

1 **Altitudinal effects on habitat selection in two sympatric pipistrelle species**

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22

23 **Abstract**

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

38

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

41

42 **Introduction**

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

55

56 The associations between altitude and bat abundance are thought to be due to a
57 combination of temperature, influencing thermoregulatory constraints, and water and
58 habitat, influencing food resources (Cryan et al. 2000; McCain 2007). Altitude
59 influences prey availability, which tends to decrease with increasing altitude (Wolda
60 1987; McCoy 1990; but see also Stoneburner, 1977), and upper altitudes can tend to be
61 characterised by elevationally widespread generalists (Moreira et al. 2009).

62

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

67 *Pipistrellus pygmaeus* (Leach, 1825), were recognised as separate species in 1993, and
68 are distinguished by differing echolocation call frequencies (Jones and van Parijs 1993),
69 social calls (Barlow and Jones 1997) and gross morphology (Jones and van Parijs
70 1993). Following molecular confirmation (Barratt et al. 1997) several studies have
71 examined ecological differences between the species, finding differences in diet
72 (Barlow 1997) and foraging habitat (Vaughan et al. 1997a; Russ et al. 2003) that
73 suggest *P. pygmaeus* specialises more in wetland habitats than *P. pipistrellus*, which is
74 more of a generalist (Barlow 1997; Vaughan et al. 1997a). More recent studies have
75 also found *P. pipistrellus* to have larger home and foraging range sizes than *P.*
76 *pygmaeus* (Davidson-Watts and Jones 2006; Nicholls and Racey 2006a; Nicholls and
77 Racey 2006b).

78

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

87

88 Different species are adapted to different ‘optimum’ altitudes across a broad altitudinal
89 range (Sanchez-Cordero 2001), but any altitudinal effects on a smaller scale tend to be
90 overlooked in studies of habitat usage by mammals. Here, we investigate firstly,
91 whether altitude is a significant factor affecting the distribution of either *P. pipistrellus*

92 or *P. pygmaeus*; and secondly, whether altitude is merely a confounding factor in
93 determining habitat availability and therefore influencing distribution, or whether
94 altitude per se is important in limiting distribution and should therefore be taken into
95 consideration when designing and implementing mammalian conservation strategies.
96
97

98 **Materials and methods**

99 *Sites*

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

110

111 *Bat monitoring*

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

120

121 Transects were walked on warm evenings (air temperature $>10^{\circ}\text{C}$ at the start of the
122 transect) which were dry (no rain or mist) and still (≤ 2 on the Beaufort Scale). Strong

123 wind, rain or low temperatures may adversely affect bat activity or the clarity of the
124 recording. Recording in each transect began 30 minutes after sunset in order to allow
125 pipistrelles to reach their foraging areas (Jones and Rydell 1994). It was assumed that
126 pipistrelles forage at a constant rate until 2 hours after sunset (Maier 1992).

127

128 *Classification of variables*

129 Altitude was measured in bands of 20m intervals using 1:4000 scale maps provided by
130 the Isle of Man Government MannGIS project. Habitat classifications and contour lines
131 were taken from the same set of mapping data; habitat classifications were according to
132 the Nature Conservancy Council Phase I Habitat Survey (1990) and summarised in
133 Table 1. Habitat was then sub-classified as either having water present (for the length
134 of transect for which a fresh water body was less than 10m away) or absent; and
135 according to position in habitat where an edge position was defined as any point within
136 10m of the habitat edge (for woodland and scrub habitats only), and a centre position
137 was any point further than 10m from the habitat edge. Some bat species are edge
138 habitat specialists (e.g. Hillien et al. 2011); whereas others are better adapted to
139 foraging in more cluttered environments, such as the centre of habitats (e.g. Kanuch et
140 al. 2008), and another study showed *P. pipistrellus* and *P. pygmaeus* to differ in their
141 use of central and edge habitats (Nicholls & Racey 2006b).

142

143 *Analysis of recordings and definition of data*

144 Spectrographic analysis of recordings was carried out using Spectrogram 5.0.4 in order
145 to identify the call frequency with maximum energy (FMAXE) and therefore identity of
146 pipistrelle species. Calls were identified with reference to Jones & van Parijs (1993):
147 calls up to 1.5 standard deviations either side of the mean for each species were taken as

148 belonging to that species (*P. pipistrellus* 43.3 – 49.3 kHz; *P. pygmaeus* 51.2 – 59.0
149 kHz). Calls in between these values were regarded as indeterminate and were excluded
150 from analysis. Calls above both these ranges were taken as *P. pygmaeus* and calls
151 below both these ranges were taken as *P. pipistrellus*; *Pipistrellus nathusii* has not been
152 recorded on the Isle of Man and no calls were low enough to definitively be classified
153 as *P. nathusii*. Social calls and ambiguous calls from which the frequency of the CF tail
154 could not be determined were excluded from analysis. A bat pass was defined as a
155 sequence of at least one pulse of echolocation of a passing bat; the next bat pass was
156 recorded after a break the length of at least three pulses in the echolocation sequence.
157
158 The position of each bat pass was marked on a 1:4000 map. Each transect was split into
159 sections of known transect length according to altitude band, habitat type, position
160 within habitat, and presence or absence of water within 10m; thus, each combination of
161 habitat and altitude category was replicated on between 1 and 16 transects (mean \pm se:
162 4.45 ± 0.43). Data were expressed as number of bat passes of each species within each
163 combination of habitat and altitude category, taking into account positioning within
164 habitat (middle or edge) and presence or absence of a water body within 10m.

165

166 *Statistical analysis*

167 Statistical analyses were carried out in R (www.r-project.org). A generalised linear
168 model was fitted to the data using iteratively reweighted least squares fits with
169 quasipoisson error distributions to control for overdispersion. Bat activity was
170 designated as the response variable, and the minimum model contained only transect
171 length as a continuous covariate, to control for the distance covered within each habitat
172 and altitude category. Main effects examined to determine their influence on bat

173 abundance were altitude (as a continuous variable defined by the lower limit of each
174 20m altitude band), habitat, position within habitat (centre or edge) and presence or
175 absence of water (all categorical variables). Each main effect was added into the model
176 in turn and model comparisons made using F tests to determine the importance of each
177 term: the most significant term was added into the model each time and the process
178 repeated until no more terms significant at $p < 0.05$ remained. To determine whether *P.*
179 *pipistrellus* and *P. pygmaeus* differed in their activity in relation to habitat and altitude
180 variables, interactions between the Species term and each main effect were tested in the
181 same manner as above. Interactions between altitude and all three habitat terms were
182 also considered, to determine whether altitude influenced habitat selection.
183

184 **Results**

185 Activity differed between species (Table 2), with a total of 693 *Pipistrellus pipistrellus*
186 but only 49 *Pipistrellus pygmaeus* recorded over the study period. However, there was
187 no evidence that the two species differed in any aspect of their habitat use (Table 2),
188 thus the remaining results refer to both species together. Altitude and habitat interacted
189 to influence bat activity (Table 2), with activity declining sharply with increasing
190 altitude within deciduous woodland, mixed woodland and scrub land, but declining
191 more gently in arable, heathland and conifer woodland (Figure 1a). Bat activity was
192 also influenced by interactions between altitude and each of the presence of water and
193 position within habitat (Table 2). Activity was higher in the centre of habitats at low
194 altitudes but declined more sharply with increasing altitude until activity was lower
195 compared to edge habitats (Figure 1b). At low altitudes with water, activity was higher
196 than habitats without water; however, activity declined more sharply with increasing
197 altitude until at higher altitudes, habitats without water had greater bat activity (Figure
198 1c).

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205 **Discussion**

206 *Pipistrellus pipistrellus* was present at consistently higher densities than *Pipistrellus*
207 *pygmaeus* and was more widespread, being found across all transects walked, compared
208 to *P. pygmaeus* of which 70% of records were found within a region of 9km² south of
209 Ramsey and all records occur within the north or east of the island (J. Dunn, unpubl.
210 data). Whilst our data are not directly comparable, they suggest concordance with data
211 from radiotracking studies of the two species, which suggest that *P. pipistrellus* has
212 larger home ranges and spends more time foraging than *P. pygmaeus* (Davidson-Watts
213 and Jones 2006; Nicholls and Racey 2006a). We found no evidence for differential
214 habitat use between the two species, although this may be due to our relatively small
215 sample of *P. pygmaeus*. Both species were more common in deciduous woodland,
216 conifer woodland and scrub than in arable heath or mixed woodland, but no differential
217 preferences were found for riparian habitats, in contrast to previous studies of these two
218 species (Vaughan et al. 1997a; Nicholls and Racey 2006b).

219

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

228

229 Both bat species showed a significant decrease in activity with altitude over a very
230 small scale. Although some of this relationship can be explained by habitat availability,
231 as the area of woodland does begin to decrease with increasing altitude, the relationship
232 was still present within habitats. This could be due either to decreasing prey availability
233 with increasing altitude, or to the decrease in temperature with increasing altitude. The
234 observation of Vaughan *et al.* (1997a) that the activity of *P. pipistrellus* is affected by
235 temperature but feeding rate was not suggests that temperature per se may be
236 responsible for the declining activity with altitude, although another study over a wider
237 altitudinal range found reduced prey capture rates at higher altitudes (Grindal et al.
238 1999). If temperature was responsible for the decreasing activity with altitude then we
239 might expect to see corresponding relationships with latitude, which are not apparent
240 from UK pipistrelle distribution (Mitchell-Jones et al., 2002). Alternatively, increased
241 temperature variability at higher altitudes may make reduce the predictability of these
242 foraging habitats, leading to the increased utilisation of lower altitude habitats.

243

244 The scale of the decline in activity with altitude within habitats that we show has
245 implications for the conservation strategies of chiroptera, and warrants further
246 investigation of small-scale altitudinal effects on other mammal species. Low altitudes
247 may be disproportionately important in providing foraging habitat for some bat species,
248 especially for females during the breeding season (e.g. Cryan et al 2000; Russo 2002).
249 This may lead to sexual segregation along an altitudinal gradient as has been shown for
250 *Myotis daubentonii* (Russo 2002) and suspected for species of *Nyctalus* (Ibáñez et al.
251 2009). Since it was not possible to record the sex of the individual bats in this study, the
252 changes in habitat selection with altitude may be additionally due to different foraging
253 requirements between sexes. Altitudinal effects on activity may also differ depending

254 on the scale of the local and surrounding habitat: habitats on the Isle of Man show large
255 variation over a small scale. Mammals may be likely to utilise heterogeneous habitat
256 (such as woodland-arable mosaic) differently to larger-scale, more homogeneous
257 habitats (such as large areas of woodland) and thus the results of this study may be more
258 applicable to heterogeneous habitats: this warrants further work. Our results also
259 suggest that further investigation of altitudinal impacts on activity is warranted for other
260 species of both volant and non-volant mammals, especially those with more restricted
261 distributions, as relatively small altitudinal changes may limit distribution and
262 potentially act as barriers to dispersal independently of habitat availability.

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373

374

375

376 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

377

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

379

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

Variable	df	F	p	Estimate	SE
Transect length	1, 272	247.533	<0.001	<0.001	<0.001
Species (<i>Pipistrellus pygmaeus</i>)	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

382

383 Parameter estimates for habitat are for the level stated when compared to arable.

384 Parameter estimates for other variables are for the stated level when compared to the

385 other. Two way-interactions of Species with habitat ($F_5=0.76$, $p=0.58$), altitude

386 ($F_1=1.13$, $p=0.29$), habitat position ($F_1=0.04$, $p=0.85$), and presence of water ($F_1=0.90$,
387 $p=0.34$) were not included in the model as they significantly influenced neither the
388 response variable nor the fit of the model.

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390

391 Figure legends

392

393 Figure 1. Altitude and a) habitat, b) position within habitat and c) presence of water

394 interact to predict bat activity. Points show raw data; lines shows relationship from the

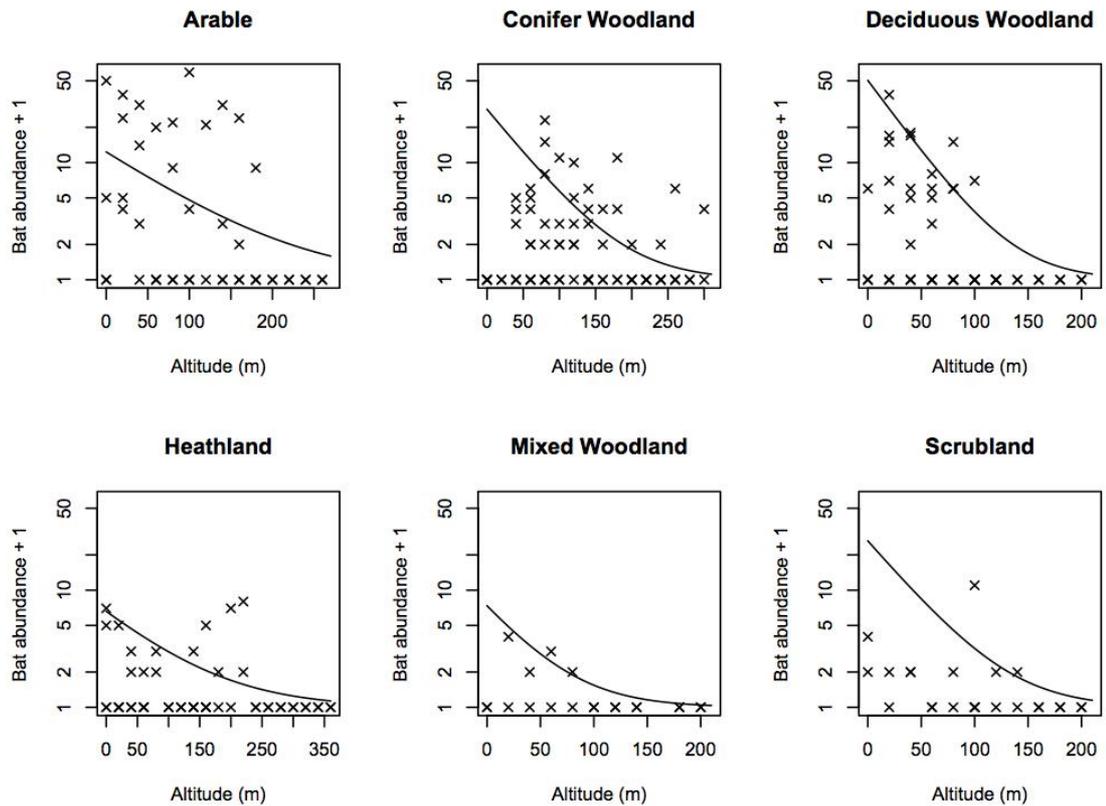
395 final model (Table 1) when correcting for the transect length walked within each habitat

396 and altitude band (predictions for the mean transect length, 1012 m), with factors levels

397 set where necessary for *Pipistrellus pipistrellus* with water present in the centre of

398 deciduous woodland. Note log y-axes.

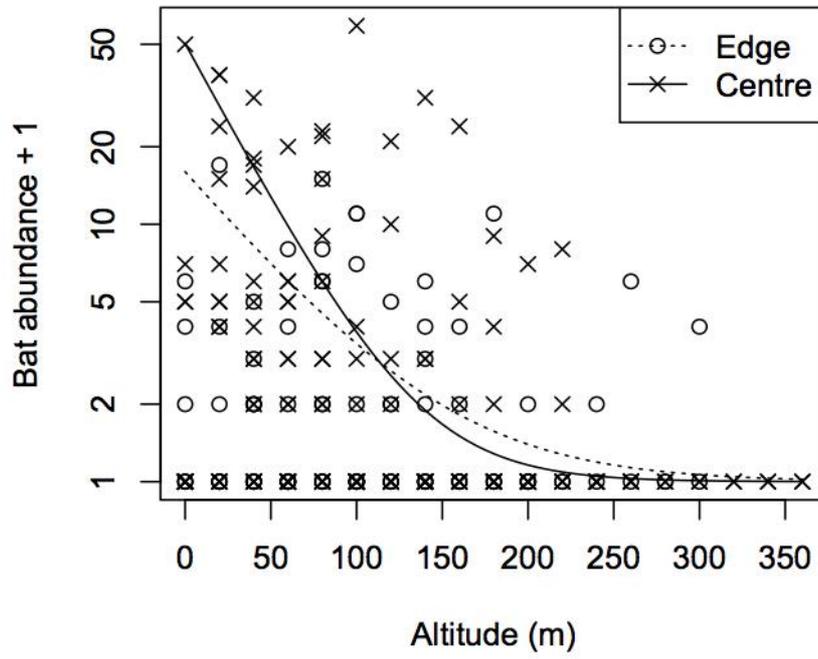
399 a)



400

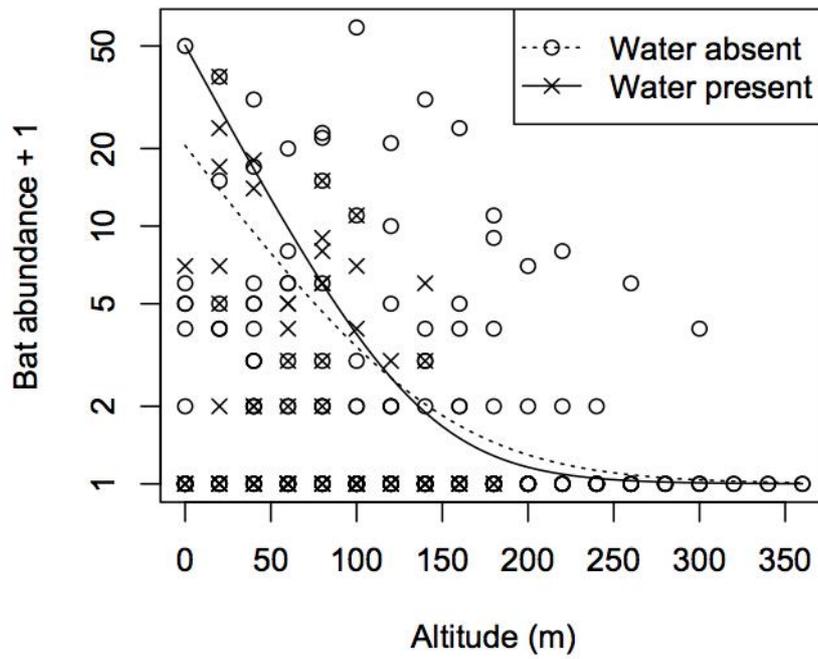
401

402 b)



403

404 c)



405