Roosts, echolocation calls and wing morphology of two phonic types of *Pipistrellus pipistrellus*

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Abstract

Variation in the number of bats in maternity roosts of two phonic types of *P. pipistrellus* was investigated. Also, bats of the two phonic types were caught at maternity roosts, and their wing morphology and echolocation calls studied. 45 kHz *P. pipistrellus* maternity roosts contained significantly fewer bats than 55 kHz *P. pipistrellus* roosts. There was significant variation in mean frequency of maximum energy (FMAXE) of echolocation calls used by bats among roosts of 55 kHz *P. pipistrellus*, but not among roosts of 45 kHz *P. pipistrellus*. However, within each phonic type differences among roosts only accounted for a small proportion of the variation in echolocation call frequency; a much larger proportion was due to differences among individuals. Forearm length, an indicator of body size, was larger in 45 kHz *P. pipistrellus* than in 55 kHz *P. pipistrellus*, but there was no relationship between body size and geographic roost location in either phonic type. Variation in echolocation call frequency was not correlated with body size in either phonic type. Variation in echolocation call frequency among individuals may allow roost members to identify others in their group, but it is more likely to have evolved as a result of other influencing factors. Some variables of wing morphology differed between the two phonic types, but it is not clear how these differences relate to flight performance.

Key words: *Pipistrellus pipistrellus*, cryptic species, ultrasound, body size, ecomorphology

Introduction

Maternity roosts of the vespertilionid bat *Pipistrellus pipistrellus* (Schreber, 1774) are formed from May to July in the British Isles. These maternity roosts are aggregations of mainly adult female bats and their pups (Stebbings 1968; Speakman et al. 1991) and are usually found in buildings (Corbet and Harris 1991). Adult females may occupy a number of different roosts during the year, but are often loyal to the same set of roosts for several years (Thompson 1992). The number of females in roosts of *P. pipistrellus* in the British Isles varies widely from a few bats to over a thousand in some cases (Speakman et al. 1991); up to double that number emerge from roosts when young bats are flying, usually during July.

In this study, we investigated the roosting ecology and wing morphology of *P. pipistrellus* in the British Isles. *P. pipistrellus* exists as two phonic types over much of Europe (Jones and van Parijs 1993). Search-phase echolocation calls (Griffin et al. 1960) of these phonic types have a frequency of maximum energy (FMAXE) at around 55 kHz in one type, and at around 45 kHz in the other. We will refer to the phonic types as 45 kHz *P. pipistrellus* and 55 kHz *P. pipistrellus* throughout this study, though there is now unequivocal evidence that they are cryptic species (Barratt et al. 1997; Barlow

1997; Barlow and Jones 1997 a, b; Barlow et al. 1997; Jones 1997). The nomenclature of *P. pipistrellus* is currently being amended accordingly by the International Commission on Zoological Nomenclature.

There are several benefits to animals living in groups, which may include increased access to resources, information transfer, decreased risk of predation, and increased reproductive success (Hamilton 1971; Ward and Zahavi 1973; Pulliam and Caraco 1984; Brown 1988; Wilkinson, 1992; Speakman et al. 1992; Speakman et al. 1995; Fenton et al. 1994). Roosting communally may also have energetic benefits (Trune and Slobodchikoff 1976; Roverud and Chappell 1991). There are costs, however, of coloniality, including for example increased parasite loads (Brown and Brown 1986; Barclay 1988; Lewis 1996). Optimal colony size will differ according to ecological circumstances. We predicted that the two phonic types of *P. pipistrellus* might have different colony sizes since they show differences in diet (Barlow 1997) and in habitat use (Vaughan et al. 1997 a).

Group cohesion may be achieved by bats if individuals produce individually identifiable communication calls specifically to maintain group coherence or to identify their relatives (e.g. Balcombe 1990; Rasmuson and Barclay 1992; Scherrer and Wilkinson 1993) or their group mates (e.g. Cheney and Seyfarth 1982; Ford 1989; Wilkinson and Boughman 1998). Bat echolocation calls may function in communication (Fenton 1985, 1994). Pearl and Fenton (1996) suggest that echolocation call structure may be colony-specific and used in group recognition, and therefore in the maintenance of group cohesion. There is variation in echolocation call frequency among individual *P. pipistrellus* (Miller and Degn 1981), which could allow individual or colony identification, although individual variation may be caused by sex, or body size effects (Jones 1995).

Bats of the two phonic types of *P. pipistrellus* use separate maternity roosts (Jones and van Parijs 1993). First, we counted and compared the numbers of bats in maternity roosts of the two phonic types. Second, we measured body size, indicated by forearm length, and variables of wing morphology of the phonic types. We also investigated variation in body size with geographical roost location in the two phonic types. Third, we investigated whether variation in echolocation call frequency could be explained at the individual level by correlating with body size, or at the roost level by varying among roosts.

Material and methods

Roost counts

The number of adult bats in maternity roosts of the two phonic types were counted at evening emergence between late May and early July 1992-6. In most cases, time-expanded recordings of echolocation calls were recorded as bats emerged from the roosts, and a Sona-Graph was used to determine the phonic type of the bats. Overlap in the frequency of maximum energy in echolocation calls between phonic types is small (<5%, Jones and van Parijs 1993), and roosts can be ascribed to phonic type unambiguously when large numbers of bats are recorded. For some roosts the heterodyne output of a bat detector (S-25; Ultra Sound Advice, London, UK), tuned first to 45 kHz and then to 55 kHz, was used to determine phonic type. Roost counts were transformed with the square root transformation to achieve normality (Zar 1984). The number of bats in roosts of each phonic type was compared with a t-test.

Bat capture at roosts

Adult female bats were caught with a hand-net during evening emergence at 16 roosts of each of the two phonic types during June 1993–1996. The length of the left forearm was measured to the nearest 0.1 mm with dial callipers, as an index of body size, and a wing tracing was made of the left wing of each captured bat. A magnetic tablet (SummaSketch III, Summagraphics, Fairfield, USA) and software written by Professor J. M. V. Rayner (School of Biological Sciences, University of Bristol) were

used to digitise the wing tracings and morphological variables were measured from them (NORBERG and RAYNER 1987). Variables measured were wingspan (B), total wing area (S), hand-wing area (HWA), hand-wing length (HWL), arm-wing area (AWA), and arm-wing length (AWL); variables calculated were aspect ratio (AR), tip length ratio (TL), tip area ratio (TS), and tip shape index (I).

Each bat was released from the hand in open habitat, and its echolocation call sequence was recorded via the high frequency output of a bat detector (S-25) to a Portable Ultrasound Processor (PUSP; Ultra Sound Advice, London, UK). A 2.2 s sequence of digitised signal (sampled at 448 kHz) was stored in the PUSP and replayed to a Walkman (WM-D6C; Sony, Tokyo, Japan) at one tenth of the original speed. The bat detector (S-25) microphone had a response of ± 3 dB from 20–120 kHz; the Walkman had a response of ± 3 dB from 40 Hz to 15 kHz. The recordings were analysed by using a Digital Signal Processing Sona-Graph (5500; Kay Elemetrics, Pine Brook, New Jersey, USA; 512 point fast Fourier transform with Hamming window, 400 Hz frequency resolution). The mean frequency containing most energy (FMAXE) of calls produced by each bat was calculated from power spectra of 3–6 echolocation calls. Each roost was considered to be composed of either 45 kHz *P. pipistrellus* or 55 kHz *P. pipistrellus*, on the basis of the mean FMAXE of all bats caught from that roost. Roosts were assigned to 45 kHz *P. pipistrellus* if the roost mean FMAXE was less than 49 kHz, and to 55 kHz *P. pipistrellus* if the roost mean FMAXE was greater than 52 kHz (JONES and VAN PARIJS 1993). This categorisation allowed unambiguous separation of the phonic types, with each phonic type corresponding to the two different genotypes with a sequence divergence of >11% in the cytochrome *b* gene of mitochondrial DNA identified by BARRATT et al. (1997).

Variation in FMAXE of echolocation calls among roosts of each phonic type was investigated by using analysis of variance (ANOVA). Variance component estimates were calculated to determine how much variation in FMAXE was explained by differences among roosts, and how much by differences among individuals (SOKAL and ROHLF 1995). Variables of wing morphology were compared between phonic types with t-tests or Mann Whitney tests. Geographical variation in forearm length, according to roost location, was investigated by using multiple least squares regression analysis on roost latitude and longitude for each phonic type. The relationship between individual forearm length and FMAXE was investigated in the two phonic types.

Results

Roost counts

The number of bats in 33 roosts of 45 kHz *P. pipistrellus* ranged from 20 to 223, with a median of 76 bats. The number of bats in 40 roosts of 55 kHz *P. pipistrellus* ranged from 30 to 650, with a median of 203 bats. There were significantly more bats in 55 kHz *P. pipistrellus* roosts than in 45 kHz *P. pipistrellus* roosts ($t_{71} = 6.15$, $P < 0.001$; Fig. 1).

Echolocation calls

The 16 roosts of each of the two phonic types at which bats were caught are shown in figure 2; between 6 and 20 adult female bats were caught at each roost. Figure 3 shows the distribution of individual FMAXE in the two phonic types. A comparison of FMAXE of echolocation calls found in this study and in previous studies of the two phonic types of *P. pipistrellus* is shown in table 1. In 45 kHz *P. pipistrellus*, there was no significant difference in FMAXE among roosts ($F_{15,165} = 1.66$, NS; Tab. 2). Variance component estimates showed that only 5.5% of the variation in FMAXE was explained by differences among roosts, whereas 94.5% was explained by differences among individuals. In 55 kHz *P. pipistrellus*, there was a significant difference in FMAXE among roosts ($F_{15,204} = 3.45$, $P < 0.00$, Tab. 2). Variance component estimates showed that 15.2% of the variation in FMAXE was explained by differences among roosts, and 84.8% by differences among individuals. Three bats (of 401 recorded) which were assigned to 45 kHz *P. pipistrellus* on the basis of roost mean FMAXE, had FMAXE in the range 52–54 kHz (Fig. 3). These three individuals were therefore not included in further analysis.
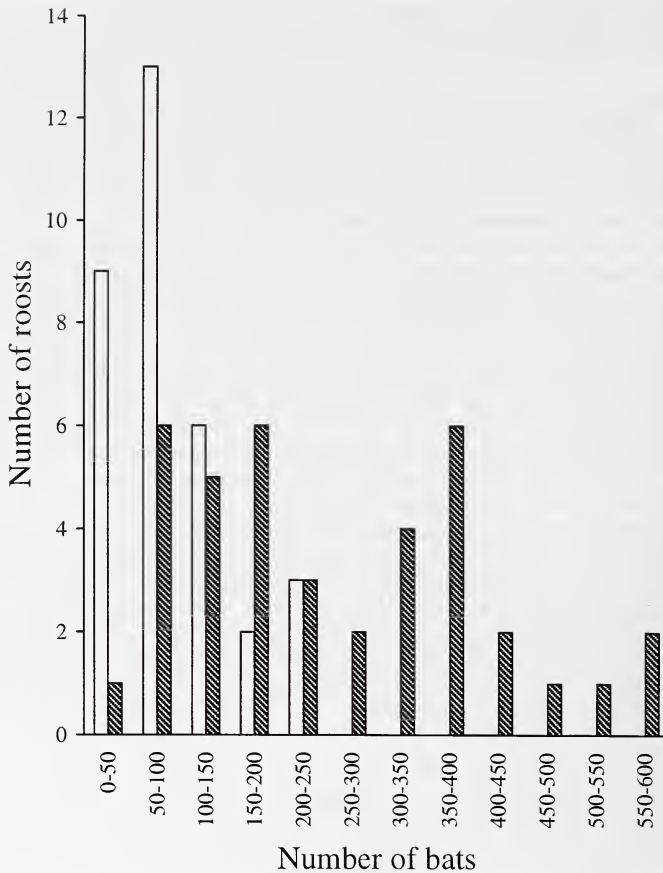
Fig. 1. Histogram showing the frequency distribution of the number of bats in 45 kHz *P. pipistrellus* roosts (white bars) and in 55 kHz *P. pipistrellus* roosts (hatched bars). There were significantly more bats in 55 kHz *P. pipistrellus* roosts than in 45 kHz *P. pipistrellus* roosts.

Wing morphology

There was much overlap in forearm length (mm) between the two phonic types (45 kHz *P. pipistrellus*: mean = 32.0, sd = 0.82, range 29.9–33.9, n = 178; 55 kHz *P. pipistrellus*: mean = 31.7, sd = 0.77, range 29.9–33.7, n = 220; Fig. 4). However, forearm length was significantly longer in 45 kHz *P. pipistrellus* than in 55 kHz *P. pipistrellus* ($t_{396} = 3.87$, P < 0.001). Multiple regression analysis of forearm length on two measures of geographical roost location, latitude and longitude, showed that there was no relationship between forearm length and roost location in either 45 kHz *P. pipistrellus* ($r^2 = 0.024$, $F_{2,175} = 2.12$, NS) or 55 kHz *P. pipistrellus* ($r^2 = 0.012$, $F_{2,217} = 1.28$, NS). There was also no correlation between forearm length and FMAXE of echolocation calls in either 45 kHz *P. pipistrellus* ($r_{176} = 0.08$, NS), or 55 kHz *P. pipistrellus* ($r_{218} = -0.05$, NS). The variables B, S, HWA, HWL, AWL, TS, and I were all significantly larger in 45 kHz *P. pipistrellus* than in 55 kHz *P. pipistrellus* (Tab. 3). However, there was much overlap in all these variables between the two phonic types.

Fig. 2. A map of mainland Britain showing the roosts at which bats of the two phonic types of *P. pipistrellus* were caught. Open circles represent 45 kHz *P. pipistrellus* roosts (n = 16); closed circles represent 55 kHz *P. pipistrellus* roosts (n = 16).

Discussion

Wing morphology and echolocation calls

The FMAXE of echolocation calls of the two phonic types of *P. pipistrellus* recorded in this study was similar to that found in previous studies (JONES and VAN PARIJS 1993; VAUGHAN et al. 1997b), the two types differing by 8–9 kHz on average. It is unclear whether the three bats (0.75% of total) that were classified as 45 kHz *P. pipistrellus*, but whose FMAXE fell within the range of 55 kHz *P. pipistrellus* were in fact individuals of 45 kHz *P. pipistrellus* with unusually high FMAXE, or were individuals of 55 kHz *P. pipistrellus* in a 45 kHz *P. pipistrellus* roost.
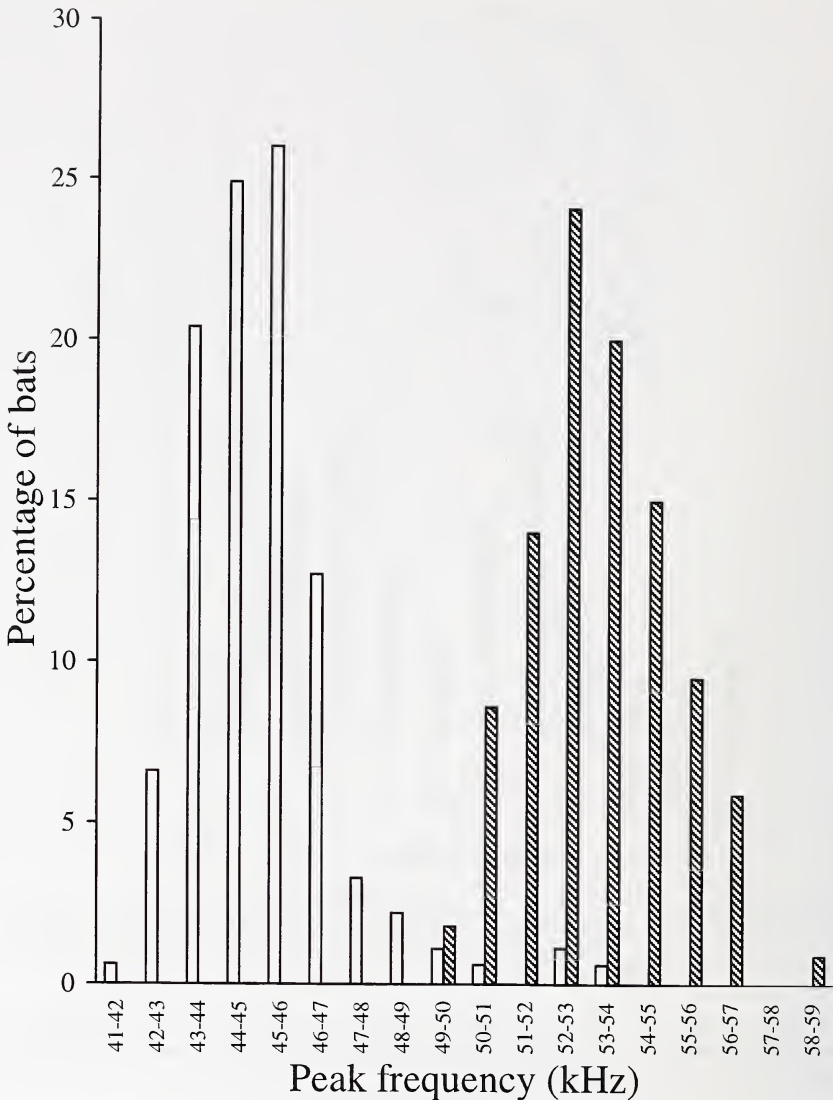
Fig. 3. Histogram showing the percentage distribution of FMAXE (kHz) of echolocation calls of bats of the two phonic types recorded as they were released from the hand. White bars represent the percentage of 45 kHz *P. pipistrellus* in each category (n = 181); hatched bars represent the percentage of 55 kHz *P. pipistrellus* in each category (n = 220).

In some species that produce FM echolocation calls, FMAXE decreases with increasing body size (JONES and RAYNER 1991; JONES and KOKUREWICZ 1994). In several other species, however, FMAXE of echolocation calls is not related to body size (NEUWEILER et al. 1987; JONES et al. 1992; JONES and RANSOME 1993; OBRIST 1995), and no such relationship has been found in *P. pipistrellus* (JONES et al. 1991; JONES and VAN PARIJS 1993). The absence of any relationship between FMAXE of echolocation calls and forearm length in the two phonic types is therefore not unexpected.

Table 1. Echolocation call FMAXE (kHz) of bats of the two phonic types of *P. pipistrellus*. Data are from this study, Jones and van Parijs (1993), and Vaughan et al. (1997 b). In the studies by Jones and van Parijs (1993) and Vaughan et al. (1997 b), bats were recorded as they emerged from roosts. In this study, bats were recorded as they were released from the hand.

	Mean	sd	Range	n
45 kHz *P. pipistrellus*				
This study	45.1	1.77	41.8–53.0	181
Jones and van Parijs (1993)	46.3	1.97	–	174
Vaughan et al. (1997 b)	46.0	1.77	41.6–50.8	60
55 kHz *P. pipistrellus*				
This study	53.2	1.76	49.6–58.0	220
Jones and van Parijs (1993)	55.1	2.62	–	398
Vaughan et al. (1997 b)	53.8	1.7	49.2–57.6	59

Table 2. Frequency of maximum energy (FMAXE) of echolocation calls (kHz) and forearm lengths (mm) of bats from 16 roosts of 45 kHz *P. pipistrellus* and 16 roosts of 55 kHz *P. pipistrellus*. Roosts are listed from north to south by latitude in each phonic type.

| Roost	FMAXE (kHz)		FA (mm)	
	Mean ± sd	Range	Mean ± sd	n
45 kHz *P. pipistrellus*				
Killiekrankie	46.7 ± 1.90	43.2–50.4	32.0 ± 0.87	14
Bleaton Hallet	45.3 ± 1.70	41.8–48.3	31.7 ± 0.57	18
Earswick	44.9 ± 1.47	42.7–47.6	32.8 ± 0.75	11
Claphouse Fold	44.5 ± 0.97	42.1–45.5	32.3 ± 0.68	9
Stone	44.9 ± 1.23	43.1–47.8	32.0 ± 0.76	18
Newton	44.3 ± 1.73	42.3–48.1	31.6 ± 0.73	9
Llanspyddid	45.0 ± 1.00	42.9–46.7	31.5 ± 0.82	9
Cambridge	45.0 ± 1.76	43.2–49.3	32.1 ± 0.88	10
Woodchester	43.9 ± 1.41	42.7–46.7	31.7 ± 0.61	6
Bwlch	44.2 ± 1.18	42.5–45.9	32.0 ± 0.88	10
Priston	45.2 ± 0.99	43.9–46.8	32.0 ± 0.51	7
Frensham	45.1 ± 1.55	42.7–47.2	31.9 ± 0.57	13
Ditcheat	44.5 ± 0.94	43.6–46.3	32.2 ± 0.97	10
Tracebridge	46.1 ± 1.45	44.9–48.9	31.6 ± 0.65	6
Trendeal	45.3 ± 2.06	42.4–49.0	31.5 ± 0.86	15
Trenowth	45.2 ± 0.66	44.1–46.4	32.3 ± 0.96	16
55 kHz *P. pipistrellus*				
Haddoo	53.6 ± 1.28	51.5–55.9	31.9 ± 0.92	19
Glen O'Dee	53.3 ± 1.87	50.6–56.7	32.0 ± 0.71	20
Larochmore	53.6 ± 1.82	50.0–56.2	31.5 ± 0.82	20
Inchmaggranakhan	55.0 ± 1.80	51.1–58.0	31.8 ± 0.64	14
Bretton	52.4 ± 1.69	49.9–56.1	31.5 ± 0.69	13
Beaumaris	52.6 ± 0.91	50.5–53.4	31.5 ± 0.60	9
Doveridge	52.0 ± 1.38	50.4–54.7	31.4 ± 0.70	18
Bromham	53.6 ± 0.59	52.7–54.5	31.8 ± 0.76	6
Llangors	53.0 ± 1.97	49.7–55.8	31.4 ± 0.86	10
Barrow	53.2 ± 1.57	50.5–56.2	31.7 ± 0.78	18
Winsley	53.4 ± 1.66	51.5–55.7	32.0 ± 0.71	9
Waterham	51.9 ± 1.33	49.6–53.7	31.5 ± 0.65	17
Sheephatch	54.4 ± 1.26	52.5–56.0	32.5 ± 0.43	7
Castle Cary	53.6 ± 1.67	50.9–56.2	31.0 ± 0.73	16
Puckington	53.4 ± 1.34	51.4–55.6	31.9 ± 0.92	9
High Hampton	52.8 ± 2.30	50.0–58.0	31.7 ± 0.58	15
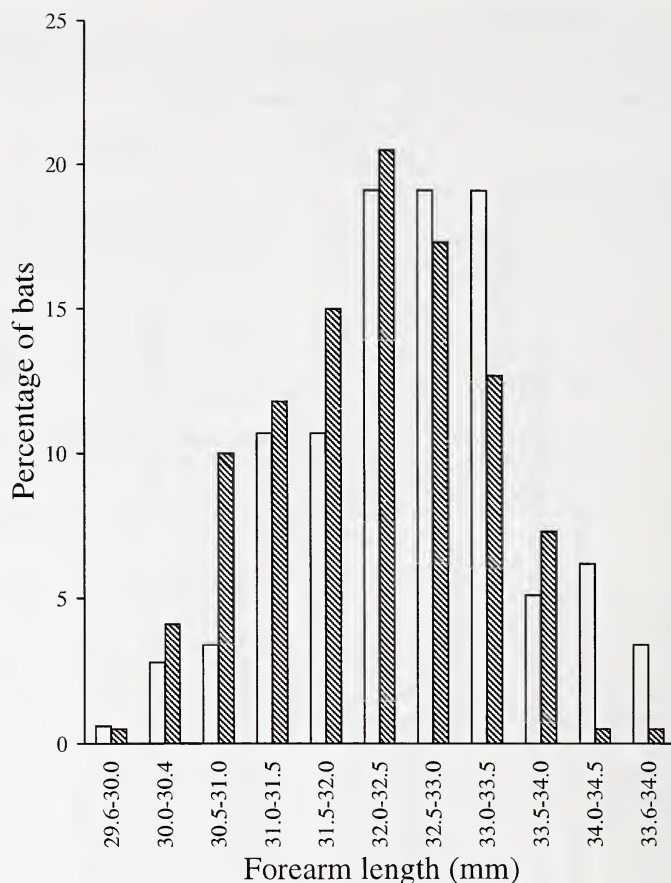
Fig. 4. Histogram showing the percentage distribution of forearm length (mm) of bats of the two phonic types. White bars represent the percentage of 45 kHz *P. pipistrellus* in each category (n = 178); hatched bars represent the percentage of 55 kHz, *P. pipistrellus* in each category (n = 220). Forearm was significantly longer in 45 kHz *P. pipistrellus* than in 55 kHz *P. pipistrellus*.

Table 3. Wing morphology of two phonic types of *P. pipistrellus*. Data are from 226 bats from 16 roosts of 45 kHz *P. pipistrellus* and 253 bats from 16 roosts of 55 kHz, *P. pipistrellus*. Statistics are from t-tests or Mann Whitney tests (W statistic) between phonic types. *P < 0.05, **P < 0.01, ***P < 0.001.

Variable	45 kHz *P. pipistrellus*		55 kHz *P. pipistrellus*		t
	Mean ± sd	range	Mean ± sd	range	
wingspan, B (mm)	217 ± 6.7	200–234	215 ± 7.2	192–232	2.62**
wing area, S (cm^2)	71.1 ± 4.5	57.0–84.4	70.1 ± 5.2	57.1–88.5	2.44*
hand-wing area, HWA (cm^2)	13.9 ± 0.9	10.7–16.1	13.4 ± 1.0	10.4–16.4	5.06***
arm-wing area, AWA (cm^2)	17.5 ± 1.7	13.2–21.9	17.3 ± 1.8	12.9–22.0	1.30
hand-wing length, HWL (mm)	53.5 ± 1.8	48.0–59.0	52.9 ± 0.2	47.0–58.0	3.50***
arm-wing length, AWL (mm)	44.8 ± 2.1	40.0–50.0	44.2 ± 2.4	38.0–50.0	2.78**
aspect ratio, AR	6.62 ± 0.28	5.83–7.43	6.62 ± 0.31	5.57–7.61	0.14
tip area ratio, TS	0.80 ± 0.08	0.63–1.03	0.78 ± 0.07	0.64–1.02	W = 57 144*
tip length ratio, TL	1.20 ± 0.06	1.02–1.39	1.20 ± 0.07	0.98–1.47	W = 61 118
tip shape index, I	2.11 ± 0.7	1.20–6.28	1.94 ± 0.5	1.15–5.63	W = 56 156**

In both phonic types, only a small percentage of the overall variation in FMAXE (around 3 kHz in each phonic type) was attributable to differences among roosts (5.5% in 45 kHz *P. pipistrellus*; 15.2% in 55 kHz *P. pipistrellus*). The small among-roost variation and the large interindividual variation found in FMAXE in both phonic types provide little support for the hypothesis of group recognition by echolocation call frequency suggested by Pearl and Fenton (1996). The results of this study suggest that it is more likely that interindividual variation in FMAXE in the two phonic types of *P. pipistrellus* has evolved as a result of factors not functionally related to group recognition. Whatever the reason for the observed interindividual variation, it may possibly allow recognition among bats in a roost (Masters et al. 1995). Odour may be more important in individual recognition in *P. pipistrellus*. Individuals of *P. pipistrellus* can recognise and discriminate between odours of conspecifics, both from their own and from other colonies (De Fanis and Jones 1995), suggesting that scent cues may be used by individuals in the identification of others, perhaps in conjunction with acoustic cues.

The small but significant difference found in body size, indicated by forearm length, between the two phonic types was in accordance with Jones and van Parijs (1993): 45 kHz *P. pipistrellus* is larger than 55 kHz *P. pipistrellus*. In some vespertilionids including *P. pipistrellus*, body size increases with increasing latitude north (Findley and Traut 1970; Stebbings 1973; Burnett 1983; Bogdanowicz 1990). Stebbings (1973) found that adult female *P. pipistrellus* tended to have longer forearms in the north and east of the British Isles. In this study, however, no such relationship between geographical roost location and forearm length was found in either of the two phonic types. There were small but significant differences between the two phonic types in most of the wing morphology variables measured, suggesting that they may differ in flight performance (Norberg and Rayner 1987). Aldridge (1986) showed that even small differences in wing morphology between morphologically similar bat species have significant effects on flight performance. Other studies, however, have found little evidence that small differences in wing morphology between species significantly affect foraging behaviour (e.g. Brigham et al. 1992; Saunders and Barclay 1992). We found no difference between the phonic types in aspect ratio (AR), an important parameter for flight efficiency (Norberg and Rayner 1987; Norberg 1994). This is in contradiction to Jones and van Parijs (1993), who found a significant difference in AR between the two phonic types. The larger tip shape index of 45 kHz *P. pipistrellus* suggests that it has more rounded wings than 55 kHz *P. pipistrellus* and may fly more slowly (Norberg and Rayner 1987).

In summary, differences in the roosting ecology and wing morphology found in this study between the two phonic types of *P. pipistrellus* corroborate existing evidence that they are cryptic species. Within each phonic type, variation in echolocation call frequency was small at the roost level and greater at the individual level, but could not be accounted for by body size variation.

Acknowledgements

Zusammenfassung

Quartiere, Echoortungslaute und Flügelmorphologie von zwei akustischen Typen von Pipistrellus pipistrellus

Bei zwei akustischen Typen von *Pipistrellus pipistrellus* wurden Unterschiede in der Zahl der Tiere in den Wochenstubenquartieren, in der Flügelmorphologie und bei den Ultraschallrufen untersucht. In Wochenstubenquartieren der 45 kHz *P. pipistrellus* waren signifikant weniger Tiere als in den Quartieren der 55 kHz *P. pipistrellus*. Die mittlere Hauptfrequenz der Ultraschallrufe variierte zwischen den Quartieren der 55 kHz *P. pipistrellus*; bei den 45 kHz *P. pipistrellus* wurde kein solcher Unterschied gefunden. Diese Unterschiede erklärten jedoch immer nur einen kleinen Teil der Variabilität in der Hauptfrequenz der Ultraschallrufe, ein weit größerer Teil wurde durch Unterschiede zwischen den Individuen erklärt. Bei den 45 kHz *P. pipistrellus* war die mittlere Unterarmlänge ein Maß für die Körpergröße, größer als bei den 55 kHz *P. pipistrellus*. Bei beiden Gruppen konnte jedoch kein Zusammenhang zwischen Körpergröße und geographischer Lage der Quartiere festgestellt werden. Bei beiden Gruppen waren die individuellen Unterschiede in der Hauptfrequenz der Ultraschallrufe nicht mit der Körpergröße korreliert. Individuelle Unterschiede in der Frequenz der Ultraschallrufe könnten der Erkennung anderer Koloniemitglieder dienen, wahrscheinlicher ist jedoch eine evolutive Entfaltung bedingt durch andere Faktoren. Verschiedene Merkmale der Flügelmorphologie unterschieden sich bei den Gruppen; es ist jedoch noch unklar, wie diese die Flugweise bestimmen.

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