Acta Chiropterologica, 8(2): 391–401, 2006
PL ISSN 1508-1109 © Museum and Institute of Zoology PAS

Songflight behaviour and mating system of the pipistrelle bat (*Pipistrellus pipistrellus*) in an urban habitat

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The songflight and the territorial behaviour of courting male pipistrelles (*Pipistrellus pipistrellus*) were observed in an urban habitat of this bat species, in the city of Bayreuth in Bavaria. (1) Within the city limits, from the middle of July to the end of October but most intensively in September, the male bats occupied courtship territories averaging about 200 m in diameter. At night they patrolled these territories along regular flight routes emitting characteristic advertisement calls. By day they sheltered in crevices in buildings. (2) The courtship territories were densely distributed in the center of the inner city and rarer at the outskirts. As all known larger winter roosts as well as the 'invasion centers' (typical late summer swarming sites of this species) also were in the inner city, territories were situated around winter quarters, but not in the vicinity of the nursery roosts, which were lying at the edge of the city and outside it. (3) The males evidently arrange their courtship territories in such a way that as many females as possible pass through them when they inspect the winter roosts. That is, they are not defending resources important to the females; instead, they position their courtship territories near the resources the females require. As male territories are densely packed, the males offer a possibility for mate choice to the females, so that the mating system also bears some likeness to a lek.

Key words: *Pipistrellus pipistrellus,* songflight, mating, courtship territories, urban habitat

INTRODUCTION

The pipistrelles, like all temperate-zone bats, have an annual rhythm that includes hibernation for several winter months. The cycle is thus essentially triphasic: after hibernation, which usually occurs in roosts occupied by large number of bats, the males and females separate; while the females gather in nursery roosts to bear and raise their young (e.g., Swift, 1980; Feyerabend and Simon, 2000), the males generally lead basically solitary lives in summer (e.g., Park *et al*., 1996). When the young no longer need their mothers' care, the females leave the nursery roosts and migrate toward the winter roosts. It is in this phase that mating occurs, as well the remarkable 'invasion behaviour' of the pipistrelle bat. During 'invasions' many bats, mainly young bats born the same year, gather at certain places, a behavior comparable with the swarming behaviour of other bats, the biological significance of which is still unclear (see, e.g., Grummt and Haensel, 1966; Grimmberger and Bork, 1978; von Helversen *et al*., 1987; Sachteleben, 1991; Smit-Viergutz and Simon, 2000).

Due to Gerell and Lundberg's studies in Sweden, the mating system of the common

pipistrelles was supposed to be well-known (Gerell and Lundberg, 1985; Lundberg and Gerell, 1986; Lundberg, 1989), but in the last years it turned out that these observations referred to a related species, the pygmy pipistrelle. Although it was known for a long time, that two types of pipistrelle bats with echolocation calls around 45 and around 55 kHz exist in many parts of Europe (see, e.g., Ahlén, 1981; Weid and von Helversen, 1987; Jones and van Parijs, 1993), only much later the bats described as 'pipistrelles' were separated into two species with the aid of DNA analysis (Jones and Barratt, 1999; Mayer and von Helversen, 2001): the pipistrelle bat *Pipistrellus pipistrellus* (Schreber, 1774) and the pygmy pipistrelle *Pipistrellus pygmaeus* (Leach, 1825).

Barlow and Jones (1997) described the different songflight calls of the two species. Because of their study it was obvious that the Swedish bats were pygmy bats (see Lundberg, 1989). Consequently the mating behaviour of *P. pipistrellus* is still unknown. In the present paper we describe the songflight behaviour of this species in a typical urban habitat.

Materials and Methods

Study Area

Common pipistrelles were observed in the city of Bayreuth in northeastern Bavaria (49°57'N, 11°35'E; population — 70,000 inhabitants, ca. 9 km^2 built-up area) and its immediate surroundings (cf. Fig. 2). The terrain is hilly (325–400 m a.s.l.) and falls off towards the northwest. The surroundings of the city are quite densely wooded (ca. 20% of the total area); the agricultural areas consist at least partly of pasture and grassland. Several streams bordered by trees and shrubs flow through the region. The city itself is characterized by a relatively high proportion of parks, tree-lined streets, gardens and the like. The only fairly large local body of still water is situated within the city. Day roosts available to the bats are many and varied, ranging from unplastered cracks in old walls to the facings of modern multistory buildings.

Inside the city some old sandstone buildings with cavity walls are used as winter roosts. In the inner city 'invasions' regularly occur in August and September (Sachteleben, 1991). The nearest nursery roosts are within the study area, but most are further away. The population is substantially stationary (ringed animals were recovered over a 3-year-period, with one exception, in the immediate vicinity — Sachteleben, 1991).

Technical Equipment

The bats were detected with either a QMC-Mini or a FLAN 2.2 Detector. Their calls were recorded with a BRÜEL and KJÆR 4135 microphone on magnetic tape (RACAL 4 Store DS) or with FLAN 2.2 Detector or QMC microphone on a converted video recorder (cf. Weid and von Helversen, 1987). The recordings were evaluated by means of a sonagraph (MOSIP-FFT-Processor, MEDAV/Erlangen). A residual-light amplifier from the firm LITTON was used as a night-vision device.

Observations

On the basis of unsystematic observations in 1985 and 1986, in 1987 eight localities, where the songflight regularly could be observed, were selected for a more detailed study, as well as another locality in which the bats frequently hunted. From April 22 to October 21, 1987 these nine sites were visited hourly one night per week throughout April and during the courtship period, from July to October, and one night per month in May and June, always in the same order (observation series A). At each site four minutes were spent making the following counts: number of pipistrelles present, echolocation calls, final buzzes, advertisement calls (i.e., series of ≥ 10 songflight-calls — sensu Barlow and Jones, 1997) and agonistic calls (i.e., < 4 calls in a series). On each visit various weather parameters (temperature, wind strength, % cloud cover, rain) were also recorded.

In a second observation series (series B) the observer bicycled slowly through the region on 70 nights, at various times of the night. The routes were subdivided into 598 different localities on the basis of similar biotope structures. Each time a locality was checked (a total of 2,597 site checks) the above data were collected. Whenever a pipistrelle was encountered, the duration of the contact was measured and feeding buzzes, agonistic and advertisement calls were counted.

The procedure for estimating the number and spatial distribution of courtship territories was as follows: first all individual territories of routinely

observed males with known daytime roosts, or territories sufficiently isolated, so that the male observed there could be assumed always to be the same individual, were entered on a map of Bayreuth. In the inner city the density of courting males was so great that this procedure was not always possible. Here the places, where courting males where regularly heard, were first marked on the map. Then these marked areas were filled with the smallest possible number (i.e., with no overlap) of circles 200 m in diameter (which had been found to be the mean diameter of courtship territories). The number of territories derived in this manner is certainly a minimum, because the territories in the densely populated part of the inner city tended to be smaller than 200 m.

Statistics

In addition to nonparametric tests (χ^2, Mann-Whitney *U*), a stepwise logistic regression was carried out to describe the dependence of the target variable 'songflight activity' upon a minimal number of independent environmental variables, and in the results section only relations, that were significant (at the 5% level) in both observation series, are reported.

RESULTS

Songflight Display and Courtship Territories

During the songflight display the bats patrolled in a territory around their roosts. They flew, mainly near their roosts and at the boundaries of the territory, along regular routes that often followed conspicuous linear structures such as a street, the wall of a building or the edge of woodland (an example is given in Fig. 1). The bats normally flew at a height from 3 up to 10 m. The flying style during the songflight was often distinctly different from the typical hunting flight style: the normal flapping flight was interrupted at regular intervals by brief phases of gliding. The flight routes were evidently patrolled in a regular sequence — often for hours, and on many nights. The routes of neighbouring male pipistrelles normally did not intersect one another. Only rarely the bats made brief pursuit excursions, presumably to chase intruders out of their courtship territory.

Some of the courtship territories were occupied for several years, and every year approximately the same flight routes were used — probably indicating that the routes were to a great extent influenced by the given spatial configuration (buildings, rows of trees, etc.) of the area.

For seven territories, in which all the flight routes normally used by the occupying male were known, we were able to measure the distance between the route points furthest removed from one another. The mean value so obtained, an estimate of territory diameter (d), was 204 m (SD = 88 m, range = 125–375 m), thus indicating territory sizes ranging between about 1.2 up to 10 ha.

In five courtship territories the male's daytime roost could be located. All were crevices in the outer walls of buildings: (1) joint between sandstone blocks in the wall of the 'New Palace', (2) gap under the copper-sheated spire of the 'Old Palace' in the Eremitage, (3) joint under a board of a wooden bell tower in the 'Thiergarten' quarter, (4) crack at the jalousie box of a window of the 'Old Hospital', (5) gap under the outer edge of the roof facing of a multistory building.

Because these roosts were hard to reach, it was possible in only two cases to catch the occupant in a net and prove that it was indeed an adult male. One of these males was marked with a wing ring to which reflecting foil had been glued, so that he could be followed during the songflight in the next nights.

The songflying bats were occasionally (especially in the vicinity of their roots) observed to fly to certain places on the walls of buildings (especially corners recessed into the buildings or nooks under projecting parts of the wall) several times in the night and to land at these places

repeatedly (corresponding to the 'false landings').

Only once, just before dawn, a territorial male was observed to give loud calls frequently out of his roost while another bat was flying towards him. The male was presumably trying to attract a female into his roost. Unfortunately, it was impossible to look into any of the daytime roosts, so the various males' success in courtship could not be evaluated.

Songflight Calls

The songflights are characterized primarily by the specific and loud social calls, termed 'advertisement calls' or 'songflight calls'. The character of these calls of the investigated bats can be described as follows: (1) they are repeated in series with a mean interval of 0.8 s (SD = 0.38 s, n = 24); (2) an individual call usually consisted of 4 sweeps, less often of 3, 5 or 6; (3) the mean

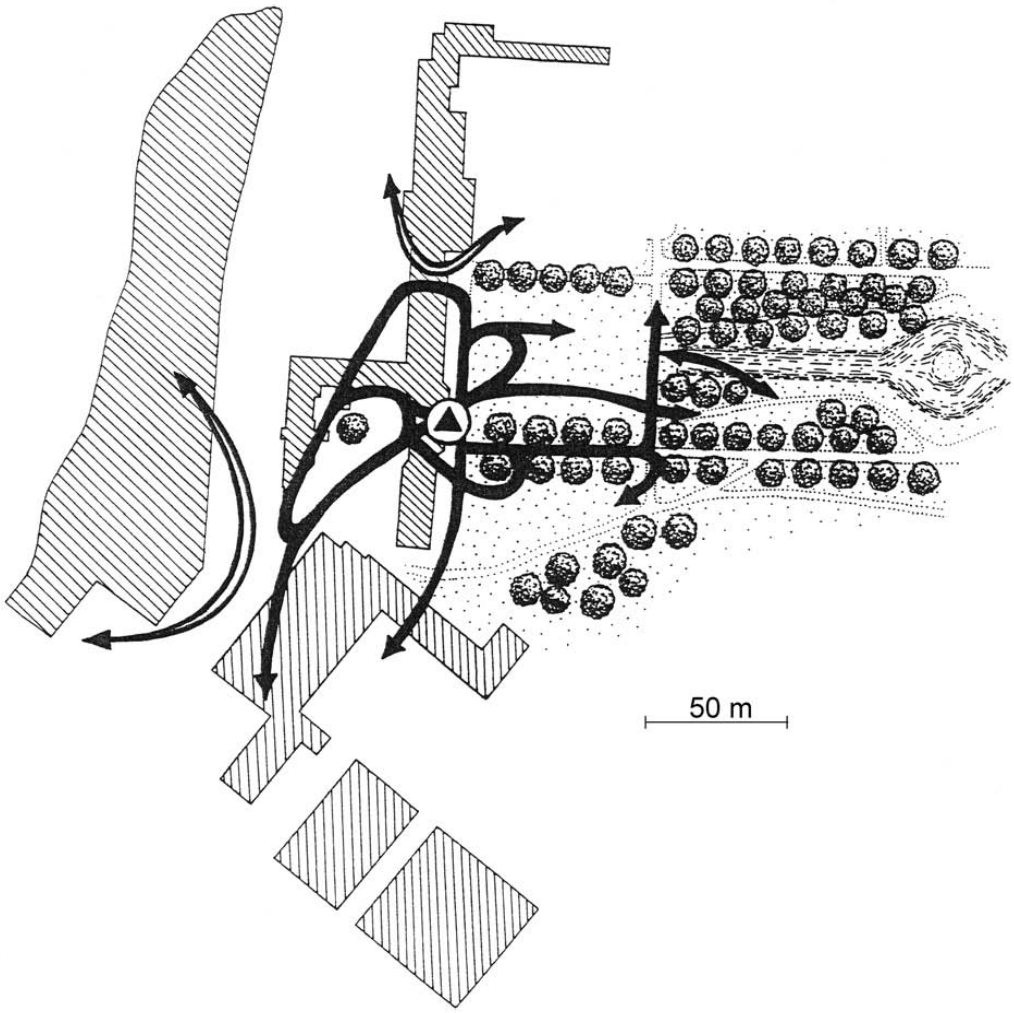

FIG. 1. Songflight paths of a male *P. pipistrellus* at the 'New Palace' in the center of Bayreuth; triangle = roost site of the territorial male, solid lines = songflight paths of the male, open lines = songflight paths of two adjacent males. At the right of the building complex (hatches) is a park with lawn (dotted), predominantly old trees and an elongated pond (broken lines)

frequency of maximum energy was 17.6 kHz (SD = 0.96 kHz, n = 16, 3 ♂♂); (4) the CF part of the echolocation calls following the advertisement call had a mean amplitude maximum at 48 kHz (SD = 1.89 kHz, 16 calls of three ♂♂).

In the field the individual calls are indistinguishable from the social calls emitted throughout the year during intraspecific interactions while hunting; we propose to call the latter 'agonistic calls'. Agonistic calls are never repeated more than three or four times, whereas the advertisement calls are given in long series at regular intervals. In the present paper, call series were counted as advertisement calls if they comprised at least 10 calls at regular intervals.

Spatial Distribution of Territories

We identified a total number of 92 songflight territories, which is a conservative estimate, as towards the center of the city the territories tended to be smaller. The highest concentration of territories was clearly near to the center of the old city. In this area there are three traditional large hibernation roosts of pipistrelles, and in this region also most of the known 'invasion centers' were situated (Fig. 2).

Within a diameter of about one km around the hibernation roosts the density of courtship territories was 10.8 territories/km^2, whereas the density out of this range was 2.1 territories/km^2. The distance to the

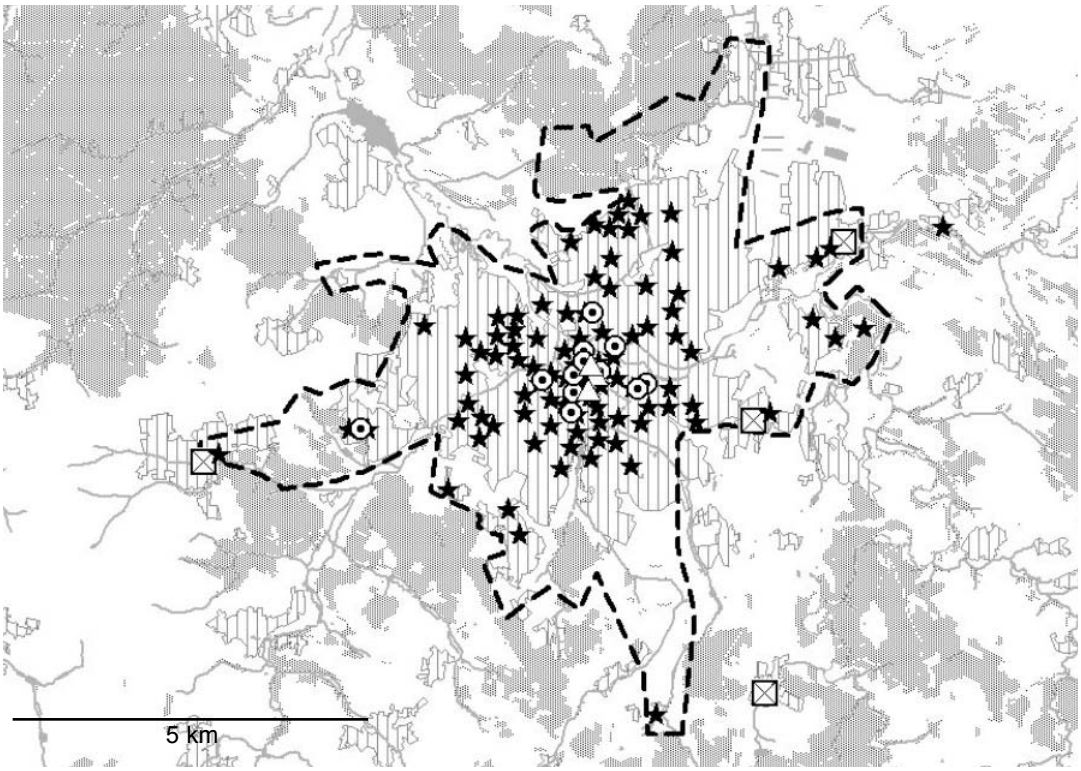

FIG. 2. Distribution of 'songflight territories' of pipistrelle males in Bayreuth. Stars = songflight territories; open crossed squares = nursery roosts; triangles = winter roosts with more than 15 individuals; dotted circles = 'invasion roosts' with more than 15 individuals. The diameter of the stars corresponds to the average size of a songflight territory (diameter 200 m). Hatched: built-up area of the city; dotted: forested area; white: open, mostly agricultural land or pasture; broken line: border of the city

known nursery colonies, which were situated at the edge of the city or even further away from the centre, outside the city limits, had no effect on territory density (Fig. 2).

Temporal Differences in Songflight Activity

Songflight displays were observed from the middle of July to mid-October. The songflight activity was maximal in September, about the same time when the 'invasions' occurred (Fig. 3). The male reproductive organs developed in parallel with songflight activity: the testes were largest in July/August and the epididymes in September/October (authors' unpubl. data).

There was considerable variation in the time course of songflight activity at different nights. On average, activity did not reach its maximum until several hours after hunting had begun, then remaining relatively high for the rest of the night until an hour or two before sunrise, when it declined dramatically (Fig. 4).

As the mating period went on, songflight activity began progressively earlier at night. Whereas in the period from 16 July to 20 August no advertisement calls could be heard during the first hour after the onset of hunting activity, between 21 August and 21 October the bats regularly called earlier in the night (difference: Mann-Whitney *U*-test, $Z = -3.865$, $P < 0.001$).

Climatic Factors

Regardless of the time of year or of the night, songflight activity increased with temperature (Fig. 5). During heavy rain no songflight display was performed. Other weather parameters (wind, cloud, moon) had no statistically significant influence on this activity.

Individual Differences in Songflight Activity and Interactions with Other Pipistrelle Bats

Individual territorial males differed considerably from one another in the intensity of their courtship activity (Table 1).

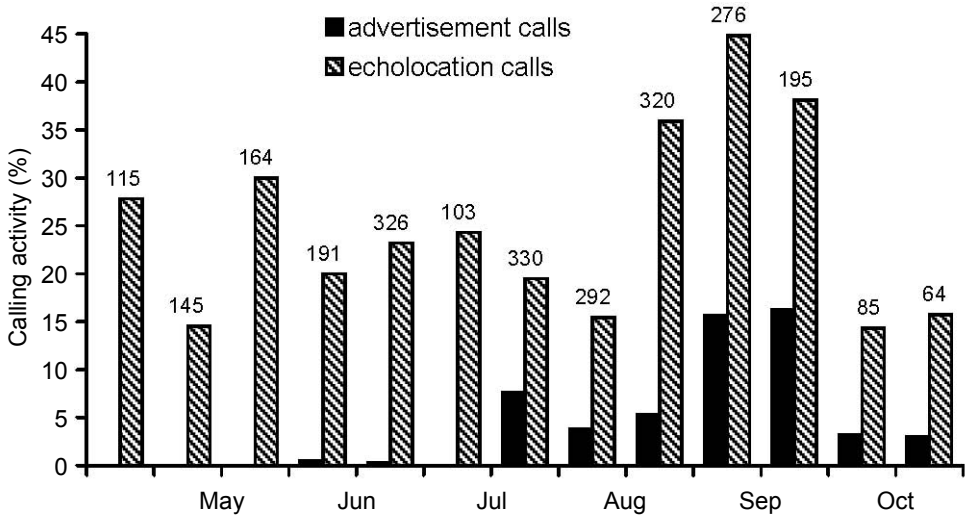

FIG. 3. Calling activity (percentage of site checks with calls) of pipistrelles during the year. Each column (representing half a month) gives the percentage of site checks, during which echolocation calls were observed (hatchend columns), either alone or together with advertisement calls (black columns) (observation series B, see methods). The bars under the graph identify the most important sections in the life cycle of the pipistrelles. The total number of site checks is shown above each column

Both agonistic and advertisement calls were heard significantly more frequently when at least one other pipistrelle was present during the observation in addition to the singing male (Table 2). Unfortunately, it was impossible to discern whether the other bats were male or female. The increase of calling in the presence of a conspecific was even greater for the agonistic calls than for the advertisement calls.

During the songflight displays the territorial males often emitted feeding buzzes

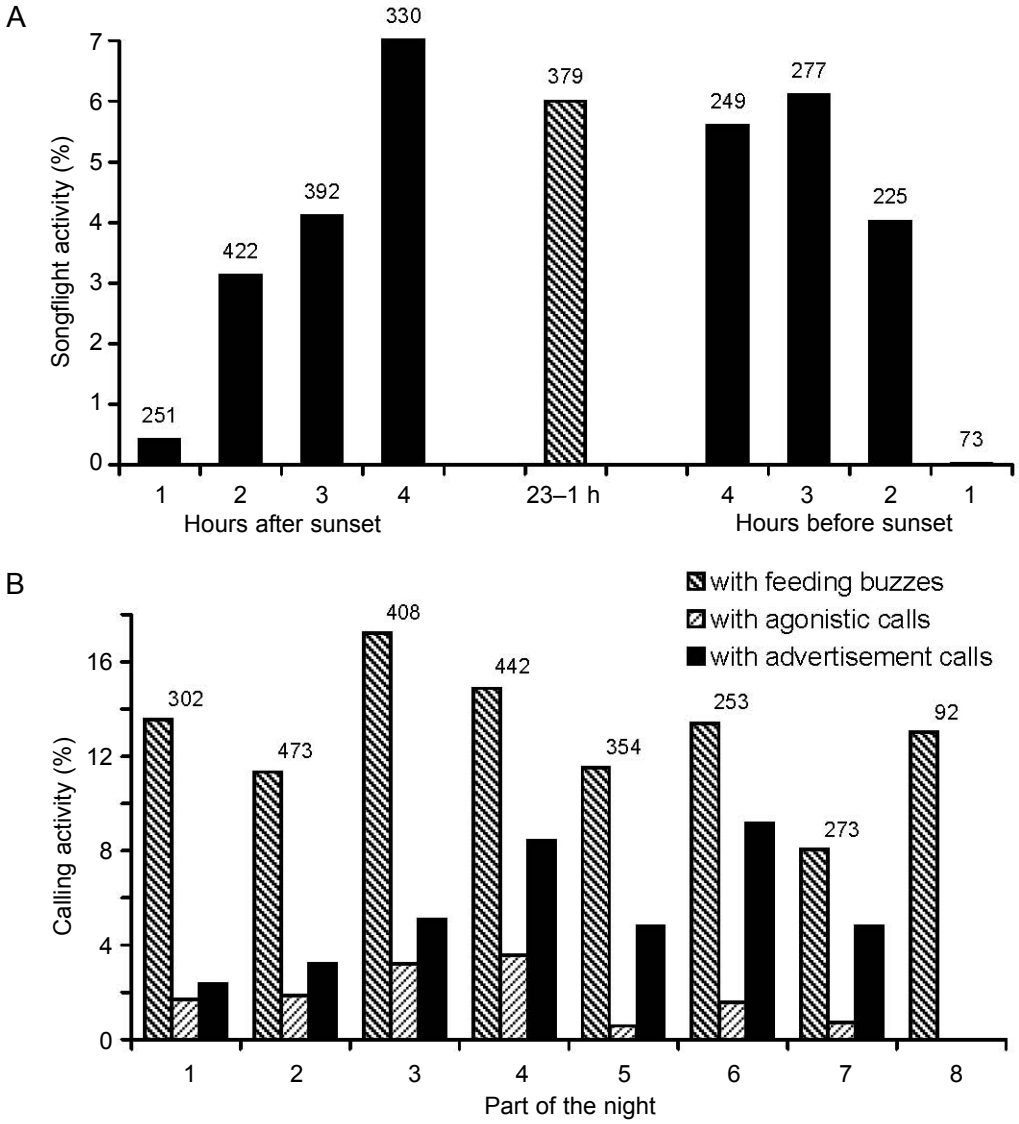

FIG. 4. Course of songflight activity of pipistrelles over the night (observation series B). A) — Songflight activity (percent of site checks) in the first and the last four hours of the night (hours after sunset and before sunrise); for comparison, the activity in the two hours around midnight (23:00–01:00) is also shown. B — Songflight activity (percent of site checks) during the night in comparison to hunting (feeding buzzes) and agonistic behaviour (agonistic calls). To compensate for the differences in duration of the night over the course of the year, each night of observation was divided into eight equally long sections and the activity was recorded for each section. The number above the column is the total number of site checks in the associated time interval

TABLE 1. Intensity of songflight activity in different territories between July 16th and October 15th (observation series A; n = 101–102)

Territory No.	Percentage of 4-minute units with advertisement calls	Songflights per 4 minutes ($\bar{x}$ ± SD)
1	12	0.26 ± 0.89
2	30	0.53 ± 0.97
3	30	0.76 ± 1.54
4	60	3.85 ± 4.63
5	14	0.16 ± 0.44
6	28	0.77 ± 1.96
7	28	1.05 ± 2.27
8	12	0.43 ± 1.44

and made flight manoeuvres indicating that they were hunting insects. Agonistic calls were much more likely to occur when the second individual was hunting (i.e., emitting feeding buzzes) compared to not hunting (Table 3).

DISCUSSION

Although as yet there are no reliable data to document the attraction of females in mating condition by the territorial songflight of the male pipistrelles in Bayreuth, such attraction is very likely, since it has been shown to occur in *P. pygmaeus* in southern Sweden (summarized by Lundberg, 1989), *P. kuhlii* in Israel (Barak and Yom-Tov, 1991) and *P. nanus* in East Africa (O'Shea, 1980). The songflying males in Bayreuth, like the bats observed by Lundberg and Gerell (1986) in Sweden, were sexually active (large epididymes). The songflight is conspicuous not only acoustically (low-pitched calls, which can thus be heard at a great distance) but also because of the flight style, flapping interrupted by brief phases of gliding flight. It is probably also accompanied by olfactory signals, which are very likely placed during 'false landings' (see Lundberg and Gerell, 1986).

Most striking, however, are the regularly emitted calls, readily detectable even by the human ear (Barlow and Jones, 1997). Because the advertisement calls have nearly the same acoustic structure as the agonistic calls, but, because they are regularly repeated, are considerably more

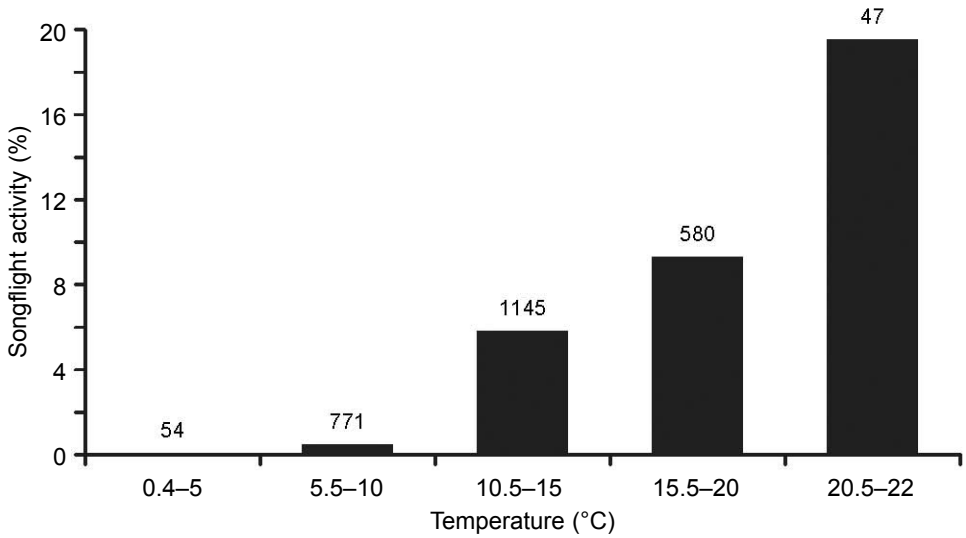

FIG. 5. Songflight activity of pipistrelles at different temperatures. The 2,597 site checks made during observation series B were classified according to the mean temperature at the time of the check, and for each class the percentage of site checks in which courtship activity was observed was calculated. The number of checks is given above each column. On warm nights courtship activity was much greater than in cool nights, and this effect was independent of the time of the year

TABLE 2. Frequency of advertisement calls and agonistic calls in relation to the number of pipistrelles at the observation site (observation series B)

Bats detected by their echolocation calls	*n*	Percentage of localities with	
		agonistic calls[1]	advertisement calls[2]
Only one bat	1,038	8.5	16.8
More than one bat	137	45.3	36.5

[1] — $\chi^2 = 143.71$, $P < 0.001$; [2] — $\chi^2 = 29.28$, $P < 0.001$

conspicuous, they can be interpreted as a ritualized form of a general social call. Agonistic calls can be heard when two bats in hunting flight encounter one another, and brief pursuit flights are also common in this situation.

Gerell and Lundberg (1985) and Lundberg (1989) interpreted the mating system of the pygmy bat and other members of the genus *Pipistrellus* as 'resource defence polygyny'. By this they meant that the females choose as reproductive partners those males that defend roosts as a resource, though they also notice the 'quality of the food resources in the surroundings of the roost site'. Our observations in Bayreuth show that this interpretation is very unlikely to apply to the common pipistrelles in southern Germany. The courtship territories are most densely packed in the city center (Fig. 2), where the proportion of buildings to open space is relatively high and hence, presumably, the density of prey animals tends to be low. In the peripheral regions of the city, where the nursery roosts are located (Arnold and Sachteleben, 1993) and the food supply is certainly greater, hardly any courtship territories could be found, although suitable roosts are present there as well.

We propose an alternative explanation: the males set up their courtship territories where the females are most likely to be during the time after they have left the nursery roosts. A number of bat-ringing studies have shown that the pipistrelles in Central Europe live in stationary populations, populations that do not migrate far and are often centered around large winter roosts (von Helversen *et al*., 1987). According to most studies, the bats come to these winter roosts from a surrounding region with a radius of about 20–40 km (Grimmberger and Bork, 1978; von Helversen *et al*., 1987; Hůrka, 1988, Sachteleben, 1991; Haensel, 1992; Feyerabend and Simon, 2000). After the young have been raised, the females leave the vicinity of the nursery roosts and, as early as end of July, make their way to the winter roosts, where a 'swarming' behaviour can be observed (Grimmberger and Bork, 1978; Sachteleben, 1991; Smit-Viergutz and Simon, 2000). During this phase the animals inspect the hibernation quarters, probably to make sure that the winter roosts still exist and remain suitable. This is also the time of the year (mainly August and September) when the 'invasions' occur, a phenomenon characteristic for the pipistrelle bat: sometimes hundreds

TABLE 3. Frequency of advertisement calls and agonistic calls in relation to feeding activity of pipistrelles, monitored by the occurrence of 'feeding buzzes' (observation series B)

Situations with or without feeding activity	*n*	Percentage of localities with	
		agonistic calls[1]	advertisement calls[2]
Only normal echolocation calls	335	2.1	20.6
Echolocation calls and feeding buzzes	340	12.6	16.8

[1] — $\chi^2 = 25.9$, $P < 0.001$; [2] — $\chi^2 = 1.4$, $P > 0.1$

of bats gather, often at unexpected places like a room the windows of which have left open and the inhabitants left for a holiday week. Because in Bayreuth the invasion centers were observed to be near to the winter roosts (Sachteleben, 1991) and hence close to the courtship territories, possibly young females involved in the invasions are visiting the territorial males in the vicinity to mate with them in their daytime roosts; but as yet there is no direct evidence for this idea.

The male pipistrelles thus neither defend resources for the females, nor can they prevent the females from leaving their territories. Instead they choose territories where many females may be expected to pass.The territories are the more favourably situated the closer they are to the flight routes which the females follow to the winter roosts. The territories are densely packed there, thus females can choose between many males, favourable also seen out of the females' view. Thus the mating system of the pipistrelle bat also bears some likeness to a lek mating system (in a broader sense, see, e.g., Höglund and Alatalo, 1995).

Acknowledgements

For important critical discussions we thank K.-G. Heller. We are also grateful to M. Hammer, F. Matt, F. Mayer and W. Schulze for reading the manuscript and their critical comments, and to two anonymous referees for many detailed and helpful suggestions.

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Received 13 February 2006, accepted 04 April 2006