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Foraging strategy and predation risk as factors influencing emergence time in echolocating bats

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SUMMARY

We hypothesized that interspecific differences in evening emergence time among echolocating bats are subject to natural selection through effects of variation in food availability and predation risk, both of which are related to flight technique and foraging strategy. We predicted that bats that feed on small aerial insects emerge relatively early to get access to the peak in flight activity of small dipterans at dusk. By emerging well before dark, however, they expose themselves to increased risks of predation and/or harassment from raptorial or insectivorous birds which may still be active. Bats that can feed independently of the dusk peak of dipterans, i.e. those that are adapted to feed on moths, on flightless or diurnal prey or on plants, would be expected to emerge later, thus minimizing the predation risk. We tested these predictions by analysis of two data bases: one including European bats only and another including a worldwide sample. The predictions were largely supported. The evening emergence time appears to be a function of dietary specializations and foraging strategy, and is probably also affected by the ability to avoid predation.

1. INTRODUCTION

The time that bats emerge to feed in the evening varies substantially from species to species even in the same place. In northern Europe, for example, noctules *Nyctalus noctula* often feed together with swifts at high elevation soon after sunset, and yet Daubenton's bat *Myotis daubentonii* and the brown long-eared bat *Plecotus auritus* typically do not emerge until half an hour or more later (personal observations).

The evening emergence of bat colonies is one of the most easily and most frequently studied aspects of bat behaviour. For example, emergence studies of bats have been done to illuminate questions about circadian rhythms (see, for example: DeCoursey & DeCoursey 1964; Voûte *et al.* 1974; Erkert 1982) and clustering behaviour (see, for example: Swift 1980; Speakman *et al.* 1994).

The general question of why bats nearly always feed during the night rather than during the day has received attention recently (see, for example: Speakman 1991, 1993, 1995). Here we address the related problem of why the emergence time differs so much among the various species of bats. This specific question has only been considered in one previous study as far as we know. Taake (1985) analysed a small (and biased) subset of European bats, and found that smaller species tended to fly out early in the evening whereas those with white bellies or long ears, which are mainly gleaners, tended to fly out late. He ascribed the late emergence of gleaners to increased

predation risk associated with their foraging technique, which demands slow flight.

The aim of this paper was to summarize the available data on evening emergence in echolocating bats and produce a functional hypothesis that may explain the interspecific variations observed, and hence to provide a basis for further, more detailed, studies. We concentrate on European species, with which we are most familiar, but we also make comparisons with bat faunas in other areas, including the tropics.

2. HYPOTHESES AND PREDICTIONS

Despite their taxonomic and ecological diversity, bats are almost universally nocturnal. Speakman (1991, 1993, 1995) suggests that this trait may be explained by increased predation risk for bats that fly in daylight, compared with those that fly in darkness, and perhaps also by increased competition from diurnal birds. At least in the temperate zone, the main predators on bats that fly in daylight or at dusk are the small hawks, e.g. *Accipiter* spp., and falcons, *Falco* spp., and the main potential competitors are aerial insectivorous birds like swallows, e.g. *Hirundo rustica*, and swifts, e.g. *Apus apus* (Speakman 1993).

Echolocating bats are probably much more susceptible to aerial predation and harassment than aerial insectivorous birds, because most bats are relatively slow fliers and also rely on echolocation rather than vision. Compared with vision, echoloca-

tion is a short range and relatively directional operation, and therefore probably less suitable for detection of approaching predators (Speakman 1993). Overall, owls and house cats may take many more bats than hawks and falcons do (Gillette & Kimbrough 1970), but since they are active and feed mainly during the night, they presumably have much less influence on the bats' emergence times than diurnal or crepuscular predators.

Some insects that constitute potential prey of bats, such as Nematocera and other small flies, often show marked peaks in flight activity around dusk and dawn and little activity during most of the night (see, for example: Lewis & Taylor 1965; Racey & Swift 1985). To exploit such crepuscular insects, bats may therefore have to leave their roost before it gets dark, hence exposing themselves to avian predators and competitors which may still be active at dusk.

We assume that the time bats emerge from their roost to feed in the evening is subject to natural

selection and we hypothesize that differences in evening emergence time between bat species reflect differential abilities to avoid predation and harassment from diurnal birds on one hand and the dependence on the dusk peak in insect flight activity on the other.

Fast flying, agile bats are probably less likely to be caught in flight by raptorial birds than slow flying, more manoeuvrable ones under the same prevailing conditions (high manoeuvrability demands slow flight, but high agility, i.e. ability to change direction rapidly, does not; Norberg & Rayner 1987). Hence, we predict that emergence time will be related to flight speed, which in turn depends on wing morphology and body mass, or, more specifically, on the wing loading (Norberg 1987, 1990). Fast flying bats, or those with high wing loadings, would thus be expected to emerge earlier, i.e. in brighter light conditions, than slow flying ones, or those with low wing loadings, everything else being equal.

Table 1. *Emergence times for 17 species of European bats together with data on wing loading (L), flight speed (V) and diet* (All wing loading data were measured by G.J. except for *Vespertilio murinus* and *Eptesicus nilssonii*, where data from Norberg & Rayner (1987) were used. A body mass of 10.2 g was used for *E. nilssonii* (J.R., unpublished), since this is more realistic than the value given by Norberg & Rayner (1987). Flight speeds were measured by multiple flash photography either by G.J. or by Baagøe (1987). Emergence times (minutes after local sunset) are medians, measured during at least five evenings in June, except for *V. murinus*, where only one value was available, and *M. bechsteini*, where data from August were used. All data were from Europe except for *N. lasiopterus*, which was observed in Japan. Dietary data are expressed either as percentage of total volume (*v*) or as percentage frequency of recovered fragments (*f*). Where several studies have been made on one species, mean values of all studies are given. The sources are: 1, G.J. (unpublished data); 2, Jones (1993); 3, Jones (1990); 4, McAney & Fairley (1988); 5, A.M. Hollyfield (personal communication); 6, McAney & Fairley (1989); 7, Baagøe (1987); 8, Wolz (1988); 9, Taake (1992); 10, Norberg & Rayner (1987); 11, Voûte *et al.* (1974); 12, Jones & Rayner (1988); 13, S.M. Swift (personal communication); 14, Nyholm (1965); 15, Sullivan *et al.* (1993); 16, Swift & Racey (1983); 17, DeCoursey & DeCoursey (1964); 18, Böhme & Natuschke (1967); 19, Bauerová (1978); 20, Laufens (1973); 21, Bauerová & Červený (1986); 22, Shiel *et al.* (1991); 23, Jones & Rayner (1989); 24, Bullock *et al.* (1987); 25, Swift *et al.* (1985); 26, T. Guillen (personal communication); 27, Maeda (1974); 28, McAney & Fairley (1990); 29, Pottier (1993); 30, Kronwitter (1988); 31, J. R. (unpublished data); 32, Rydell (1989); 33, Degn (1983); 34, Catto (1993); 35, Bauerová & Ruprecht (1989); 36, Rydell (1992); 37, Frylestam (1969); 38, R. Arlettaz (personal communication).)

bat species	$L/N\text{ m}^{-2}$	$V/\text{m s}^{-1}$	emergence time/min	latitude °N	small aerial insects (%)	moths (%)	flightless prey (%)	<i>f</i> or <i>v</i> sources
Rhinolophidae								
<i>Rhinolophus hipposideros</i>	5.1	3.5	31	53	13.5	18.7	2.5	<i>f</i> 2,4-6
<i>R. ferrumequinum</i>	10.6		25	51	3.8	40.6	0	<i>v</i> 1-3
Vespertilionidae								
<i>Myotis bechsteini</i>	9.0	4.9	33	49	0	0	47.1	<i>f</i> 2,7-9
<i>M. dasycneme</i>	10.4	6.0	64	53				7,10-11
<i>M. daubentonii</i>	7.0	4.1	84	60,57	41.7	2.9	4.2	<i>f</i> 2,12-16
<i>M. myotis</i>	11.2		66	51,49	0	0	82.0	<i>v</i> 10,17-19
<i>M. mystacinus</i>	6.4	4.3	32	51	49.3	34.7	7.8	<i>f</i> 2,5,7
<i>M. nattereri</i>	6.0	4.5	75	51,51	2.7	3.3	14.8	<i>v,f</i> 2,7,18,20-22
<i>Pipistrellus pipistrellus</i>	6.0	4.4	32	56	60.1	3.0	1.1	<i>f</i> 1,2,7,15,23-25
<i>Nyctalus lasiopterus</i>	19.7		-2	43				26,27
<i>N. leisleri</i>	15.2		18	53,49	24.1	10.7	0.1	<i>f</i> 1,2,15,28,29
<i>N. noctula</i>	17.3	6.8	5	48	21.7	18.4	0	<i>v</i> 1,2,7,30
<i>Eptesicus nilssonii</i>	9.1	5.0	26	58	46.9	17.1	1.9	<i>v</i> 1,7,10,31,32
<i>E. serotinus</i>	11.1	6.2	20	55,51	14.8	3.5	0	<i>f</i> 2,7,33,34
<i>Vespertilio murinus</i>	10.2	6.1	35	58	66.8	7.7	0.1	<i>v</i> 7,10,31,35,36
<i>Plecotus auritus</i>	5.9	3.2	54	57,58	5.1	31.4	18.2	<i>v,f</i> 2,5,7,13,22,32,37
Molossidae								
<i>Tadarida teniotis</i>			39	44	0	90.0	0	38

For bat species that are adapted to feed independently of the dusk peak in insect flight activity, there may be little or no benefit from flying out early, but only an added risk of doing so. Such bats may include those that catch their prey by gleaning from surfaces (see, for example, Bell 1982), and hence are able to exploit flightless or inactive prey, or those that specialize by feeding on moths (see, for example, Jones 1990), at least some of which are active more or less throughout the night (Taylor & Carter 1961; Lewis & Taylor 1965). Hence, gleaning bats and those that feed extensively on moths are predicted to emerge later than aerial-hawking species that feed on small flying insects. By the same argument, bats that feed on fruit, pollen or nectar in the tropics are predicted to emerge relatively late. While the predation risk presumably increases with the light level, the availability of fruit, for example, may be more or less the same throughout the 24h period.

3. DATABASES AND ANALYSIS

Ideally, data on evening emergence times of bats should be given as the mean or median of the whole colony over several nights and in relation to the local sunset time (Bullock *et al.* 1987), but, unfortunately, this has not always been done in the past. The time of emergence of the first bat, as given in most papers, is strongly dependent on colony size (Avery 1986), and may not reflect the typical behaviour of all individuals in the colony. To overcome this problem, we compiled two databases, the first including data that conform with the suggestions of Bullock *et al.* (1987), on European species (table 1), and a second much more extensive one (table 2), which also contains data that do not conform with Bullock *et al.* (1987).

The first database includes standardized measurements of wing loading, mostly made by G.J. (Jones 1993 and unpublished data), and in some cases flight speed of foraging bats measured, by multiple flash photography, by G.J. (unpublished data) or Baagøe (1987). It also includes median emergence times collected at nursery roosts during at least five evenings in June, which corresponds to the time of pregnancy in most European bats. For each colony, the emergence time is given as the mean across all nights of observation. Some species have been studied at more than one locality (colony). In these cases, the species' emergence time was computed as the mean across all colonies observed. The data in the European database were collected between 43 and 60°N and in most cases between 48 and 58°N degrees. To some extent, this restricts the possible confounding effects of latitude. By limiting the database to studies performed during pregnancy, possible seasonal effects on emergence time (see, for example, Rydell 1993) were minimized.

The worldwide database was primarily used to extend and confirm the results obtained from the European database. However, it was also used to test predictions on bats that do not feed on insects and to investigate whether emergence time varies according to latitude. For this database we had to use time of

emergence of the first bat in the colony, rather than median emergence time, because the former has been reported much more frequently. Fortunately, both were given by some authors, and they were significantly correlated ($r_{42} = 0.67$, $P < 0.001$). For this database, we did not restrict the emergence time data to the period of pregnancy, but also included observations made at other times of the year.

To test predictions related to the foraging strategy and diet, each bat species for which food habits have been investigated was classified according to the most important (most frequent or most voluminous) component in the diet. We assumed that the diet reflects the prevailing foraging strategy. The following categories were used: (i) small aerial prey, i.e. nocturnal or crepuscular dipterans excluding the relatively large tipulids, indicating an aerial-hawking foraging strategy, (ii) moths, which may indicate either a gleaning or an aerial-hawking foraging strategy or both, (iii) flightless or mainly diurnal (nocturnally inactive) arthropods, indicating a gleaning foraging strategy, and (iv) fruit, nectar or pollen, likewise indicating a gleaning foraging strategy. In addition, we considered bats that normally feed low over open water as a special case (v). These species sometimes fly in extremely exposed situations, but yet differ in an important respect from most other bats that fly in the open in that they often have low wing loadings, which indicate slow and manoeuvrable flight (Norberg & Rayner 1987).

In some cases, beetles (Coleoptera) were reported to be the most important prey items. However, we did not include 'beetle feeders' as a special category, because little is known about the activity patterns of the beetles in question. Instead, we used the second most important prey category of these bats in the analysis.

Throughout the paper, emergence times are related to local sunset times at sea level, as given by almanacs. The analyses were performed by using MINITAB release 9 for Microsoft Windows. Analyses of Covariance (ANCOVAs) were performed under the GLM command, since models were of unbalanced design.

4. RESULTS

(a) European database

The correlation between wing loading and flight speed across the species for which both have been measured ($n = 10$) was highly significant ($r = 0.91$, $P < 0.001$). This may justify the use of wing loading as a predictor of flight speed.

The correlation between latitude of observation and emergence time across all species ($N = 17$) was low and non-significant ($r = 0.27$, $P > 0.1$, Spearman's Rank Correlation). This suggests that differences in latitude may not confound the results seriously.

In accordance with our predictions, emergence time was negatively correlated with wing loading ($r_{14} = -0.50$, $P < 0.05$; figure 1a), and also with actual flight speed ($r_{10} = -0.58$, $P < 0.05$; figure 1b). On average, large bats left the roost earlier than small

Table 2. *Emergence times of bats studied worldwide together with data on wing loading (L) and flight speed (V)*

(Tropical species are denoted by Tr and temperate ones by Te. Dietary categories, according to the most frequent or most voluminous prey, are: D, small aerial prey (mainly dipterans); G, flightless or diurnal arthropods, i.e. gleaners; L, moths; C, beetles; W, bats that mainly feed low over water; P, pollen and nectar; and F, fruit. Emergence times listed here may differ from those in table 1 because more studies were included (the criteria for inclusion were less rigid). The sources are: 1, Norberg & Rayner (1987); 2, Gaur (1980); 3, Subbaraj & Chandrashekar (1977); 4, Tiedemann *et al.* (1985); 5, McDonald *et al.* (1990); 6, Fenton *et al.* (1977); 7, Funakoshi & Uchida (1980); 8, Jones (1990); 9, Jones (1993); 10, G.J. (unpublished data); 11, A. M. Hollyfield (personal communication); 12, McAney & Fairley (1988); 13, Gaisler (1963); 14, Harmata (1960); 15, Vaughan (1977); 16, Marimuthu (1984); 17, Link *et al.* (1986); 18, Silva Taboada (1979); 19, Goodwin (1928); 20, Vaughan (1959); 21, Ross (1967); 22, Morrison (1980); 23, Silva Taboada & Pine (1969); 24, Taake (1992); 25, Wolz (1988); 26, Baagøe (1987); 27, Voûte *et al.* (1974); 28, Nyholm (1965); 29, Swift & Racey (1983); 30, S. M. Swift (personal communication); 31, Krull *et al.* (1991); 32, Bauerová (1986); 33, Nagorsen & Brigham (1993); 34, Warner (1985); 35, O'Farrell & Studier (1975); 36, Griffith & Gates (1985); 37, Anthony & Kunz (1977); 38, Whitaker & Lawhead (1992); 39, Belwood & Fenton (1976); 40, Buchler (1976); 41, Whitaker *et al.* (1977); 42, Patterson & Hardin (1969); 43 Kuthe (1989); 44, Böhme & Natuschke (1967); 45, DeCoursey & DeCoursey (1964); 46, Roer (1968); 47, Bauerová (1978); 48, Bauerová & Červený (1986); 49, Shiel *et al.* (1991); 50, Erkert (1978); 51, Twente (1955); 52, Kunz (1974); 53, Barclay (1985); 54, Funakoshi & Uchida (1978); 55, Prakesh (1962); 56, Isaac & Marimuthu (1993); 57, Jones & Rayner (1989); 58, Negro *et al.* (1992); 59, Swift (1980); 60, VENABLES (1943); 61, Bullock *et al.* (1987); 62, Stebbings (1968); 63, Swift *et al.* (1985); 64, Sullivan *et al.* (1993); 65, Maeda (1974); 66, T. Guillen (personal communication); 67, McAney & Fairley (1990); 68, Pottier (1993); 69, Kronwitter (1988); 70, Brigham & Saunders (1990); 71, J. R. (unpublished data); 72, Rydell (1989); 73, Eisentraut (1952); 74, Catto (1993); 75, Degn (1983); 76, Glas (1980–81); 77, Bauerová & Ruprecht (1989); 78, Rydell (1992); 79, Clem (1992); 80, Whitaker & Clem (1992); 81, Cueva (1992); 82, Barclay (1989); 83, Frylestam (1969); 84, Clark *et al.* (1993); 85, Sample & Whitmore (1993); 86, Leonard & Fenton (1983); 87, Easterla & Whitaker (1972); 88, Freeman (1981); 89, Black (1974); 90, Bell (1982); 91, O'Shea & Vaughan (1977); 92, Funakoshi & Uchida (1975); 93, Dwyer (1964); 94, Herreid & Davis (1966); 95, R. Arlettaz (personal communication); 96, Gould (1961); 97, McWilliam (1989); 98, Norberg (1987); 99, Chase *et al.* (1991).)

bat species	time of first emergence/min	time of median emergence/min	$L/N\text{ m}^{-2}$	$V/\text{m s}^{-1}$	diet class	source
Rhinopomatidae						
<i>Rhinopoma microphyllum</i> (Tr)	32		20.5			1,2
Emballonuridae						
<i>Taphozous melanopogon</i> (Tr)	24		25.9			1,3
Megadermatidae						
<i>Macroderma gigas</i> (Tr)		86	12.0		G	1,4
Rhinolophidae						
<i>Rhinolophus capensis</i> (Te)	20					5
<i>R. clivosus</i> (Te)	42				C	5,6
<i>R. cornutus</i> (Te)	3	14				7
<i>R. ferrunquinum</i> (Te)	19	25	10.6		L	8,9
<i>R. hipposideros</i> (Te)	19	30	5.1	3.5	L	9,10–14
Hipposideridae						
<i>Hipposideros commerconi</i> (Tr)	30		15.7		C	1,15
<i>H. speoris</i> (Tr)	10		8.9			1,16,17
Noctilionidae						
<i>Noctilio leporinus</i> (Tr)	3	20	12.0	8.9	W	18,19
Mormoopidae						
<i>Pteronotis parnellii</i> (Tr)	10	23	6.5		L	18
<i>P. quadridens</i> (Tr)	–11	–1	5.0		D	18
<i>P. macleayii</i> (Tr)	8	19	5.5		D	18
<i>Mormoops blainvillii</i> (Tr)	22	39	4.8		L	18
Phyllostomidae						
<i>Macrotus californicus</i> (Te)	51		10.2		G	1,20,21
<i>M. waterhousii</i> (Tr)	26	34	7.7		L	18
<i>Monophyllus redmani</i> (Tr)	28	49	8.6		P	18
<i>Vampyroides caraccioli</i> (Tr)	45		14.5		F	1,18
<i>Artibeus jamaicensis</i> (Tr)	4	26	12.7	8.2	F	18,22
<i>Brachyphylla nama</i> (Tr)	48	65	12.9		P	18
<i>Erophylla sezekorni</i> (Tr)	53	77	14.5		F	23
<i>Phyllonycteris poeyi</i> (Tr)	32	52	12.7		P	18

Table 2. Continued

bat species	time of first emergence/min	time of median emergence/min	$L/N \text{ m}^{-2}$	V/ms^{-1}	diet class	source
Natalidae						
<i>Natalus micropus</i> (Tr)	14		3.0		L	18
<i>N. lepidus</i> (Tr)	-8	1	3.6		D	18
Vespertilionidae						
<i>Myotis bechsteinii</i> (Te)	30	33	9.0	4.9	G	9,24-26
<i>M. dasycneme</i> (Te)	43	64	10.4	6.0	W	1,26,27
<i>M. daubentonii</i> (Te)	73	84	7.0	4.1	W	9,26,28-30
<i>M. emarginatus</i> (Te)	17				G	31,32
<i>M. evotis</i> (Te)	25		6.1		L	33,34
<i>M. lucifugus</i> (Te)	6	23	7.5	5.7	D	1,35-42
<i>M. myotis</i> (Te)	34	69	11.2		G	1,14,43-47
<i>M. mystacinus</i> (Te)	28	33	6.4	4.3	D	9,11,26
<i>M. nattereri</i> (Te)	31	60	6.0	4.5	G	9,24,26,44,48,49
<i>M. nigricans</i> (Tr)	23		6.1			1,50
<i>M. tricolor</i> (Te)	57		8.2			1,5
<i>M. velifer</i> (Te)	25	37	6.3	6.2	D	1,20,51,52
<i>Lasionycteris noctivagans</i> (Te)	36		8.2		D	1,53
<i>Pipistrellus abramus</i> (Te)	12	15				54
<i>P. mimus</i> (Te)	5	9	6.2			1,55,56
<i>P. pipistrellus</i> (Te)	21	33	6.0	4.4	D	9,10,14,26,57-64
<i>Nyctalus lasiopterus</i> (Te)		-2	19.7			65,66
<i>N. leisleri</i> (Te)	3	17	15.2		D	9,10,64,65,68
<i>N. noctula</i> (Te)	8	8	17.3	6.8	D	9,10,26,69
<i>Eptesicus fuscus</i> (Te)	20	5	9.4	9.3	D	1,18,33,36,42,70
<i>E. nilssonii</i> (Te)	9	26	9.1	5.0	D	1,10,26,71,72
<i>E. serotinus</i> (Te)	26	21	11.1	6.2	D	9,14,26,73-76
<i>Vespertilio murinus</i> (Te)	19	35	10.2	6.1	D	1,26,71,77,78
<i>V. superans</i> (Te)	10	25			L	54
<i>Nycticeius humeralis</i> (Te)		11	10.7		L	1,79,80
<i>Lasiurus borealis</i> (Tr)	9		6.6	6.6	C	18,81
<i>L. cinereus</i> (Te)	25	40	16.5	7.0	L	1,81,82
<i>Plecotus auritus</i> (Te)	33	44	5.9	3.2	L	9,11,26,29,48,72,83
<i>P. townsendii</i> (Te)	19	46	7.2		L	1,84,85
<i>Euderma maculatum</i> (Te)	32	49			L	86-88
<i>Anthrozous pallidus</i> (Te)	41		8.1		G	1,50,89,90,91
<i>Miniopterus schreibersii</i> (Te)	12	37	10.2		D	1,5,92,93
Molossidae						
<i>Tadarida brasiliensis</i> (Tr, Te)	4	19	11.5		D	1,18,88,94
<i>T. teniotis</i> (Te)		38			L	95
<i>T. femorosacca</i> (Tr)	45				L	96
<i>T. pumila</i> (Tr)	27		11.8	8.3		97,98
<i>Mormopterus minutus</i> (Tr)	-16	2	8.9		D	18
<i>Eumops glaucinus</i> (Tr)	4	19	15.4			18
<i>E. perotis</i> (Te)	50		25.1		L	1,20,88
<i>Molossus ater</i> (Tr)	9		23.4		D	1,50,88
<i>M. molossus</i> (Tr)	-15	0	16.0		D	18,99

bats, but the correlation between emergence time and body mass was not significant ($r_{15} = -0.47$, $P > 0.05$).

Emergence time was related to diet and hence to the predominant foraging strategy used. For example, late emergence was significantly associated with a high proportion of flightless taxa in the diet, which is indicative of a gleaning foraging strategy ($r_{12} = 0.82$, $P < 0.001$, Spearman's Rank Correlation; figure 2).

The effect of diet on emergence time was further analysed by using ANCOVA with wing loading, as an indicator of flight speed, as a covariate. The analysis showed that both wing loading and diet affected the emergence time significantly ($F_{1,10} = 5.68$, $P < 0.05$ and $F_{3,10} = 9.23$, $P < 0.01$, respectively). The

adjusted mean emergence times were 27.2 min after sunset (s.d. 4.8, $n = 7$) for bats that feed mainly on small aerial prey (i), 31.3 min (s.d. 7.4, $N = 4$) for those that feed mainly on moths (ii), 56.1 min (s.d. 7.0, $N = 3$) for those that feed on flightless or diurnal prey, i.e. the gleaners (iii), and 72.1 min (s.d. 8.6, $N = 2$) for those that feed mainly low over water (v). Significant differences ($P < 0.05$) existed between two of the pairs of adjusted means (i and iii, i and v; Gabriel comparison intervals; Sokal & Rohlf 1981). Thus bats that feed mainly on small aerial prey emerged significantly earlier than gleaners and bats that fly low over water, even after variation in wing loading among groups was controlled for.

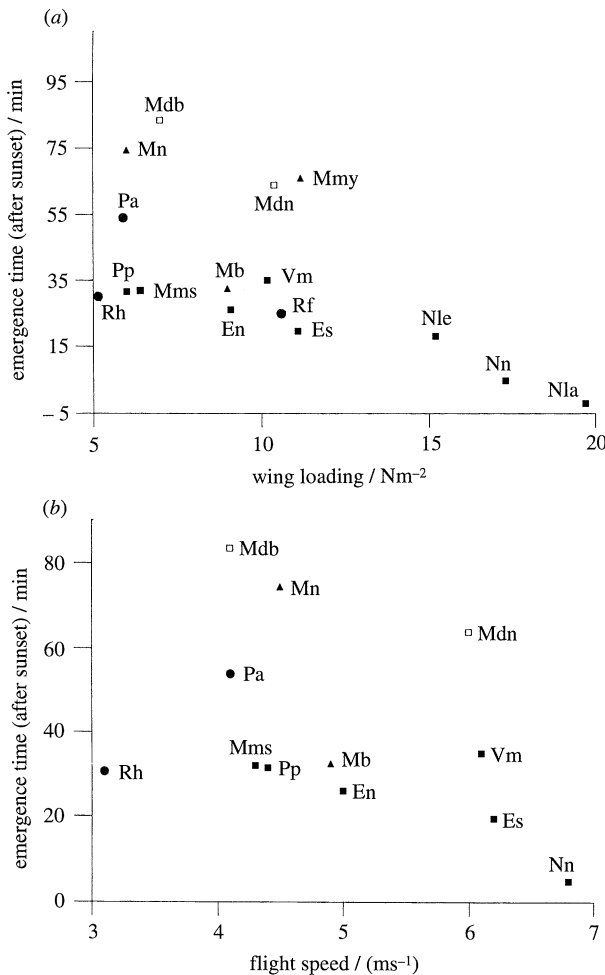


Figure 1. The relation between emergence time and (a) wing loading and (b) flight speed in samples of European bats. Emergence times are medians. All data are from table 1. Closed squares are for bats that eat mainly small aerial prey, closed circles are for bats that eat mainly lepidopterans, closed triangles are for bats that feed mostly on flightless or diurnal prey, i.e. gleaners, and open squares are for bats that usually feed low over water. Rh, *Rhinolophus hipposideros*; Rf, *R. ferrumequinum*; Nla, *Nyctalus lasiopterus*; Nle, *N. leisteri*; Nn, *N. noctula*; En, *Eptesicus nilssonii*; Es, *E. serotinus*; Vm, *Vespertilio murinus*; Pp, *Pipistrellus pipistrellus*; Pa, *Plecotus auritus*; Mb, *Myotis bechsteinii*; Mdb, *M. daubentonii*; Mdn, *M. dasycneme*; Mms, *M. mystacinus*; Mmy, *M. myotis*; Mn, *M. nattereri*.

Among the bats that feed mainly on small aerial prey, there was still a significant correlation between wing loading and emergence time ($r_5 = 0.87$, $P < 0.05$), which suggests that there was an independent effect of wing loading at least within this diet category. Thus, both flight speed and foraging strategy appear to influence the emergence time in European bats.

(b) *Worldwide database*

In accordance with the previous analysis, the worldwide database showed that bats adapted for high flight speed emerge earlier than other bats ($r_{18} = 0.44$, $P = 0.05$; figure 3). A two-way ANOVA showed that emergence time was significantly affected

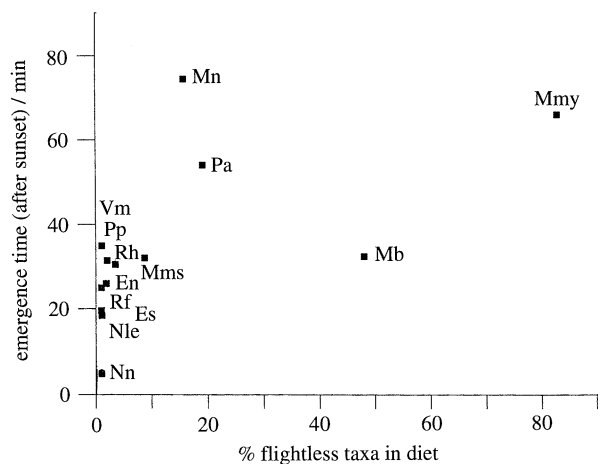


Figure 2. The relation between emergence time and the percentage of flightless or diurnal arthropods in the diet. Emergence times are medians. All data are from table 1. Abbreviations are as in figure 1.

by diet as before ($F_{4,40} = 11.73$, $P < 0.001$; figure 4) and also by latitude ($F_{1,40} = 8.47$, $P < 0.01$), with tropical species tending to emerge earlier than their counterparts in temperate areas. The absence of frugivores, nectarivores and pollen eaters in temperate zone localities made the ANOVA table unbalanced; so it was not possible to test for a diet \times latitude interaction.

In a reduced analysis that considered only bats that feed mainly on small aerial prey and bats that feed mainly on moths, the main effects remained significant while the interaction term was non-significant (diet, $F_{1,28} = 19.65$, $P < 0.01$; latitude, $F_{1,28} = 9.11$, $P < 0.01$; diet \times latitude interaction, $F_{1,28} = 3.72$, $P > 0.05$).

Comparison of means in figure 4, by using Tukey's multiple comparisons, showed that tropical bats that mainly feed on small aerial prey emerged significantly

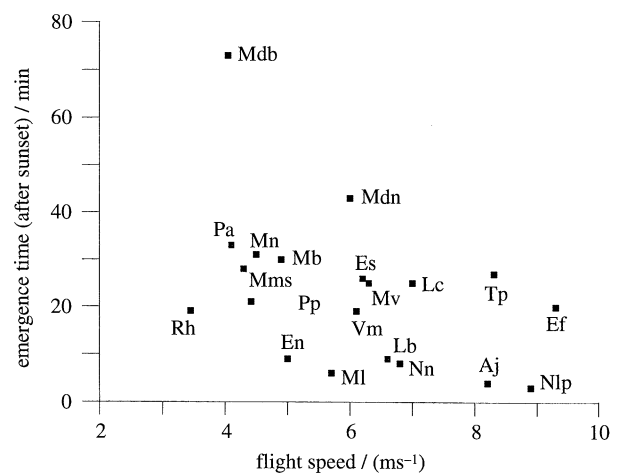


Figure 3. The relation between emergence time and flight speed for bats in the worldwide database (table 2). Emergence times are for the first bat in the colony. Abbreviations are as in figure 1 with the addition of: Nlp, *Noctilio leporinus*; Aj, *Artibeus jamaicensis*; MI, *Myotis lucifugus*; Mv, *M. velifer*; Ef, *Eptesicus fuscus*; Lc, *Lasiurus cinereus*; Lb, *L. borealis*; Tp, *Tadarida pumila*.

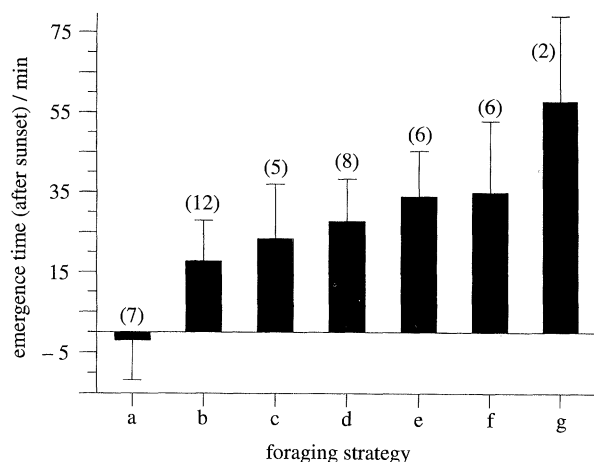


Figure 4. Time of emergence in relation to diet for bats grouped into seven foraging classes: a, tropical species that feed mainly on small aerial insects; b, their temperate zone counterparts; c, tropical species that feed mainly on moths; d, their temperate zone counterparts; e, temperate zone bats that feed mainly on flightless or diurnal arthropods, i.e. gleaners; f, tropical bats that feed mainly on fruit, nectar or pollen; and g, temperate zone bats that mainly feed low over water. Columns show means positive standard deviations for each class, with sample sizes (number of species) in brackets above. Species used in the analysis are given in the appendix.

earlier than all other groups. Similarly, temperate zone bats that eat mainly small aerial prey and tropical bats that eat mainly moths emerged significantly earlier than temperate zone bats that feed low over water.

Table 3. Emergence times of bats within four families

(Comparisons are for species that eat mainly small aerial prey against bats that eat mainly lepidopterans or flightless prey. For the tropical species, emergence times refer to the emergence of the first bat in the colony. For the temperate zone species, emergence times refer to the median emergence times (except*, which refer to emergence of the first bat). Emergence times are given in minutes after local sunset and were extracted from the worldwide database (table 2).)

	Bats that eat mainly small aerial prey		Bats that eat mainly flightless prey or moths	
Tropical				
Mormoopidae	<i>Pteronotis macleayi</i>	19	<i>Pteronotis parnellii</i>	23
	<i>P. quadridens</i>	-1	<i>Mormoops blainvillii</i>	39
Natalidae	<i>Natalus lepidus</i>	-8	<i>Natalus micropus</i>	14
Molossidae	<i>Tadarida brasiliensis</i>	18	<i>Tadarida femorosacca</i>	45
Temperate				
Vespertilionidae	<i>Myotis mystacinus</i>	33	<i>Myotis myotis</i>	69
	<i>M. velifer</i>	37	<i>M. nattereri</i>	60
	<i>Pipistrellus pipistrellus</i>	33	<i>Plecotus auritus</i>	44
	<i>Nyctalus leisleri</i>	17	<i>P. townsendii</i>	46
	<i>Eptesicus fuscus</i>	35	<i>Euderma maculatum</i>	49
	<i>E. serotinus</i>	21		
	<i>Vespertilio murinus</i>	35		
	<i>Nycticeius humeralis</i>	11		
	<i>Miniopterus schreibersii</i>	37		
	Molossidae	<i>Tadarida brasiliensis</i>	8	<i>Tadarida teniotis</i>
			<i>Eumops perotis</i>	50*

(c) Phylogenetic analysis

Since the species was used as the unit of analysis, the observed relation between emergence time and foraging strategy could have been confounded by phylogenetic effects (Harvey & Pagel 1991). Therefore, each family was analysed separately to test if the trends were consistent at this level, and therefore must have evolved several times. In both tropical and temperate areas, and indeed across all phylogenetic comparisons ($N = 4$ families), bats that feed mainly on small aerial prey emerged earlier than those that feed on flightless prey or on moths (table 3). This suggests that emergence time is indeed determined by ecological factors rather than by the phylogeny.

5. DISCUSSION

The prediction that bats that feed mainly on small, aerial prey, and that therefore may be more or less dependent on the dusk peak in flight activity of dipterans, tend to emerge earlier than other bats was supported by both the European and the worldwide data sets. Most of these bats are relatively fast fliers, and may therefore be relatively well adapted to face the additional risks of early emergence. The correlation between wing loading and emergence time suggests that the ability to avoid predation may be an important predictor of emergence time within this group.

The prediction that gleaners and those that feed mainly on moths should emerge relatively late was also generally supported, although the emergence time of moth feeders only differed significantly from that of other groups in the worldwide data set.

Frugivores and pollen eaters also emerged relatively late, as predicted. Taake's (1985) suggestion that small bats tended to emerge earlier than larger bats was not supported. Instead, there was a (non-significant) trend that larger bats, which had higher wing loadings on average, emerge before small bats. However, his suggestion that bats with long ears and light bellies, i.e. characteristics of many gleaners and species that feed low over water, tended to emerge relatively late seems to be justified.

The diet categories used in the analysis were selected arbitrarily and did not conform precisely with different foraging strategies, although they may indicate the predominant strategy used. For example, bats that feed mainly on small dipterans may be considered as aerial foragers, since such prey items are rarely taken by gleaning bats (see, for example: Bauerová 1978; Rydell 1989). On the other hand, moth eaters may be either aerial foragers, e.g. the spotted bat *Euderma maculatum* (Leonard & Fenton 1983), predominantly gleaners, e.g. the brown long-eared bat *Plecotus auritus*, or both, e.g. the horseshoe bats *Rhinolophus* spp. (see, for example: Swift & Racey 1983; Rydell 1989; Jones 1990; Shiel *et al.* 1991).

Among the species that feed mainly on moths, large molossids, which are fast flying aerial foragers (Norberg & Rayner 1987), emerged as late as the gleaners like the brown long-eared bat and the greater horseshoe bat *Rhinolophus ferrumequinum* and much later than other large aerial-hawking bats like, for example, the noctules *Nyctalus* spp. However, moths are probably less available to noctules than to large molossids, because the former use echolocation call frequencies that are audible to most tympanate moths (20–25 kHz; Zingg 1988; Zbinden 1989), which hence may detect the bats and take evasive action (see, for example, Fullard 1987), whereas the latter use frequencies well below the hearing range of most moths (11 kHz in *Tadarida teniotis*; Zbinden & Zingg 1986). Hence while the noctules may be more or less dependent on crepuscular dipterans, and therefore must emerge early, the large molossids are not.

Another discrepancy worth mentioning is the lesser horseshoe bat *Rhinolophus hipposideros*, which emerged earlier than other moth feeders. This species is very small (5–9 g) and also feeds extensively on small flying dipterans (McAney & Fairley 1989).

The time of evening emergence apparently reflects the light level that the bat is prepared to tolerate. However, the differences in tolerable light level probably differ much more among the bat species than the differences in emergence time suggest, because the prevailing light level also varies between habitats. Most bats that fly out early also feed in relatively open habitats, while those that fly out later, e.g. gleaning insectivores, more often fly under tree canopies. On the other hand, some bats tend to avoid the most exposed habitats until it has become dark, and instead concentrate their initial foraging activities at dusk to more protected areas near vegetation (see, for example: Nyholm 1965; Rydell 1986).

Bats that regularly feed low over open water, like Daubenton's bat *Myotis daubentonii* and the pond bat

Myotis dasycneme, emerge even later than the gleaners. Such late emergence may perhaps be caused by the timing of the hatching and flight of insects over water, or, alternatively, by a high predation risk associated with the exposed feeding conditions over open water far away from protective cover. The first explanation seems unlikely, since most aquatic insects emerge and fly during the day or early in the evening, rather than during the middle of the night (Morgan & Waddell 1961). The second hypothesis is perhaps more likely. Birds, such as small hawks and falcons and perhaps also gulls, may be potential predators of relatively slow bats that fly away from cover before dark (Gillette & Kimbrough 1970). Bats that fly low over water may also expose themselves to predation by fishes, if their silhouettes are visible against the sky. The white belly of most temperate zone bats that feed low over water seems to support this idea. There is yet little evidence that fish prey on bats however (see, for example, Gillette & Kimbrough 1970).

Although our hypothesis was largely supported by the data, it is clearly an oversimplification of the real situation, and much of the scatter in the data sets may represent additional constraints on the individual species. For example, variations in commuting time may potentially have a confounding effect if some bat species emerge earlier than others in order to reach more distant feeding sites. Such an effect may be expected if the species that fly out early also are those that form the largest colonies and hence experience the most intense competition for feeding sites near the roost. This possibility is difficult to evaluate at present, because information on the length of commuting flights in bats is scarce. However, among the European bats included in the analysis, the largest colonies are generally those of *Pipistrellus* and *Myotis* spp., species that emerge relatively late. Those that emerge early, e.g. *Nyctalus* spp. and *Eptesicus* spp., generally form small colonies (see, for example: Sluiter & van Heerdt 1966; Rydell 1989; Catto 1993).

Tropical bats tended to emerge earlier in relation to sunset than temperate species that use similar foraging strategies. This is to be expected, since the duration of the twilight period is shorter at lower latitudes, i.e. the light level prevailing a given time after sunset is much lower in the tropics than at temperate latitudes. Latitudinal effects may also have added variance to the European data set, since it included data from a range of 17°.

The relation between foraging strategy and emergence time was upheld within families of bats, and was therefore not an effect of a phylogenetic bias. Overall, the foraging strategy seems to be a good predictor of emergence time. This, in turn, would suggest that interspecific differences in emergence time may be explained by variations in activity patterns of various types of insects in combination with limitations on prey detectability and/or specializations on certain types of insects by the bats. There was also a significant effect of wing loading on the emergence time of aerial hawking bats, which suggests that predator avoidance ability may also be important.

APPENDIX

Bats used in the analysis of figure 4 according to foraging class (a–g).

(a) *Pteronotus macleayi*, *P. quadridens*, *Natalus lepidus*, *Tadarida brasiliensis*, *Mormopterus minutus*, *Molossus ater*, *M. molossus*.

(b) *Myotis lucifugus*, *M. mystacinus*, *M. velifer*, *Lasiorycteris noctivagans*, *Pipistrellus pipistrellus*, *Nyctalus leisleri*, *N. noctula*, *Eptesicus fuscus*, *E. nilssonii*, *E. serotinus*, *Vespertilio murinus*, *Miniopterus schreibersii*.

(c) *Pteronotus parnellii*, *Mormoops blainvillii*, *Macrotus waterhousii*, *Natalus micropus*, *Tadarida femorosacca*.

(d) *Rhinolophus ferrumequinum*, *R. hipposideros*, *Myotis evotis*, *Lasiurus cinereus*, *Plecotus auritus*, *P. townsendii*, *Euderma maculatum*, *Eumops perotis*.

(e) *Macrotus californicus*, *Myotis bechsteini*, *M. emarginatus*, *M. myotis*, *M. nattereri*, *Antrozous pallidus*.

(f) *Monophyllus redmani*, *Vampyrodes caraccioli*, *Artibeus jamaicensis*, *Brachyphylla nana*, *Erophylla sezekorni*, *Phyllostonycteris poeyi*.

(g) *Myotis dasycneme*, *M. daubentonii*.

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REFERENCES

- Anthony, E.L.P. & Kunz, T.H. 1977 Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology* **58**, 775–786.
- Avery, M.I. 1986 Factors affecting the emergence times of pipistrelle bats. *J. Zool.* **209**, 296–299.
- Baagøe, H.J. 1987 The Scandinavian bat fauna: adaptive wing morphology and free flight in the field. In *Recent advances in the study of bats* (ed. M.B. Fenton, P.A. Racey & J.M.V. Rayner), pp. 57–74. Cambridge: Cambridge University Press.
- Barclay, R.M.R. 1985 Long- versus short-range foraging strategies of hoary (*Lasiurus cinereus*) and silver-haired (*Lasiorycteris noctivagans*) bats and the consequences for prey selection. *Can. J. Zool.* **63**, 2507–2515.
- Barclay, R.M.R. 1989 The effect of reproductive condition on the foraging behavior of female hoary bats *Lasiurus cinereus*. *Behav. Ecol. Sociobiol.* **24**, 31–37.
- Bauerová, Z. 1978 Contribution to the trophic ecology of *Myotis myotis*. *Folia zool.* **27**, 305–316.
- Bauerová, Z. 1986 Contribution to the trophic bionomics of *Myotis emarginatus*. *Folia zool.* **35**, 305–310.
- Bauerová, Z. & Červený, J. 1986 Towards an understanding of the trophic ecology of *Myotis nattereri*. *Folia zool.* **35**, 55–61.
- Bauerová, Z. & Ruprecht, A.L. 1989 Contribution to the knowledge of the trophic ecology of the parti-coloured bat, *Vespertilio murinus*. *Folia zool.* **38**, 227–232.
- Bell, G.P. 1982 Behavioral and ecological aspects of gleaning by the desert insectivorous bat, *Antrozous pallidus* (Chiroptera: Vespertilionidae). *Behav. Ecol. Sociobiol.* **10**, 217–223.
- Belwood, J.J. & Fenton, M.B. 1976 Variation in the diet of *Myotis lucifugus* (Chiroptera: Vespertilionidae). *Can. J. Zool.* **54**, 1674–1678.
- Black, H.L. 1974 A north temperate bat community: structure and prey populations. *J. Mamm.* **55**, 138–157.
- Böhme, W. & Natuschke, G. 1967 Untersuchungen der Jagflugaktivität freilebender Fledermäuse in Wochenstuben mit Hilfe einer doppelseitigen Lichtschranke und Ergebnisse an *Myotis myotis* (Borkhausen, 1797) und *Myotis nattereri* (Kuhl, 1818). *Säugetierk. Mitt.* **15**, 129–238.
- Brigham, R.M.R. & Saunders, M.B. 1990 The diet of big brown bats (*Eptesicus fuscus*) in relation to insect availability in southern Alberta, Canada. *N.W. Sci.* **64**, 7–10.
- Buchler, E.R. 1976 Prey selection by *Myotis lucifugus* (Chiroptera: Vespertilionidae). *Am. Nat.* **110**, 619–628.
- Bullock, D.J., Combes, B.A., Eales, L.A. & Pritchard, J.S. 1987 Analysis of the timing and pattern of emergence of the pipistrelle bat (*Pipistrellus pipistrellus*). *J. Zool.* **211**, 267–274.
- Catto, C.M.C. 1993 *Aspects of the ecology and behaviour of the serotine bat (Eptesicus serotinus)*. PhD thesis, University of Aberdeen.
- Chase, J., Small, M.Y., Weiss, E.A., Sharma, D. & Sharma, S. 1991 Crepuscular activity of *Molossus molossus*. *J. Mamm.* **72**, 414–418.
- Clark, B.S., Leslie, D.M.Jr. & Carter, T.S. 1993 Foraging activity of adult female Ozark big-eared bats (*Plecotus townsendii ingens*) in summer. *J. Mamm.* **74**, 422–427.
- Clem, P.D. 1992 Seasonal population variation and emergence patterns in the evening bat, *Nycticeius humeralis*, at a west-central Indiana colony. *Proc. Indiana Acad. Sci.* **101**, 33–44.
- Cueva, H. de la 1992 Vertebrates' flight speeds during the reproductive season. *Am. Zool.* **32**, 90A.
- DeCoursey, G. & DeCoursey, P.J. 1964 Adaptive aspects of activity rhythms in bats. *Biol. Bull.* **126**, 14–27.
- Degn, H.J. 1983 Field activity of serotine bats. *Nyctalus* **1**, 521–530.
- Dwyer, P.D. 1964 Seasonal changes in activity and weight of *Miniopterus schreibersi blepotis* (Chiroptera) in north-eastern New South Wales. *Aust. J. Zool.* **12**, 52–69.
- Easterla, D.A. & Whitaker, J.O.Jr. 1972 Food habits of some bats from Big Bend National Park, Texas. *J. Mamm.* **53**, 887–890.
- Eisentraut, M. 1952 Beobachtungen über Jagdroute und Flugbeginn bei Fledermäusen. *Bonn zool. Beitr.* **3**, 211–220.
- Erkert, H.G. 1978 Sunset-related timing of flight activity in Neotropical bats. *Oecologia* **37**, 59–67.
- Erkert, H.G. 1982 Ecological aspects of bat activity rhythms. In *Ecology of bats* (ed. T. H. Kunz), pp. 201–242. New York: Plenum Press.
- Fenton, M.B., Boyle, N.G.H., Harrison, T.M. & Oxley, D.J. 1977 Activity patterns, habitat use, and prey selection by some African insectivorous bats. *Biotropica* **9**, 73–85.
- Freeman, P.W. 1981 Correspondence of food habits and morphology in insectivorous bats. *J. Mamm.* **62**, 166–173.
- Frylestam, B. 1969 Studier över långörade fladdermusen. *Fauna Flora, Stockh.* **65**, 72–84.
- Fullard, J.H. 1987 Sensory ecology and neuroethology of moths and bats: interactions in a global perspective. In *Recent advances in the study of bats* (ed. M.B. Fenton, P.A. Racey & J.M.V. Rayner), pp. 244–272. Cambridge: Cambridge University Press.
- Funakoshi, K. & Uchida, T.A. 1975 Studies on the physiological and ecological adaptations of temperate insectivorous bats. I. Feeding activities in the Japanese long-fingered bats, *Miniopterus schreibersi fuliginosus*. *Jap. J. Ecol.* **25**, 217–234.
- Funakoshi, K. & Uchida, T.A. 1978 Studies on the

- physiological and ecological adaptations of temperate insectivorous bats. III. Annual activity of the Japanese house-dwelling bat, *Pipistrellus abramus*. *J. Fac. Agric. Kyushu Univ.* **23**, 95–115.
- Funakoshi, K. & Uchida, T.A. 1980 Feeding activity of the Japanese lesser horseshoe bat, *Rhinolophus cornutus cornutus*, during the hibernation period. *J. Mamm.* **61**, 119–121.
- Gaisler, J. 1963 Nocturnal activity in the lesser horseshoe bat, *Rhinolophus hipposideros* (Bechstein, 1800). *Folia zool.* **12**, 223–230.
- Gaur, B.S. 1980 Roosting ecology of the Indian desert rat-tailed bat, *Rhinopoma kinneari* Wroughton. In *Proceedings of the fifth International Bat Research Conference* (ed. D.E. Wilson & A.L. Gardner), pp. 125–128. Lubbock: Texas Tech Press.
- Gillette, D.D. & Kimbrough, J.D. 1970 Chiropteran mortality. In *About bats* (ed. B.H. Slaughter & D.W. Walton), pp. 26–283. Dallas: Southern Methodist University Press.
- Glas, G.H. 1980–81 Activities of serotine bats (*Eptesicus serotinus*) in a nursing-roost. *Myotis* **18–19**, 164–167.
- Goodwin, G.G. 1928 Observations on *Noctilio*. *J. Mamm.* **9**, 104–112.
- Gould, P.J. 1961 Emergence time of *Tadarida* in relation to light intensity. *J. Mamm.* **42**, 405–407.
- Griffith, L.A. & Gates, J.E. 1985 Food habits of cave-dwelling bats in the central Appalachians. *J. Mamm.* **66**, 451–160.
- Harmata, W. 1960 Obserwacje etologiczne i ekologiczne nad nietoperzami z Lasu Wolkiego. *Zeszyty Naukowe Univ. Jag. Krakow, Zool.* **33**, 163–203.
- Harvey, P.H. & Pagel, M.D. 1991 *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- Herreid, C.F. & Davis, R.B. 1966 Flight patterns of bats. *J. Mamm.* **47**, 78–86.
- Isaac, S.S. & Marimuthu, G. 1993 Early outflying and late homeflying in the Indian pygmy bat under natural conditions. *Oecologia* **96**, 426–430.
- Jones, G. 1990 Prey selection by the greater horseshoe bat (*Rhinolophus ferrumequinum*): optimal foraging by echolocation? *J. Anim. Ecol.* **59**, 587–602.
- Jones, G. 1993 Flight morphology, flight performance and echolocation in British bats. In *Proceedings of the first European bat detector workshop* (ed. K. Kapteyn), pp. 59–78. Amsterdam: Netherlands Bat Research Foundation.
- Jones, G. & Rayner, J.M.V. 1988 Flight performance, foraging tactics and echolocation in the trawling insectivorous bat *Myotis adversus* (Chiroptera: Vespertilionidae). *J. Zool.* **225**, 393–412.
- Jones, G. & Rayner, J.M.V. 1989 Optimal flight speed in pipistrelle bats, *Pipistrellus pipistrellus*. In *European bat research 1987* (ed. V. Hanák, I. Horáček & J. Gaisler), pp. 247–253. Prague: Charles University Press.
- Kronwitter, F. 1988 Population structure, habitat use and activity patterns of the noctule bat, *Nyctalus noctula* Schreb., 1774 (Chiroptera: Vespertilionidae) revealed by radio-tracking. *Myotis* **26**, 23–85.
- Krull, D., Schumm, A., Metzner, W. & Neuweiler, G. 1991 Foraging areas and foraging behavior in the notch-eared bat, *Myotis emarginatus* (Vespertilionidae). *Behav. Ecol. Sociobiol.* **28**, 247–253.
- Kunz, T.H. 1974 Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). *Ecology* **55**, 693–711.
- Kuthe, C. 1989 Aktivitätsuntersuchungen an einer Mausohrwochenstube (*Myotis myotis*). In *European bat research 1987* (ed. V. Hanák, I. Horáček & J. Gaisler), pp. 533–536. Prague: Charles University Press.
- Laufens, G. 1973 Untersuchungen zur Aktivitätsperiodik von *Myotis nattereri* Kuhl, 1818. *Lynx* **10**, 45–51.
- Leonard, M.L. & Fenton, M.B. 1983 Habitat use by spotted bats (*Euderma maculatum*, Chiroptera: Vespertilionidae): roosting and foraging behavior. *Can. J. Zool.* **61**: 1487–1491.
- Lewis, T. & Taylor, L.R. 1965 Diurnal periodicity of flight by insects. *Trans. R. ent. Soc. Lond.* **116**, 393–479.
- Link, A., Marimuthu, G. & Neuweiler, G. 1986 Movement as a specific stimulus for prey catching behaviour in rhinolophid and hipposiderid bats. *J. comp. Physiol. A* **159**, 403–413.
- Maeda, K. 1974. Éco-éthologie de la grand noctule, *Nyctalus lasiopterus*, a Sapporo, Japon. *Mammalia* **38**, 461–487.
- Marimuthu, G. 1984 Seasonal changes in the precision of the circadian clock of a tropical bat under natural photoperiod. *Oecologia* **61**, 352–357.
- McAney, C.M. & Fairley, J.S. 1988 Activity patterns of the lesser horseshoe bat *Rhinolophus hipposideros* at summer roosts. *J. Zool.* **216**, 325–338.
- McAney, C.M. & Fairley, J.S. 1989 Analysis of the diet of the lesser horseshoe bat *Rhinolophus hipposideros* in the west of Ireland. *J. Zool.* **217**, 491–498.
- McAney, C.M. & Fairley, J.S. 1990 Activity of Leisler's bat *Nyctalus leisleri* (Kuhl, 1818) at a summer roost in Ireland. *Myotis* **28**, 83–91.
- McDonald, J.T., Rautenbach, I.L. & Nel, J.A.J. 1990 Foraging ecology of bats observed at De Hoop Provincial Nature Reserve, southern Cape Province. *S. Afr. J. Wildl. Res.* **20**, 133–145.
- McWilliam, A.N. 1989 Emergence behaviour of the bat *Tadarida (Chaerephon) pumila* (Chiroptera: Molossidae) in Ghana, West Africa. *J. Zool.* **219**, 698–701.
- Morgan, N.C. & Waddell, A.B. 1961 Diurnal variation in the emergence of some aquatic insects. *Trans. R. ent. Soc. Lond.* **113**, 123–134.
- Morrison, D.W. 1980 Flight speeds of some tropical forest bats. *Am. Midl. Nat.* **104**, 189–192.
- Nagorsen, D.W. & Brigham, R.M. 1993 *The bats of British Columbia*. Vancouver: University of British Columbia Press.
- Negro, J.J., Ibáñez, C., Pérez Jordá, J.L. & Riva, M.J. de la 1992 Winter predation by common kestrel *Falco tinnunculus* on pipistrelle bats *Pipistrellus pipistrellus* in southern Spain. *Bird Study* **39**, 195–199.
- Norberg, U.M. 1987 Wing form and flight mode in bats. In *Recent advances in the study of bats* (ed. M.B. Fenton, P.A. Racey & J.M.V. Rayner), pp. 43–56. Cambridge: Cambridge University Press.
- Norberg, U.M. 1990 *Vertebrate flight*. Berlin: Springer-Verlag.
- Norberg, U.M. & Rayner, J.M.V. 1987 Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Phil. Trans. R. Soc. Lond. B* **316**, 335–427.
- Nyholm, E.S. 1965 Zur Ökologie von *Myotis mystacinus* (Leisl.) und *M. daubentoni* (Leisl.) (Chiroptera). *Ann. Zool. Fennici* **2**, 77–123.
- O'Farrell, M.J. & Studier, E.H. 1975 Population structure and emergence activity patterns in *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae) in northeastern New Mexico. *Am. Midl. Nat.* **93**, 368–376.
- O'Shea, T.J. & Vaughan, T.A. 1977 Nocturnal and seasonal activities of the pallid bat, *Antrozous pallidus*. *J. Mamm.* **58**, 269–284.
- Patterson, A. & Hardin, J. 1969 Flight speeds of five species of vespertilionid bats. *J. Mamm.* **50**, 152–153.
- Pottier, T. 1993 Presence et reproduction de la noctule de Leisler (*Nyctalus leisleri*, Kuhl, 1818) en Normandie (France). *Le petit Lérot* **46**, 13–23.

- Prakesh, I. 1962 Times of emergence of the pipistrelle. *Mammalia* **26**, 133–135.
- Racey, P.A. & Swift, S.M. 1985 Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. *J. Anim. Ecol.* **54**, 205–215.
- Roer, H. 1968 Zur Frage der Wochenstuben-Quartier-treue weiblicher Mausohren (*Myotis myotis*). *Bonn zool. Beitr.* **19**, 85–96.
- Ross, A. 1967 Ecological aspects of the food habits of insectivorous bats. *Proc. west. Found. Vert. Zool.* **1**, 205–264.
- Rydell, J. 1986 Feeding territoriality in female northern bats *Eptesicus nilssoni*. *Ethology* **72**, 329–337.
- Rydell, J. 1989 Food habits of northern (*Eptesicus nilssoni*) and brown long-eared (*Plecotus auritus*) bats in Sweden. *Holarct. Ecology* **12**, 16–20.
- Rydell, J. 1992 The diet of the parti-coloured bat *Vespertilio murinus* in Sweden. *Ecography* **15**, 195–198.
- Rydell, J. 1993 Variation in foraging activity of an aerial insectivorous bat during reproduction. *J. Mamm.* **74**, 503–509.
- Sample, B.E. & Whitmore, R.C. 1993 Food habits of the endangered Virginia big-eared bat in West Virginia. *J. Mamm.* **74**, 428–435.
- Shiel, C.B., McAney, C.M. & Fairley, J.S. 1991 Analysis of the diet of Natterer's bat *Myotis nattereri* and the common long-eared bat *Plecotus auritus* in the West of Ireland. *J. Zool.* **223**, 299–305.
- Silva Taboada, G. 1979 *Los murcielagos de Cuba*. Havana: Editorial Científico-Técnica, Ciudad de La Habana.
- Silva Taboada, G. & Pine, R.H. 1969 Morphology and behavioral evidence for the relationship between the bat genus *Brachyphylla* and the Phyllonycterinae. *Biotropica* **1**, 10–19.
- Sluiter, J.W. & van Heerdt, P.F. 1966 Seasonal habits of the noctule bat (*Nyctalus noctula*). *Arch. Neerl. Zool.* **16**, 423–439.
- Sokal, R.R. & Rohlf, F.J. 1981 *Biometry*. (2nd edn). San Francisco: W. H. Freeman.
- Speakman, J.R. 1991 Why do insectivorous bats in Britain not fly in daylight more frequently? *Funct. Ecol.* **5**, 518–524.
- Speakman, J.R. 1993 The evolution of echolocation for predation. In *Mammals as predators* (ed. N. Dunstone & M. L. Gorman), pp. 39–63. Oxford: Clarendon Press.
- Speakman, J.R. 1995 Chiropteran nocturnality. In *Ecology, evolution and behaviour of bats* (ed. P.A. Racey & S.M. Swift). Oxford: Clarendon Press. (In the press.)
- Speakman, J.R., Stone, R.D. & Kerslake, J.D. 1994 Emergence patterns of pipistrelle bats (*Pipistrellus pipistrellus*) are consistent with an anti-predator response *Anim. Behav.* (In the press.)
- Stebbing, R.E. 1968 Measurements, composition and behaviour of a large colony of the bat *Pipistrellus pipistrellus*. *J. Zool.* **156**, 15–33.
- Subbaraj, R. & Chandrashekar, M.K. 1977 'Rigid' internal timing in the circadian rhythm of flight activity in a tropical bat. *Oecologia* **29**, 341–348.
- Sullivan, C.M., Shiel, C.B., McAney, C.M. & Fairley, J.S. 1993 Analysis of the diets of Leisler's *Nyctalus leisleri*, Daubenton's *Myotis daubentoni* and pipistrelle *Pipistrellus pipistrellus* bats in Ireland. *J. Zool.* **231**, 656–663.
- Swift, S.M. 1980 Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. *J. Zool.* **190**, 285–295.
- Swift, S.M. & Racey, P.A. 1983 Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. *J. Zool.* **200**, 249–259.
- Swift, S.M., Racey, P.A. & Avery, M.I. 1985 Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. II. Diet. *J. Anim. Ecol.* **54**, 205–215.
- Taake, K.H. 1985 Einige verhaltensökologische Aspekte der Rauber-Beute-Beziehungen europäischer Fledermäuse (Chiroptera). *Z. Säugetierk.* **50**, 202–208.
- Taake, K.H. 1992 Strategien der Ressourcennutzung an waldgewässern jagender Fledermäuse (Chiroptera: Vespertilionidae). *Myotis* **30**, 7–73.
- Taylor, L.R. & Carter, C.I. 1961 The analysis of numbers and distribution in an aerial population of macrolepidoptera. *Trans. R. ent. Soc. Lond.* **113**, 369–386.
- Tidemann, C.R., Priddel, D.M., Nelson, J.E. & Pettigrew, J.D. 1985 Foraging behaviour of the Australian ghost bat, *Macroderma gigas* (Microchiroptera: Megadermatidae). *Aust. J. Zool.* **33**, 705–713.
- Twente, J.W. 1955 Some aspects of habitat selection and other behavior of cavern-dwelling bats. *Ecology* **36**, 706–732.
- Vaughan, T.A. 1959 Functional morphology of three bats: *Eumops*, *Myotis*, *Macrotus*. *Univ. Kansas Publ. Mus. nat. Hist.* **12**, 1–153.
- Vaughan, T.A. 1977 Foraging behaviour of the giant leaf-nosed bat (*Hipposideros commersoni*). *E. Afr. Wildl. J.* **15**, 237–249.
- Venables, L.S.V. 1943 Observations at a pipistrelle bat roost. *J. Anim. Ecol.* **12**, 19–26.
- Voûte, A.M., Sluiter, J.W. & Grimm, M.P. 1974 The influence of the natural light-dark cycle on the activity rhythm of pond bats (*Myotis dasycneme* Boie, 1825) during summer. *Oecologia* **17**, 221–243.
- Warner, R.M. 1985 Interspecific and temporal dietary variation in an Arizona bat community. *J. Mamm.* **66**, 45–51.
- Whitaker, J.O. Jr & Clem, P. 1992 Food of the evening bat *Nycticeius humeralis* from Indiana. *Am. Midl. Nat.* **127**, 211–214.
- Whitaker, J.O. Jr & Lawhead, B. 1992 Foods of *Myotis lucifugus* in a maternity colony in central Alaska. *J. Mamm.* **73**, 646–648.
- Whitaker, J.O. Jr, Maser, C. & Keller, L.E. 1977 Food habits of bats of western Oregon. *Northwest. Sci.* **51**, 46–55.
- Wolz, I. 1988 Ergebnisse automatischer Aktivitätsaufzeichnungen an Wochenstubenkolonien der Bechsteinfledermaus (*Myotis bechsteini*). *Z. Säugetierk.* **53**, 257–266.
- Zbinden, K. 1989 Field observations on the flexibility of the acoustic behaviour of the European bat *Nyctalus noctula* (Schreber, 1774). *Rev. Suisse Zool.* **96**, 335–343.
- Zbinden, K. & Zingg, P. 1986 Search and hunting signals of echolocating European free-tailed bats, *Tadarida teniotis*, in southern Switzerland. *Mammalia* **50**, 9–25.
- Zingg, P. 1988 Search calls of echolocating *Nyctalus leisleri* and *Pipistrellus savii* (Mammalia: Chiroptera) recorded in Switzerland. *Z. Säugetierk.* **53**, 281–293.

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