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Habitat Preferences of Soprano Pipistrelle *Pipistrellus pygmaeus* (Leach, 1825) and Common Pipistrelle *Pipistrellus pipistrellus* (Schreber, 1774) in Two Different Woodlands in North East Scotland

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Alek Rachwald, Tim Bradford, Zbigniew Borowski, and Paul A. Racey (2016) The habitat preferences of the soprano pipistrelle *Pipistrellus pygmaeus* and the common pipistrelle *Pipistrellus pipistrellus* living in sympatry, were investigated in north east Scotland, using bat detector transects. Bat flight, foraging and social activity in natural birch woodland was compared with that in managed non-native coniferous woodland. Each area consists of riparian habitat, meadow-forest ecotone and dense forest. The activity of bats was highest in riparian habitat, then meadow, and lowest in dense woodland. *P. pygmaeus* was more abundant than *P. pipistrellus* in both areas, although in managed coniferous woodland only narrowly so (43.7% of all recorded bat flights, compared to 40.0% for common pipistrelle). In natural birch woodland, meadow habitat was most preferred by *P. pipistrellus*, and there was no significant difference between the use of riparian and woodland habitats, whereas in coniferous woodland, riparian habitat was most preferred. *P. pygmaeus* in both sites preferred riparian habitat, then meadow and forest least of all. The foraging activity of soprano pipistrelles was higher in birch than in coniferous woodland, whereas for the common pipistrelle, it was more evenly distributed. In both sites the lowest number of feeding buzzes was recorded in dense forest. In both study areas social calls were recorded, but many more for *P. pygmaeus* than for *P. pipistrellus*, especially in birch woodland. Soprano pipistrelle is a specialist species, focused mostly on riparian habitat, whereas common pipistrelle shows more generalistic behaviour. High number of social calls recorded near the waterbodies could suggest, that such habitat partitioning could be caused also by competitive behaviour.

Key words: Bats, Scotland, Soprano pipistrelle, Common pipistrelle, Woodland.

BACKGROUND

Riparian and woodland habitats are important for insectivorous bats of the temperate zone. In Europe in the last 1000 years, large scale landscape changes have occurred, creating agricultural and urban areas, exploiting natural forests and replacing them with managed plantations. But even after such profound changes, many bat species remain strongly associated with managed woodland and river valleys, since they provide abundant insects and many tree hole shelters, both of which are important for bat populations (Walsh and Mayle 1991; Walsh and Harris 1996; Racey 1998).

The common pipistrelle *Pipistrellus pipistrellus* (Schreber 1774) and the soprano pipistrelle *P. pygmaeus* (Leach 1825) are ubiquitous in the British Isles, with the exception of a few Scottish islands (Altringham 2003). *Pipistrellus pipistrellus* and *P. pygmaeus* were, for a long time, thought to be a single biological species. The first indication that cryptic species may be present, was the description by Jones and van Parijs (1993) of

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the bimodal distribution of echolocation call frequencies, which they attributed to two 'phonic types'. This discovery was then supported by further studies of echolocation (Barlow and Jones 1997), morphology (Altringham 2003), behaviour (Park et al. 1996), and genetics (Barratt et al. 1997; Mayer and von Helversen 2001a; Racey et al. 2007). Finally, the acceptance of *P. pygmaeus* as the name of the new species is recorded in the Bulletin of Zoological Nomenclature (Anon 2003).

Pipistrellus pipistrellus and *P. pipistrellus* are the two most common bat species in Britain (Altringham 2003; Dietz et al. 2009). Both species have extensive ranges in Europe, with *P. pygmaeus* having the most northerly range in Scandinavia, and *P. pipistrellus* extending into the Middle East. Both species occur in central and western Europe (Mayer and von Helversen 2001b; Dietz et al. 2009; Sztencel-Jabłonka and Bogdanowicz 2012). Their distribution in Britain, although overlapping, differs in relative abundance; the soprano pipistrelle is more abundant in the north, whilst the common pipistrelle is more abundant in the south of Britain (Altringham 2003). Although hybridization between both species in continental Europe does occur, this phenomenon is not yet confirmed for British Isles (Racey et al. 2007; Sztencel-Jabłonka and Bogdanowicz 2012).

Both pipistrelle species have a similar diet with some slight differences (Barlow 1997), perhaps connected with their habitat preferences, although to prove selection, choice experiments are necessary. Both species are aerial hawkers and prefer smaller prey items (Arnold et al. 2002).

The study had two aims - to determine how the two sibling species of pipistrelles use mixed forest landscapes in this part of Scotland and to investigate their habitat preferences in relation to natural birchwoods and managed non-native conifers. By habitat use we mean flight, foraging and social activity of bats. Establishment of habitat preferences will assist management and will help to formulate appropriate conservation measures for these species.

MATERIALS AND METHODS

The study was conducted in the valley of the River Dee, north east Scotland. The river is approximately 140 km long, emptying into the North Sea at about 57° in the city of Aberdeen. The river catchment consists of grassland, commercial woodland, rough grazing and moorland (Pugh 1985). Human population density in the catchment area is low outside Aberdeen.

Riparian woodland covers approximately 40% of the river banks (Racey et al. 1998). Some native pinewoods remain in Glentanar National Nature Reserve, but non-native Sitka and Norway spruce are common on Deeside. Birchwood in mixed form is common in the study area; from the towns of Ballater to Aboyne, birch makes up about 25% of the woodland area (Forster and Green 1985). The study was conducted in two areas near Dinnet, Aberdeenshire: Torphantrick Wood (owned by Glentanar Estate), a managed woodland of about 4,328 ha adjacent to the River Dee, with Norway spruce, Sitka spruce, Douglas fir and birch, and Muir of Dinnet, former moorland covered by a 60 year-old birch forest of natural origin, about 600 ha with almost no other tree species, in the centre of which are two small lochs or lakes, each about 1 km^2. Muir of Dinnet is managed by Scotland's statutory nature conservation organization, Scottish Natural Heritage. The average distance between the two areas was approximately 4.5 km. The activity of the bats was recorded along two 2.5 km transects, one in each study area, which incorporated the meadow-forest and river-forest ecotones, and areas within the forest (in equal proportion).

Muir of Dinnet birch woodland is unique and consists of former moorland pastures which were abandoned in the 1940s and are now covered by naturally grown birch trees. Because it is the only example of naturally grown birch forest in this part of Scotland, it is protected as a nature reserve. The area of birch woodland with no coniferous trees is relatively limited and our study transect crossed most of it, which explains why it was possible to establish only one transect at this site.

The conversion and recording of signals involved the use of two D 980 bat detectors (Pettersson Elektronik AB, Sweden), together with Sony WM-D6C cassette recorders. For bat recording we used the frequency division and time expansion systems. The frequency division system reduces the frequency of the ultrasound call by a factor of 10 and it works in real time. Time expansion reduces the playback speed of the signal by a factor of 10; three seconds of signal are recorded digitally by the detector and these are played-back over 30 seconds. Bat activity (number of passes, number of feeding buzzes and social calls) was measured with frequency division real time continuous recordings, whereas the time expansion system was used for detailed recognition of species and signal measurements, when it was necessary. The data were collected over a total number of 41 nights throughout June, July and August 2004; during the period of greatest bat activity. Transects were walked twice each night; from one end to the other and then back again. Both transects (in Torphantrick Wood and in Muir of Dinnet, 2500 m each), were walked simultaneously. The first walk of the transect began approximately 45 minutes after sunset and each walk lasted for 30 minutes. For the purposes of data analysis both walks were treated as one whole sample period. At the end of one transect walk, the time was recorded and then the transect was repeated in the opposite direction. The purpose of the repetition was to record bat species emerging at different times. Starting points were changed alternately. The tape recordings were analysed using a licensed copy of Batsound® for MS Windows (Pettersson Elektronik AB). The recorded data were stored as a .WAV file, at 16 bits per sample, 22 050 samples per second in two channels. Spectrograms were calculated using Fast Fourrier Transformation (FFT).

The three types of acoustic activity identified were flight activity, foraging and social calls. The first activity, flight, consisted of a number of bat passes, or flights; recorded as a series of echolocation calls, in any given period; and confirmed by at least two signals (Furlonger et al. 1987). The second activity, foraging, was recorded as the number of feeding buzzes accompanying some echolocation "flight" sequences. A "buzz" is a short sequence of calls where the pulse repetition rate increases to a point at which it is impossible to distinguish individual pulses. This pattern indicated the bat was attacking prey. Flights with accompanying feeding buzzes were also counted as "flight activity" for calculation purposes, whereas foraging activity was calculated separately and is based only on the number of buzzes. The third type of acoustic activity, social calls, occur when individuals interact either inter- or intra-specifically.

The total number of recorded bat passes; feeding buzzes and social calls, together with the frequency of signals were recorded in a MS Excel datasheet. The Lavene test and GLM modelling were carried out with post-hoc LSD and Tukey tests. Dependent variables were flight, foraging and social activities. Independent variable was walk of the transect, whereas independent categorizing variables were habitat, site and species. Statistical calculations were provided using the statistical package Statistica.

RESULTS

During the study 1997 bat call sequences were recorded. *Pipistrellus pipistrellus* and *P. pygmaeus* accounted for 1748 (up to 90%) of these: most of the remaining signals were attributed to small *Myotis* bats. Ninety five percent of recorded *Pipistrellus* bats were divided between two classes: 45-50 kHz range (*P. pipistrellus*) and 52-62 kHz range (*P. pygmaeus*). Records of *Pipistrellus* at a frequency of 51 kHz ($n = 18$) were assigned to *Pipistrellus* spp. In both sites the most common bat was *P. pygmaeus*. (Table 1)

Generally, activities of both species of bats were different between different sites and habitats (GLM, $F_{2,48} = 4.566$, $p = 0.01086$). Flight activity of *P. pygmaeus* was significantly higher than *P. pipistrellus* in all habitats in birch woodland (Muir of Dinnet) (HSD Tukey's post hoc test, edge: $p < 0.05$; forest: $p < 0.001$; water: $p < 0.001$). In coniferous woodland (Torphantrick Wood) was not found any significant differences (HSD Tukey's post hoc test: $p > 0.05$) (Fig. 1).

Analysis of differences of flight activity between species and habitats revealed that in birch woodland, *P. pipistrellus* was equally active near the water and in the forest (HSD Tukey's post hoc test, $p > 0.05$), whereas slightly higher activity of this species was recorded along the meadow, but not significantly so (HSD Tukey's post hoc test,

Table 1. Pipistrelle bats species composition in Muir of Dinnet and Torphantrick Wood measured as number of recorded flights. The table contains the number and percentage of recordings identified to species level

	Muir of Dinnet		Torphantrick Wood	
species	n	%	n	%
P. pygmaeus	754	78.3	410	52,2
P. pipistrellus	209	21.7	375	47,8
total	963	100	785	100

$p > 0.05$). At the same site *P. pygmaeus* was most active near the water, (HSD Tukey's post hoc test water - forest: $p < 0.001$; water-edge: $p > 0.001$; forest-edge: $p > 0.05$). In coniferous woodlands both species were most active near the water, and least in the forest (HSD Tukey's post hoc test, water-edge: $p > 0.05$; water-forest: $p < 0.001$ edge-forest: $p < 0.01$ for *P. pipistrellus* and the same result for *P. pygmaeus* with one exception water-edge: $p < 0.01$) (Fig. 1.).

The foraging activity of *P. pygmaeus* was similar both in Dinnet as well as in Torphantrick (GLM, $F_{2.81} = 0.63$, HSD Tukey's post hoc test, $p > 0.05$) (Fig. 2), as well as *P. pipistrellus* in this species foraging activity between both sites was similar (Fig. 3).

Comparing bat activity between sites and habitats (GLM, $F_{2.127} = 1.5911$, $p = 0.20774$), differences between two species in foraging activity are not significant within the habitats, but significant between some habitats, *e.g.* between *P. pipistrellus* in Torphantrick edge and *P. pygmaeus* in Torphantrick water (HSD Tukey's post hoc test, $p < 0.05$). It is an effect of differences between habitats rather than differences in bat preferences.

Social activity of bats of the genus *Pipistrellus* (measured as the number of social calls per unit time) in birch woodland was three times higher than in coniferous woodland (proportion birch woodland to conifers: 194/66). The proportion of social calls of the two species varied greatly between the two sites: from 1:2 (*P. pipistrellus*/ *P. pygmaeus* respectively) in the coniferous woodland of Torphantrick Wood, to 1:13 in birch woodland of Muir of Dinnet. The number of social calls of *P. pipistrellus* was too small for statistical analysis. In the case of *P. pygmaeus*, the number social calls varied both between sites and between habitats (GLM: $F_{2.28} = 3.9$; $p = 0.032$). Social activity was higher in Dinnet than in Torphantrick, and generally this kind of activity was lowest in the woodland habitat (HSD Tukey's post hoc test,: Torphantrick and Dinnet "near the water" activity higher than Torphantrick "forest" activity, $p < 0.05$) (Fig. 4). In Torphantrick social calls of this species were not present in woodland habitat at all.

DISCUSSION

The two woodlands in this study were used by bats in different ways, with the birch woodland

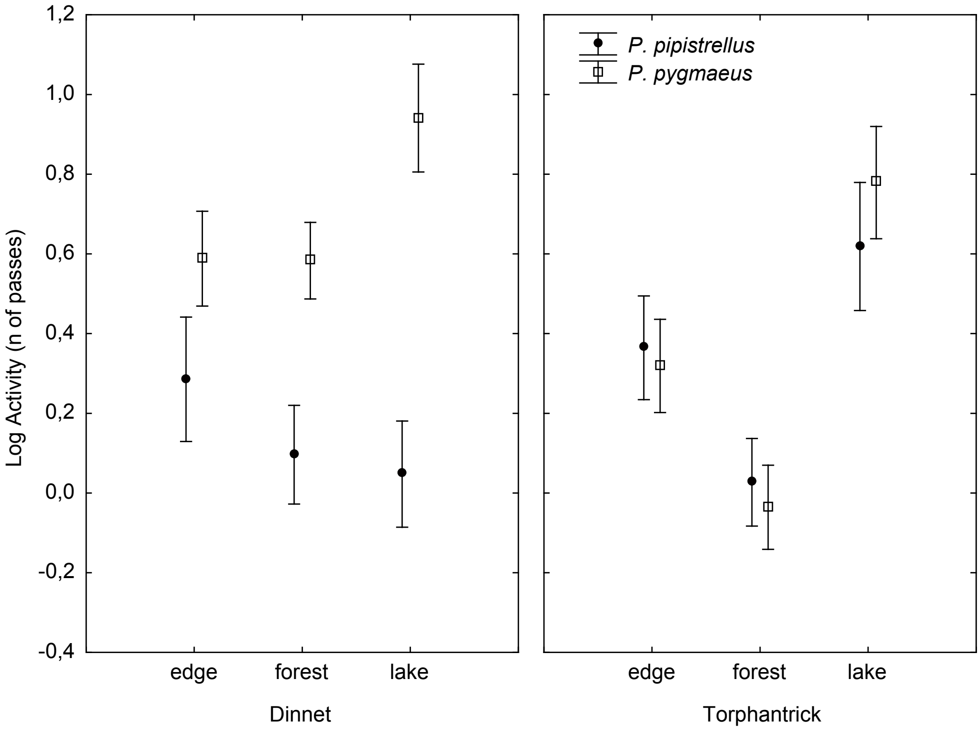

Fig. 1. The comparison of general (flight) activity of common (*P. pipistrellus*) and soprano (*P. pygmaeus*) pipistrelles between three habitats (near the water, meadow ecotone and forest) and both sites. Activity = average number of recorded bat passes (flights) throughout one transect control (logarithmically transformed). Vertical poles = SE.

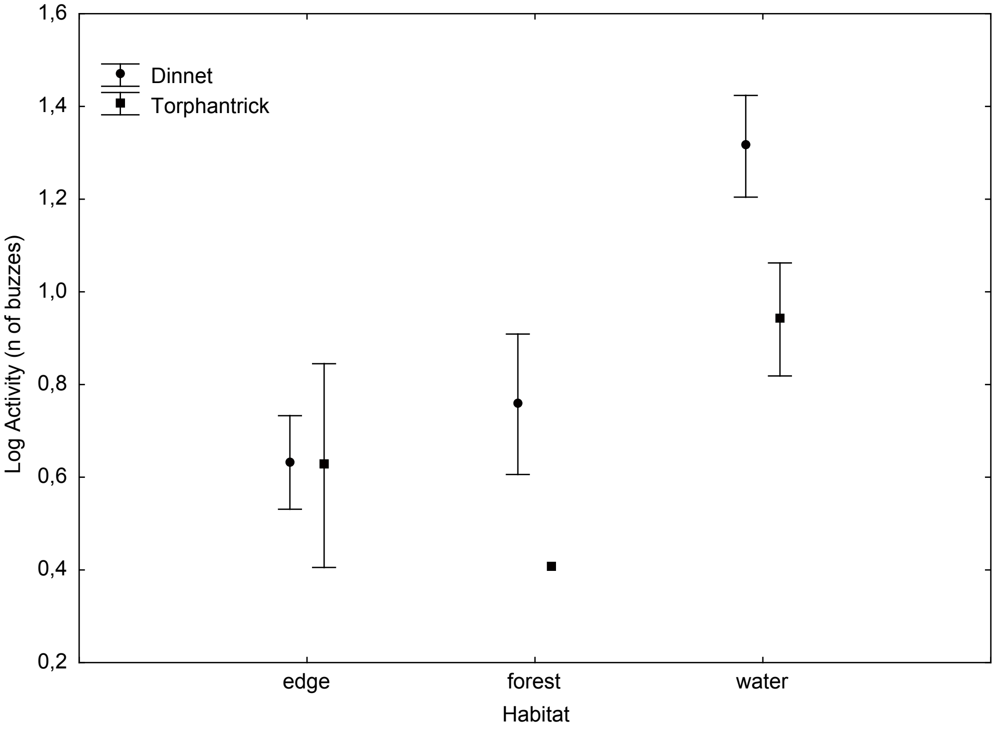

Fig. 2. The comparison of foraging activity of soprano pipistrelle (*P. pygmaeus*) between different habitats (near the water, meadow ecotone and forest) and sites. Activity = average number of recorded bat feeding buzzes (attacks) throughout one transect control (logarithmically transformed). Vertical poles = SE.

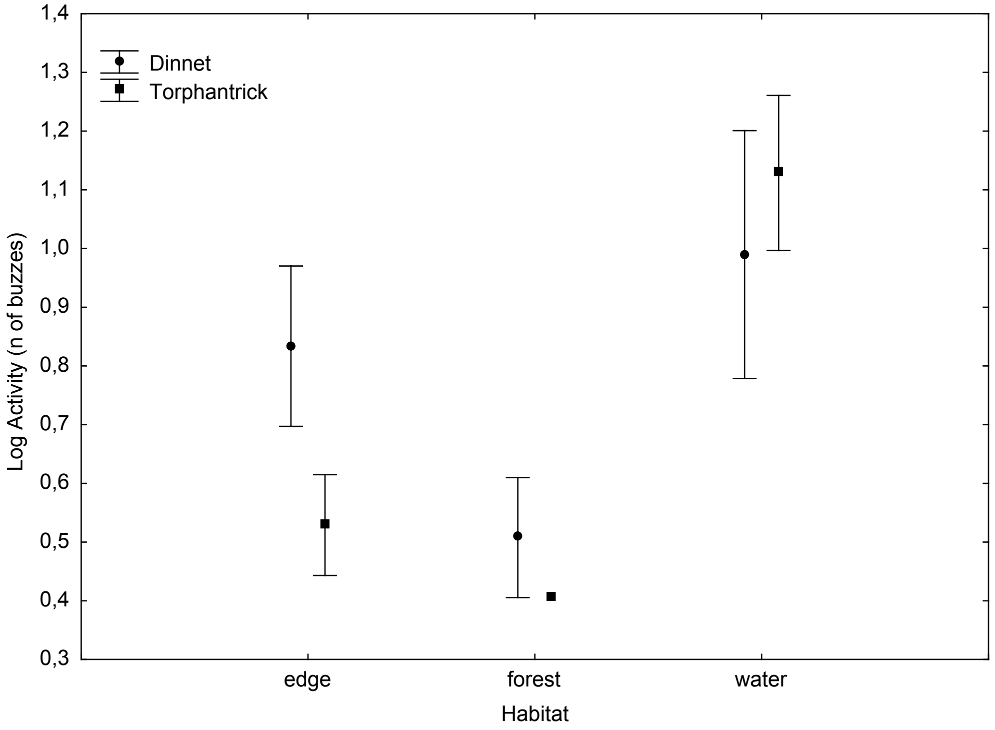

Fig. 3. The comparison of foraging activity of common pipistrelle (*P. pipistrellus*) between different habitats (near the water, meadow ecotone and forest) and sites. Activity = average number of recorded bat feeding buzzes (attacks) throughout one transect control (logarithmically transformed). Vertical poles = SE.

being much more attractive as a foraging area than the neighbouring mixed conifers. Bat activity in the birch forest was also more evenly distributed in comparison to the coniferous area. In both kinds of woodland, bats were most active near the water, but activity of bats inside the coniferous forest was minimal, whereas activity was relatively high throughout the birch forest.

Although both of these woodlands consist mostly of a single tree species, they differ in spatial structure (Forster and Green 1985). Species-rich bat communities can be found in both broadleaved and coniferous forests, as well as in mixed ones (Thomas 1988). However, age and spatial structure of a forest is considered to be one of the most important factors influencing the density and diversity of its inhabitants (McCaffery et al. 1981; Thomas 1988; Overcashet al. 1989; Rachwald 1992). Such factors as natural tree holes, the presence of dead trees and canopy gaps, influence bats directly (through the provision of shelters and space suitable for foraging) and indirectly (by impact on the number and diversity of flying insects). In Europe, spatial structure is usually a result of forest history, and past and present exploitation. From this point of view, the two areas compared in the present study differ substantially. Whereas Muir of Dinnet birch forest is a self-grown natural woodland 60+ years old, nowadays protected as a nature reserve, Torphantrick Wood, although of similar age, is a managed forest, partly artificially created, consisting mainly of introduced coniferous species like Douglas fir and Norway and Sitka spruce, with only a minor component of native birch. The dense structure of Torphantrick Wood, with only a few clearings made by woodcutting, is the result of forest management, whereas the less dense structure of Muir of Dinnet (which in part is almost park-like) is caused only by natural factors. The spatial structure of Muir of Dinnet is more favorable for bat foraging, especially for bats of the genus *Pipistrellus*, which prefer semi-open foraging areas and edge habitat (*e.g.* Walsh and Harris 1996; Racey and Swift 1985; Verboom and Huitema 1997). Only along the waterbodies was bat activity similar between these two sites. Another factor which could account for flight activity of a bat species is the presence of maternity colonies in the neighborhood. Both species studied are predominantly house-dwelling bats. From unpublished data (authors' observations) we know that a colony of soprano pipistrelles was located in Cambus O'May Hotel, less than 1 km from Torphantrick Wood, and

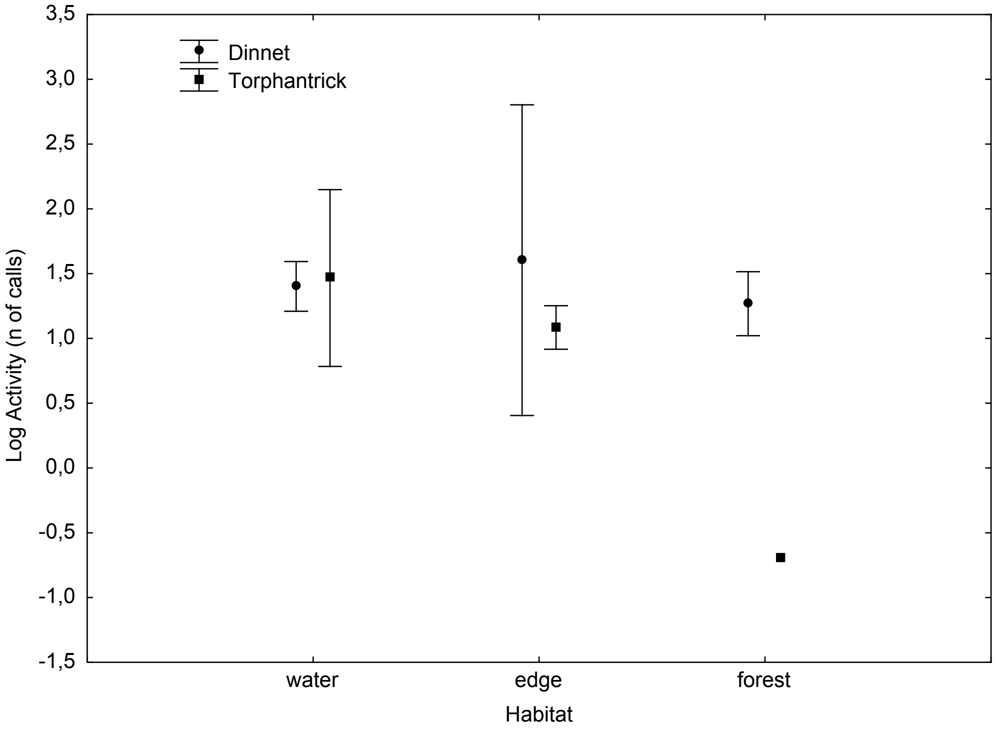

Fig. 4. The comparison of social activity (average number of sequences of social calls) of soprano pipistrelle (*P. pygmaeus*) between three habitats (near the water, meadow ecotone and forest) in both study sites. Activity = average number of recorded bat social calls throughout one transect control (logarithmically transformed). Vertical poles=SE.

another in a guest house in Lockhead (3 km from study area). Bat faeces were also found in several buildings in the vicinity of the study area.

The niche separation of the sympatric pipistrelles has been the subject of recent studies (Davidson-Watts and Jones 2006; Nicholls and Racey 2006; Kusch and Schmitz 2013; Ciechanowski 2015). Possible explanations of this could be based on several hypotheses: interspecific food competition (*e.g.* Birch 1979), interspecific non-competitive aggression/avoidance, a competitive situation in the species' evolutionary history (Connell 1980) or allopatric evolution (Mayr 1977; Hulva et al. 2004). According to the published literature, the habitat preferences of these two species are different (Walsh and Harris 1996; Vaughan et al. 1997), but the mechanism that causes these differences is not fully described. Although Barlow (1997) found differences in diet composition between these species in England, they were most manifest in the least important elements of the diet. On the other hand, Arnold et al. (2002) showed no significant differences in the diet of *P. pipistrellus* and *P. pygmaeus* in Germany. The slightly larger size of the common pipistrelle compared with the soprano pipistrelle suggests that differences in size of preferred food is possible, and could be associated with a slightly different ability to catch and eat bigger prey. Preliminary results from contemporary morphological studies (Sztencel et al. 2005) have shown that the jaw and mandible of *P. pipistrellus* is able to crush larger and harder prey than that of *P. pygmaeus*. But such evidence is two-sided: without supporting data from diet studies it shows only that *P. pipistrellus* can eat more diverse prey items than *P. pygmaeus.*

Usually *P. pygmaeus* prefers to forage in riparian habitats, whereas *P. pipistrellus* is less choosy, hunting in riparian, meadow and small woodland habitats (*e.g.* Bartonička and Řehák 2004). Such patterns of behaviour are most visible in the areas where these two species live sympatrically (Nicholls and Racey 2006; Ciechanowski 2015). According to Kusch and Schmitz (2013) a restricted distribution of *P. pygmaeus* (and another similar species *P. nathusii*) compared to *P. pipistrellus* may indicate a weaker habitat specialization of the latter species. The present study also found that *P. pygmaeus* was much more abundant than *P. pipistrellus* close to waterbodies. However, riparian habitats offer a higher density of potential prey than other habitats (Barclay 1991; de Jong and Ahlen 1991; Iwata et al. 2003), and because of this they are optimal foraging areas, particularly for generalist species. The fact that social vocalizations of *P. pygmaeus* were much more frequent near water, and that they were vocalizing proportionally much more frequently than *P. pipistrellus*, suggests that such a situation can be caused by interspecific competition. However, the results of playback experiments (Barlow and Jones 1997) do not support the hypothesis of direct interspecific influence of social calls on behaviour of these bats. Substantial data, concerning the habitat preferences of *P. pipistrellus* where it occurs allopatrically, are lacking. It is possible that the results of such research could help to solve the question of whether *P. pipistrellus* is a true habitat generalist.

CONCLUSIONS

In naturally-grown birch woodland soprano pipistrelles preferred mostly riparian habitats, whereas common pipistrelle was less choosy, flying in riparian, meadow and small woodland habitats more equally (Fig. 1). Neighbouring coniferous woodland area constituted generally less attractive habitat. Soprano pipistrelles were generally more abundant (Table 1), although its abundance was significally highest near waterbodies. Social activity of this species was also especially high in riparian areas (Fig. 4), which could suggests possible competitive interactions, both intra- and interspecific. Further studies of habitat preferences of common pipistrelle living in allopatry (without influence of sibling species) are needed for conclusion, is the observed distribution of common pipistrelle between habitats result of preferences of this species, or mostly interspecific competition.

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