Altitudinal effects on habitat selection in two sympatric pipistrelle species

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Abstract

Altitude can profoundly influence the distribution of mammals, although the majority of studies of altitudinal impacts on distribution and abundance examine large-scale effects in mountainous environments. We investigate the potential for altitudinal effects on within-habitat distribution in common and soprano pipistrelle bats (*Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*) over relatively small scales on the Isle of Man, an island with a maximum altitude of 620 m above sea level. Whilst we found no differences in habitat or altitude usage between the two species, both showed a sharp decline in activity with small increases in altitude within all habitats. This decline was steepest in deciduous and conifer woodland, and more gradual in arable and heathland. Activity also declined more quickly with increasing altitude in the centre of habitats compared to the edge, and where water was present compared to where water was absent. We suggest that altitude may limit distribution independent of habitat, and thus is an important factor to take into account, in combination with habitat, when designing mammalian conservation strategies.

Keywords: Altitude; conservation; habitat; *Pipistrellus pipistrellus*; *Pipistrellus pygmaeus*.

Introduction

Altitude can profoundly influence the distribution of mammals, although the majority of studies of altitudinal impacts on distribution and abundance examine large-scale effects in mountainous environments. In these environments, species richness and abundance of both volant and non-volant mammals can either decrease with increasing altitude or, in some environments, form a peak at mid-elevations (e.g. Hunter and Yonzon 1993; Geise et al 2004; McCain 2007). This mid-elevation peak can be caused by the overlap of species adapted to high and low altitudes (Pyrcz and Wojtusiak 2002), although in bats, where both mid-elevation peaks and declines in abundance with increasing altitude are found, patterns of altitudinal variation in abundance depend on the local climatic context (McCain 2007). In this case, peaks in abundance are tightly linked to water availability, with mid-elevation peaks found on mountains with dry bases, and declines in abundance with increasing altitudes on mountains with wet bases (McCain 2007).

The associations between altitude and bat abundance are thought to be due to a combination of temperature, influencing thermoregulatory constraints, and water and habitat, influencing food resources (Cryan et al. 2000; McCain 2007). Altitude influences prey availability, which tends to decrease with increasing altitude (Wolda 1987; McCoy 1990; but see also Stoneburner, 1977), and upper altitudes can tend to be characterised by elevationally widespread generalists (Moreira et al. 2009).

Knowledge of the ecological differences between morphologically similar species is important in understanding the ecological requirements and evolution of sympatric species, as well as the design and implementation of conservation strategies. The common and soprano pipistrelle, *Pipistrellus pipistrellus* (Schreber, 1774) and

Pipistrellus pygmaeus (Leach, 1825), were recognised as separate species in 1993, and are distinguished by differing echolocation call frequencies (Jones and van Parijs 1993), social calls (Barlow and Jones 1997) and gross morphology (Jones and van Parijs 1993). Following molecular confirmation (Barratt et al. 1997) several studies have examined ecological differences between the species, finding differences in diet (Barlow 1997) and foraging habitat (Vaughan et al. 1997a; Russ et al. 2003) that suggest *P. pygmaeus* specialises more in wetland habitats than *P. pipistrellus*, which is more of a generalist (Barlow 1997; Vaughan et al. 1997a). More recent studies have also found *P. pipistrellus* to have larger home and foraging range sizes than *P. pygmaeus* (Davidson-Watts and Jones 2006; Nicholls and Racey 2006a; Nicholls and Racey 2006b).

Dietary differences between species may affect altitudinal distribution through a differential distribution of preferred insects, with species reliant upon aquatic invertebrates restricted to lower elevations (Graham 1990), or alternatively, altitude may influence the distribution of both species through a reduced diversity and abundance of invertebrates at higher altitudes (Jacobsen et al. 1997). This, along with the larger foraging ranges of *P. pipistrellus* (Nicholls and Racey 2006a) may lead to the expectation that this species would use a wider range of altitudes and habitats than *P. pygmaeus* (Warren et al., 2000)

Different species are adapted to different ‘optimum’ altitudes across a broad altitudinal range (Sanchez-Cordero 2001), but any altitudinal effects on a smaller scale tend to be overlooked in studies of habitat usage by mammals. Here, we investigate firstly, whether altitude is a significant factor affecting the distribution of either *P. pipistrellus* or *P. pygmaeus*; and secondly, whether altitude is merely a confounding factor in determining habitat availability and therefore influencing distribution, or whether altitude per se is important in limiting distribution and should therefore be taken into consideration when designing and implementing mammalian conservation strategies.

Materials and methods

Sites

Transects were located on the Isle of Man, an island covering 572 km sq located in the northern part of the Irish Sea with a maximum altitude of 620 m above sea level (between latitude 54˚4 'N and 54˚22 'N longitude 4˚20 'W and 4˚50 'W). Forty-two transects spanning six broad habitat types (detailed in Table 1) and altitudes between 0 and 400 m above sea level were walked once between June and September 2003 to monitor bat activity. Transects were selected to cover as broad a range of habitats and altitudes as possible. Within each transect; each combination of habitat and altitude band was replicated on between 1 and 16 transects (mean ± se: 4.45 ± 0.43). Forty-two transects totalling 141.2km in length were walked between June and September 2003 (mean ± se: 3.36 ± 0.19 km; range: 1.55 km – 6.08 km).

Bat monitoring

Bats were monitored using a Tranquility II time expansion bat detector (Courtpan Design Ltd, Gloucester, UK) and 10x time expanded calls recorded onto the right channel of a stereo tape recorder (Radio Shack, Fort Worth, TX). The left channel of the tape recorder was used as a dictaphone to record any landmarks such as field boundaries or buildings. The position of the observer was used as a surrogate for the position of the recorded bat, as the detection distance of the bat detector was approximately 10-15 m for a pipistrelle; since the recording ran continuously each bat pass could be positioned accurately on a map using these landmarks.

Transects were walked on warm evenings (air temperature >10°C at the start of the transect) which were dry (no rain or mist) and still (≤ 2 on the Beaufort Scale). Strong wind, rain or low temperatures may adversely affect bat activity or the clarity of the recording. Recording in each transect began 30 minutes after sunset in order to allow pipistrelles to reach their foraging areas (Jones and Rydell 1994). It was assumed that pipistrelles forage at a constant rate until 2 hours after sunset (Maier 1992).

Classification of variables

Altitude was measured in bands of 20m intervals using 1:4000 scale maps provided by the Isle of Man Government MannGIS project. Habitat classifications and contour lines were taken from the same set of mapping data; habitat classifications were according to the Nature Conservancy Council Phase I Habitat Survey (1990) and summarised in Table 1. Habitat was then sub-classified as either having water present (for the length of transect for which a fresh water body was less than 10m away) or absent; and according to position in habitat where an edge position was defined as any point within 10m of the habitat edge (for woodland and scrub habitats only), and a centre position was any point further than 10m from the habitat edge. Some bat species are edge habitat specialists (e.g. Hillien et al. 2011); whereas others are better adapted to foraging in more cluttered environments, such as the centre of habitats (e.g. Kanuch et al. 2008), and another study showed *P. pipistrellus* and *P. pygmaeus* to differ in their use of central and edge habitats (Nicholls & Racey 2006b).

Analysis of recordings and definition of data

Spectrographic analysis of recordings was carried out using Spectrogram 5.0.4 in order to identify the call frequency with maximum energy (FMAXE) and therefore identity of pipistrelle species. Calls were identified with reference to Jones & van Parijs (1993): calls up to 1.5 standard deviations either side of the mean for each species were taken as belonging to that species (*P. pipistrellus* 43.3 – 49.3 kHz; *P. pygmaeus* 51.2 – 59.0 kHz). Calls in between these values were regarded as indeterminate and were excluded from analysis. Calls above both these ranges were taken as *P. pygmaeus* and calls below both these ranges were taken as *P. pipistrellus*; *Pipistrellus nathusii* has not been recorded on the Isle of Man and no calls were low enough to definitively be classified as *P. nathusii*. Social calls and ambiguous calls from which the frequency of the CF tail could not be determined were excluded from analysis. A bat pass was defined as a sequence of at least one pulse of echolocation of a passing bat; the next bat pass was recorded after a break the length of at least three pulses in the echolocation sequence.

The position of each bat pass was marked on a 1:4000 map. Each transect was split into sections of known transect length according to altitude band, habitat type, position within habitat, and presence or absence of water within 10m; thus, each combination of habitat and altitude category was replicated on between 1 and 16 transects (mean ± se: 4.45 ± 0.43). Data were expressed as number of bat passes of each species within each combination of habitat and altitude category, taking into account positioning within habitat (middle or edge) and presence or absence of a water body within 10m.

Statistical analysis

Statistical analyses were carried out in R (www.r-project.org). A generalised linear model was fitted to the data using iteratively reweighted least squares fits with quasipoisson error distributions to control for overdispersion. Bat activity was designated as the response variable, and the minimum model contained only transect length as a continuous covariate, to control for the distance covered within each habitat and altitude category. Main effects examined to determine their influence on bat abundance were altitude (as a continuous variable defined by the lower limit of each 20m altitude band), habitat, position within habitat (centre or edge) and presence or absence of water (all categorical variables). Each main effect was added into the model in turn and model comparisons made using F tests to determine the importance of each term: the most significant term was added into the model each time and the process repeated until no more terms significant at $p<0.05$ remained. To determine whether *P. pipistrellus* and *P. pygmaeus* differed in their activity in relation to habitat and altitude variables, interactions between the Species term and each main effect were tested in the same manner as above. Interactions between altitude and all three habitat terms were also considered, to determine whether altitude influenced habitat selection.

Results

Activity differed between species (Table 2), with a total of 693 *Pipistrellus pipistrellus* but only 49 *Pipistrellus pygmaeus* recorded over the study period. However, there was no evidence that the two species differed in any aspect of their habitat use (Table 2), thus the remaining results refer to both species together. Altitude and habitat interacted to influence bat activity (Table 2), with activity declining sharply with increasing altitude within deciduous woodland, mixed woodland and scrub land, but declining more gently in arable, heathland and conifer woodland (Figure 1a). Bat activity was also influenced by interactions between altitude and each of the presence of water and position within habitat (Table 2). Activity was higher in the centre of habitats at low altitudes but declined more sharply with increasing altitude until activity was lower compared to edge habitats (Figure 1b). At low altitudes with water, activity was higher than habitats without water; however, activity declined more sharply with increasing altitude until at higher altitudes, habitats without water had greater bat activity (Figure 1c).

Discussion

Pipistrellus pipistrellus was present at consistently higher densities than *Pipistrellus pygmaeus* and was more widespread, being found across all transects walked, compared to *P. pygmaeus* of which 70% of records were found within a region of 9km^2 south of Ramsey and all records occur within the north or east of the island (J. Dunn, unpubl. data). Whilst our data are not directly comparable, they suggest concordance with data from radiotracking studies of the two species, which suggest that *P. pipistrellus* has larger home ranges and spends more time foraging than *P. pygmaeus* (Davidson-Watts and Jones 2006; Nicholls and Racey 2006a). We found no evidence for differential habitat use between the two species, although this may be due to our relatively small sample of *P. pygmaeus*. Both species were more common in deciduous woodland, conifer woodland and scrub than in arable heath or mixed woodland, but no differential preferences were found for riparian habitats, in contrast to previous studies of these two species (Vaughan et al. 1997a; Nicholls and Racey 2006b).

Woodland tends to be the most important habitat type for foraging bats: deciduous woodland in particular is considered to be an important foraging habitat for both species of pipistrelle (Russ and Montgomery, 2002) although surprisingly we found conifer woodlands to also contain high levels of bat activity, in contrast to previous studies that have shown bats to actively avoid conifer plantations (e.g. Racey and Swift, 1985; Russo and Jones, 2003). However, the Isle of Man has three times as much conifer plantation as deciduous woodland (Sharpe et al. 2007) and bats on the Island may have adapted to utilise this habitat given its relatively high availability.

Both bat species showed a significant decrease in activity with altitude over a very small scale. Although some of this relationship can be explained by habitat availability, as the area of woodland does begin to decrease with increasing altitude, the relationship was still present within habitats. This could be due either to decreasing prey availability with increasing altitude, or to the decrease in temperature with increasing altitude. The observation of Vaughan *et al*. (1997a) that the activity of *P. pipistrellus* is affected by temperature but feeding rate was not suggests that temperature per se may be responsible for the declining activity with altitude, although another study over a wider altitudinal range found reduced prey capture rates at higher altitudes (Grindal et al. 1999). If temperature was responsible for the decreasing activity with altitude then we might expect to see corresponding relationships with latitude, which are not apparent from UK pipistrelle distribution (Mitchell-Jones et al., 2002). Alternatively, increased temperature variability at higher altitudes may make reduce the predictability of these foraging habitats, leading to the increased utilisation of lower altitude habitats.

The scale of the decline in activity with altitude within habitats that we show has implications for the conservation strategies of chiroptera, and warrants further investigation of small-scale altitudinal effects on other mammal species. Low altitudes may be disproportionately important in providing foraging habitat for some bat species, especially for females during the breeding season (e.g. Cryan et al 2000; Russo 2002). This may lead to sexual segregation along an altitudinal gradient as has been shown for *Myotis daubentonii* (Russo 2002) and suspected for species of *Nyctalus* (Ibáñez et al. 2009). Since it was not possible to record the sex of the individual bats in this study, the changes in habitat selection with altitude may be additionally due to different foraging requirements between sexes. Altitudinal effects on activity may also differ depending on the scale of the local and surrounding habitat: habitats on the Isle of Man show large variation over a small scale. Mammals may be likely to utilise heterogeneous habitat (such as woodland-arable mosaic) differently to larger-scale, more homogeneous habitats (such as large areas of woodland) and thus the results of this study may be more applicable to heterogeneous habitats: this warrants further work. Our results also suggest that further investigation of altitudinal impacts on activity is warranted for other species of both volant and non-volant mammals, especially those with more restricted distributions, as relatively small altitudinal changes may limit distribution and potentially act as barriers to dispersal independently of habitat availability.

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Table 1. Definitions of the six habitat classifications used in this study.

Habitat	Description
Conifer plantation (CP)	Vegetation dominated by trees more than 5m high when mature; 90% or more of the canopy consists of conifer trees; woodland is obviously planted
Deciduous woodland (DW)	Vegetation dominated by trees more than 5m high when mature; 90% or more of the canopy consists of broadleaved trees; woodland may be obviously planted or semi-natural.
Mixed woodland (MW)	Vegetation dominated by trees more than 5m high when mature; 10-90% of the canopy consists of either broadleaved or conifer trees. Woodland may be obviously planted or semi-natural.
Scrub (S)	Vegetation dominated by locally native shrubs usually less than 5m tall
Heath (H)	Includes vegetation dominated by herbs and ferns; dwarf gorse species; lichens and bryophytes. Coastal heath and grassland are also included in this category
Arable (A)	Includes arable cropland, intensively managed grassland and horticultural land as well as improved and poor semi-improved grassland which may or may not be used as grazing land

Definitions are broadly based on those of the Nature Conservancy Council (1990).

Table 2. Minimum adequate model from a General Linear Model describing variation in bat activity.

Variable	**df**	**F**	**p**	**Estimate**	**SE**
Transect length	1, 272	247.533	<0.001	<0.001	<0.001
Species (*Pipistrellus pygmaeus*)	1, 271	217.778	<0.001	-2.648	0.258
Altitude	1, 270	40.598	<0.001	-0.003	0.001
Habitat (Conifer woodland)	5, 265	5.571	<0.001	0.887	0.440
Habitat (Deciduous woodland)				1.471	0.346
Habitat (Heath)				-0.706	0.476
Habitat (Mixed woodland)				-0.579	0.984
Habitat (Scrub)				0.805	0.759
Position in habitat (edge)	1, 264	5.493	0.020	-1.192	0.323
Presence of water (present)	1, 263	4.619	0.033	0.927	0.267
Altitude x Habitat (Conifer)	5, 258	3.289	0.007	0.007	0.004
Altitude x Habitat (Deciduous)				0.018	0.005
Altitude x Habitat (Heath)				0.001	0.003
Altitude x Habitat (Mixed)				0.014	0.015
Altitude x Habitat (Scrub)				0.014	0.008
Altitude x position in habitat (edge)	1, 257	11.253	0.001	0.010	0.004
Altitude x Presence of water (present)	1, 256	5.194	0.023	0.008	0.004

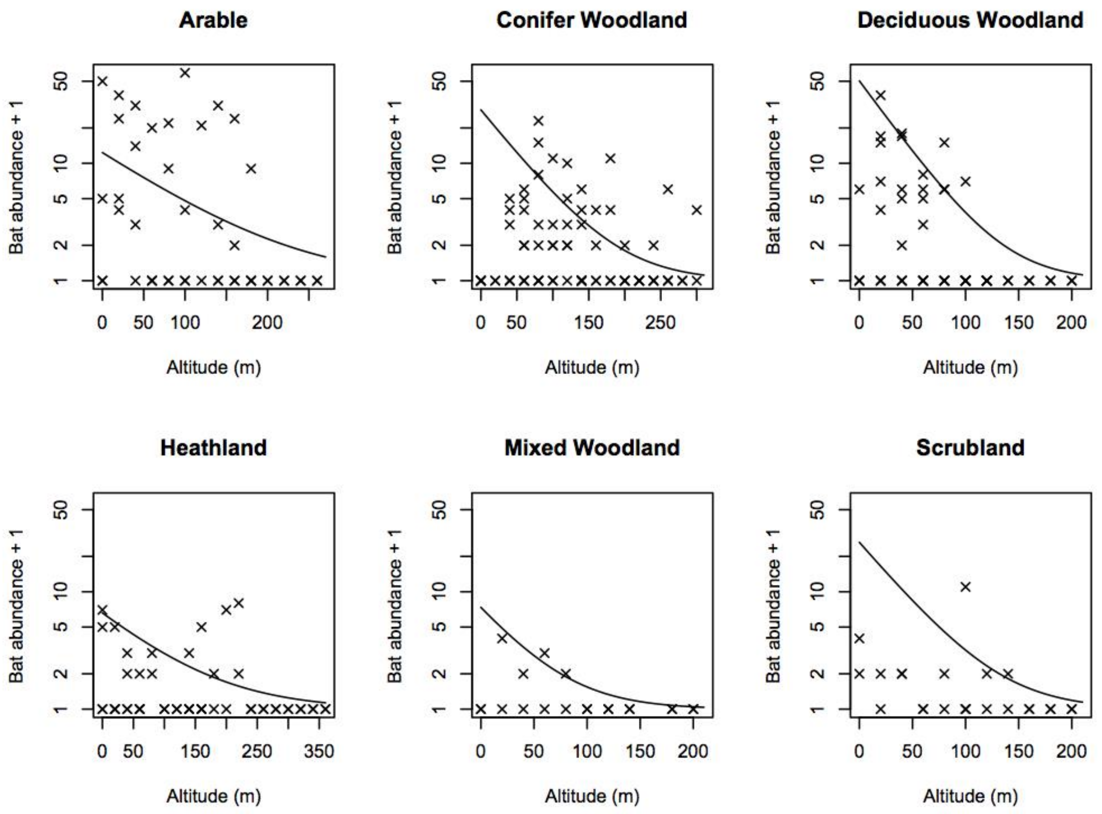
Parameter estimates for habitat are for the level stated when compared to arable. Parameter estimates for other variables are for the stated level when compared to the other. Two way-interactions of Species with habitat (F_5=0.76, p=0.58), altitude

(F_1=1.13, p=0.29), habitat position (F_1=0.04, p=0.85), and presence of water (F_1=0.90, p=0.34) were not included in the model as they significantly influenced neither the response variable nor the fit of the model.

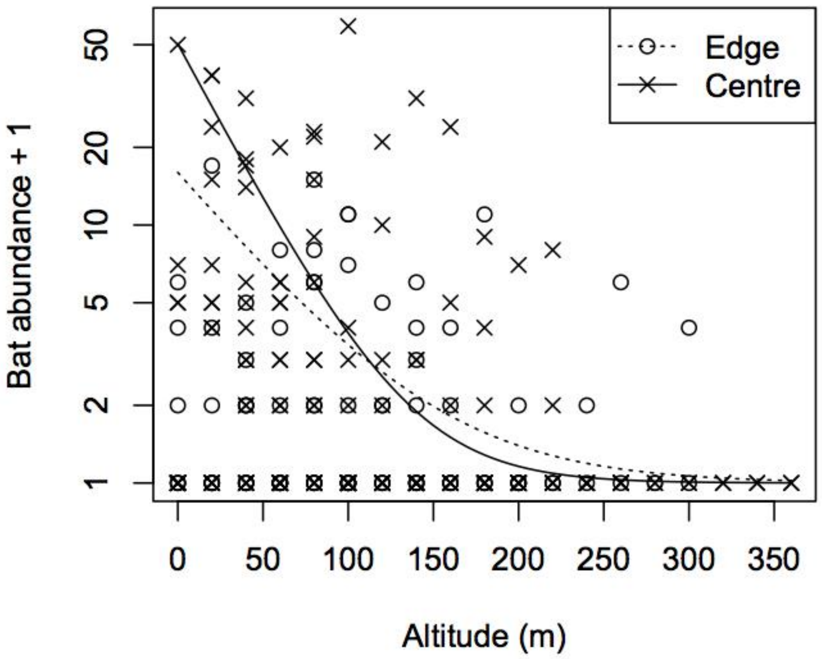
Figure legends

Figure 1. Altitude and a) habitat, b) position within habitat and c) presence of water interact to predict bat activity. Points show raw data; lines shows relationship from the final model (Table 1) when correcting for the transect length walked within each habitat and altitude band (predictions for the mean transect length, 1012 m), with factors levels set where necessary for *Pipistrellus pipistrellus* with water present in the centre of deciduous woodland. Note log y-axes.

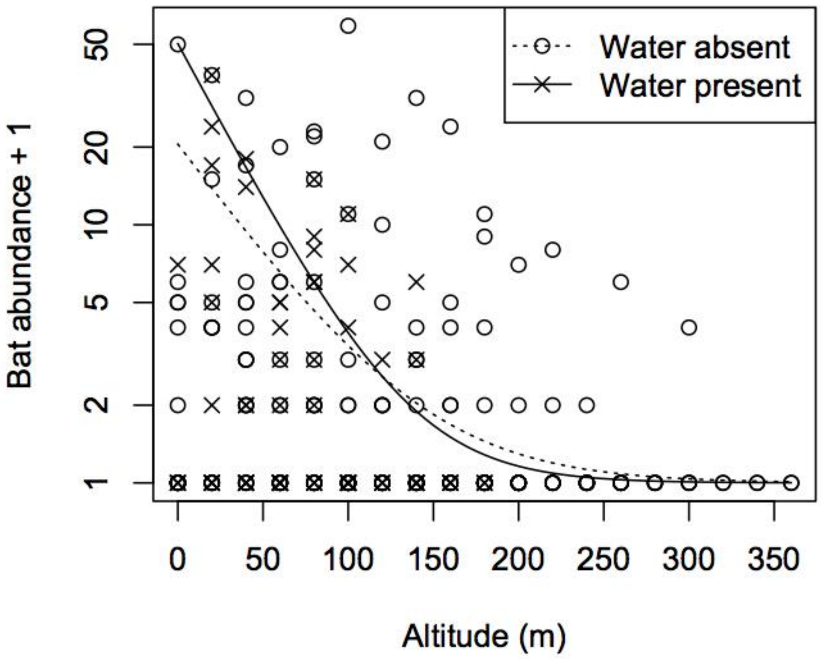
a)



b)


Edge
Centre
Bat abundance + 1
1
2
5
10
20
50
0
50
100
150
200
250
300
350
Altitude (m)

c)


Water absent
Water present
Bat abundance + 1
1
2
5
10
20
50
0
50
100
150
200
250
300
350
Altitude (m)