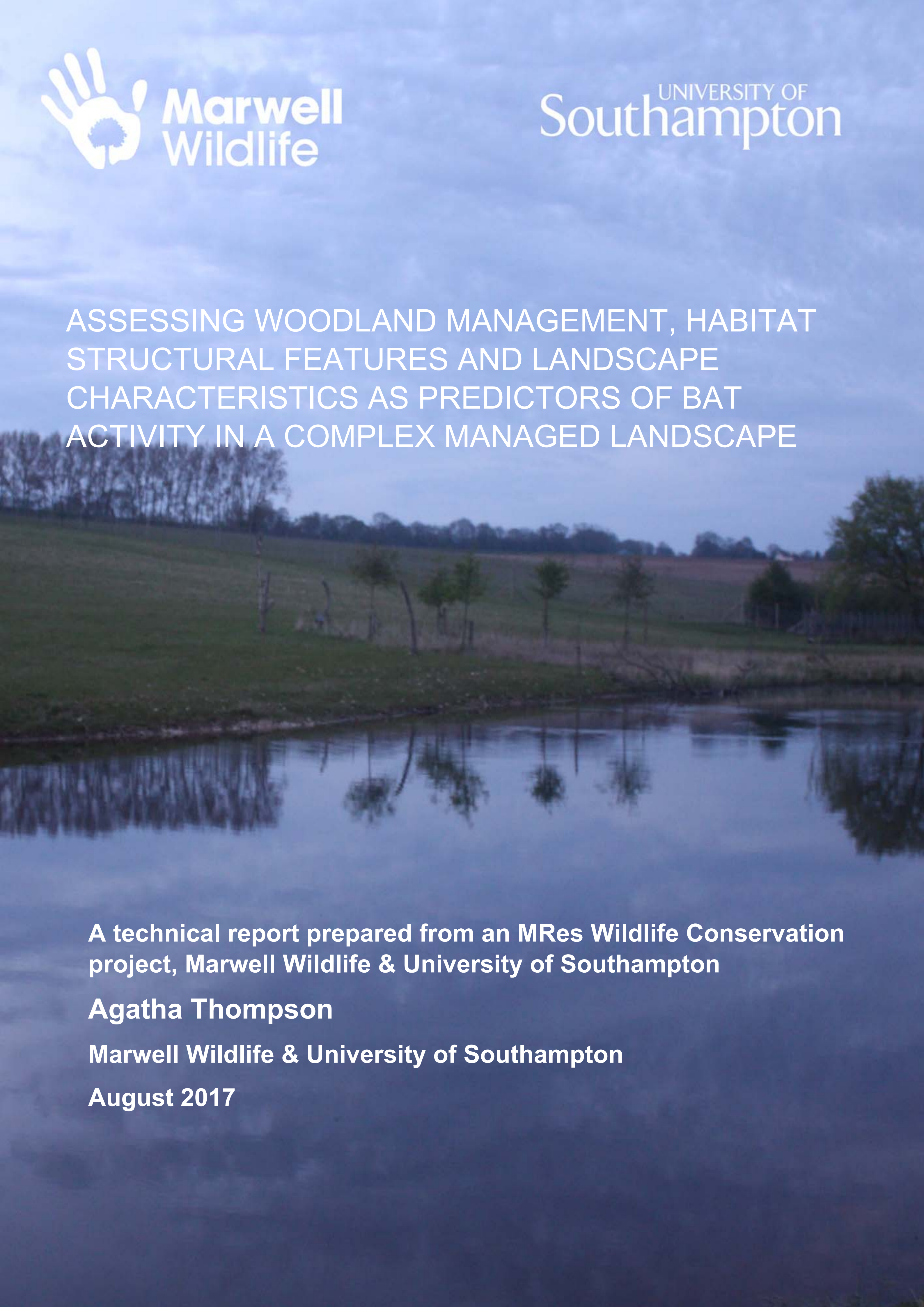

ASSESSING WOODLAND MANAGEMENT, HABITAT STRUCTURAL FEATURES AND LANDSCAPE CHARACTERISTICS AS PREDICTORS OF BAT ACTIVITY IN A COMPLEX MANAGED LANDSCAPE

A technical report prepared from an MRes Wildlife Conservation project, Marwell Wildlife & University of Southampton

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Abstract

UK bat populations have undergone severe historical declines due to factors that include: urbanisation, habitat degradation and commuting route severance. All 17 species breeding in the UK are listed on the IUCN red list and protected by European and UK law. These species are important bioindicators of habitat quality and change, but also provide a valuable ecosystem service: regulating insect populations and suppressing pests and invasive species, both in natural and agricultural landscapes. There have been relatively few studies investigating the effect of woodland management in an agricultural landscape on bat populations in the UK, so a quantitative assessment of the habitats utilised by bat species is important for understanding the impacts of land use on bat populations, especially within a multifunctional landscape.

The research here assesses the impact of both localised structural features and landscape influences on bat populations using acoustic surveys at a mixed use site in Hampshire. There were three main aims: firstly to assess woodland structural features and woodland management intensity as predictors of total bat activity and species level bat activity inside woodland, secondly to evaluate the impact of land use and woodland management intensity on bat activity and species level bat activity along woodland edges, and thirdly to assess the importance of woodland connectivity to bats foraging inside woodland and along woodland edges.

A total of 9950 bat passes were recorded, with the results showing a dramatic disparity in the significant predictors of bat activity for different species and highlighting the importance of a heterogeneous landscape which incorporates both managed and unmanaged woodland. Management recommendations were made, including incorporation of minimally managed woodland and buffer strips along managed woodland edge to facilitate foraging by species more sensitive to disturbance.

The results will be used both at the local scale, with reports disseminated to local land managers to provide specific advice on managing woodland to maximise land suitability for all bat species, and on a greater scale, considering implications for wider context woodland management across the UK. The results can be used to validate conservation management decisions and to provide advice on the best methods for the integration of bats into an agricultural landscape.

Keywords: bats, woodland management, land use, connectivity, agriculture, Hampshire

Target journal: Agriculture, Ecosystems & Environment

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Contents

1 Literature Review

1.1 UK Agriculture

Six thousand years ago 75% of the UK was covered by woodland (Watts, 2005). Following the development of woodland clearance practices to make space for agriculture this figure has declined to 13%, whilst 74.8% of UK land use is agricultural (Khan and Powell, 2011). Approximately half of the existing wooded areas are exotic conifer plantations, with only 5% of woodland area being ancient semi-natural woodland (Khan and Powell, 2011).

Mixed agriculture is an important part of the UK's cultural and economic landscape, but the loss in wildlife communities has been pronounced, particularly for species which are sensitive to changes in landscape and habitat structure (Green, 1990; Pretty *et al.*, 2000; Walker *et al.*, 2004). These dramatic changes have led to severe fragmentation, placing increased importance on the existence of linear remnants of intact vegetation and scattered trees in fields. These, combined with less-intensive land uses and the integration of "wildlife friendly farming" and "land sparing" techniques such as unimproved pastures, are of landscape level importance to a number of species, including bats (Lentini *et al.*, 2012), .

1.2 Chiroptera

The order Chiroptera contains around 1300 bat species distributed across most geographical regions of the world (Graham, 1994). There are 17 resident bat species in the UK (Bat Conservation Trust, 2015), and all hold favourable conservation status (Collins, 2016). Bat populations have undergone serious historical declines due to urbanisation, which has caused habitat degradation and fragmentation, loss of roosts through building development and intersection of commuting routes (Bat Conservation Trust, 2015). Whilst populations have begun to recover as a result of the implementation of legislation and conservation action (Bat Conservation Trust, 2017a), there are still many gaps in knowledge relating to the impact of management practises both of conservation and agricultural purpose, particularly at the landscape level.

Bats perform an essential ecological function and provide a valuable ecosystem service through insect foraging. They regulate natural insect populations and suppress pest and invasive species, which benefits both agricultural and natural ecosystems (Kunz *et al.*, 2011; Maine and Boyles, 2015). They are also important bioindicators as they occupy high trophic levels and are therefore sensitive to alterations in their ecosystem, for example due to prey decline or habitat disturbance

(Jones *et al.*, 2009). They are particularly sensitive to human-caused disturbance, including artificial light and noise (Berthinussen and Altringham, 2012; Bunkley *et al.*, 2015; Kuijper *et al.*, 2008; Mathews *et al.*, 2015; Schaub *et al.*, 2008; Stone *et al.*, 2015). Hence, understanding bat abundance and distribution within an ecosystem can indicate the overall health of that ecosystem. Using indicator species is therefore particularly important in the process of habitat alterations as part of post-implementation adaptive management, involving constant monitoring and adjustment of procedures to cause as little impact as possible to non-target species.

1.3 Bats and Ecological Requirements

The conservation of bats as an Order relies upon the detailed understanding of the variety of habitats utilised by different bat species, and requires a landscape-scale approach encompassing all habitat types and foraging localities used by bats. Whilst all UK bat species are nocturnal foragers of insects, different species rely on different foraging strategies, habitat types and resources (Vaughan, 1997). For example, the Leisler's bat *(Nyctalus leisleri)* prefers to forage at woodland margins (Waters *et al.*, 1999), whilst the brown long-eared bat *(Plecotus auritus)* shows preference for complete tree cover with a dense understorey (Entwistle *et al.*, 1996). Species which rely on foraging over water sources for insects such as the Daubenton's *(Myotis daubentonii)* bat can become negatively affected by changes in freshwater habitats (Downs and Racey, 2006; Vaughan *et al.*, 1996).

The reduced availability of suitable roost sites within the landscape can significantly reduce bat abundance and individual bat size, as they provide shelter from the cold or wet conditions, and protection from predation (Humphrey, 1975). This protection allows bats to enter a state of torpor during colder weather, the process of which minimises daily energy expenditure and is particularly important for pregnant or lactating females, or in the process of overwintering (Humphrey, 1975). Barbastelles *(Barbastella barbastellus)* prefer to roost in untouched mature woodlands, hence areas of untouched mature woodland should be preserved as suitable roosting sites for this species (Russo *et al.*, 2004).

1.4 Bats and Woodland Management in Mixed Use Agricultural Landscapes

The retention of natural foliage structures and an understorey have been identified as important for insectivorous bats in Australia (Lentini *et al.*, 2012). The presence of small forest openings has also been shown to increase bat activity due to the provision of foraging opportunities. It was suggested that managed cutblocks can function as edge habitat for foraging bats (Grindal and Brigham, 1998). In south-eastern Australia, the peak tree density has been identified as 20 – 30 trees per hectare, with an increase above this leading to a decline in bat activity (Lumsden and Bennett, 2005). The study highlighted the value of scattered trees as foraging habitats as well as the provision of resources by small and isolated habitat components in rural land mosaics.

Bats rely on landscape level continuity and availability of resources, hence fragmentation and patch quality deterioration may lead to a reduction in bat abundance (Walsh and Harris, 1997). A study on frugivorous and nectivorous bats in Paraguay showed that species abundance increased with increased forest cover, patch size and patch density (Gorresen and Willig, 2004).

The presence of linear features connecting these patches can reduce the impact of fragmentation as they provide passages for travel for bat species, including both the common *(Pipistrellus pipistrellus)* and the soprano pipistrelle *Pipistrellus pygmaeus)*. Conversely, the noctule *(Nyctalus noctula)* appears to remain uninfluenced by the density of linear features, once again confirming the importance understanding species specific requirements and creating a heterogeneous landscape (Boughey *et al.*, 2011).

1.5 Context of this Research

There have been few studies investigating the effects of management interventions on bats in agricultural landscapes, with even fewer based in the UK (Fuentes-Montemayor *et al.*, 2013; Park, 2015). There is also a gap in knowledge of species specific habitat requirements of bats (Murphy *et al.*, 2012). Hence, whilst fragments of information pertaining to the habitat preferences of individual bat species exist, this research provides a landscape study comparing the relative predictors of bat activity according to land use and woodland connectivity at the landscape scale, and woodland management intensity and woodland structural features at the local habitat scale.

Systematic bat surveys are also lacking for the area, hence this research also seeks to improve knowledge of bat distribution within the landscape to inform future conservation management decisions and studies.

Dissemination of the results will not only inform local landowners surrounding the study site of suggested alterations to management practices, but provide important insight to land managers across the UK of potential changes which can be made to improve the landscape in its support of all UK bat species, as well as give insight into the impacts that woodland management has already caused. By improving the landscape for occupancy by bats, the maximum benefits from the ecological services they provide can be reaped. In the context of agricultural land, this is delivered in the form of insect regulation and pest control.

1.6 Research Aims

1. Assess woodland structural features and woodland management intensity as predictors of total bat activity and species level bat activity inside woodland in an agricultural landscape.
2. Evaluate the impact of land use and woodland management intensity on bat activity and species level bat activity along woodland edges in an agricultural landscape
3. Assess the importance of woodland connectivity to bats foraging inside woodland and along woodland edges.

1.7 Research Objectives

a. Implement a series of acoustic bat surveys both inside woodland blocks and along woodland edge and collect recordings of bat calls.
b. Carry out habitat assessments at the landscape scale for land use distribution and connectivity calculations, and at the local scale to measure structural features within woodland.
c. Assess woodland habitats and assign management categories.
d. Analyse recordings of bat calls and identify to species level.
e. Perform statistical analysis to determine the predictors of total bat activity and species level activity along woodland edges and inside woodland blocks.
f. Translate species level predictors of activity into relative habitat requirements of different species.
g. Interpret habitat requirements of bat species into woodland management recommendations.
h. Contribute results to the National Bat Monitoring Scheme and Hampshire Bat Group database to inform future conservation endeavours.

2 Methodology

2.1 Study Site

The South Downs National Park (SDNP) is situated in the south of England and is administered by the South Downs National Park Authority (SDNPA), and managed according to the Environment Act 1995 (The Environment Agency, 1995). The study site lies within the SDNP and centres on a 30 hectare area of woodland surrounding the Marwell Zoological Park in Hampshire. It also extends to two areas of privately owned agricultural farmland to the north: Hensting Farm, and to the east: Roughay Farm (Figure 1).

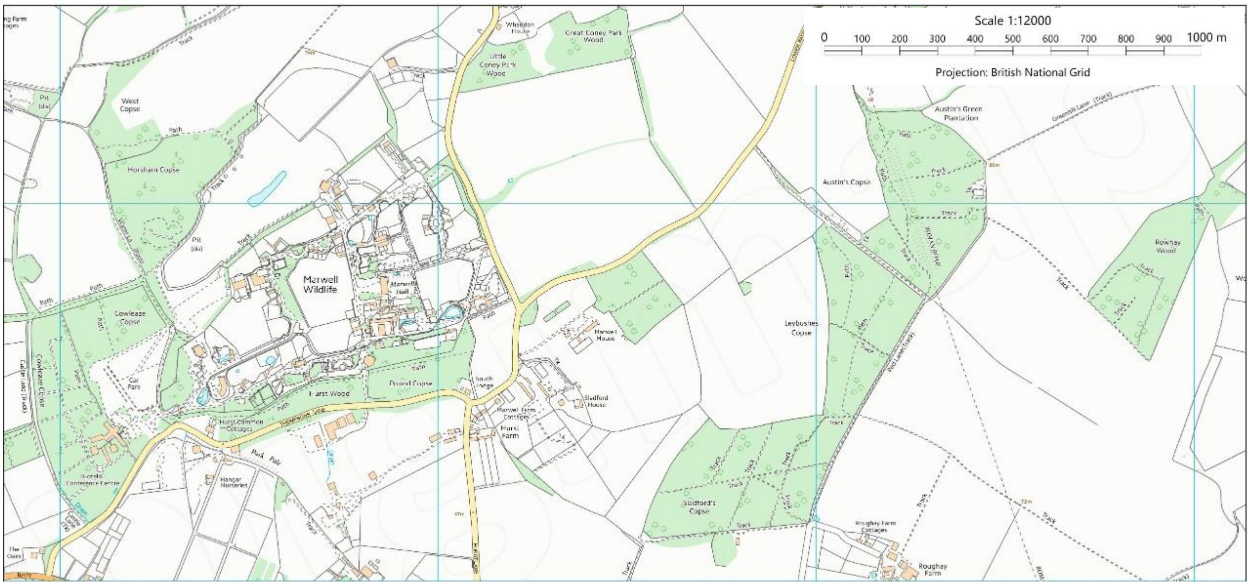

Figure 1 - Map of study site with Marwell Zoo and the surrounding woodland in the west, Hensting Farm to the north of Horsham Copse and Roughay Farm to the east. Source: Digimap (http://digimap.edina.ac.uk/roam/os).

The woodland at the Marwell site is managed by Marwell Wildlife, and is considered to be of significant ecological value as approximately half of the total area contains semi-natural woodland, the protection of which is now considered a UK conservation priority. The woodlands have been designated as three separate Sites of Importance for Nature Conservation (SINC) (Parker *et al.*, 2010).

A small portion of deciduous woodland at Hensting Farm is included in the study site and is directly connected to the woodland at the Marwell site. A significant portion of the woodland at Roughay Farm is lowland mixed deciduous woodland, which is considered a BAP priority habitat (The Hampshire Biodiversity Information Centre, 2011). A mixture of woodland management is carried out on this site, including hazel coppice rotation previously on a seven year basis, but presently on a five year rotation. Other management techniques include harvesting for hurdle making, cutting and clearing. Additionally the site is also used for game rearing and hosts game shoots in late summer.

Woodland management at Marwell has been carried out for over 400 years, but with minimal intervention until the zoological park began to expand throughout the 1970s and 1980s. Recent management has included hazel coppicing, thinning of larch and subsequent restocking with several species including oak, ash, hazel, maple, re-establishment of rides and a herb and shrub layer, creation of new native woodland areas and edge habitat and removal of invasive species (Parker, Wilkie and Woodfine, 2010).

The site is surrounded by a mix of grassland, woodland and farmland. The nearest urbanised areas are Colden Common and Bishopstoke, approximately 1.7km north west and 2.5km south west of the site respectively, whilst Eastleigh is the nearest town, 5km west of Marwell.

2.2 Bat Surveys

Acoustic surveys have become a widely used method of surveying bats (Bender *et al.*, 2015; Grindal and Brigham, 1998; Russo *et al.*, 2007; Williams-Guillén *et al.*, 2011). They can be implemented without a bat license, which is required for other types of bat survey including radio-tagging, mist-netting and roost surveying (Collins, 2016). They allow bat activity data to be collected and subsequently identified, providing as easier process of identification than for in situ observations.

Survey protocol and data collection were performed in line with the Bat Surveys for Professional Ecologists Good Practice Guidelines (Collins, 2016). The main aim was to cause as little disturbance to bat activity as possible, including keeping surveyor-caused noise and light pollution to a minimum.

2.2.1 Woodland Edge Surveys

Transect surveys were carried out between May and July 2017. A “fair-weather” approach was taken, where surveys were only carried out on nights where there was no rain or strong wind, and where the mean temperature was above 10^{o}C. This is because extremes in these three factors are widely accepted to affect bat activity (Bender and Hartman, 2015; Lacki, 1984; Maier, 1992), and is the approach suggested by the Bat Conservation Trust in their Good Practice Guidelines (Collins, 2016) in order to avoid incorrectly attributing variations in bat activity to abiotic factors.

Six transects (Figure 2) were selected across the study area to provide coverage of a range of different woodland edge types. Waypoints were marked using a Garmin GPSMAP 64s at 50 metre intervals along the length of each transect, providing the locations at which bat calls were recorded. Since the data will not be analysed according to transect, but rather according to the individual characteristics of each waypoint, the aim of transect design was to optimise the data collection process, where one transect was surveyed on each data collection night to fit within the survey window as described below.

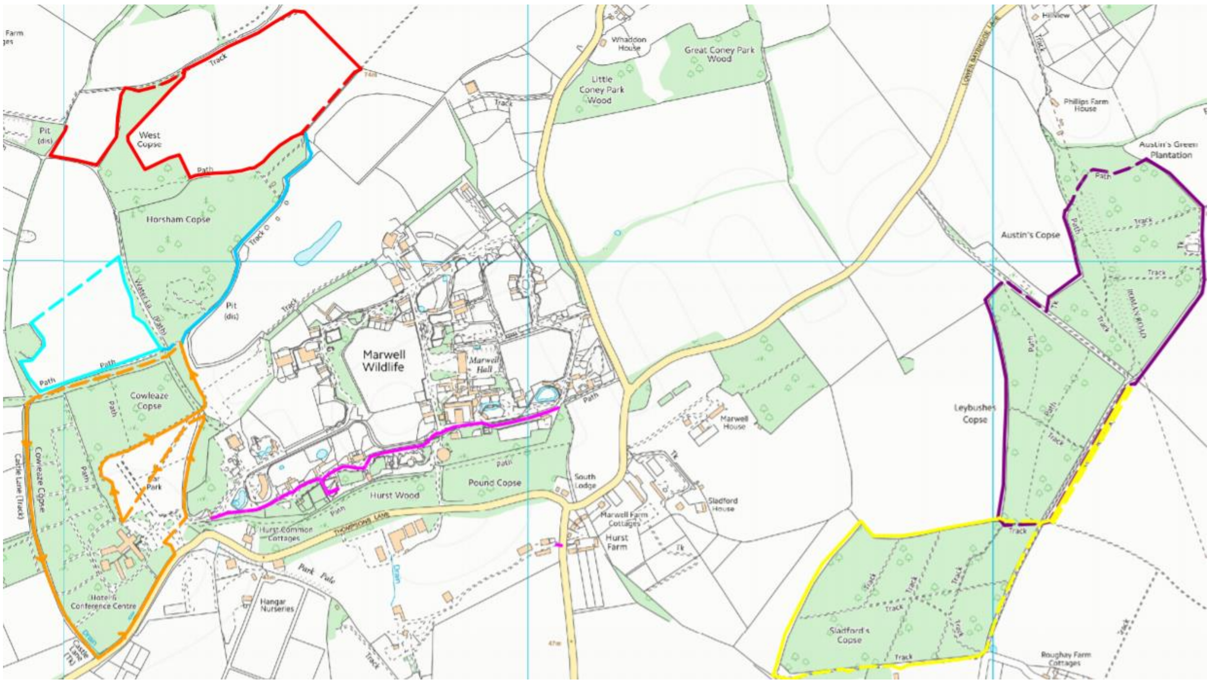

Figure 2 – Map showing six transects used for woodland edge surveys. Two surrounding the woodland at Marwell (blue and orange), one inside the zoo (pink), one at Hensting Farm (red) and two at Roughay Farm (purple and yellow). Source: Digimap (http://digimap.edina.ac.uk/roam/os).

With the exception of the transect within the zoological park (pink), each transect was approximately 1.5 kilometres in length with around 30 waypoints each. A two minute recording was made at each waypoint using a Batbox Duet dual-mode bat detector (Batbox Ltd, 2007) with heterodyne and frequency division channels connected to a Roland Edirol R-09 Digital Recorder (Roland, 2006).

The same equipment was used throughout data collection and was calibrated against artificial bat calls in a laboratory environment prior to survey commencement. The input level on the recording device was used to locate the peak recording level to avoid distortion caused by clipped recordings and the addition of unwanted harmonics and background noise.

The detector on the Batbox was always help upright pointing directly upwards at a height of 1.5 metres during recording in order to detect the highest number of bats and to keep the chance of detection equal across all waypoints. The recordings made were full spectrum, however the detector was kept tuned to a frequency of 45 kHz during the recording process in order to keep recordings constant across all waypoints. The sound quality of bats recorded further from the tuned frequency will be slightly different to those recorded at their peak frequency, so this was kept in mind during subsequent call analysis. The frequency of 45 kHz was chosen as it represents a frequency where the most UK bat species will be heard, including the most common UK bat: the common pipistrelle.

Data collection was implemented in the two hour window beginning 20 minutes post-sunset. This time frame was chosen as all bat species will typically be active within this window. It also allowed a reasonable balance between transect length and survey length. Each transect was surveyed four times and the start point for each repeat was varied. This is because bat activity varies across the two hour survey window, with different species emerging at different times (Collins, 2016). Hence, rotating the start point allowed each quarter of each transect to be surveyed in each four quarters of the survey window. The four repeats for each transect were distributed across the survey period to avoid scheduling bias and climatic variation between transects.

Figure 3 - Photograph taken from one of the waypoints at Roughay Farm, showing the location of the transect at the border of woodland and arable field.

The following local environmental conditions were also recorded at each waypoint, as is standard procedure for bat surveys: temperature, relative humidity, background noise, light intensity and wind speed both parallel and perpendicular to the transect route. For both the wind speed and background recordings, three readings were taken at each waypoint at intervals of five seconds and were subsequently converted into mean values. This was to allow for the substantial variation in these variables which can occur due to fluctuations, for example those caused by gusts of wind. The time at each waypoint was noted down from the recording device so that the timings matched with the recordings.

2.2.2 Inner Woodland Surveys

Four static bat detectors were rotated around 12 locations inside woodland blocks between May and July 2017. Three Wildlife Acoustics Song Meter SM2BAT+ Ultrasonic Bat Detector and Recorders (Wildlife Acoustics, 2011) along with one Song Meter SM4BAT FS Ultrasonic Bat Detector and Recorder (Wildife Acoustics, 2016) were used (Figure 4). They were configured to listen for bat calls for a two and a half hour period beginning thirty minutes before sunset and make full spectrum recordings. This period was chosen as all recording locations were situated inside woodland blocks where roost emergence and early foraging occur before bat activity reaches its peak (Collins, 2016).

Figure 4 - SM2BAT+ bat detector (left) and SM4BAT FS bat detector (right)

Upon detecting a bat, the devices begin to record for the duration of the bat call, before ending the recording and beginning the listening process. Each of the SM2BAT+ devices has two microphone connections, one with a three metre cable and one with a fifty metre cable. This enabled two separate locations to be sampled at the same time by the same device. Hence this allowed seven locations to be monitored in the same evening, to maximise the volume of recordings collected during the study period. Three sets of seven locations were used, and the detectors made two full rotations around these location sets to provide a total of 8 nights of data collection per each of the 21 survey locations (Figure 5).

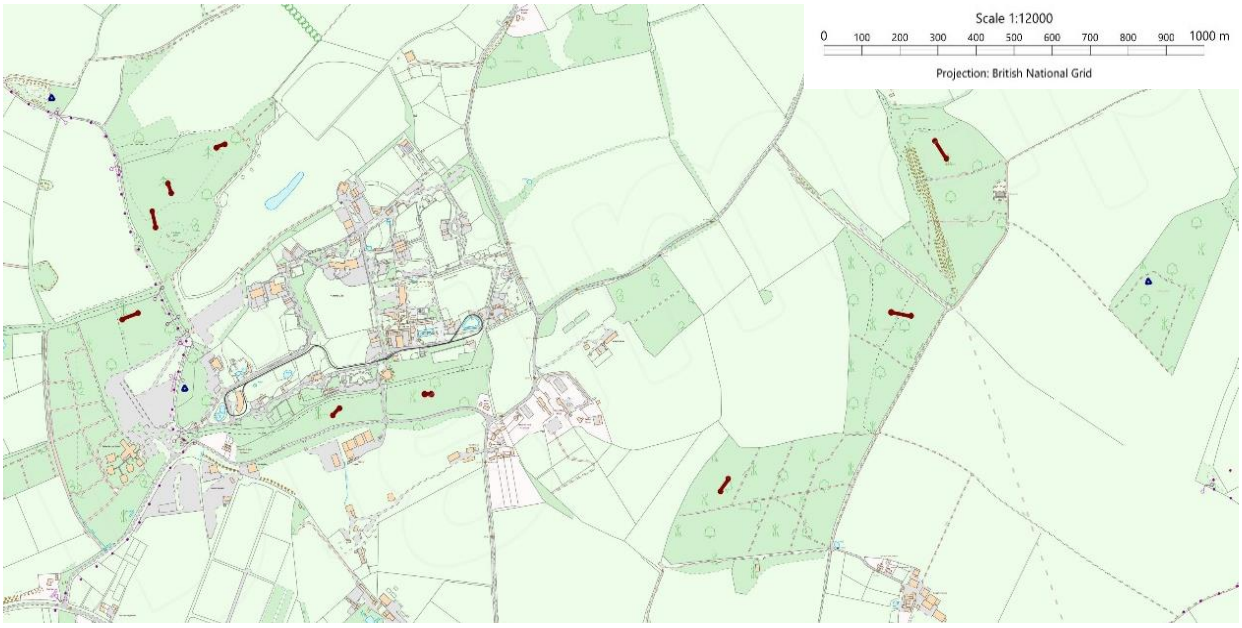

Figure 5 - Map showing nine paired microphone locations (SM2BAT locations, shown as red dots and lines) and three single microphone locations (SM4BAT, shown as blue triangles). Source: Digimap (http://digimap.edina.ac.uk/roam/os).

The microphones were positioned to point directly upwards at a height of two metres from the ground on plastic poles attached to metal ground stakes. Microphones were not placed directly below branches which would lead to acoustical echos.

Below the microphone attached via the three metre cable, the detector was suspended on the metal stake in a protective bag with a waterproof covering, since the detectors themselves are not waterproof. The microphones are fitted with a protective foam cover to prevent moisture running down inside the microphone, however whenever significant rain was forecast the microphones and detectors were removed from the field. Hence, as with the woodland edge sampling, fair-weather sampling was used.

The environmental conditions, temperature and humidity, were sourced online following data collection (Time and Date, 2017) along with lunar illumination percentages (Moon Phases, 2017).

2.3 Habitat Analysis

The woodland edges for the transect surveys and inner woodland plots where static detector microphones were located were assessed using two separate techniques.

2.3.1 Woodland Edge

2.3.1.1 Land Use Classifications

Land use classifications were designated for the non-woodland side of the transects (Figure 3). They were considered to be of more value as categorical variables than raw measurements as they are more easily interpreted and communicated to land managers (McConville *et al.*, 2013). Land use was assessed using aerial imagery (Google Earth, 2017) and each waypoint was assigned to one of five categories (see Table 1).

Table 1 - Land use classifications and descriptions for the non-woodland side of each waypoint.

Land Use	Description
Agricultural Field	Fields used for agriculture, including wheat, corn and rapeseed, located at Roughay Farm and Hensting Farm.
Livestock Field	Fields containing livestock, located at Roughay Farm and to the west of Cowleaze Copse at the Marwell site.
Conservation Field	Westcopse field at the Marwell site, a mixture of grasses and wildflowers, the field is occasionally harvested for forage for zoo animals and has a public right of way around the perimeter.
Human Use	Quiet car parks and roads.
Zoological Park	Half of the waypoints were situated along a tarmacked road inside the zoo between woodland and animal enclosures. The other half were along a grass track over-looking the African Valley enclosure.

2.3.1.2 Woodland Management Intensity Rating

Each waypoint was given a woodland management intensity rating (Table 4) based on two factors: time since last management practice (Table 2), and intensity of last management practice (Table 3).

Table 2 - Woodland management intensity rating: time since last management practice. Time refers to the length of time since the most recent management intervention was carried out.

Rating	0	1	2	3	4
Description	No management has ever been carried out or was implemented over 30 years ago	Management has been implemented between 10 and 30 years ago	Management has been implemented between 5 and 10 years ago	Management has been implemented between 1 and 5 years ago	Management has been implemented within the last year

Table 3 - Woodland management intensity rating: intensity of last management practice. Intensity refers to the most recent management intervention that was implemented.

Rating	0	1	2	3	4
Description	No management	Management causing minimal disturbance and structural change	Management causing moderate disturbance and structural change	Management causing significant disturbance and structural change	Intensive management causing major disturbance and structural change

Table 4 – Woodland management intensity rating: matrix for selecting the overall woodland management intensity rating based on the time (Table 2) and intensity rating (Table 3).

		Time				
Intensity		**0**	**1**	**2**	**3**	**4**
	0	0	-	-	-	-
	1	-	1	2	2	3
	2	-	2	2	3	3
	3	-	2	3	3	4
	4	-	3	3	4	4

Connectivity metrics were generated per woodland block using the software: graphab (Clauzel *et al.*, 2016). A raster file was generated in ArcMAP (ESRI, 2017) containing all woodland blocks within a six kilometre radius from the study site. This distance was chosen as it represents the core sustenance zone (CSZ) of the UK species with the largest CSZ (Bat Conservation Trust, 2016a). Minimum patch area was set to 0.5 hectares with the link set maximum distance at 350 metres (see Figure 6).

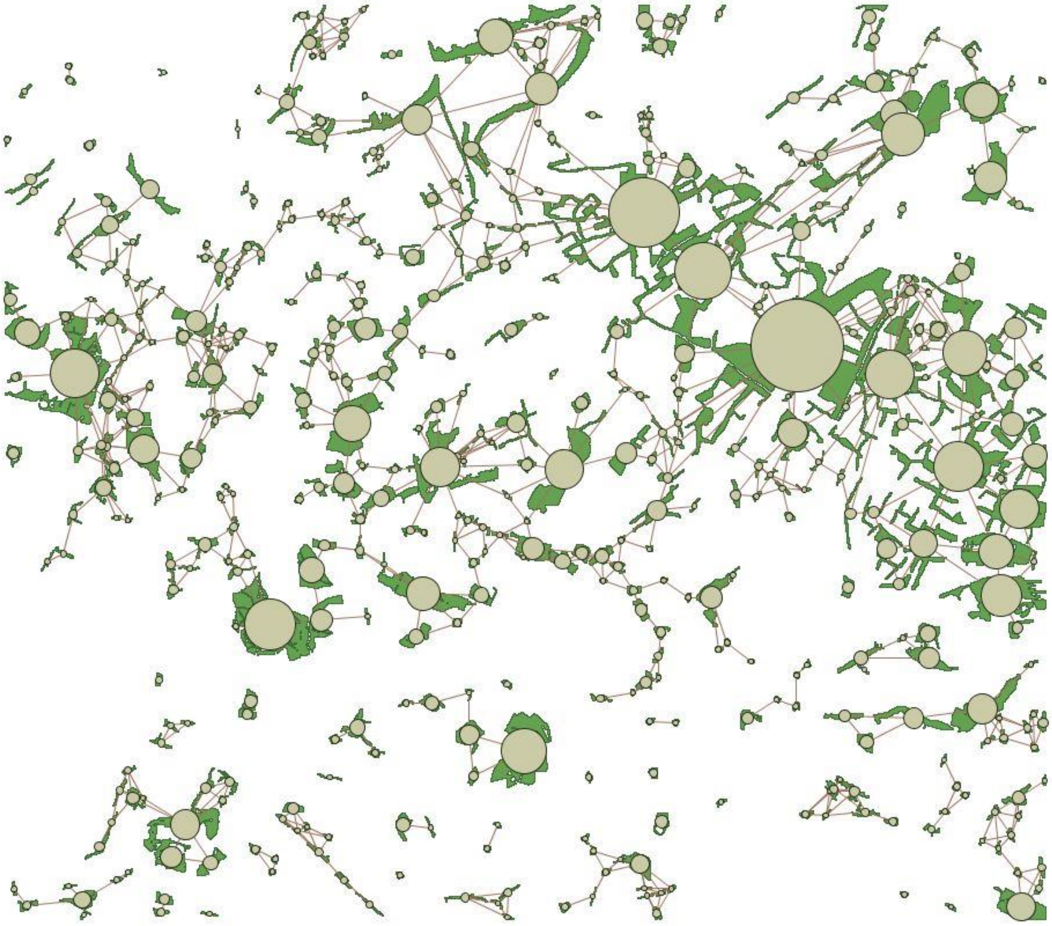

Figure 6 - Map showing woodland connections in a 195km^2 (15 km west-east x 13 km north-south) square around the study site. Size of circle indicates more connections, red lines indicate connected woodlands.

2.3.2 Inner Woodland

Habitat evaluation surveys were carried out for each of the 21 static detector microphone locations. Using the microphone location as the centre, a 144m^2 grid was marked out using a guide cord with coloured indicators at four metre intervals. Within the sample square, 16 sample points were located using these coloured indicators, and at each of these points two measurements were recorded: understorey height and canopy density. The height of the understorey was estimated by eye and recorded in metres, whilst canopy density was recorded by taking a photograph pointed upwards at the canopy using a Canon EOS 1200D with an 18-55mm lens set at 18mm (Canon Inc, 2016). The image numbers were recorded and the photos were subsequently analysed using the program ImageJ (Ferreira and Rasband, 2012) with the macro Hemisphere 2.0 (Beckschäfer, 2015) to produce a gap fraction percentage per habitat survey location. This method holds improved accuracy over manual estimation methods (Chianucci, 2016).

The number of trees was recorded within each 144m^2 survey square. Along with circumference measurements at breast height for every tree of height four metres or above, a clutter index was calculated using Equation 1.0.

$$Clutter\ index\ = \left(\frac{\sum \pi \left(\frac{x}{2\pi}\right)^2}{144}\right) x\ 100 \qquad \textit{Equation 1.0}$$

Where *x* is tree circumference in metres, thus providing a percentage for the total sample area occupied by trees. For coppiced trees, only the largest trunk was measured. The connectivity metrics calculated for the woodland edge analysis were also used.

2.4 Call Analysis

2.4.1 Woodland Edge Survey Data

Calls were analysed using the software: BatSound 4 (Pettersson, 2014), a screenshot of which is shown in Figure 7. Each two minute recording was loaded into the program and manually scanned for bat passes. Any pass which could confidently be identified to a species category was recorded in a spreadsheet. Identification was carried out on the basis of the analyst's existing knowledge and training, and all calls were checked against a list of five species parameters: peak frequency, start frequency, end frequency, inter-pulse interval and call duration, as well as taking into consideration their call shape, sound qualities and rhythm (Bat Conservation Trust, 2017b). Where difficult to identify whether an object appearing in the recordings was either due to a weak bat call or noise caused by a non-bat source, the objects were marked as unidentified and excluded from final analysis.

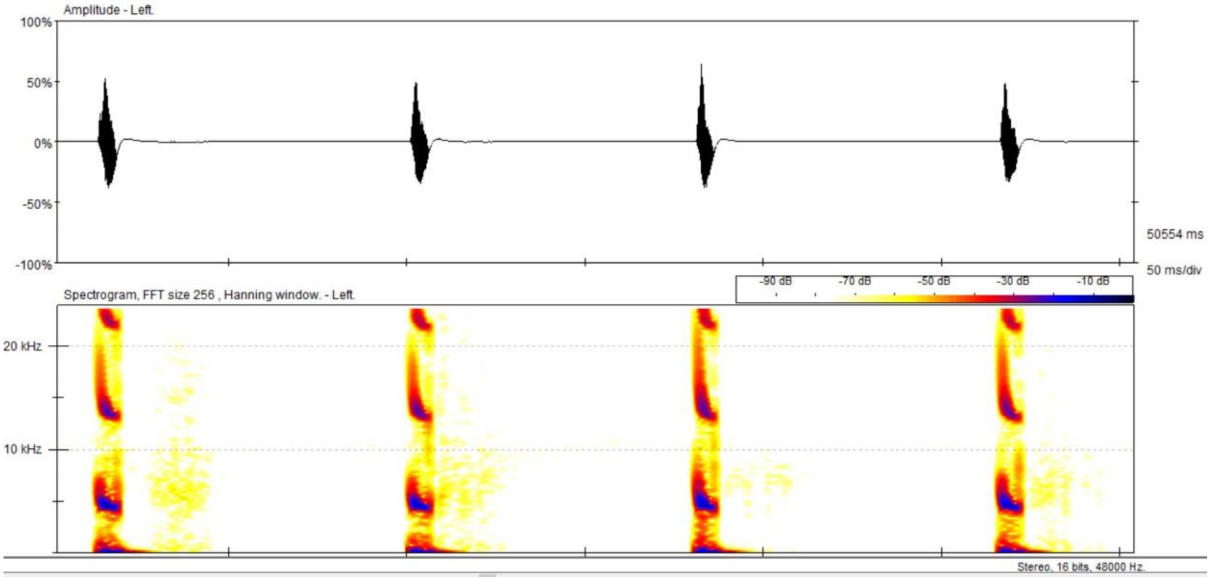

Figure 7 - Screenshot from BatSound 4 showing four pulses from a common pipistrelle. Bottom panel shows pulse frequency against time, top panel shows pulse amplitude against time.

A bat pass was defined as a sequence of one or more call pulses separated by less than 1 second (Hayes, 1997; O'Farrell *et al.*, 1999).

2.4.2 Inner Woodland Survey Data

All static detector data was analysed via the Automatic Species Identification feature of Kaleidoscope Pro 4 using the Bats of Europe 4.3.0 classifier (Wildlife Acoustics, 2017). This method was chosen to allow quick analysis of the 168 nights of data collected by the static bat detectors across the survey period. To achieve an acceptable level of confidence in identification results, the number of matching pulses required for identification confirmation was set at three, with the classification confidence level set at neutral. The results were also checked manually, including verification of results returned for species which are not native to the UK but which are rare vagrants. Calls which were not assigned to a species category were labelled "No ID". It should be noted that automatic identification is likely to provide both false positives and negatives. One of the drawbacks of this sampling method is that occasionally bat passes were missed if they occurred at the same time as another pass being recorded, this is because Kaleidoscope only makes one identification per file. The results obtained were reported as the number of bat passes per night according to species.

2.5 Statistical Analysis

The presence of overdispersion led to the consideration of a GLM with quasipoisson family or a negative binomial model from the R package MASS (Ripley *et al.*, 2017; Ver Hoef and Boveng, 2007). From reviewing diagnostic plots for both models, the negative binomial model showed the best fit as the variance showed an approximately quadratic relationship with the mean for both sets of data. The R package DHARMa (Hartig, 2017) was then used to plot the residuals and a goodness of fit test was implemented [(Woodland edge, K-S: D = 0.028, p = 0.661); (Inner woodland, K-S: D = 0.059, p = 0.612)]. Tests were also carried out for species distributions (see Appendices A and B). The data structure fits the assumptions of the model in terms of the independence of data points, distribution of counts and the variance structure. For the categorical predictors, the following reference levels were selected: level 0 for woodland management intensity level, the land use with the lowest bat activity for land use type (excluding land uses with no activity). Zero-inflated poisson (ZIP) and hurdle models were also considered (Xu *et al.*, 2015), however the negative binomial GLM provided a better fit and are considered to be more robust models.

3 Results

A total of 9950 bat passes were recorded across both sampling methods. 8210 of these were identified to species level from 13 of the 17 UK native bat species (Figure 8). The most frequent calls belonged to common pipistrelles, followed by soprano pipistrelles. Whilst not currently known to be breeding in the UK, three calls from the greater mouse-eared bat were identified using Kaleidoscope Pro. Whilst occasional individuals of this species have been recorded in the past twenty years since it was declared extinct in the UK in 1990 (Bat Conservation Trust, 2010a), it should be kept in mind that this result is potentially a false positive as *Myotis* species are often difficult to separate from one another. From here on, species will be referred to using their common names for ease of understanding.

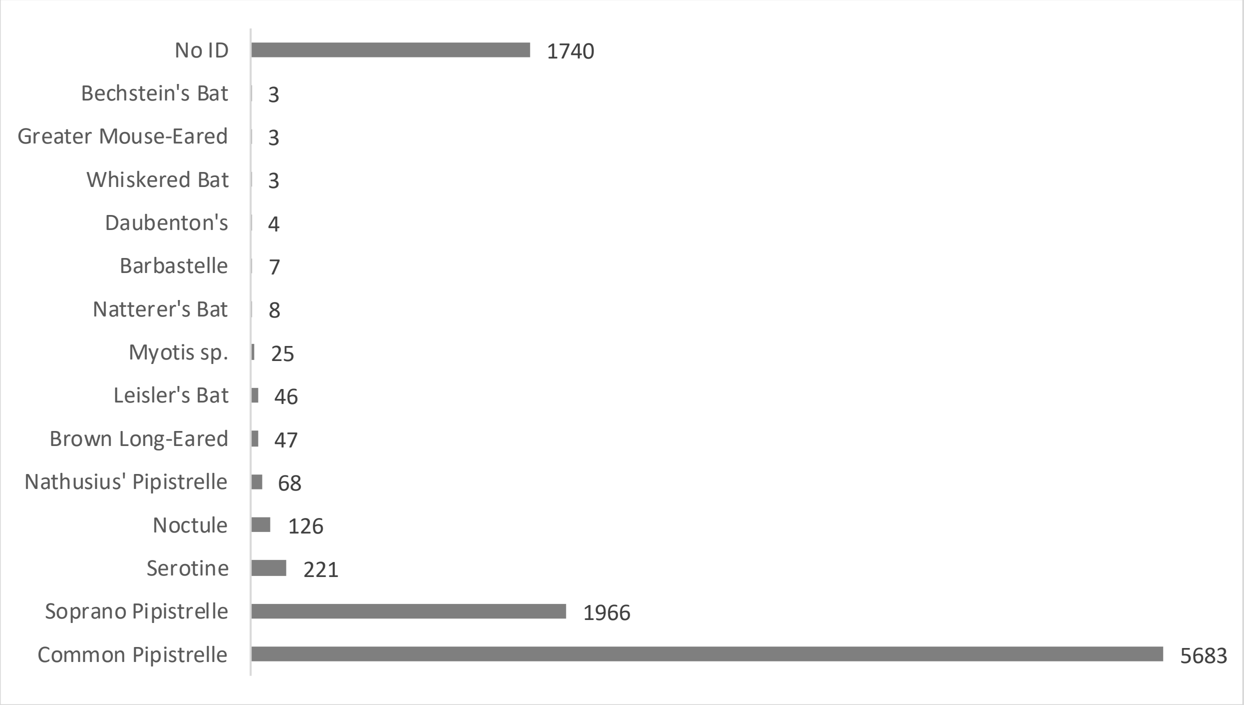

Figure 8 – Total passes recorded throughout data collection, grouped by species. 46 calls from Myotis bats could not be identified to species level and have therefore been assigned to a grouped category. 1740 bat calls could not be identified to species level.

3.1 Woodland Edge

3.1.1 Total Bat Passes

1918 bat passes were recorded from the woodland edge surveys, with the most frequent calls belonging to the common pipistrelle. Each of the environmental variables were tested for their individual relationship with bat activity (Table 5).

*Table 5 - Results from negative binomial GLM (689 d.f.), indicating individual relationships between predictors and total bat passes per waypoints. * denotes a significant result.*

Predictor Variables	**Estimate**	**Std. Error**	**Z Value**	**P value**
Temperature	-0.062	0.023	-2.716	0.007 *
Humidity	0.043	0.009	4.734	<0.001 *
Moon Illumination	-0.002	0.002	-1.24	0.216
Wind Parallel	-0.392	0.161	-2.426	0.015 *
Wind Perpendicular	-1.010	0.342	-2.953	0.003 *
Light Intensity	-0.149	0.030	-4.973	<0.001 *
Background Noise	-0.036	0.013	-2.774	0.006 *

Humidity showed a significant positive relationship with bat activity, whilst temperature, wind, light intensity and background noise showed a significant negative relationship. There was no significant relationship between moon illumination and bat activity. From graphically assessing the means, standard deviations and standard errors of environmental conditions across each habitat and land use category, they were deemed to not vary significantly from one another. Hence, the predictor variables: temperature, humidity, moon illumination, wind, light intensity and background noise were not included in the final model (Appendix C).

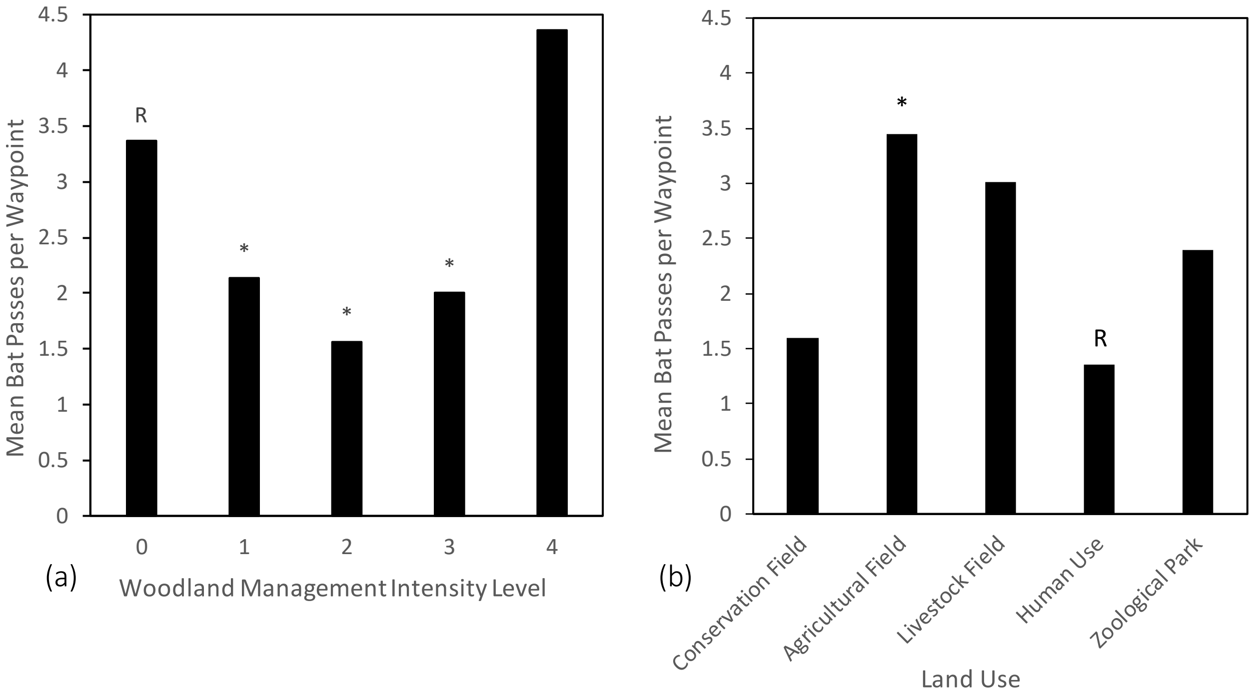

Figure 9 - The mean number of bat passes per waypoint for all species against: a) ascending woodland management intensity level (0-4), b) land use type. (*) indicates a category with a significant difference in bat activity to the reference level (R).

The highest levels of bat activity were recorded at waypoints adjacent to woodland of management intensity levels four and zero (non-managed), with levels one (GLM (n = 1918): Z = -2.238, d.f. = 689, p = 0.025), two (GLM (n = 1918), Z = -3.904, d.f. = 689, p < 0.001) and three (GLM (n = 1918), Z = -2.666, d.f. = 689, p = 0.008) associated with significantly lower levels of bat activity than the reference level: non-managed land (level zero) (Figure 9). Land use was also a significant predictor of total bat activity, with waypoints situated in agricultural land exhibiting significantly more bat activity than those situated in the reference level: human use land (GLM (n = 1918), Z = 2.315, d.f. = 689, p = 0.021). Connectivity did not have a significant relationship with total bat activity (GLM (n = 1918), Z = -0.693, d.f. = 689, p = 0.488).

3.1.2 Woodland Management Intensity

Key results are reported in this section, see Appendix E for full table of statistical results.

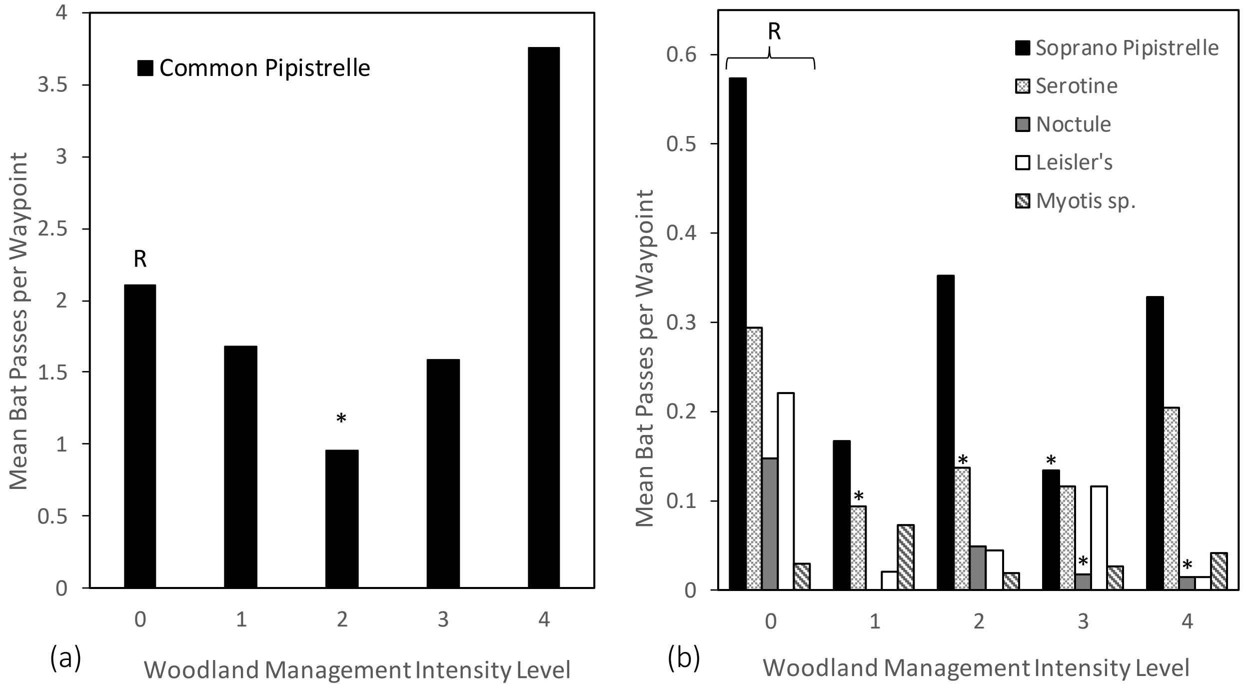

Figure 10 – The mean number of passes per waypoint for (a) common pipistrelle, and (b) soprano pipistrelle, noctule, serotine, Leisler's and Myotis spp. according to woodland management intensity level (0: non-managed, 4: most intensively managed). (*) indicates a category with a significant difference in bat activity to the reference level (R).

The majority of common pipistrelle calls were recorded at waypoints located adjacent to woodland of management intensity level four, whilst level two showed significantly less activity at points near woodland of management level two (GLM (n = 1489) : Z = -3.281, d.f. = 686, p = 0.001) (Figure 10). The highest levels of soprano pipistrelle, serotine and noctule activity were recorded at waypoints adjacent to the reference level: non-managed woodland (level zero). Soprano pipistrelle activity was significantly lower than the reference level at waypoints near level three managed woodland GLM (n = 213) : Z = -2.140, d.f. = 686, p = 0.032, whilst serotine activity was significantly lower than the reference level at waypoints near level one (GLM (n = 114) : Z = -2.398, d.f. = 686, p = 0.017) and two woodland (GLM (n = 114) : Z = -2.936, d.f. = 686, p = 0.003). Noctule activity was significantly lower than the reference level at waypoints adjacent to woodland of management level three (GLM (n = 25) : Z = -2.451, d.f. = 686, p = 0.014) and four (GLM (n = 25) : Z = -2.021, d.f. = 686, p = 0.043). There is a potential interaction between common and soprano pipistrelles at management level two, where common pipistrelles decrease and soprano pipistrelles increase.

The Leisler's bat also showed highest activity levels near non-managed woodland, however statistical analysis was not carried out for this species as the excess of zeroes and unique distribution of the data meant that no statistical models provided a satisfactory fit. Similarly, whilst not statistically significant, the highest level of activity exhibited by *Myotis* species was recorded near woodlands of management intensity level one.

3.1.3 Land Use

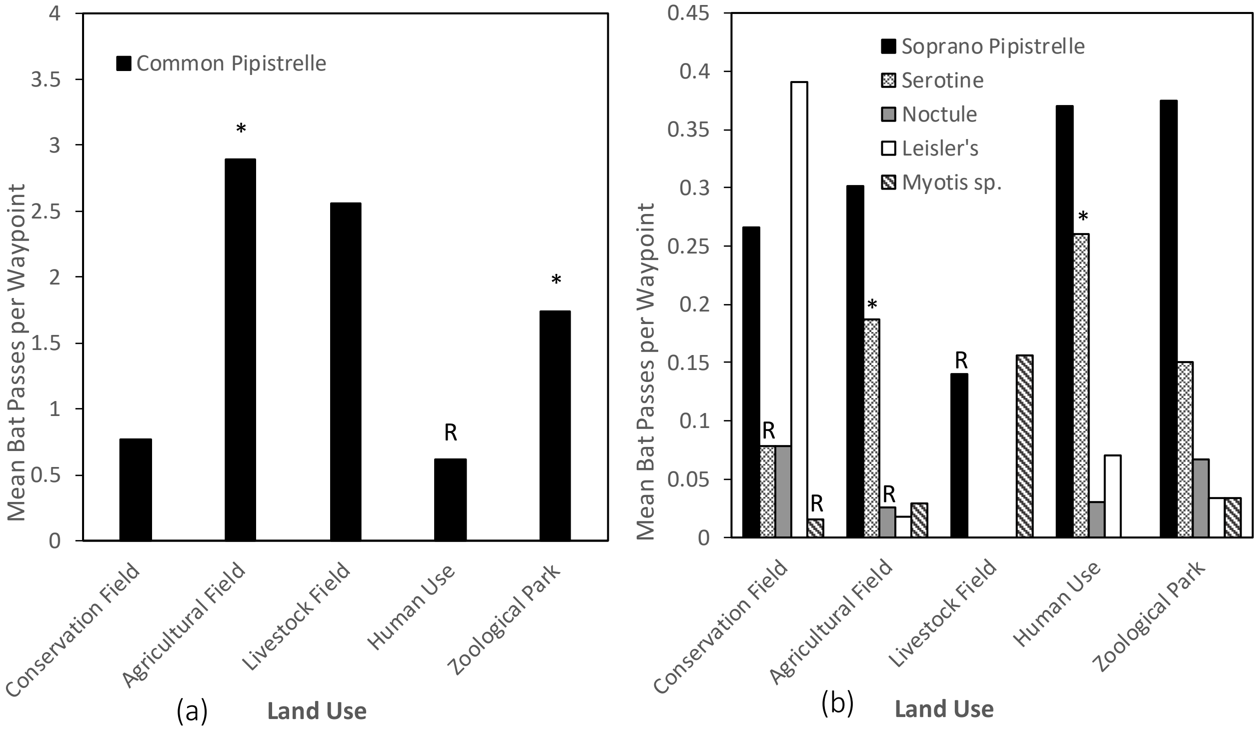

Figure 11 - The mean number of passes per waypoint for (a) common pipistrelle, and (b) soprano pipistrelle, noctule, serotine, Leisler's and Myotis spp. according to land use type. (*) indicates a category with a significant difference in bat activity to the reference level (R).

Waypoints situated along agricultural fields (GLM (n=1489): Z = 3.170, d.f. = 686, p = 0.002) and inside the zoological park (GLM (n = 1489): Z = 2.514, d.f. = 686, p = 0.012) recorded significantly higher levels of common pipistrelle activity compared to the reference level: human use (Figure 11). There were significantly higher levels of serotine activity at waypoints on human use land (GLM (n = 114): Z = 3.028, d.f. = 686, p = 0.002) and in agricultural fields (GLM (n = 114): Z = 2.608, d.f. = 686, p = 0.009) than the reference level: conservation field.

Only three groups were recorded in the livestock fields: common pipistrelles, soprano pipistrelles and *Myotis* species. It was the land use type where most *Myotis* activity was recorded. The majority of Leisler's bat passes were recorded in the conservation field. Waypoints situated in land predominantly for human use showed the lowest common pipistrelle activity, but the highest level of serotine activity. Waypoints inside the zoological park recorded the highest soprano pipistrelle activity. Woodland block connectivity rating was a positive predictor of activity for two species: soprano pipistrelle (GLM (n = 213): Z = 2.131, d.f. = 686, p = 0.033) and serotine (GLM (n = 114: Z = 2.105, d.f. = 686, p = 0.035).

Insufficient brown long-eared bat activity was recorded for statistical analysis (N=10), however all 10 passes were recorded at the same waypoint on the same night (woodland management category = 1, land use = livestock field, connectivity metric = 2.857). The recording was made in a woodland ride along the edge of the woodland, and it is suspected that the 10 passes belonged to one foraging individual.

3.2 Inner Woodland

3.2.1 Total Bat Passes

8032 bat passes were recorded from the inner woodland surveys, with the most frequent calls belonging to the common pipistrelle. Each of the environmental variables were tested for their individual relationship with bat activity (Table 6).

*Table 6 - Results from individual GLM with negative binomial distribution, with 167(166) degrees of freedom. * denotes significant result.*

Predictor Variables	Estimate	Std. Error	T Value	P value
Temperature	-0.073	0.023	-3.225	0.001 *
Humidity	-0.006	0.007	-0.792	0.429
Moon Illumination	< -0.001	0.002	-0.071	0.934

Temperature showed a significant negative relationship with bat activity, whilst there was no significant relationship between humidity and bat activity or moon illumination and bat activity (Table 6). From graphically assessing the means, standard deviations and standard errors of environmental conditions across the 21 sampling locations, they were deemed to not vary significantly from one another. Hence, the predictor variables: temperature, humidity and moon illumination were not included in the final model (Appendix D).

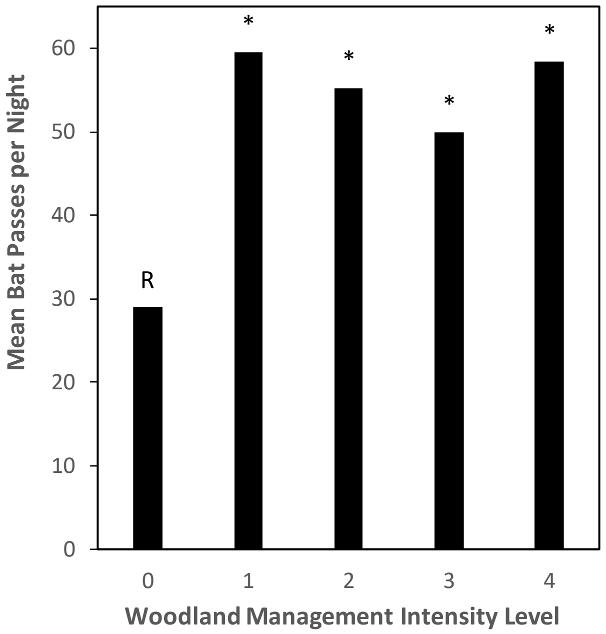

Figure 13 - The mean number of total bat passes per night according to woodland management intensity level (0: non-managed, 4: most intensively managed). (*) indicates a significant difference in bat activity to the reference level (R).

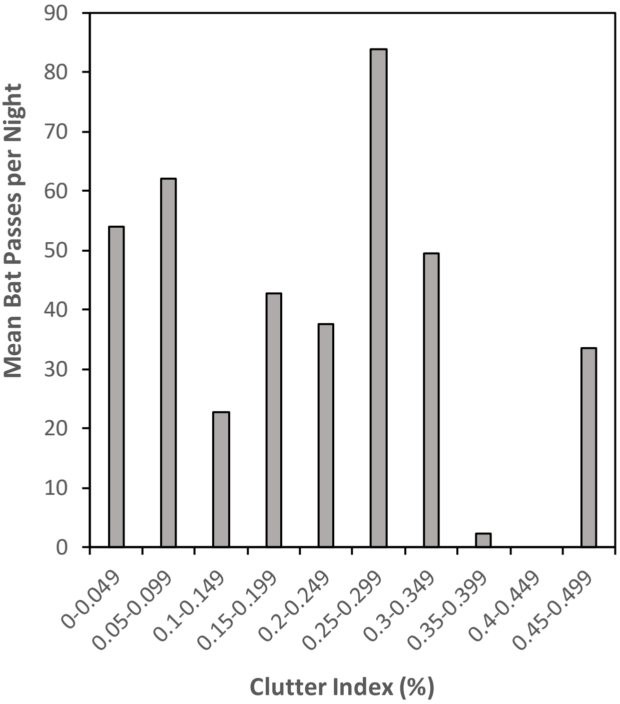

Figure 12 - The mean number of total bat passes per night according to clutter index categories (percentage of sample area occupied by vegetation).

Bat activity levels were significantly higher at woodland management intensity levels one (GLM (n = 8032): Z = 3.108, d.f. = 159, p = 0.002), two (GLM (n = 8032): Z = 3.633, d.f. = 159, p < 0.001), three (GLM (n = 8032): Z = 5.224, d.f. = 159, p < 0.001) and four (GLM (n = 8032): Z = 4.344, d.f. = 159, p < 0.001) than the reference level: non-managed woodland (level zero) (Figure 13). There was a significant positive relationship between total bat activity and clutter index (GLM (n = 8032): Z = 2.089, d.f. = 159, p = 0.037) (Figure 12). There were high levels of bat activity at lower clutter indices between 0 and 0.099, which dropped between 0.01 and 0.0149 before increasing up to between 0.25 and 0.299. Bat activity reached its lowest between 0.35 and 0.449, before increasing again between 0.45 and 0.499. There was no significant overall relationship between total bat activity and: canopy height (GLM (n = 8032): Z = 1.241, d.f. = 159, p = 0.215), canopy gap fraction (GLM (n = 8032): Z = -0.226, d.f. = 159, p = 0.821) or woodland connectivity rating (GLM (n = 8032): Z = 0.163, d.f. = 159, p = 0.870).

3.2.2 Woodland Management Intensity

Key results are reported in this section, see Appendix F for full table of statistical results.

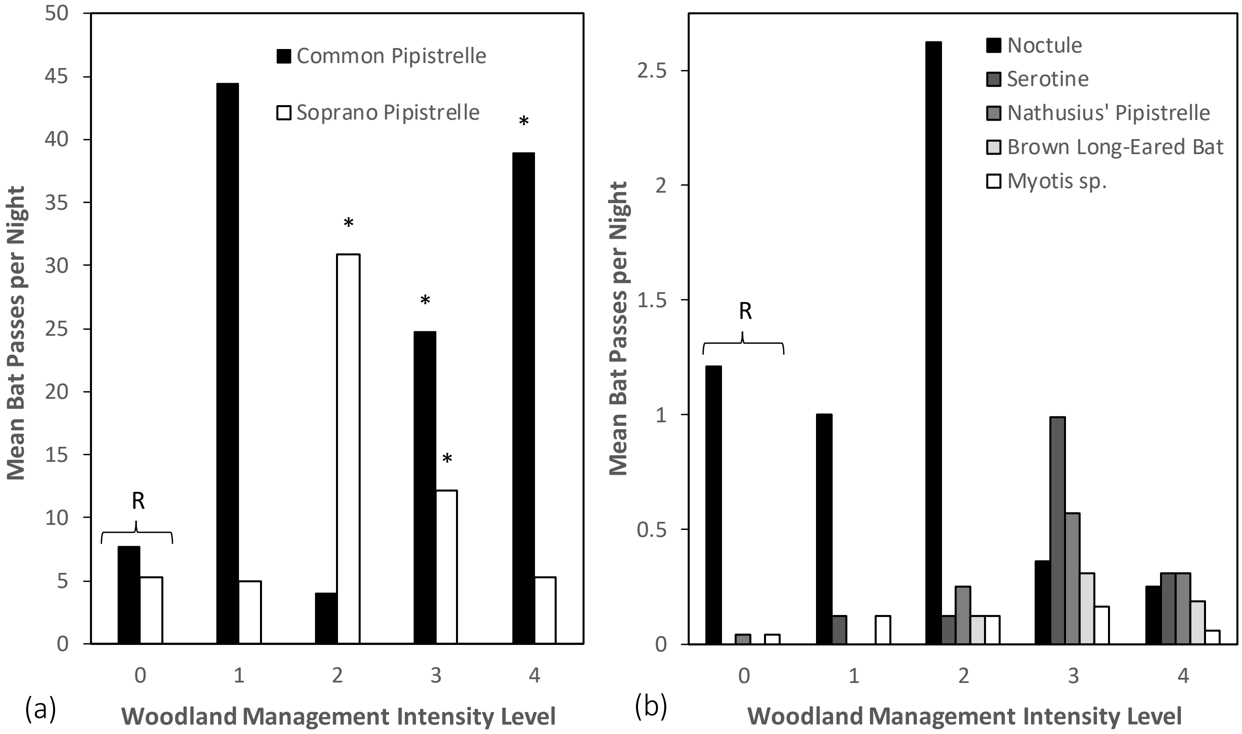

Figure 14 - The mean number of (a) common and soprano pipistrelle passes per night and (b) noctule, serotine, Nathusius' pipistrelle, brown long-eared bat and Myotis species passes per night, according to woodland management intensity level (0: non-managed, 4: most intensively managed). (*) indicates a significant difference in bat activity to the reference level (R).

The highest level of common pipistrelle activity was recorded inside woodland managed to intensity level one, though this result was not statistically significant, perhaps owing to a large variance (Figure 14). There was also a significantly higher level of common pipistrelle activity inside woodland with management levels three (GLM (n = 4194): Z = 2.672, d.f. = 159, p = 0.008) and four (GLM (n = 4194): Z = 2.817, d.f. = 159, p = 0.005) than in non-managed woodland. Soprano pipistrelles exhibited significantly higher levels of activity in woodland of intensity management levels two (GLM (n = 1753): Z = 3.924, d.f. = 159, p < 0.001) and three (GLM (n = 1753): Z = 3.859, d.f. = 159, p < 0.001) than in non-managed woodland.

The results for the other five species were not statistically significant, however noctules were most active in woodland of management level two, whilst serotines, Nathusius' pipistrelles, brown long-eared bats and *Myotis* species were most active in level three. No serotines or brown long-eared bats were found in non-managed woodland, whilst no Nathusius' pipistrelles or brown long-eared bats were found in level two.

3.2.3 Clutter Index

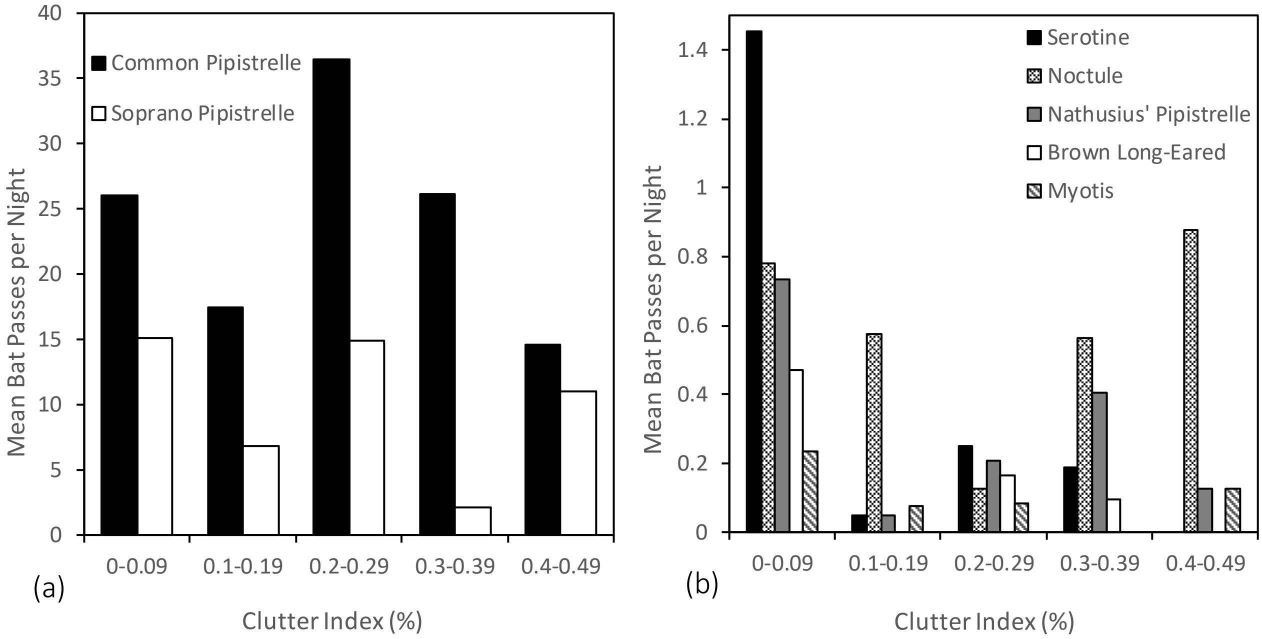

Figure 15 - The mean number of (a) common and soprano pipistrelle passes per night and (b) noctule, serotine, Nathusius' pipistrelle, brown long-eared bat and Myotis species passes per night, according to clutter index (see Section 2.3.2 for equation of calculation). Indices have been divided into categories for interpretation purposes.

Statistically, activity of common pipistrelles had a significant overall positive relationship with clutter index (GLM (n = 4194): Z = 4.268, d.f. = 159, p < 0.001), whilst serotine activity had a significant overall negative relationship with clutter index (GLM (n = 107): Z = -2.784, d.f. = 159, p = 0.005) (Figure 15). No other species had a statistically significant overall relationship with clutter index, however other trends may be observed in the data. Soprano pipistrelles followed a similar trend to common pipistrelles, except their activity was much lower in woodland with clutter indices 0.3-0.39. Noctules had high activity levels at low and high clutter indices, but reduced activity in moderately clutter woodland between 0.2 and 0.29. The Nathusius' pipistrelle followed a similar trend to the other two pipistrelle species, with activity higher in low clutter environments, before dropping between 0.1 and 0.19 then increasing up to 0.39 before dropping again between 0.4 and 0.49.

3.2.4 Canopy Gap Fraction

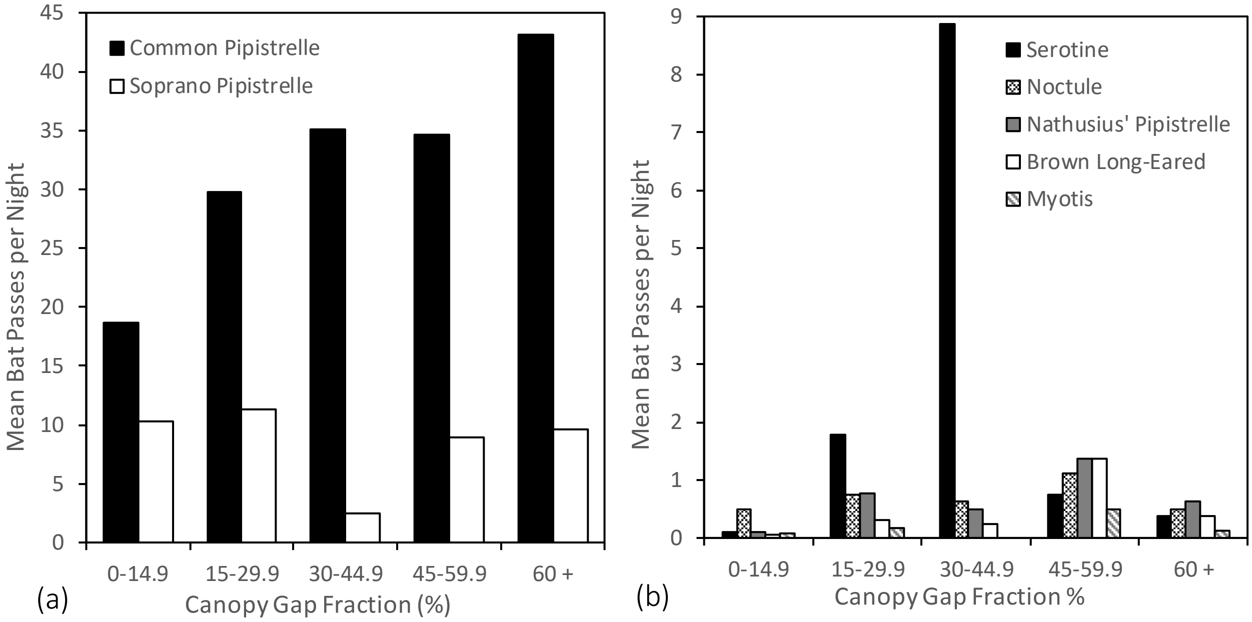

Figure 16 - The mean number of (a) common and soprano pipistrelle passes per night and (b) noctule, serotine, Nathusius' pipistrelle, brown long-eared bat and Myotis species passes per night, according to canopy gap fraction (%).

Statistically, activity of common pipistrelles had a significant overall positive relationship with canopy gap fraction (GLM (n = 4194): Z = 2.937, d.f. = 159, p = 0.003), whilst soprano pipistrelle activity had a significant overall negative relationship with canopy gap fraction (GLM (n = 1753): Z = -0.062, d.f. = 159, p < 0.001). No other species had a statistically significant overall relationship with canopy gap fraction, however other trends may be observed in the data. The highest level of serotine activity was recorded in woodland with medium canopy gap fractions, between 30% and 44.9%. Noctules, Nathusius' pipistrelles, brown long-eared bats and *Myotis* species were most active in woodland with a canopy gap fraction between 45% and 59.9%. There is a potential interaction between serotines, which increase in activity greatly in the 30% to 44.9% gap fraction category, and soprano pipistrelles, whose activity declines in this category.

3.2.5 Understorey Height

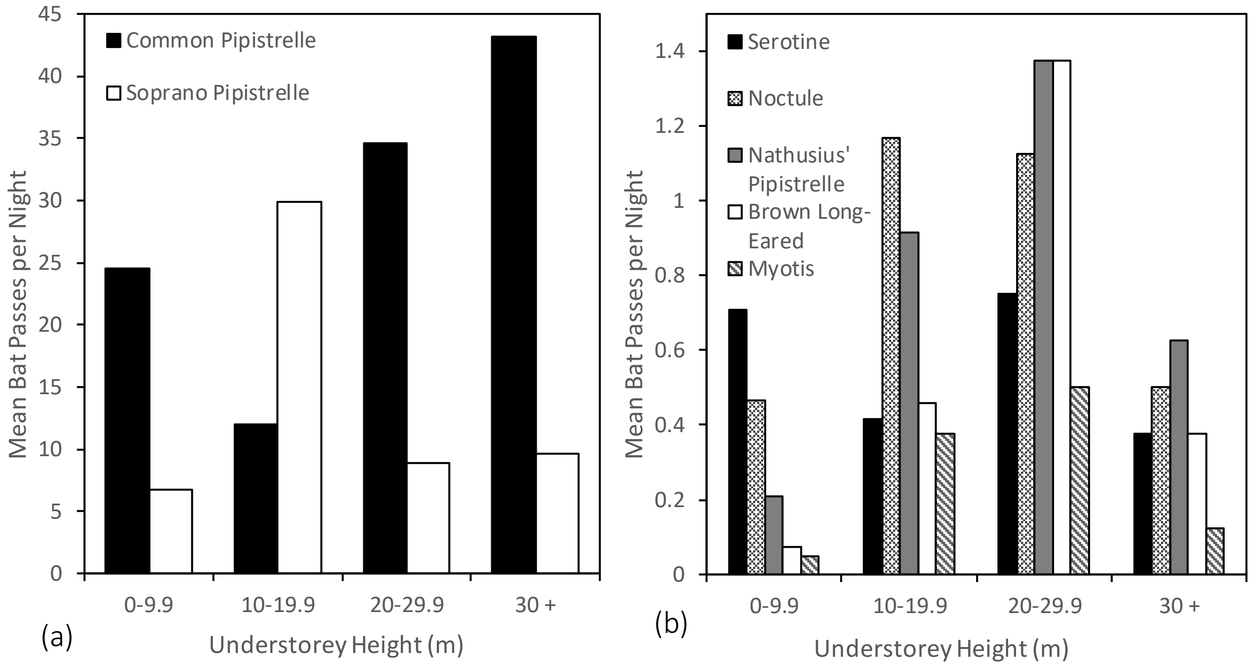

Figure 17 - The mean number of (a) common and soprano pipistrelle passes per night and (b) noctule, serotine, Nathusius' pipistrelle, brown long-eared bat and Myotis species passes per night, according to understorey height (m).

Statistically, activity of soprano pipistrelles (GLM (n = 1753): Z = 7.002, d.f. = 159, p < 0.001) and *Myotis* species (GLM (n = 21): Z = 2.072, d.f. = 159, p = 0.038) had a significant overall positive relationship with understorey height, whilst serotine activity had an overall negative relationship with understorey height (GLM (n = 107): Z = -3.313, d.f. = 159, p < 0.001) (Figure 17). No other species had a statistically significant overall relationship with understorey height, however other trends may be observed in the data. There appears to be a potential interaction between common and soprano pipistrelles at canopy heights between 10 and 19.9 m, as the dominant species changes to soprano pipistrelle in this category, whilst it is common pipistrelles at all other heights. Noctules, Nathusius' pipstrelles and brown long-eared bats were most active between understorey heights of 10 m to 29.9 m, whilst low canopy heights recorded low activity rates of Nathusius' pipistrelles, brown long-eared bats and *Myotis* species.

3.2.6 Connectivity Index

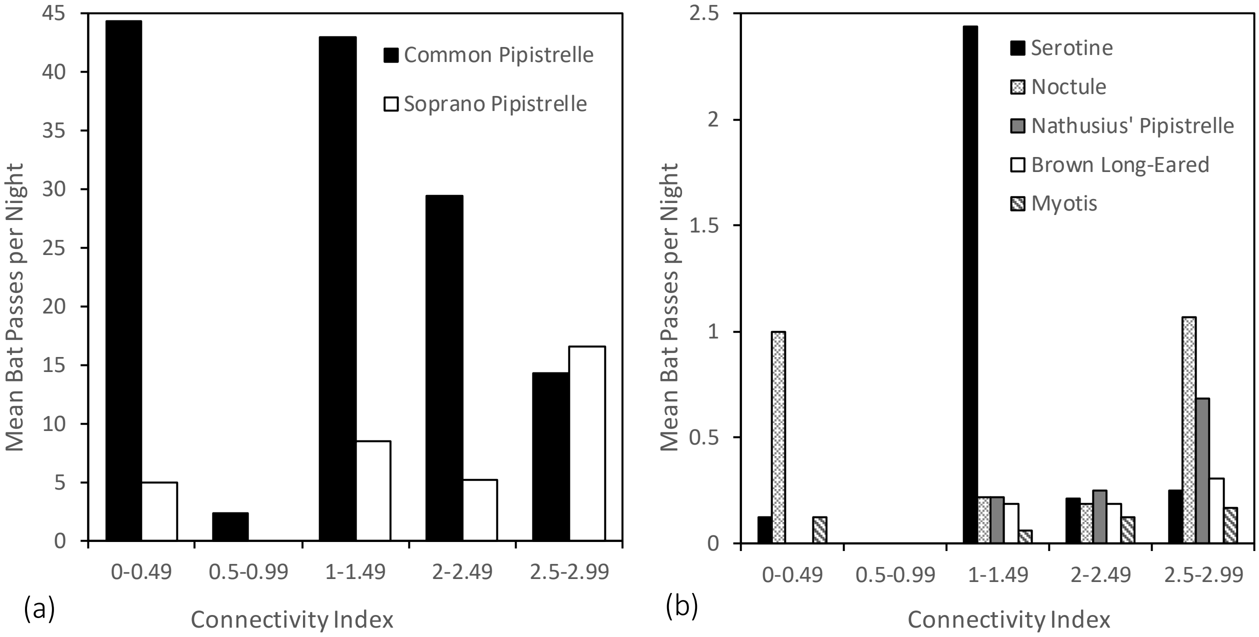

Figure 18 - The mean number of (a) common and soprano pipistrelle passes per night and (b) noctule, serotine, Nathusius' pipistrelle, brown long-eared bat and Myotis species passes per night, according to connectivity index. No sites had a connectivity index between 1.49 and 2.

Statistically, activity of common pipistrelles had a significant overall negative relationship with connectivity index (GLM (n = 4194): Z = -4.085, d.f. = 159, $p < 0.001$) (Figure 18). No other species had a statistically significant overall relationship with connectivity index, however other trends may be observed in the data. Soprano pipistrelles were most active in the more connected woodland blocks, whilst serotines were most active in moderately connected woodland blocks. Little activity across all species was recorded in woodland with connectivity indices between 0.5 and 0.99. No Nathusius' pipistrelles or brown long-eared bats were recorded in woodland below a connectivity index of 1. Noctules were most active at either end of the connectivity scale, between 0 and 0.49, and 2.5 and 2.99.

4 Discussion

The distribution of species recorded follows what would be expected from UK bat surveys, with common pipistrelles constituting the majority of calls. Five of the species recorded are listed as UK BAP (Biodiversity Action Plan) priority species: noctule, soprano pipistrelle, brown long-eared bat, Bechstein's bat and barbastelle (Bat Conservation Trust, 2016b). The latter two are also currently listed as near threatened on the IUCN red list (Paunović, 2016; Piraccini, 2016a), and are listed in Annex II of the Habitats Directive (JNCC, 2016). Hence the results of this study show that the Marwell site and surrounding agricultural landscape are essential in providing important resources to populations of the majority of UK bat species, including those of specific conservation interest. The only two BAP priority species not recorded in this study were the greater and lesser horseshoe bats. This was not unexpected as the site is located at the outskirts of their geographic range (Piraccini, 2016b; Taylor, 2016).

It should be considered that some species may be more easily picked up by a bat detector, such as pipistrelles and large bats with low frequency calls. Quieter calls such as some *Myotis* species or long-eared bats may not have been picked up in the recordings, or may not have been assigned a species ID due to a faint recording. However, the chance of detecting the quieter bats remains even across all sampling locations, hence only the overall counts of bat populations may have been affected, but not the conclusions here drawn.

4.1 Abiotic Conditions

Artificial lighting has been shown to negatively affect the activity of several bat species, including the common pipistrelle and Leisler's bat (Fure *et al.*, 2006; Mathews *et al.*, 2015; Stone *et al.*, 2015). However, artificial lighting was not the cause of positive light intensity readings for this study, instead they are due to the natural light before sunset, where approximately the first 20 minutes of each survey registered positive readings on the lux meter. Since light intensity did not vary across sites, the negative relationship between bat activity and light intensity observed here can be attributed to the natural variation of species emergence times, with many species not emerging until after sunset, including *Myotis* species, long-eared bats and horseshoe bats (Collins, 2016; Duvergé *et al.*, 2000).

Temperature was shown to have a negative relationship with bat activity. This was unexpected as the positive effect of temperature on bat activity is well documented (Bender and Hartman, 2015;

Maier, 1992). However, since fair-weather sampling was implemented throughout data collection, the recorded temperature range was between 10 and 23 ^{0}C, with the higher temperatures corresponding to recordings earlier in the evening. Hence, it is possible that an interaction between temperature and time occurred, leading to the peak activity time later in the evening being associated with lower temperatures. As shown in this study, increased relative humidity has previously been shown to be associated with increased bat activity levels of some species (Lacki, 1984), but only up to a certain level as echolocatory calls become compromised following the atmospheric attenuation of high frequency sounds that occurs at higher humidities (Griffin, 1971).

The negative impact of background noise on bat activity is also well documented. For example, for passive listening bats such as *Myotis* species, traffic noise, vegetation noise and broadband computer-generated noise caused a repellent effect (Schaub *et al.*, 2008). It has also been shown that loud noise produced by machinery can reduce bat activity by up to 70% in bat species with low frequency calls (Bunkley *et al.*, 2015). In this study, the majority of louder background noise readings were caused by aeroplanes flying over the site, either flying out or returning to Southampton Airport. Hence an interesting effect has been recorded here, since no significant research investigating the impact of airports on bat calls is presently available. Since bat calls were recorded before and after the aeroplane noise, it appears bats withhold echolocation calls if there is significant background noise where possible.

Less sheltered waypoints with higher wind speeds led to reduced bat activity. This can partly be explained by the reduction of insect activity occurring in high winds (Peng *et al.*, 1992), and also by the alterations in flight behaviour that high wind speeds can lead to, including a reduction in the distance travelled from tree lines (Verboom and Spoelstra, 1999). This highlights the importance of shelter for bats, provided by different configurations and orientations of woodland edges to provide pathways and foraging locations without strong winds, such as for serotines (Robinson and Stebbings, 1997).

A negative relationship between bats and lunar illumination has previously been documented (Lang *et al.*, 2006), whilst no effect was observed in this study. In Canada, bats were shown to not reduce their activity, but to alter habitat foraging between vertical forest levels, based on spatial structure and degree of light penetrating the canopy (Hecker and Brigham, 1999).

4.2 Woodland Management Intensity

The responses of total bat passes to both increased woodland management intensity and land use type follow the same trend shown by the common pipistrelle, as this was by far the most abundant species. The overall lack of relationship between total bat passes and connectivity rating implies that it is not the most important feature of woodland habitats for bat activity. However, it is also possible that woodland connectivity is an important feature for some species, but that those effects are masked by indifferent responses of other species to connectivity rating. It is difficult to make suggestions for conservation management based on these results alone, as the effects of landscape indicators on individual species are hidden by the response of the common pipistrelles, which are a generalist bat species capable of exploiting a variety of woodland habitats (Davidson-Watts and Jones, 2006; Vaughan *et al.*, 1997). Hence, due to the likelihood of a wide range of interspecific differences in foraging technique, site selection and response to disturbance, results will be interpreted at the species level. This will provide the most informative evidence on which management recommendations can be made to suit the requirements of each species.

With the exception of common pipistrelles and *Myotis* species, all bats species showed higher activity levels along non-managed woodland edge as opposed to managed woodland edge. Some species were particularly negatively affected by increased woodland management intensity, with noctules showing very low levels of activity inside woodlands of management intensity categories above two. Noctules show a strong preference for roosting in old woodland stands, aged over 100 years, and avoidance of young forest stands (Mackie, 2002; Ruczyński *et al.*, 2010). Since there is low availability of this preferred woodland type in the near vicinity of the level four managed land at Roughay Farm, the vast reduction in noctule activity in intensively managed woodlands could be in part attributed to this. However it does not explain why management level three woodland also exhibited significantly lower noctule activity levels. Following the birth of young in late June and July (Bat Conservation Trust, 2010b), lactating females avoid foraging in marginal habitat, such as agricultural land (Mackie, 2002), perhaps adding to the explanation for the reduction in noctule activity. Since the reduced activity of noctules on intensively managed land is not well documented, these findings could represent new information. Suggestions for alterations to woodland management include leaving areas of old forest untouched in order to maintain suitable roosting sites for noctules and other species which show roosting preference in this woodland type, including the barbastelle (Russo *et al.*, 2004) and Bechstein's bat (Dietz and Pir, 2009).

Whilst this study did not find significant predictors of brown long-eared activity, coppicing practices and woodland grazing have been shown to negatively impact the species (Murphy *et al.*, 2012). The study suggested management strategies to suit brown long-eared habitat preferences: maintenance of native species cover in understorey layer and hedgerows to provide a degree of connectivity between woodland blocks.

Noctules and Leisler's bats are known to mostly forage in the open (Rachwald, 1992; Vaughan *et al.*, 1997; Waters *et al.*, 1999), with Leisler's typically selecting roosts in more open areas with low tree density (Spada *et al.*, 2008). The conservation field at the Marwell site was of particular importance to these species, recording their highest levels of activity. This supports the suggestion for the implication of reduced intensity land practices (Lentini *et al.*, 2012; Robinson and Stebbings, 1997), but more realistically, to include areas of open land with minimal management within the landscape, balanced with a variety of land uses. The installation of buffer zones along woodland edges could suit this purpose, providing suitable foraging habitat for species which prefer to forage in the open and along woodland edges.

Conversely, common pipistrelles were not negatively affected by increased management intensity. There was significant common pipistrelle activity across all woodland edge management categories, with the exception of level two, with their woodland edge activity highest adjacent to the most intensively managed woodland. The lower level of activity at woodland edge waypoints of management level two corresponds with an increase in activity of soprano pipistrelles. This may imply a level of competition or avoidance between the two species. The common pipistrelle is slightly larger than the soprano pipistrelle, and is capable of pursuing a more diverse and potentially larger range of prey (Rachwald *et al.*, 2016). The soprano also shows stronger preference for riparian habitats, typically travelling further than the common pipistrelle to reach specific foraging sites (Davidson-Watts and Jones, 2006; Lisón and Calvo, 2013), whilst the common pipistrelle is more of a generalist, travelling to more foraging sites per evening, but across wider range of habitat types (Vaughan *et al.*, 1997).

Hence the common pipistrelle usually holds competitive advantage over the soprano pipistrelle in habitats other than riparian. In this study, the displacement of common pipistrelles by sopranos at sites both at the woodland edge and inside woodland blocks of woodland management level two were all situated near to Fisher's Pond (between 0.6 and 1.2 kilometres) or inside the zoo, where there are water sources within animal enclosures and near the main entrance.

Furthermore, the highest level of soprano pipistrelle activity at the woodland edge was near non-managed woodland, of which a large proportion of the waypoints were located along the eastern edge of Horsham Copse, which faces the African Valley lake inside the zoo. Hence an important predictor of soprano pipistrelle activity was proximity to water sources, and the foraging activity of this species appears to have led to a decrease in common pipistrelle activity in these areas. This effect is also present when categorised by land use type, with high activity levels of soprano pipistrelles on human use land and in the zoological park being associated with lower common pipistrelle activity and corresponding to two of the same sites in close proximity to Fisher's Pond.

The increases in soprano pipistrelle activity inside woodland of management ratings two and three, along with serotine and Nathusius' pipistrelle activity in level three woodland, could also be attributed to the structural profile of these habitats. Woodland in this category is mostly located at the Marwell site, where woodland management is of conservation intent with the aim to enhance sites for biodiversity (Parker *et al.*, 2010). Increases in invertebrate abundance may also be present in these woodlands due to the thinning of mature oak and ash trees to increase light to ground level flora. Indeed, one of the key predictors of habitat use by serotines are shifts in prey availability (Robinson and Stebbings, 1997). This combined with the diversification of woodland structure through coppicing is likely to provide suitable foraging sites for bats. Hence, the specific quantitative structural measurements of inner woodland sites were considered as predictors.

4.3 Structural Characteristics

High levels of total bat activity were recorded in uncluttered environments, which is supported by the fact that all species were physiologically capable of foraging in these areas, including large bats. Low to mid-levels of clutter had lower bat activity as some species begin to lose their ability to fly in these conditions, such as noctules (Brigham *et al.*, 1997; Rachwald, 1992; Waters *et al.*, 1999). The peak of total bat activity was in moderately cluttered environments, which was caused by the increase in common pipistrelle activity in these areas and was likely due to the competitive advantages presented by their fast and manoeuvrable flight (Norberg and Rayner, 1987). Activity tailed off for most species at the highest clutter indices, with the exception of *Myotis* species and noctules. *Myotis* species and long-eared bats are able to forage in cluttered environments (Fuentes-Montemayor *et al.*, 2013), and can reduce foraging flight costs and increase insect encounter rate by exploiting areas where insects accumulate, such as inside dense woodland or on the leeward side of woodland copses (Aldridge and Rautenbach, 1987). Hence the practice of clearing some large trees to allow penetration of light through the canopy should be carried out to allow growth of the herb layer in some areas, providing that large trees with high roost suitability are not removed.

The presence of noctules in highly cluttered habitat was unexpected and is incongruous with previous findings for noctules foraging behaviour, large morphology and low frequency calls which make large bats less adept at manoeuvrable flight and acoustic fine-tuning (Brigham *et al.*, 1997; Rachwald, 1992; Vaughan *et al.*, 1997; Waters *et al.*, 1999). It is likely that the noctules recorded in these highly cluttered environments were actually flying over the woodland, either to forage above the canopy or through travel to foraging sites. Serotines showed preference for the lowest category of woodland clutter and were infrequently recorded in more cluttered environments. This is the trend which would have been expected for noctules. Both species have low frequency calls, enabling them to forage for prey above woodland and over long distances (Vaughan *et al.*, 1997). Similarly, serotines showed a negative relationship with canopy height which was again an unexpected result, as they typically forage in open environments like noctules (Park, 2015). Hence, this may also be explained by serotines flying over the canopy being picked up on the recordings, due to the lower height of the canopy and far-reaching low frequency calls. This effect has also been observed in Canada, where an increase in the activity of three large bat species was recorded in artificially enhanced cluttered environments, the result of which was eventually attributed to an artefact of study design, as is likely present in these findings (Brigham *et al.*, 1997).

Conversely, common pipistrelles showed higher activity in more cluttered environments. All pipistrelle species have been shown to alter their echolocation calls as a response to different habitats, including the production of calls with wider bandwidths of up to 15 kHz to aid manoeuvrability in cluttered environments (Kalko and Schnitzler, 1993). Hence pipistrelles are able to successfully forage in a complex habitat type, displacing other species which avoid of navigating cluttered environments where foraging costs are higher than in less cluttered environments.

Common pipistrelles also showed increased activity in woodland areas with a larger canopy gap fraction. This finding is supported by a study by two studies which found common pipistrelles preferred an open understorey(Fuentes-Montemayor *et al.*, 2013; Kusch *et al.*, 2004). However, their results contradict the findings in this study for soprano pipistrelles, also aerial hawkers, which were more active in woodland with a more closed and high canopy. This may be a result of interspecific competition leading to displacement of soprano pipistrelles, or could imply that soprano pipistrelles are well suited to woodland habitat with a high degree of shelter and space, as they are a low mobility species (Fuentes-Montemayor *et al.*, 2013). Aerial hawking species are more constrained to forage earlier in the evening before complete darkness, when their small Dipteran prey is at peak abundance or just beginning to decline, whilst gleaning species such as the brown long-eared bat and *Myotis* species are able to forage whilst their prey base of moths and non-flying insects is increasing, approximately an hour after sunset. Hence, aerial hawkers are at more risk of predation during foraging, and can benefit from increased tree cover to permit earlier emergence and foraging (Rydell *et al.*, 1996), implying the maintenance of this feature in some woodland areas is important. This feature appears to be of less importance to the more generalist common pipistrelle.

Myotis species showed higher levels of activity in woodland with higher canopies. Perhaps protection provided by a low canopy is of less importance to these species as they begin to forage after dark (Rydell *et al.*, 1996), and preference is shown for habitats with space for more shrubs and vegetation beneath the canopy associated with higher insect densities.

4.4 Land Use

Land designated as human use showed a significant level of soprano pipistrelle and serotine activity along the woodland edge, which is supported by evidence of these two species travelling along woodland edge features (Lesiński *et al.*, 2011; Park, 2015; Robinson and Stebbings, 1997). After dark, the road and car parks which constituted the human use land in this study would have been very quiet, with minimal light or noise pollution from vehicles, which are known to negatively affect bat activity (Bunkley *et al.*, 2015; Fure *et al.*, 2006; Mathews *et al.*, 2015; Schaub *et al.*, 2008).

However, the lowest level of common pipistrelle activity was recorded on human use land, possibly indicating that this species preferred to utilise habitats with fewer urbanised features and more natural land covering. Alternatively, the result is indicative of the displacement and interspecific competition between the two pipistrelle species discussed previously. No *Myotis* species were recorded on human use land, implying they tend to avoid using developed land. This finding is supported by a study by Vaughan *et al.* (Vaughan *et al.*, 1997), which found *Myotis* species utilised nine out of ten land types, excluding villages.

Only two groups were recorded in livestock fields: soprano pipistrelles and *Myotis* species. In fact, this land use recorded the highest level of *Myotis* activity across the whole site. This could be a result of a drawback of the study methods, since the majority of waypoints along livestock fields were situated just inside a woodland ride as it was not possible to gain land access inside the fields. Hence the high *Myotis* activity can most likely be attributed to their affinity for foraging in cluttered woodland with high vegetation volumes. It also explains the absence of other species which are unable to forage in cluttered environments (see Structural Characteristics), since serotines for example are known to forage along the edge of grazed pasture due to increased insect density caused by dung (Robinson and Stebbings, 1997).

Foraging opportunities can also be gained from arable land by aerial hawkers including pipistrelle species and serotines (Davidson-Watts and Jones, 2006; Robinson and Stebbings, 1997), which showed high activity levels on agricultural land in this study. Roughay Farm used manure to fertilise fields, with piles left alongside fields for a number of weeks prior to application, providing a novel foraging opportunity. Intensively managed coffee plantations in Mexico have also been identified as suitable foraging habitats for insectivorous bat species (Williams-Guillén *et al.*, 2011).

4.5 Connectivity

Higher connectivity ratings predicted increased activity by serotines and soprano pipistrelles. Serotines have previously been shown to prefer to travel along tree lines, hedgerows and woodland edges (Robinson and Stebbings, 1997), whilst it is not thought to be a main predictor of serotine activity as they tend to travel large distances foraging over open habitats (Park, 2015). Soprano pipistrelles are known to prefer to travel along woodland corridors (Park, 2015), and it has been identified that habitat loss and fragmentation leads to two issues: firstly it leads to an increase in the cost of commuting, and secondly to reduced travel away from their home ranges due to overlapping territories and potential conflicts and competition with neighbouring territories.

On the other hand, common pipistrelle activity actually declined with increased woodland connectivity. It has been suggested that this phenomenon may be explained by more intensive usage by bats of isolated woodland in locations where this habitat type is not abundant (Fuentes-

Montemayor *et al.*, 2013). The generalist common pipistrelle may therefore be able to exploit isolated woodland blocks which other species frequent less often. It should also be kept in mind that the woodland in the study site is relatively well connected to the surrounding landscape. Hence, the woodland with the lowest connectivity rating was not completely isolated within the habitat, and results may have been different if blocks with very low connectivity ratings were included. In an urban environment connectivity of tree lines has been identified as an important factor in the resilience of some bat species (Hale *et al.*, 2012). This suggests that maintaining woodland corridors and hedgerows in agricultural environments is essential to the longevity of bat species in these environments.

An essential element in the adaptation of land management in accordance with bat conservation is the education of landowners. It has been identified that many landowners are not aware of bats using their land (Lentini *et al.*, 2012), hence the dissemination of information advising landowners of the likely usage of their land by bats, as well as actions which can be taken to support these bat populations should be implemented.

4.6 Further Research

The next steps for this research would be to assess the degree of impact of these landscape characteristics and structures at increasing distances from the recording sites. The aim would be to ascertain the wider impact of woodland management practices on bat activity, as well as to investigate the effect of proximity to landscape features, such as water sources and towns. Whilst implications of the relationship between common and soprano pipistrelles have been made here, further analysis using these results to investigate the impact of the presence of certain species on the presence of others could also yield valuable information in land management.

A drawback of this study is that it does not take into account the different types of habitat use by bats, through foraging, locomotory behaviour or roosting. Information on insect communities within the landscape combined with records of feeding buzzes performed by different bat species could also provide valuable insight into their distribution and habitat preferences.

4.7 Conclusion

The reported results suggest that a high degree of habitat heterogeneity is essential for insectivorous bat conservation, as different species are better suited to foraging in different environments. Areas of old growth trees should be left undisturbed, combined with other areas of woodland managed to suit individual bat species preferences. A mixture of areas of habitat with open canopy and less clutter for bats with less manoeuvrable flight, combined with areas containing higher vegetation density created through hazel coppicing and clearance of larger trees to allow penetration of light to the herb layer, should be maintained to be suitable for foraging by gleaning bats. Proximity to water sources is also essential for soprano pipistrelles, although this is a more complex management solution to implicate. It is also necessary for areas with low or no management to exist, combined with buffer strips along the edges of more intensively managed woodland, to provide suitable foraging habitat for noctules and serotines. The maintenance of connecting tree lines and hedgerows is also important for species such as the soprano pipistrelle.

Woodlands managed intensively for profit at Roughay Farm provided an important foraging site for certain species, however a lower abundance of species was present at this site. Hence, management practices should be kept in line with the above suggestions, striving to achieve heterogeneous habitats and avoiding woodland monoculture which may be unsuitable to several bat species. On the other hand, the woodland at the Marwell site which is managed with conservation intent supported a wide range of species, including those listed as near threatened on the IUCN Red List. Implementation of the management recommendations above could potentially increase site suitability for bats even further.

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6 Appendices

6.1 Appendix A

Table 7 - Kolmogorov-Smirnov goodness of fit tests for woodland edge statistical models

Model	D value	P value
All bats	0.040	0.227
Common Pipistrelle	0.034	0.386
Soprano Pipistrelle	0.042	0.176
Serotine	0.035	0.368
Noctule	0.044	0.128
Myotis spp.	0.032	0.493
Leisler's	0.092	0.105

6.2 Appendix B

Table 8 - Kolmogorov-Smirnov goodness of fit tests for inner woodland statistical models

Model	D value	P value
All bats	0.059	0.612
Common Pipistrelle	0.051	0.830
Soprano Pipistrelle	0.088	0.251
Nathusius' Pipistrelle	0.144	0.396
Serotine	0.178	0.261
Noctule	0.164	0.100
Brown Long-Eared	0.239	0.109
Myotis spp.	0.080	0.229

6.3 Appendix C

*Table 9 - Results from negative binomial GLM (d.f = 689) assessing relative predictors of total bat activity at woodland edges. Reference levels: Level 0 (non-managed woodland), and human use land. Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

Predictor Variables	**Estimate**	**Std. Error**	**Z Value**	**P value**
Woodland Management Intensity				
1	-0.706	0.315	-2.238	0.025 *
2	-0.924	0.237	-3.904	< 0.001 ***
3	-0.667	0.250	-2.666	0.008 **
4	-0.147	0.268	-0.549	0.583
Land Use				
Agricultural Field	0.506	0.218	2.315	0.021 *
Conservation Field	-0.109	0.312	-0.349	0.727
Livestock Field	0.298	0.287	1.036	0.300
Zoological Park	0.215	0.234	0.919	0.358
Connectivity	-0.140	0.202	-0.693	0.488

6.4 Appendix D

*Table 10 - Results from negative binomial GLM (159 d.f) assessing relative predictors of total bat activity inside woodland blocks. Reference level: Level 0 (non-managed woodland). Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

Predictor Variables	Estimate	Std. Error	Z Value	P value
Under Canopy Height	0.031	0.025	1.241	0.215
Clutter Index	1.277	0.611	2.089	0.037 *
Canopy Gap Fraction	-0.002	0.009	-0.226	0.821
Connectivity	0.018	0.111	0.163	0.870
Woodland Management Intensity				
1	1.379	0.444	3.108	0.002 *
2	1.335	0.368	3.633	< 0.001 *
3	1.150	0.220	5.224	< 0.001 *
4	1.169	0.269	4.344	< 0.001 *

6.5 Appendix E

*Table 11 – Results from negative binomial GLMs (d.f. = 686) indicating relative predictors of bat activity per species at woodland edges. Reference levels: Level 0 (non-managed woodland), and human use land. Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. NA indicates absence of bat recordings in that category.*

Common Pipistrelle	Predictor Variables	Estimate	Std. Error	Z Value	P value
(n = 1489)	Habitat Management Rating				
	1	-0.366	0.360	-1.016	0.310
	2	-0.888	0.271	-3.281	0.001 **
	3	-0.432	0.286	-1.512	0.130
	4	0.153	0.305	0.500	0.617
	Land Use				
	Agricultural Field	0.819	0.258	3.170	0.002 **
	Conservation Field	-0.131	0.367	-0.358	0.721
	Livestock Field	0.557	0.330	1.688	0.091 .
	Zoological Park	0.692	0.275	2.514	0.012 *
	Connectivity	-0.362	0.226	-1.605	0.108
Soprano Pipistrelle	Habitat Management Rating				
(n = 213)	*1*	-1.126	0.758	-1.485	0.138
	2	-0.354	0.554	-0.639	0.523
	3	-1.364	0.637	-2.140	0.032 *
	4	0.387	0.741	0.524	0.601
	Land Use				
	Agricultural Field	0.662	0.610	1.085	0.278
	Conservation Field	0.827	0.964	0.858	0.391
	Human Use	0.484	0.721	0.671	0.502
	Zoological Park	0.491	0.788	0.623	0.533
	Connectivity	1.923	0.902	2.131	0.033 *
Serotine	Habitat Management Rating				
(n = 114)	*1*	-1.857	0.774	-2.398	0.017 *
	2	-1.782	0.607	-2.936	0.003 **
	3	-0.421	0.641	-0.657	0.511

	4	-0.403	0.713	-0.565	0.572
	Land Use				
	Agricultural Field	2.205	0.846	2.608	0.009 **
	Livestock Field	NA	NA	NA	NA
	Human Use	2.518	0.832	3.028	0.002 **
	Zoological Park	0.926	0.707	1.310	0.190
	Connectivity	2.031	0.965	2.105	0.035 *
Noctule *(n = 25)*	Habitat Management Rating				
	1	NA	NA	NA	NA
	2	-0.969	0.842	-1.151	0.250
	3	-2.551	1.041	-2.451	0.014 **
	4	-2.334	1.155	-2.021	0.043 *
	Land Use				
	Human Use	-0.921	0.749	-1.230	0.219
	Conservation Field	0.072	0.871	0.083	0.934
	Livestock Field	NA	NA	NA	NA
	Zoological Park	-0.582	0.715	-0.814	0.416
	Connectivity	0.536	0.918	0.584	0.559
Myotis spp. *(n = 25)*	Habitat Management Rating				
	1	-0.246	1.516	-0.162	0.871
	2	-0.262	1.093	-0.240	0.811
	3	-0.208	1.141	-0.182	0.855
	4	-0.437	1.251	-0.349	0.727
	Land Use				
	Agricultural Field	0.635	1.476	0.430	0.667
	Livestock Field	2.403	1.659	1.448	0.148
	Human Use	NA	NA	NA	NA
	Zoological Park	0.732	1.273	0.575	0.565
	Connectivity	-0.306	0.821	-0.372	0.710

6.6 Appendix F

*Table 12 - Results from negative binomial GLMs (d.f. = 159) indicating relative predictors of bat activity per species inside woodland blocks. Reference level: Level 0 (non-managed woodland). Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1. NA indicates absence of bat recordings in that category.*

	Predictor Variables	Estimate	Std. Error	Z Value	P value
Common Pipistrelle *(n = 4194)*	*Canopy Height*	-0.027	0.027	-1.002	0.316
	Clutter Index	2.951	0.691	4.268	< 0.001 *
	Canopy Gap Fraction	0.030	0.010	2.937	0.003 *
	Connectivity	-0.565	0.138	-4.085	< 0.001 *
	Woodland Management Intensity				
	1	0.448	0.529	0.846	0.398
	2	-0.277	0.447	-0.620	0.535
	3	0.735	0.275	2.672	0.008 *
	4	0.899	0.319	2.817	0.005 *
Soprano Pipistrelle *(n = 1753)*	*Canopy Height*	0.211	0.030	7.002	< 0.001 *
	Clutter Index	1.458	0.850	1.714	0.086
	Canopy Gap Fraction	-0.062	0.011	-5.566	< 0.001 *
	Connectivity	0.187	0.151	1.241	0.215
	Woodland Management Intensity				
	1	0.501	0.581	0.862	0.389
	2	1.663	0.424	3.924	< 0.001 *
	3	1.121	0.290	3.859	< 0.001 *
	4	-0.275	0.381	-0.722	0.470
Nathusius’ Pipistrelle *(n = 68)*	*Canopy Height*	0.116	0.062	1.877	0.061
	Clutter Index	2.271	2.105	1.079	0.281
	Canopy Gap Fraction	-0.020	0.013	-1.530	0.126
	Connectivity	0.065	0.349	0.186	0.853
	Woodland Management Intensity				

	1	NA	NA	NA	NA
	2	0.752	1.474	0.510	0.610
	3	1.251	1.166	1.073	0.283
	4	-0.236	1.327	-0.178	0.859
Serotine *(n = 107)*	*Canopy Height*	-0.147	0.044	-3.313	< 0.001 *
	Clutter Index	-6.497	2.334	-2.784	0.005 *
	Canopy Gap Fraction	0.024	0.014	1.681	0.093
	Connectivity	-0.204	0.328	-0.621	0.535
	Woodland Management Intensity				
	1	NA	NA	NA	NA
	2	0.019	1.729	0.011	0.991
	3	1.134	1.205	0.941	0.346
	4	1.495	1.243	1.202	0.229
Noctule *(n = 101)*	*Canopy Height*	-0.062	0.049	-1.278	0.207
	Clutter Index	-0.875	1.040	-0.841	0.404
	Canopy Gap Fraction	0.020	0.014	1.430	0.159
	Connectivity	0.177	0.301	0.587	0.560
	Woodland Management Intensity				
	1	0.331	0.858	0.386	0.702
	2	0.457	0.330	1.386	0.172
	3	-0.146	0.302	-0.484	0.631
	4	-0.302	0.910	-0.332	0.741
Brown Long-Eared *(n = 37)*	Canopy Height	0.080	0.085	0.941	0.347
	Clutter Index	0.335	2.331	0.144	0.886
	Canopy Gap Fraction	< 0.001	0.016	0.015	0.988
	Connectivity	-0.163	0.486	-0.336	0.737
	Woodland Management Intensity				
	1	NA	NA	NA	NA

	2	NA	NA	NA	NA
	3	0.133	1.121	0.119	0.906
	4	-1.698	1.897	-0.895	0.371
Myotis spp. *(n = 21)*	*Canopy Height*	0.207	0.100	2.072	0.038 *
	Clutter Index	-2.307	3.214	-0.718	0.473
	Canopy Gap Fraction	-0.035	0.023	-1.488	0.137
	Connectivity	0.155	0.582	0.266	0.790
	Habitat Management Intensity				
	1	1.073	2.056	0.522	0.602
	2	0.025	1.539	0.016	0.987
	3	0.589	1.202	0.490	0.625
	4	-2.647	2.085	-1.270	0.204