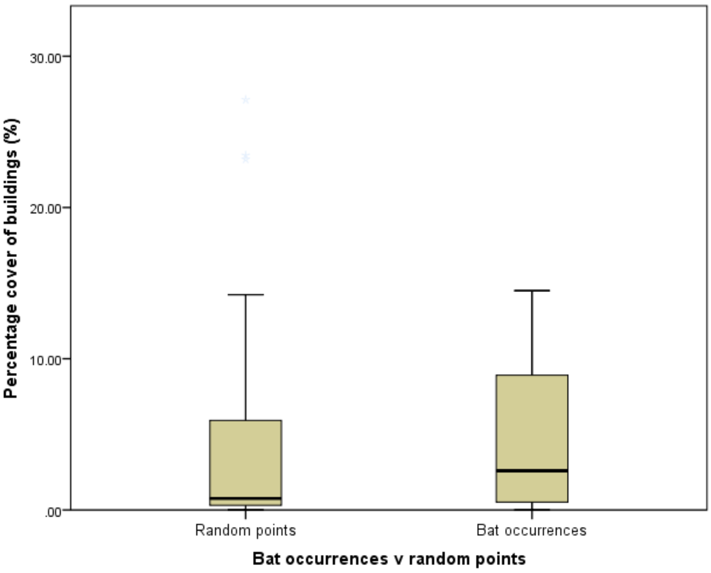


Figure 7. Boxplots showing the occurrence of *N. noctula* versus random points at different percentage covers of forest, buildings and water at a 100m scale. Medians with upper and lower quartile ranges. All EGVs showed significant differences between random points and bat occurrences. For the percentage cover of forest: X^2=24.367, n_1=104, n_2=103, n_3=207, P=0.0001, percentage cover of buildings: X^2=11.278, n_1=211, n_2=103, n_3=207, P=0.001, and percentage cover of water: X^2=16.350, n_1=211, n_2=103, n_3=207, P=0.0001.

Results for 1000m

Boxplots and statistics for the results of the percentage cover of water, forest or buildings calculated for each bat occurrence and random points at the 1000m scale.





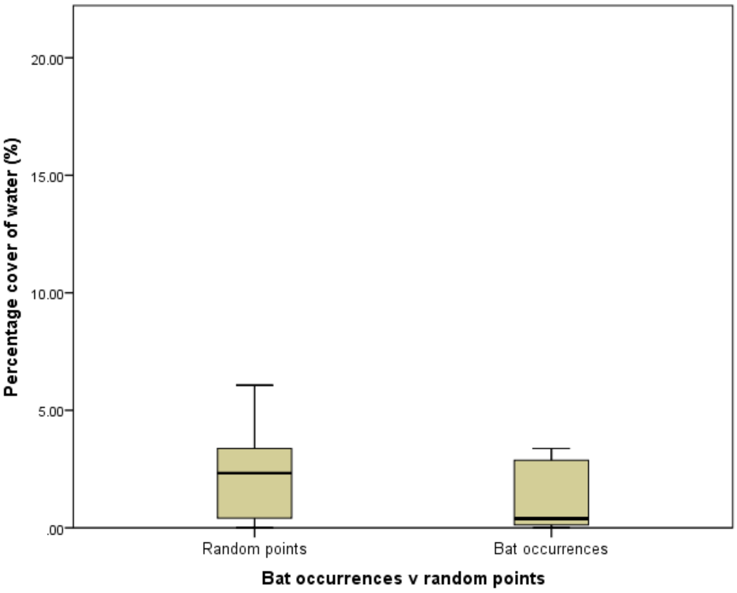


Figure 8. Boxplots showing the occurrence of *P. pipistrellus* versus random points at different percentage covers of forest (above left), buildings (above) and water (left) at a 1000m scale. Medians with upper and lower quartile ranges. There was no significant difference for the percentage cover of forest: X^2=1.154, n_1=391, n_2=385, n_3=776, P=0.283, P=0.995. The percentage cover of water was significant at: X^2=39.295, n_1=391, n_2=385, n_3=776, P=0.0001, P=0.113 as well as the percentage cover of buildings: X^2=16.768, n_1=391, n_2=385, n_3=776, P=0.0001.

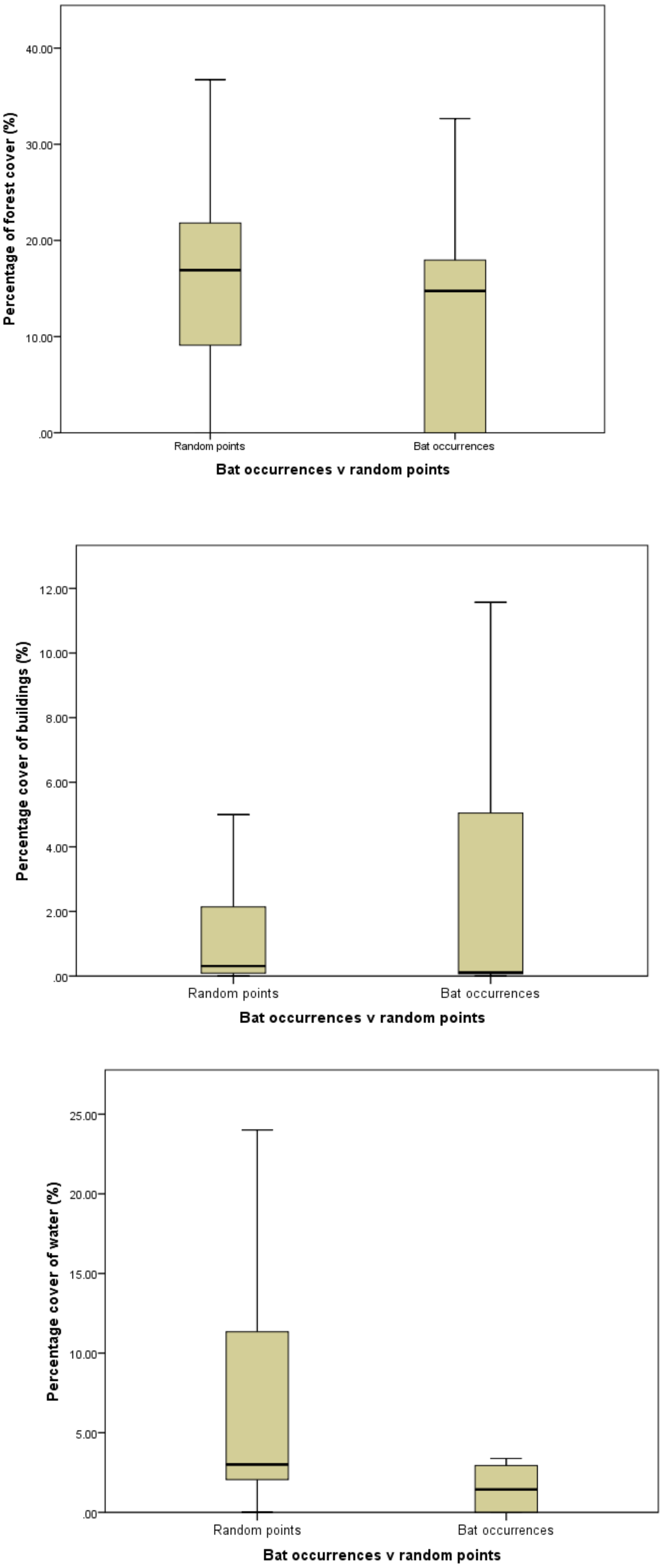


Figure 9. Boxplots showing the occurrence of *P. pygmaeus* versus random points at different percentage covers (%) of forest, buildings and water at a 1000m scale. Medians with upper and lower quartile ranges. There was no significant difference for the % cover of buildings: X^2=0.180, n_1=196, n_2=196, n_3=392, P=0.671. Highly significant difference for the % cover of water at: X^2=53.936, n_1=196, n_2=196, n_3=392, P=0.0001, P=0.113 as well as the % cover of forest: X^2=30.591, n_1=196, n_2=196, n_3=392, P=0.0001.

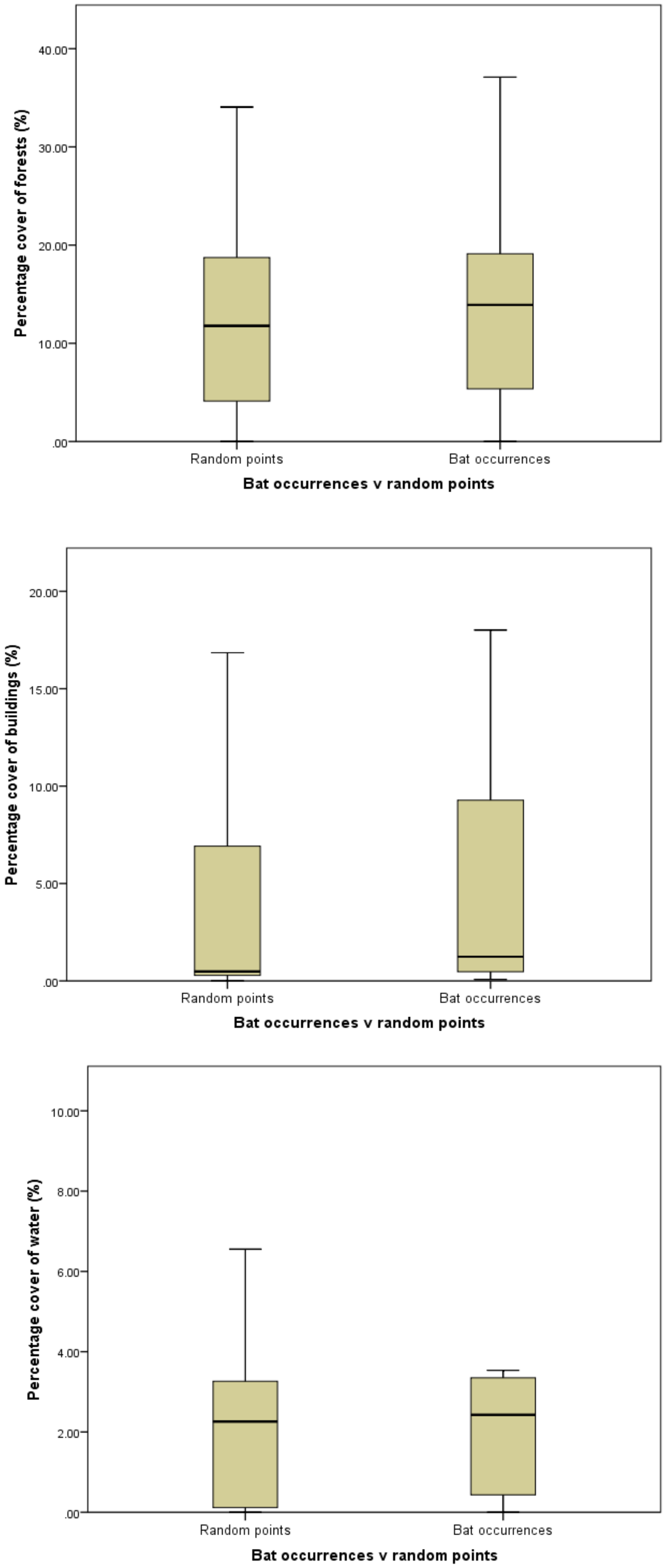


Figure 10. Boxplots showing the occurrence of versus random points at different percentage covers (%) of forest, buildings and water at a 1000m scale. Medians with upper and lower quartile ranges. There was a significant difference for the % cover of buildings: X^2=3.934, n_1=110, n_2=104, n_3=214, P=0.047. Whereas the natural features showed no significant differences; the % cover of water at: X^2=2.522, n_1=110, n_2=104, n_3=214, P=0.112, P=0.113 as well as the % cover of forest: X^2=0.727, n_1=110, n_2=104, n_3=214, P=0.394.

Species comparisons

4.4. Interspecies comparisons for distance to EGVs

A Kruskal-Wallis test was performed on the 3 bat species in order to first determine differences in distance scores for all the random bat points and bat occurrence data together (see Appendix; Table 2 and boxplots in Figure 4). All species had significantly different distance scores, and thus post hoc tests were run to compare individual species habitat preferences (see Table 4).

EGV	Species	X ² value	*P* value	d.o.f
Distance to woodland edge (m)	*P. pygmaeus-P. pipistrellus*	248.294	0.0001	2
	P. pygmaeus-N. noctula	-141.161	0.0001	
	N. noctula-P. pygmaeus	107.133	0.0001	
Distance to inland water (m)	*P.pygmaeus* and *N. noctula*	-142.729	0.0001	2
	P.pygmaeus and *P. pipistrellus*	-261.525	0.0001	
	N. noctula-P. pipistrellus	4.595	0.0001	
Distance to buildings (m)	*P. pipistrellus-N. noctula*	-85.506	0.003	2
	P. pipistrellus-P. pygmaeus	-87.765	0.008	
	N. noctula-P. pygmaeus	2.259	1.0000	
Distance to roads (m)	*P. pygmaeus-P. pipistrellus*	88.377	0.007	2
	P. pygmaeus-N. noctula	-149.045	0.0001	
	P. pipistrellus-N. noctula	-60.668	0.05	

Table 4. A pairwise comparison of all the species distance scores, (using adjusted p-values). Chi squared values, *P* values and degrees of freedom are shown. All results shown above are significant p<0.05. No significant differences in median distance scores was revealed between *N. noctula* and other combinations for distance to road, for *P. pipistrellus* and other combinations between the median distances to forest scores, and for *N. noctula* and *P. pipistrellus* between other pairwise combinations for distance to water scores.

4.5. Interspecies comparisons for percentage cover of habitat features

Scale	EGV	Species	X ² value	P value	d.o.f
100m	Percentage cover of forest (%)	*P. pipistrellus-N. noctula*	-123.949	0.0001**	2
		P. pipistrellus-P. pygmaeus	-178.802	0.0001**	
		N. noctula-P. pygmaeus	54.853	0.254	
	Percentage cover of buildings (%)	*P. pipistrellus-P. pygmaeus*	-85.729	0.0001**	2
		P. pipistrellus-N. noctula	-124.308	0.0001**	
		P. pygmaeus-N. noctula	-38.579	0.556	
	Percentage cover of water (%)	*P. pipistrellus-N. noctula*	-158.957	0.003**	2
		P. pygmaeus-P. pipistrellus	209.872	0.008**	
		N. noctula-P. pipistrellus	50.915	0.2270	
1000m	Percentage cover of forest (%)	*P. pipistrellus-N. noctula*	-101.207	0.003**	2
		P. pipistrellus-P. pygmaeus	-123.994	0.0001**	
		N. noctula-P. pygmaeus	22.787	1	
	Percentage cover of buildings (%)	*P. pipistrellus-N. noctula*	-86.401	0.015**	2
		P. pipistrellus-P. pygmaeus	-90.877	0.001**	
		N. noctula-P. pygmaeus	4.475	0.001**	
	Percentage cover of water (%)	*P. pygmaeus-N. noctula*	-240.92	0.0001**	2
		P. pygmaeus-P. pipistrellus	283.003	0.0001**	
		N. noctula-P. pipistrellus	33.083	0.849	

Table 5. Summary of the post hoc tests for the interspecies comparisons for the percentage cover of water, forest and buildings conducted separately for the two scales (100m, 1000m). Chi squared values, adjusted p-values and degrees of freedom are shown. Significant results (p<0.05) are highlighted**.

4.6. Spearman's Rank Correlation

The strength of association between the total number of bat passes and percentage cover of water, buildings and forest was assessed with a Spearman's rank correlation test. This was performed on *P. pygmaeus, P. pipistrellus* and *N. noctula.* The total number of bat recordings per species, per transect study site was used, as well as the average percentage covers for each EGV at each site. Scatter plots were generated in order to assess the data for visual linearity. Table 6 displays the statistical values of the test, and Figures 11 and 12 display scatter plots of statistically significant correlations between the bats and percentage cover of EGVs.

Scale	EGV	Species	r_S value	*P* value	*N* value
100m	Percentage cover of forest (%)	*P. pipistrellus*	0.399	0.141	15
		P. pygmaeus	0.294	0.442	9
		N. noctula	0.649	0.016**	13
	Percentage cover of buildings (%)	*P. pipistrellus*	-0.479	0.071	15
		P. pygmaeus	0.031	0.937	9
		N. noctula	-0.373	0.209	13
	Percentage cover of water (%)	*P. pipistrellus*	0.216	0.44	15
		P. pygmaeus	0.531	0.141	9
		N. noctula	0.699	0.008**	13
1000m	Percentage cover of forest (%)	*P. pipistrellus*	0.218	0.435	15
		P. pygmaeus	0.58	0.102	9
		N. noctula	0.515	0.071	13
	Percentage cover of buildings (%)	*P. pipistrellus*	-0.583	0.023**	15
		P. pygmaeus	-0.151	0.698	9
		N. noctula	-0.215	0.482	13
	Percentage cover of water (%)	*P. pipistrellus*	-0.111	0.694	15
		P. pygmaeus	0.874	0.002**	9
		N. noctula	0.671	0.012**	13

Table 6: Summary of Spearman's correlation test results for total number of bat passes at different percentage covers of water, forest and buildings at 100m and 1000m scales. *P* value r_s value, and *N* values are displayed for *P. pygmaeus, P. pipistrellus* and *N. noctula*. Two-tailed significance level of the correlation coefficient. *P* values highlighted** were statistically significant p<0.05.

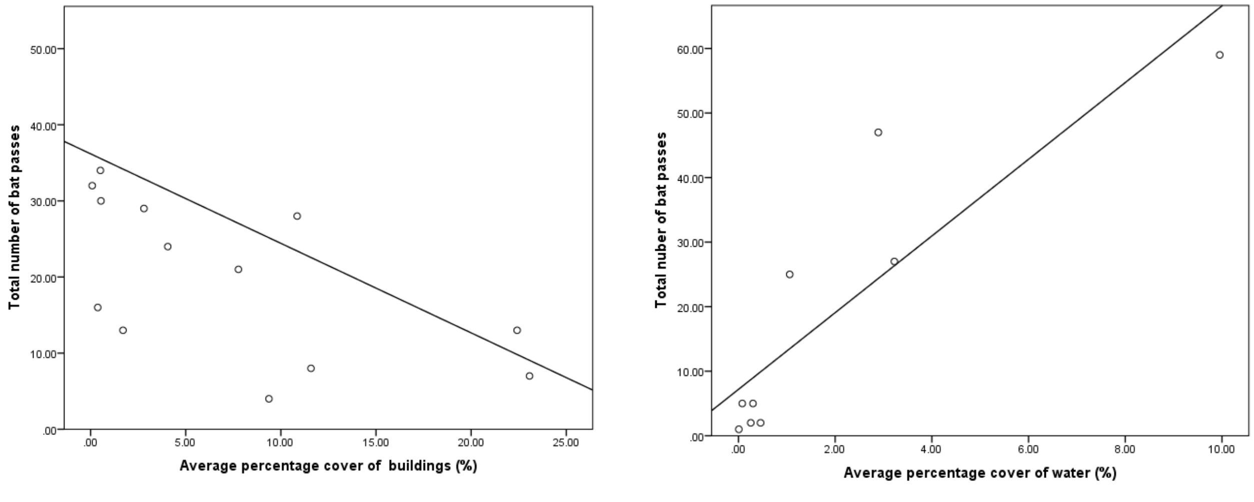


Figure 11. Scatter plot for *P. pipistrellus* (left) showing a significant negative correlation between the total number of bat passes and average percentage cover of buildings across all transect study sites, at the 1000m scale (r_s =-0.583, *P*= 0.023). *P. pygmaeus* (right) showing a significant positive correlation with percentage of water cover at 1000m scale (r_s =-0.583, *P*= 0.002). Two-tailed significance level of the correlation coefficient.

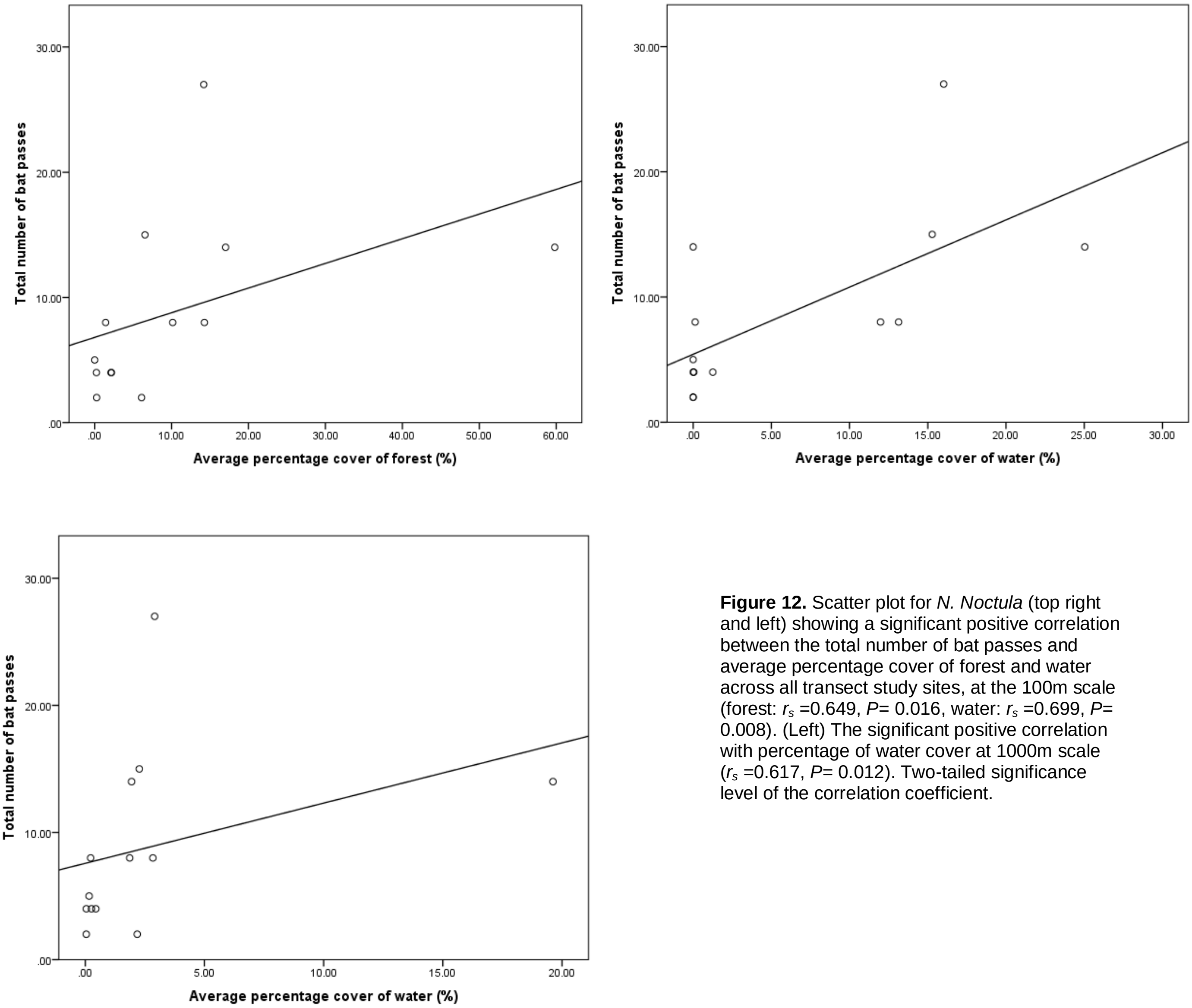


Figure 12. Scatter plot for *N. Noctula* (top right and left) showing a significant positive correlation between the total number of bat passes and average percentage cover of forest and water across all transect study sites, at the 100m scale (forest: r_s =0.649, *P*= 0.016, water: r_s =0.699, *P*= 0.008). (Left) The significant positive correlation with percentage of water cover at 1000m scale (r_s =0.617, *P*= 0.012). Two-tailed significance level of the correlation coefficient.

5. DISCUSSION

5.1. Distribution of bat species across North and West Yorkshire

Overall, *P. pipistrellus* was the most abundant and widely distributed species located at every site (and for the repeat surveys), followed by *P. pygmaeus*, *N. noctula* and *M. brandtii/mystacinus*. It was difficult to get abundance data on *M. brandtii/mystacinus* as they are generally less abundant in the region and more sensitive to urbanisation (Russo & Ancillotto, 2014; Gaisler *et al*., 1998). All species recorded were more abundant in rural areas than urban, although *P. pygmaeus* abundance was especially low in urban areas compared to *N. noctula* and *P. pipistrellus*. This could be possibly due to the lack of open bodies of water in urban areas, as well as their sensitivity to light pollution, whereas *P. pipistrellus* is known to be a better adapted synurbic species and generalist (Altringham, 2011). One particular suburban area (classified according to 25-75% building cover), Ilkley had surprisingly high numbers of bat occurrences, which could be possibly explained by the inland river, forest cover and bridges at the site, suitable for roosting and foraging. This basic description of the distribution and index of abundance of 4 bat species across the region provides the framework upon which more complex statistical analysis can be used to establish specie-habitat relationships and associations.

5.2. Bat presence and proximity relationships to habitat features

All the bat species recorded were selective of the habitat features they were recorded near, and were significantly different to the random points generated to test this hypothesis. *P. pipistrellus* was seen to be selective of all the 4 EGVs extracted for analysis, and this was especially evident for the range of distances to the road. This pattern of significance and road selectivity was seen across the other two species analysed, *P. pygmaeus* and *N. noctula*. Such associations have also been detected in studies by Brown (2013), where HSMs of *P. pipistrellus* and *P. pygmaeus* revealed positive relationships between the bats and roads at a 200m scale. Birds have also been recorded to use treeline features, street lights and hedges when navigating through urbanised landscapes, hence implying their value for a variety of species (Hale *et al.,* 2012).

Recent studies revealed that other linear man-made landscape features such as railway lines with natural verges in surrounding agricultural land are used by *N. leisleri* and *P. pipistrellus* (Vandeveldea, 2013). However, this study did not include major roads such as those assessed by Berthinussen & Altringham (2012a), which concluded bat activity decreased with increasing proximity to the M6 (Cumbria). This is principally due to acoustic pollution, and large motorways also act as barriers to feeding sites (Bennett *et al.*, 2013). Despite their negative impact, roadside verges can also provide alternative foraging areas for bats (Vandeveldea, 2013). Increased density of vegetation is also strongly associated with increased insect abundance (Russo & Ancillotto, 2014). The increased abundance of insect prey species attracted to artificial road lights has been found to improve foraging success of *P. kuhilli*, which are able to tolerate lights (Tomassini *et al*., 2014).

With *N. noctula*, the probability that the difference between the random points and bat occurrences were significantly real along all EGVs, as predicted. Noctule bats are commonly seen foraging alongside streetlights, open air spaces such as parks, roads and canals, rivers and lakes (Kronwitter, 1988). Studies in Poland looking at habitat selectivity of *N. noctula* found that bat activity was significantly higher in suburban areas, meadows as well as along forest edge, due to their ecomorphological adaptations. These long range species have well adapted wing morphologies (long, narrow wings and light body weight), suitable for high speed flight in open areas (Rachwald, 1992). Equally their frequency modulated and constant frequency calls (26-47 kHz) enable them to forage efficiently in clutter-free habitats (Altringham, 2011; Parsons & Jones, 2000). Hence the habitat features analysed in this study have been shown to influence habitat choice in this species. In studies looking at HSMs in the LDNP, the importance of distance to water and woodland was also significant in *N. noctula* (Bellamy *et al*., 2013), and linear landscape features such as tree lines and roads were also used, as seen in *P. pipistrellus*. The similarity between the species responses to certain natural habitat features indicates how important they are in determining their presence and persistence in the region. Equally in terms of conservation management, the similarity between habitat preferences may be beneficial in protecting several different species of bat (Bellamy *et al.*, 2013; Altringham, 2011).

5.3. Is bat presence driven by percentage cover of buildings, woodland or water?

P. pipistrellus presence appears to be driven by percentage cover of woodland and water, but not building cover at a 100m scale. Thus at small spatial scales natural habitat features seems to explain their pattern of presence, whereas urbanised features did not. This agrees with research on multiscale HSMs conducted in the LDNP, where *P. pipistrellus* was shown to have strong, positive associations with water cover and woodland density (Bellamy *et al*., 2013). Overall, the woodland and water variables modelled were the best positive predictors of all the species presences, with the size, distance and edge density of woodland being the most significant at smaller spatial scales (Bellamy *et al*., 2013). It was at these scales (100-500m) that natural habitat features (such as water and forest cover), were the most important and significantly associated with bat presence, as seen in this study. It is possible that at smaller scales, the behaviour of bats is predominantly concerned with feeding and roosting. In contrast, at larger spatial scales *P. pipistrellus* and *N. noctula* may be commuting over and passing buildings (due to their large core habitat ranges between 1-1.6km) rather than stopping to feed (Jones, 1995; Dixon, 2012; Bellamy *et al.*, 2013).

In this study at the 1000m scale, *P. pygmaeus* presence was strongly by the percentage cover of water and forest cover, but not building cover. This study agrees with HSMs results conducted in the Yorkshire Dales National Park and Nidderdale area of outstanding natural beauty, where *P. pygmaeus* was predicted to be within close range of water and woodland cover (Brown, 2013; Bellamy & Altringham, 2012), and have a strong positive correlation with water cover at a larger 1000-1500m scale, rather than at smaller scales. Indeed, in this study no significance was seen between percentage cover of forest or water at the 100m smaller scale. For *N. noctula,* the percentage cover of forest and water was also associated with their presence at the 100m scale. This was the same for *P. pipistrellus*, again highlighting the similarity in habitat preferences, in the context of percentage cover, despite their unique ecomorphological adaptations. This is also in accordance to results seen in both Brown (2013) and Bellamy *et al.,* (2013).

However not all results were consistent with other literature. This may be due to the varying availability of other certain key habitat features limiting in the more urbanised areas (removed or modified during development), as well as the difference in the number of spatial scales used during analysis (Brown, 2013). Habitat associations can also differ depending on the time the echolocation calls are recorded, where peak activity differs between species (Hale *et al.*, 2012). Results that differed to the literature include those for *N. noctula* at the large spatial scale (1000m), suggesting that only the percentage cover of buildings was significant associated with *N. noctula* presence. The results at larger scales suggest the presence of this species does not appear to be driven by natural habitat features, as smaller scales studies might suggest. This also contradicts suggestions made by Hale *et al.* (2012), that bats with high wing loading avoid urban areas. Again, this may be due to *N. noctula* commuting rapidly over and buildings at larger scale as their core foraging habitat ranges extends beyond the smaller and larger scales used in this study. Hence, rather than stopping to feed, *N. noctula* could be leaving the roosts, and thus appear to be selective of buildings at the 1000m scale. However overall for all the species, natural habitat features were the most important factor in determining bat presence at both spatial scales.

5.4. Correlation and interspecies habitat preferences for distance and percentage cover of EGVs

All species showed significantly different preferences for distance to the four habitat features. However, the post hoc analysis revealed that *P. pygmaeus* had the greatest number of significant habitat preferences between species, and *N. noctula* the fewest. *P. pygmaeus* was more selective than *P. pipistrellus*, and particularly significant for water. This is because *P. pygmaeus* is a water habitat specialist, and is often recorded and captured feeding on insects in such habitats (Russ & Montgomery, 2002; Bellamy *et al*., 2013; Altringham, 2011). Indeed, a strong positive correlation was seen between *P. pygmaeus* and percentage water cover at the 1000m scale, even at 10%. Despite their sympatric origin, the results do suggest both species have divergent habitat preferences, and radio tracking studies on the recently separated *P. pygmaeus* and *P. pipistrellus* tested the degree of differential habitat use and partitioning. It was found that the foraging range of *P. pygmaeus* was smaller and principally centralised towards inland water sources and riparian woodland (Nicholls & Racey, 2006). *P. pipistrellus* however was not shown to preferentially select forest or water, but significantly differ from other species in terms of distance to buildings. This highlights their more generalist nature, as species that have larger home ranges than *P. pygmaeus* and as a more urban tolerant species which can often be dependent upon man-made structures to roost in (Altringham, 2011).

Studies have shown non-linear relationships between *P. pipistrellus* activity with increasing percentage of building land cover, highlighting the potential value of buildings, with activity peaking at 40% cover. Therefore low and medium levels of building cover promotes *P. pipistrellus* activity, whilst 60% cover is considered the threshold, where reduced activity occurs beyond this (Hale *et al*., 2012). However in this study *P. pipistrellus* showed a strong negative correlation with increasing percentage cover of buildings at the 1000m scale above 25%, thus there is much variability in the tolerance of increased density of buildings and urbanisation across the UK. This may be due to an artefact of the varying urban composition between different study sites (Hale *et al.*, 2012), but equally as the scale changes so does the importance of the habitat features and the associations bats have with them (Bellamy *et al*., 2013). At smaller scales, 5-10% urban cover in the LDNP reduced bat activity, again highlighting the range of responses seen at different scales (Bellamy *et al*., 2013). Generally, bats with low aspect ratios and low wing loadings exhibit greater behavioural plasticity and urban tolerance compared to those species with long, narrow wings (Gaisler *et al.,* 1998; Hale *et al*., 2012; Altringham, 2011). *N. noctula* showed no significant differences in habitat preference for distance between species. This is potentially due to their large core foraging ranges, which may affect the viability of the results as they tend not to forage within close proximity of the transect.

Interspecific comparisons at the 100m scale, *P. pygmaeus* and *P. pipistrellus* showed the most number of significant habitat preferences, whilst at 1000m, *P. pipistrellus* only showed this probability. This agreed with the distance data that both these species showed a variable degree of selectivity for certain habitat features. *P. pygmaeus* appeared to be more selective of water at both 100m and 1000m scale compared to both *P. pipistrellus* and *N. noctula*. This again reflects the results seen in intraspeciefic species analysis of percentage cover of water and distance to inland water. At both 100m and 1000m scales, *P. pipistrellus* was shown to be more selective of forest and building cover compared to other species. The could again be due to the larger range at which pipistrelles operate at and more synurbic nature, where it is more adaptable than the other two species to urban change as seen in studies by Kusch & Schmitz (2013). Equally *P. pipistrellus* preference for forest cover at 100m can be explained by where it will forage, at more local range, smaller scales. Studies on species modelling of *P. pipistrellus, P. pygmaeus* conclude that good predictors of both species are climate and microhabitat factors, and the varying effect on both species. This could explain the significant differences in preferences for particular habitat types at different scales in this study, and has frequently been proven in other literature (Brown, 2013; Bellamy *et al.*, 2013; Davidson-Watts *et al.,* 2006). Therefore the importance of the scale at which these habitat associations are studied can affect the variation in selectivity of certain habitat features between species (Dixon, 2012).

However *N. noctula* at both spatial scales showed the most non-significant number of habitat preference differences between species, which was similar in the distance associations. This could be potentially explained again by their larger core habitat ranges compared to the pipistrelles, which operate more frequently within the 100m and 1000m buffer ranges analysed. Similar results have also been noted in Pomeranian bats which are also fast flyers and showed a lack of significant differences and preferences for habitat features (Bartonička & Zukal, 2003; Ciechanowski, 2015). Ultrasonic bat detectors can also detect calls from Noctules over large distances, leading to the misinterpretation of the bat being within the scale measured (Ciechanowski, 2015). Other factors which change distributions and habitat associations include the different regional diet preferences in *N. noctula,* as seen in the UK compared to Latvia, which preferentially feed on terrestrial insects rather than aquatic. Indeed, studies by Russ & Montgomery (2002) also concluded that the differences in microclimate could reflect the differences seen in habitat preference (Gehrt & Chelsvig, 2003; Ciechanowski, 2015). *N. noctula* did however show significant correlations between increasing percentage cover of water and forest cover, at small and large spatial scales. This association can also be seen in previous studies analysing habitat requirements, where *N. noctula* was predominantly active in open air habitats, lakes and rivers (Vaughan *et al*., 1997). Equally, studies in Poland recorded greatest *N. noctula* activity over natural habitat features, including water (Rachwald, 1992).

5.5. Evaluating methods and suggested further research

Species interaction and associations with habitat features differ at different scales, and research using multiscale HSMs in the LDNP further highlighted the importance of this (Bellamy *et al.,* 2013). In this study, bats at large scales were seen to be present when in close proximity to woodland edge, hibernacula and were affected by the density of buildings between suitable habitat patches. At small scales, the presence of slow flying bats (gleaners) as well as fast open air foragers (hawkers) were limited by their ecomorphology and echolocation call structure, and were driven by natural habitat features (Bellamy *et al.,* 2013). Thus, there are issues of what scale and what aspect of species biology different scales are acting on, which need to be taken into account. In this study, a greater number of different spatial scales could have been used to study habitat preferences in more detail, however due to the limitations of time and computing power, this was not achievable. Hence why two of the more important scales were used for the analysis. Equally, comparisons between studies are made more difficult by the varying techniques and methodologies used in HSM and studying habitat preferences (Brown, 2013; Bellamy *et al.,* 2013).

In future research, the data in this study could be used as a precursor for looking at HSM in unsurveyed regions of West and North Yorkshire, in order to determine habitat relationships which are poorly mapped in urban areas. This information can help inform conservation management and what needs to be done in particular areas to improve connectivity and increase diversity. Maximum Entropy (MaxEnt), a software program which models the distribution of species (Elith *et al.,* 2006), can be integrated with the EGVs in ArcGIS to predict the presence of bats in unsurveyed sites. This not only reduces the data required to form such models but can be readily displayed as habitat suitability maps for policy makers to maximise resources and effort into conserving specific habitats (Bellamy *et al.*, 2013). Such maps are increasingly been created and used in other Areas of Outstanding Natural Beauty, Sites of Scientific Interest, national parks such as Northumberland National Park and the North Pennines (Altringham, 2011).The concept of ecological thresholds could also be further studied in urban areas to determine future presence of different species based on habitat associations, selectivity and suitability (Hale *et al.,* 2012).

Some species were less frequently recorded such as *M. brandtii/mystacinus*, as they are not as commonly found in the region and more sensitive to urbanisation (Russo & Ancillotto, 2014; Altringham, 2011). It therefore difficult to get an accurate description of their abundance, and build up annual records of their distribution. Equally, the echolocation calls of certain species are not detectable with current ultrasonic devices, such as *Myotis nattereri* (Brown, 2013). Thus developments in such technology would prove to be invaluable in collecting informative distribution data on these cryptic and little recorded species (Bellamy *et al.,* 2013). In conjunction with acoustic data collection, additional bat capture data would also provide more accurate distribution and abundance data (Brown, 2013).

Having concluded that the barrier effect is a prevalent threat to the survival of bat populations in studies by Bernthinauss & Altringham (2012), further studies are now being conducted across the UK along major roads, motorways, and railways (Vandeveldea *et al.,* 2013). Recent revelations focusing on the importance of hedgerows, treelines and verges alongside these linear road and railway developments have fundamental applications in conservation policy and management (Altringham, 2011; Penone *et al.,* 2012). Many studies have shown that these features provide potential foraging areas at global landscape scales (Jones, 1995), and for species such as *N. noctula* and *P. pipistrellus* when surrounded by agricultural matrixes, away from core habitat and on the periphery of the colonization zone (Vandeveldea *et al.,* 2013). Equally continual, repeated annual transects could be used to compared to previous data and see whether the removal or restoration of habitat affects the abundance and distribution of bats, as well as the suitability of particular habitat features.

5.6. Conclusion

This study has demonstrated that the species and scale specific responses of bats to natural and urban habitat features needs to be considered in conservation management across North and West Yorkshire. Whilst *Nyctalus noctula* and *P. pygmaeus* species were shown to be more urban sensitive, *P. pipistrellus* showed strong associations and preferences for building cover at both scales as well as roads and could therefore be seen as more resilient to the current rate of urbanisation. *P. pygmaeus* showed strong habitat preferences and a positive correlation with increasing percentage cover of water compared to other species, and is therefore an important habitat feature for the persistence of this species. The value of green corridors, water sources and habitat networks within urban areas needs to be further assessed and tested in order to be considered in city planning (Hale *et al*., 2013). It is fundamental that underlining science is at the forefront of such policy making decisions, in order to fully quantify the effectiveness and adequacy of any mitigation strategies (Altringham, 2011). A general, more cost effective conservation strategy to conserve bats in both urban and rural areas would involve focusing on the preservation natural habitat features such as water and forest cover, rather than the more costly and idealist approach of species-specific responses (Brown, 2013). This would also provide wider benefits to other species which also persist in the same habitats, and enhance biodiversity in urban areas.

5.7. Ethics

The welfare and safety of the bats was taken into consideration through the use of non-invasive data collection methods. The broadband acoustic surveys and walking along of study transect sites would have caused minimal interference (Petit *et al.,* 2006). Possible immediate changes in behaviour at close range with the light from the head torch would have been temporary, and the continual movement would have allowed the bats to continue commuting or foraging. The disturbance in urban areas is most likely to have been insignificant for the more synanthropic species as the traffic, light pollution and other man-made disturbances would have been far greater than the impact of the study. Bat captures were not made, and so the bats were able to continue their activity. Local study sites were selected for practical expediency and to reduce the carbon miles produced to drive to them. Mock transect walks to assess their suitability of were performed 40 minutes in advance to reduce trips to the sites. Permission was granted from landowners at the Harewood Estate to access private footpaths, and public footpaths, parks or roads were freely accessible at other sites. Livestock were occasionally awoken or disturbed by the head torches, however this was brief. The overall benefit of this study outweighs any negative alterations in bat activity, as it may help inform urban conservation management strategies. Equally, the value of conserving bats as bioindicators has wider implications for the benefit of conserving other local ecological communities (Brown, 2013), and methods used in this study can help to inform conservation strategies for other species worldwide.

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8. APPENDIX

Habitat classification	Location	Bat species present	Number of each specie	Total per site
Suburban	Bramhope	*Nyctalus noctula*	2	27
		Pipistrellus pipistrellus	24	
		Pipistrellus pygmaeus	1	
Suburban	Adel	*Pipistrellus pipistrellus*	13	18
		Pipistrellus pygmaeus	5	
Rural	Chevin	*Nyctalus noctula*	5	35
		Pipistrellus pipistrellus	30	
Urban	Moortown	*Nyctalus noctula*	4	7
		Pipistrellus pipistrellus	3	
Urban	Leeds	*Nyctalus noctula*	8	15
		Pipistrellus pipistrellus	7	
Suburban	Ilkley	*Nyctalus noctula*	8	127
		Pipistrellus pipistrellus	72	
		Pipistrellus pygmaeus	47	
Rural	Denton	*Nyctalus noctula*	27	68
		Pipistrellus pipistrellus	13	
		Pipistrellus pygmaeus	27	
		Myotis brandtii/mystacinus	1	
Rural	Farnley	*Nyctalus noctula*	4	98
		Pipistrellus pipistrellus	89	
		Pipistrellus pygmaeus	5	
Urban	Rawdon	*Nyctalus noctula*	2	10
		Pipistrellus pipistrellus	8	
Rural	Harewood	*Nyctalus noctula*	14	56
		Pipistrellus pipistrellus	16	
		Pipistrellus pygmaeus	25	
		Myotis brandtii/mystacinus	1	
Urban	Pudsey	*Nyctalus noctula*	15	43
		Pipistrellus pipistrellus	28	
Rural	Swinsty	*Nyctalus noctula*	14	105
		Pipistrellus pipistrellus	32	
		Pipistrellus pygmaeus	59	
Suburban	Harrogate	*Pipistrellus pygmaeus*	21	21
Urban	Bardsey	*Nyctalus noctula*	4	35
		Pipistrellus pipistrellus	29	
		Pipistrellus pygmaeus	2	
Suburban	Addingham	*Nyctalus noctula*	8	43
		Pipistrellus pipistrellus	34	
		Pipistrellus pygmaeus	2	

Table 1. The number of each bat species in each area, with each habitat category type (urban, suburban and rural as classified by percentage cover of buildings). The highest number of bats recorded was in the suburban area of Ilkley, with the fewest in the urban area of Rawdon. Four species were recorded; *N. noctula*, *P. pipistrellus, P. pygmaeus* and *M. brandtii/mystacinus***.**

8.1. Distance to habitat features (EGVs) boxplots

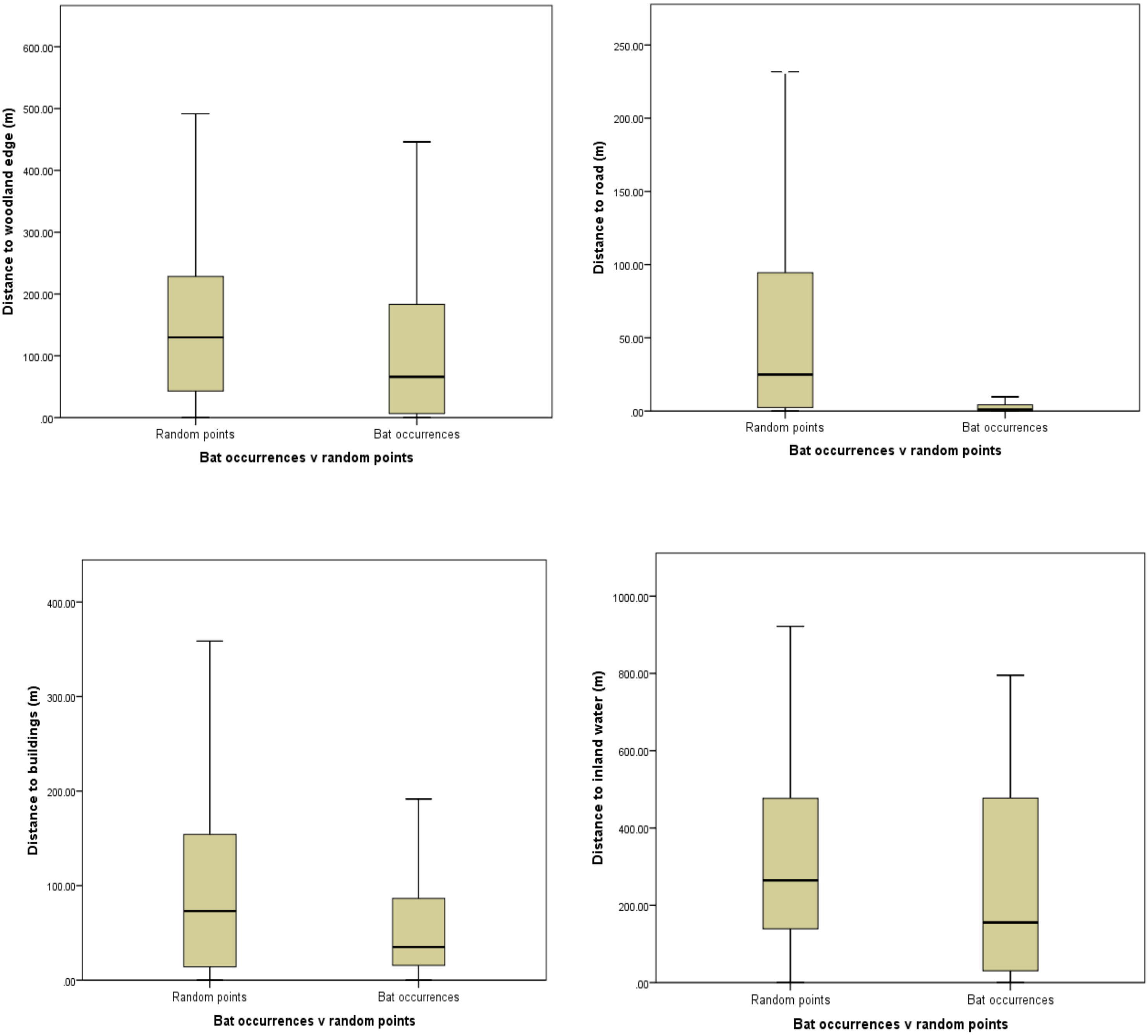

Figure 1. Boxplots showing the occurrence of *P. pipistrellus* versus random points along the range of distances to the four EGVs measured across the region. Medians with upper and lower quartile ranges. There were significant differences between all the bat occurrences and random point distances to each habitat feature. Distance to woodland edge; X^2=26.004, n_1=410, n_2=387, n_3=797, P=0.0001, distance to roads (m): X2=123.123, n_1=410, n_2=387, n_3=797, P=0.0001, distance to buildings (m): X2=19.403, n_1=410, n_2=387, n_3=797, P=0.0001, and distance to water (m): X2=24.045, n_1=410, n_2=387, n_3=797, P=0.0001.

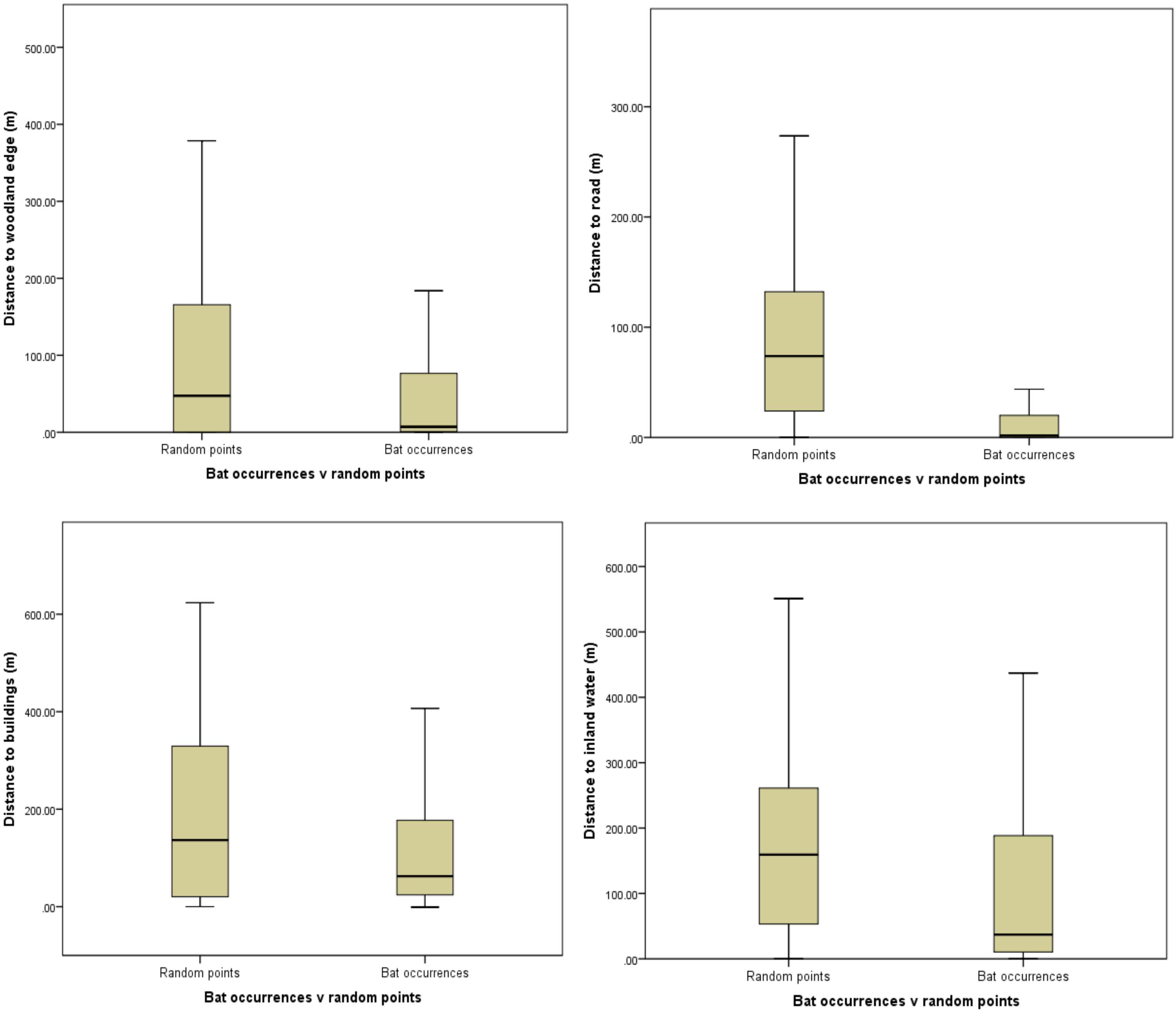

Figure 2. Boxplots showing the occurrence of *P. pygmaeus* versus random points along the range of distances to the four EGVs measured across the region. Medians with upper and lower quartile ranges. Significant differences between all the bat occurrences and random point distances to each habitat feature. Distance to woodland edge: X2=6.846, n1=146, n2=173, n3=319, P=0.009, distance to roads (m): X2=100.093, n1=146, n2=173, n3=319, P=0.000, distance to buildings (m): X2=7.384, n1=146, n2=173, n3=319, P=0.007and distance to water (m): X2=15.537, n1=146, n2=173, n3=319, P=0.000.

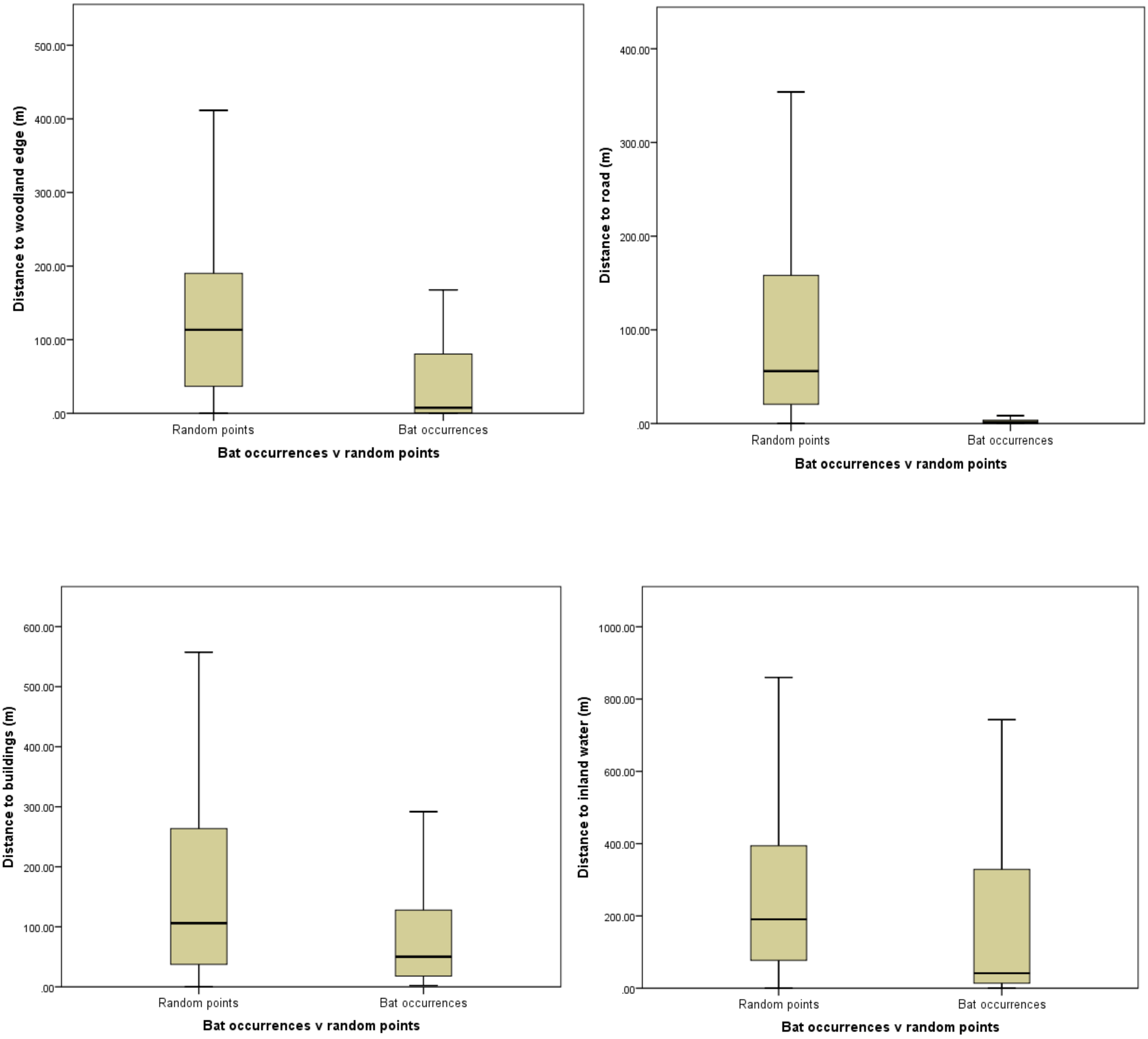

Figure 3. Boxplots showing the occurrence of *N. noctula* versus random points along the range of distances to the four EGVs measured across the region. Medians with upper and lower quartile ranges. Significant differences between all the bat occurrences and random point distances to each habitat feature. Distance to woodland edge: X2=32.390, n_1=115, n_2=115, n_3=230, P=0.0001, distance to roads (m): X2=99.929, n_1=146, n_2=173, n_3=319, P=0.0001, distance to buildings (m): X2=15.485, n_1=146, n_2=173, n_3=319, P=0.0001, and distance to water (m): X2=11.160, n_1=146, n_3=173, n3=319, P=0.00.

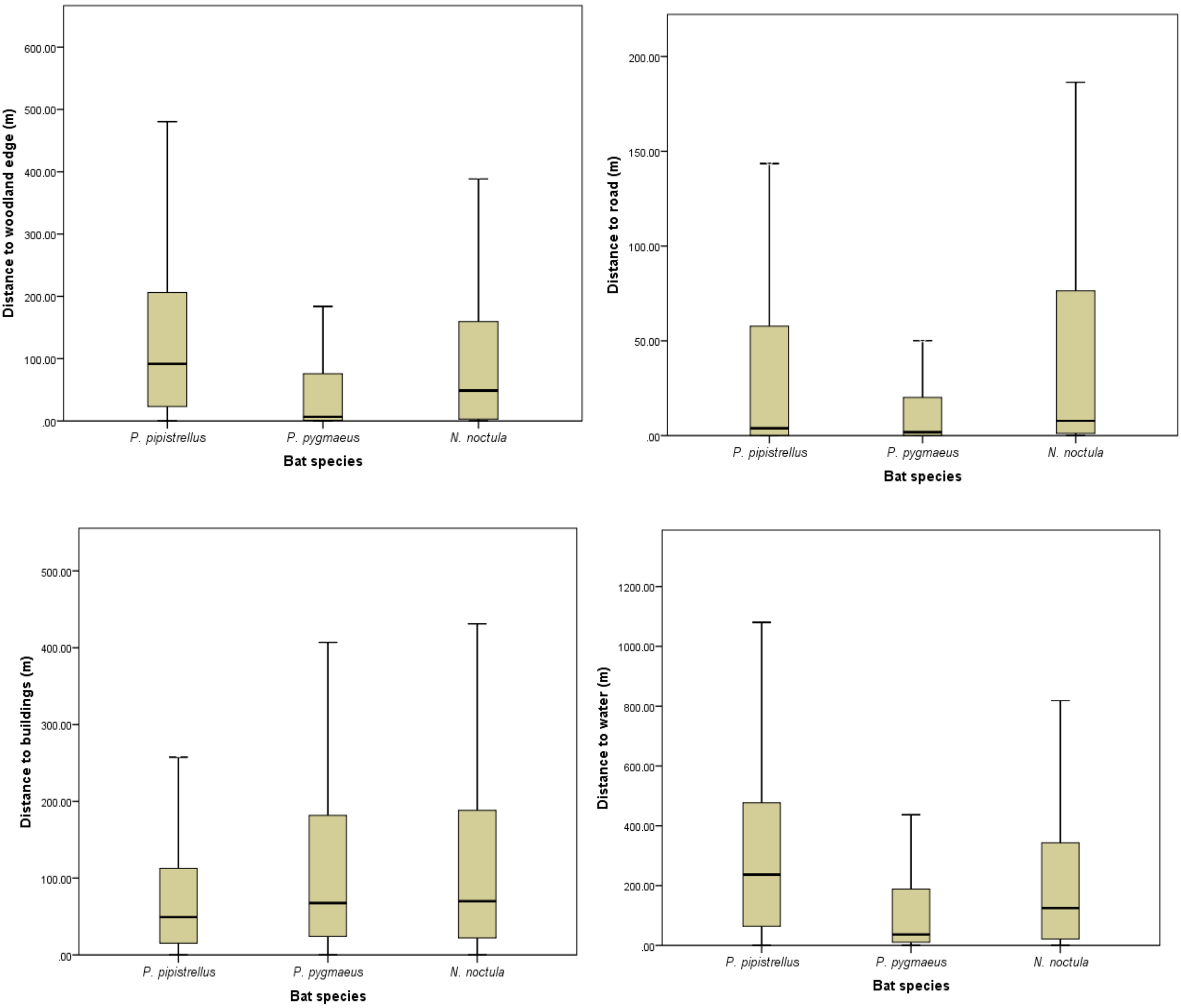

Figure 4. Boxplots showing the different median range of distances to the four EGVs measured across the region for each species. Medians with upper and lower quartile ranges. Suggests that the distribution of distance scores for are different for distance to water, woodland edge and roads, particularly for *P. pygmaeus*. The distribution of medians appears similar for all the species distance to buildings.

EGV	Species	X^2 value	P value	D.O.F
Distance to woodland edge (m)	*P. pipistrellus* *P. pygmaeus* *N. noctula*	78.50	0.0001	2
Distance to inland water (m)	*P. pipistrellus* *P. pygmaeus* *N. noctula*	88.25	0.0001	2
Distance to buildings (m)	*P. pipistrellus* *P. pygmaeus* *N. noctula*	16.67	0.0001	2
Distance to roads (m)	*P. pipistrellus* *P. pygmaeus* *N. noctula*	18.36	0.0001	2

Table 2. Distance scores for all the random bat points and bat occurrence data together. All species had significantly different distance scores. Chi squared values, P values and degrees of freedom are shown.

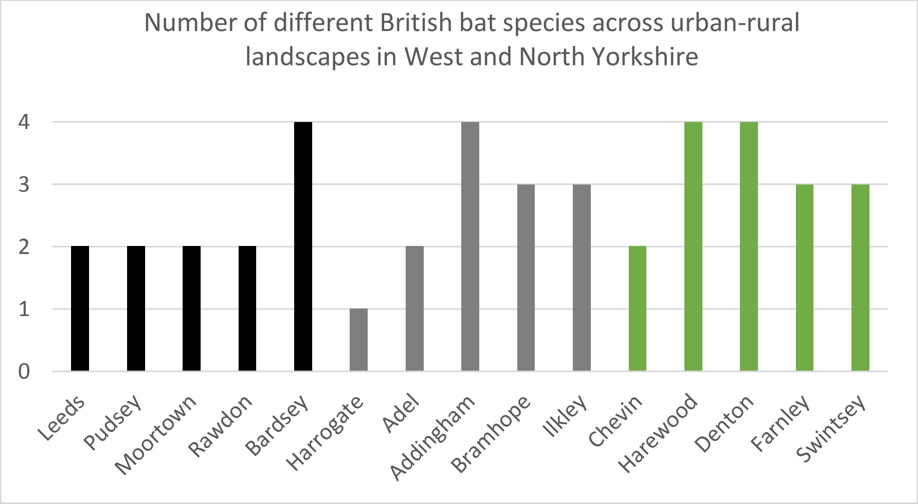

Figure 6. Bar chart illustrating the different number of British bat species within each transect area, across urban-rural landscapes in west and north Yorkshire. From the most urbanised (Leeds) to the most rural (Swinsty) area according to percentage cover of buildings within a 1000m polygon buffer around the linear transect which was walked. On average rural areas had more bat species, including *N. noctula*, *P. pipistrellus, P. pygmaeus* and *M. brandtii/mystacinus.*