Mating system of a migratory bat, Nathusius' pipistrelle (*Pipistrellus nathusii*): different male strategies*

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The mating system of European bats is often reported as 'resource-defence polygyny' where the resource is a male roost and its adjacent territory. With a large amount of field data we tested predictions of that model on the spatial dispersal of males in a resident population of a migratory species, *Pipistrellus nathusii*, well known for its complex vocal advertising by males during the mating season. The study was conducted in southern Bohemia throughout nine seasons (1999–2007) and revealed that (i) pronounced aggregations of male roosts and vocalization sites were affected by the vicinity of the breeding colony, and (ii) dyadic or triadic aggregations were observed in 65% of resident males that shared a common vocalization site. Dyadic or triadic groups were often quite stable over time (for up to seven successive years). No direct agonistic behaviour was observed between group members in contrast to regularly observed synchronization in their activity patterns and advertisement vocalizations. The busy vocalization sites were also visited by alien males that also produced advertisement vocalization and by non-vocalizing males that may have acted as sneaks. All these phenomena suggest considerable diversity in male strategies, suggesting that the mating system does not correspond entirely to 'resource-defence polygyny' nor can it be regarded as a lek mating system to which it corresponds in other characteristics (e.g., aggregations of males and the essential role of female choice). We expect that the broad diversity in mating tactics that characterises the species under study may also reveal features relevant to the mating systems of other temperate bats.

Key words: Nathusius' pipistrelle, mating system, lek, resource-defence polygyny

INTRODUCTION

As stressed already in basic texts of sociobiology (Wilson, 1975), bats (Chiroptera), the second largest order of mammals, exhibit extreme variations in reproductive strategies and social organization. Despite that, mating systems have been mostly identified as female- or resource-defence polygyny or promiscuity (sensu Clutton-Brock, 1989). This concerns not only species with a stable harem organization (Ortega *et al*., 2008; Voigt *et al*., 2008), but also temperate bats with pronounced seasonality — in which unstable harem groups are restricted to a short transitional mating period between the disintegration of maternity colonies and hibernation (Mc-Cracken and Wilkinson, 2000).

An exception to the general mammalian pattern of female or resource-defence polygyny, is mono-gamy, more likely facultative than obligate, and lekking known in a few species of bats (Bradbury and Gibson, 1983; Altringham, 1996). The lek system is characterized by the essential role of female choice and dramatic rearrangements in male territoriality that is often reduced to merely a position at the lekking site. Considerable energy is redirected to advertising displays which include visual, acoustic and olfactory signals and combinations of these (Krebs and Davies, 1993). The hammer-headed bat (*Hypsignathus monstrosus*) is often regarded as a mammalian species in which the lek mating system (Bradbury, 1977) is most pronounced and advertising behaviour results in one of the most extreme sexual dimorphism known in mammals (Starck, 1995). Males of this species form large choruses during the night that are visited by females. Males actively respond to the presence of females by increasing the repetition rate of their calls and by moving their wings (Bradbury, 1977). Patterns similar to lek systems were also found in some temperate bat species, such as *Myotis blythi* (Horáček and Gaisler,

1985) and *Miniopterus minor* (McWilliam, 1990), where males aggregate in the vicinity of maternity roost or specific mating roosts, occupy quite small territories and attract females.

The mating system of temperate bats responds to the limited availability of suitable roosts, low population density, temperate cycle with extensive seasonal rearrangements in spatial distribution, large home ranges of both males and females, and also migrating behaviour (Barclay and Harder, 2003; Kunz and Lumsden, 2003). Under these conditions, stabile harem groups can not be formed and male territoriality is often restricted to protection of relatively small 'spots' inside the foraging areas of females where single male/multi-female harem groups are formed (McCracken and Wilkinson, 2000). Clutton-Brock (1989), who provided a synoptic classification of mating strategies in mammals, classified such a system as resource-defence polygyny, where the respective resource is just the male roost (McCracken and Wilkinson, 2000).

In Nathusius's pipistrelle (*Pipistrellus nathusii*), the mating system has been repeatedly reported as 'resource-defence polygyny' — specifically, in regard to the active defence of mating territories by males with conspicuous acoustic displays (Lundberg, 1989; Gerell-Lundberg and Gerell, 1994; Barlow and Jones, 1996; Ciechanowski and Jarzembowski, 2004; Russ and Racey, 2007; Jahelková *et al.*, 2008). In contrast to the vast majority of European bats, *P. nathusii* is a species characterized by an obligatory long-distance migration from its breeding range in northern parts of Europe to hibernacula situated in southern Europe while its mating takes places just during the course of autumn migration along its migration routes (Ahlén, 1997; Strelkov, 2000; Petersons, 2004; Hutterer *et al.*, 2005). Thus the peak of the mating season appears in late July and early August in Sweden (Lundberg, 1989), in mid and late August and beginning of September in the Czech Republic (Jahelková *et al.*, 2008), north-eastern Germany (Heise, 1982, 1984; Schmidt, 1984, 1994*a*, 1994*b*) and Poland (Rachwald, 1992; Furmankiewicz, 2003), whereas it takes place in September and October in the southern parts of Europe (Bastian, 1988; Fiedler, 1998). The loud acoustic display of males is perhaps the most conspicuous phenomenon accompanying it: performed either as a songflight or as a sedentary display from males' roosts. The advertisement calls are usually composed of three motifs: the first 'main motif' is formed by several short FM notes and resembles the advertisement calls of other European pipistrelle species, the second is formed by one steep FM note, and the third is a 'trill' of several 'V-shaped' syllables (Lundberg, 1989). A fourth motif formed by several simple-curved syllables can follow (Jahelková *et al.*, 2000), as well as an additional fifth motif formed by a sequence of quite steep FM calls (Jahelková *et al.*, 2008). Some of the acoustic parameters of advertisement calls vary only minimally and can be used for individual recognition (Jahelková, 2003; Russ and Racey, 2007), while some of them are highly variable and their modification depends on the behavioural context and changes during the season (Jahelková *et al.*, 2008). Males of *P. nathusii* are known also for their fidelity to their mating roosts (Heise, 1982; Schmidt, 1984; Rachwald, 1992).

In the Czech Republic, *P. nathusii* was long considered to be a rare species (Hanák and Gaisler, 1976). By the end of the 20th century, numbers of records suddenly increased, including those from the spring and early summer period and even maternity colonies. Recently, the species has occurred in more regions throughout the year, and in some lowland areas it is ranked amongst the dominant species, although only a few records are available from the winter period (Hanák *et al.*, 2006; Anděra and Hanák, 2007). The detailed study of a resident local population of *P. nathusii* in southern Bohemia, begun in 1999, provided a large amount of data concerning the ecology and behaviour of this species, including observations on the biology of mating and related acoustic display behaviour (Jahelková *et al.*, 2008). Besides other things the data demonstrated that in comparison to congeneric species (Barlow and Jones, 1997), the advertisement calls of *P. nathusii* are more complex and show a significant increase in complexity at the peak of the mating season. This paper supplements these results with data on patterns of long-term spatial and temporal variation in the local community of advertising males, seasonal variation in display tactics, and the phenomenon of synchronous vocalization activity of dyadic males.

MATERIALS AND METHODS

Field investigations were conducted from 1999 to 2007. The study area covers 5 km² and is situated in the vicinity of the town of Veselí nad Lužnicí (49°03'N, 14°50'E), in the Třeboňsko lowland basin, southern Bohemia, a variegated landscape covered with dense patches of forest (oak, pine, birch, willow), fields, meadows and fish ponds interconnected by a canal and modified river system (Fig. 1). Within the study area, two maternity colonies of *P. nathusii* were found, a third colony being found outside the area about 3 km away. The study was focused

on male spatial distribution and male advertisement behaviour. In total, 46 resident males were individually recognized, 30 of which appeared for more than one season.

The Field Study Included

(a) Standardized transects to measure bat advertisement activity along a 6 km circular transect passing most of the male roosts twice a month from May until September 2000–2007 (starting between 0:00–1:00 and finishing at 3:00–4:00 AM).

The locations of vocalization sites and roosts were recorded by GPS with an accuracy of ± 5 m. Individual vocalization sites (mostly centred around the roost of a resident male) were denoted by numbers (1 to 33). The roosts located within a particular vocalization site (i.e., at distances less than 30 m) were distinguished by supplementary letters (a, b, c, etc., Fig. 1). The codes for males correspond to Jahelková *et al.* (2008).

(b) Recording of advertisement calls and their contextual setting (site, time, vocalization behaviour): songflight (SF),
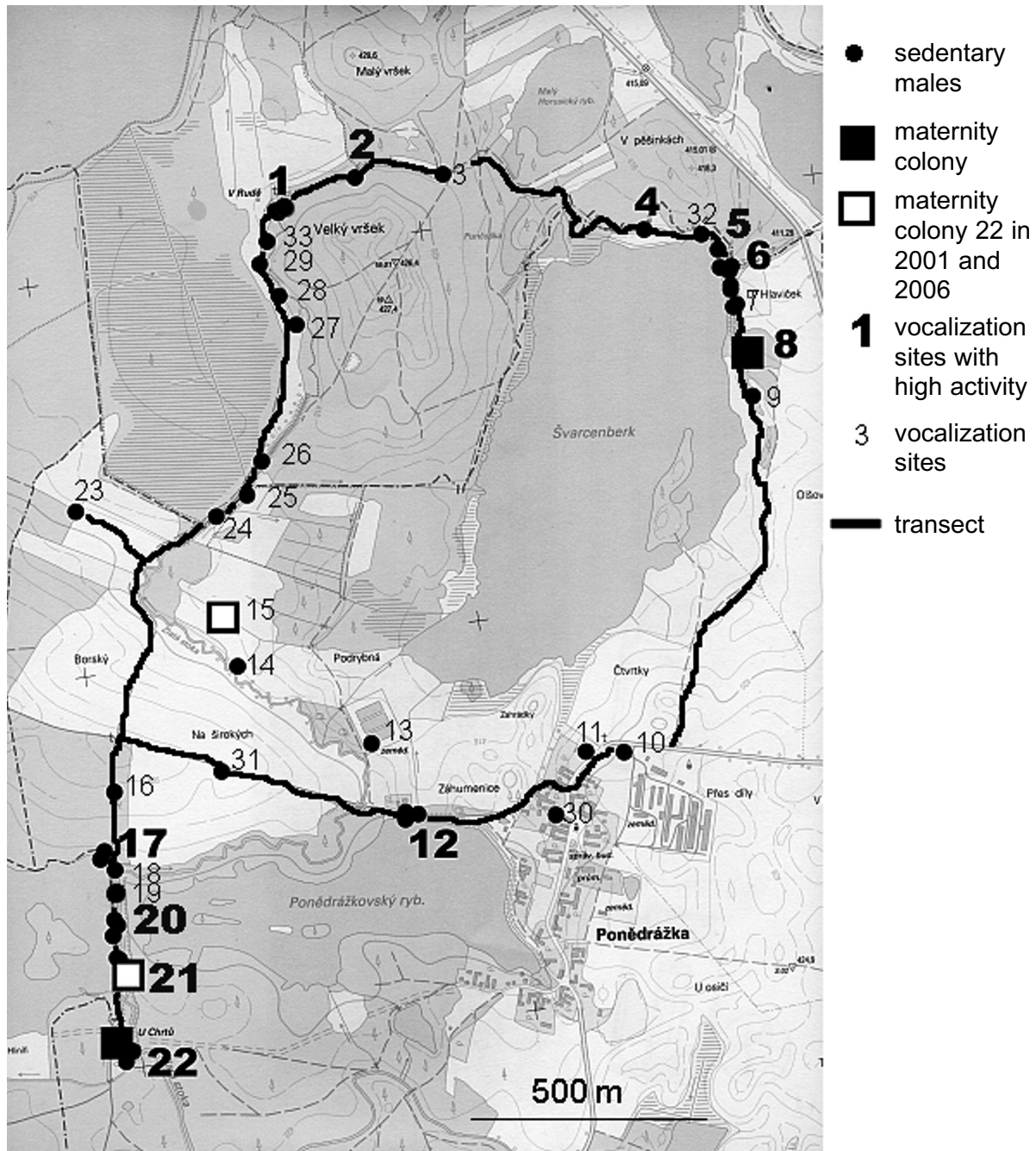

FIG. 1. A map of the study area with transect line, position of male roosts, regular roosts of maternity colonies and temporary roosts of maternity colony no. 22 (2001: no. 15, 2006: no. 21). Numbers indicate vocalization sites, with bold numbers representing areas of high activity

sedentary display (SD), and echolocation signals (ES) for subsequent sonographic analyses in 1999–2007. During 1999–2001, observations were made only during July and August and the amount of vocalization activity was estimated by using a unit of a 'positive minute' (i.e., at least 1 clear sequence of vocalization from the bat detector output during one minute was recorded as one minute of activity). During 2003–2007, males were observed from May to September, and the unit 'positive 15 seconds' was used instead of 'positive minutes' for better resolution. Based on specific individual characteristics of particular males' advertising calls (Jahelková et al., 2008), vocalizations of observed residents was distinguished from non-resident males. The total amount of whole night observations of display activity was 438 hours. In addition, the vocalization behaviour (social calls and echolocation) of maternity colonies during the end of May — beginning of July was observed in 2003–2005 (70 hours). The acoustic analysis was performed on the outputs of time expansion bat detectors D240 and D240x (Pettersson Elektronik) recorded by a digital recorder (Sony TCD-D8, Sony MZ-RH10), transferred to a computer and examined with the aid of Bat Sound 1.2 and Avisoft-SasLabPro 4.23 software (sampling frequency 22050 Hz, Hamming window, FFT size 256 and FFT overlap 87.5%).

(c) Nettings in foraging grounds and display sites of males. In total 17 males were banded, the others were marked for a particular year by individual-specific staining marks on pelage. Since 2002, all handled males were sampled for DNA with aid of a wing punches in specific pattern for each male.

(d) Day-time checks of accessible male roosts (performed only to a limited extent with particular respect to minimizing the disturbance of bats).

The study was supplemented with the radiotracking of five males (three resident males: 4, 12b, 12c and two non-residents captured at vocalization sites 4 and 12), and two females roosting at the vocalization sites (adult — 4, juvenile — 1) in August 2005 and in September 2004 and 2005 (32 nights, Holohil LB-2N transmitters, wide band receivers AR 8000, the position of each individual determined during night every minute), as well as large-scale sampling for DNA analyses (368 individuals including 45 adult males), the results were reported in Zieglerová (2008).

The statistical analysis included computation of basic statistics of temporal and spatial variables characterizing male activity, non-parametric tests used for comparisons between activity of solitary residents and group residents (Mann-Whitney U-statistics) and the quantifying of relative distances of males and maternity colony (Spearman correlation coefficient r_S). The analyses were carried out using Microsoft Excel and Statistica 6.0 software.

Definitions and Abbreviations

Resident males = males which were present at least three times during three months during a respective year at the same place; vocalization site = place where a male or males performed repeatedly advertisement display, and includes vocalization roosts of a male or group of males; vocalization roost = roost from which a male produced sedentary display; day roost = roost in which males were found during day; group = males within a relative distance of less than 30 m; neighbourhood = males at a relative distance of 30–120 m; safe distance = males at a relative distance of more than 120 m; SD = sedentary display; SF = songflight with or without echolocation calls; ES = sequence of echolocation calls with no link to advertisement call; vocalization activity = overall including SD + SF + ES; advertising activity = including SD + SF; motifs A, B, C, D, E = particular parts of the advertisement calls of P. nathusii, Fig. 7 (for details see Jahelková et al., 2008).

RESULTS

Number of Advertising Males and Vocalization Sites

The maximum number of advertising males recorded during a single transect monitoring was 30 (in August 14, 2001). The minimum number of resident males (i.e., those occupying their vocalization sites continuously throughout the season) was found in the years 2003 and 2005 (13 and 15 males respectively) and the maximum number in 2000 and 2001 (26 and 32 males — Fig. 1 and Table 1). Some vocalization sites were used yearly and males advertised there with relatively high frequency (e.g., sites 4, 6, 12, 17), whereas others were not so busy or were temporary in character (Fig. 2).

In most instances, the resident males were found at the same individual-specific vocalization sites in several subsequent seasons (2.05 ± 1.67 years on average, $n = 46$). Repeated occupancy of the same vocalization site for at least three successive years was observed in 12 males, two of which (6a, 12a) occurred at the same site for seven years and another two (4, 12b) for even eight years. The most frequent vocalization roosts during particular years

TABLE 1. Yearly account of (i) number of resident advertising males (repeatedly recorded from mid-July to mid-September), (ii) number of all males recorded during a season (April to October, includes males with unknown roost), both based on individual recognition by specific acoustic traits of advertising calls, in (iii) numbers of females in maternity colonies 8 and (iv) 22, respectively, during the study period (2000–2007). MC — maternity colony, * — counted during the first part of July (included early fledged juveniles), + — temporary roost of colony (1200 m from proper roost)

Category	2000	2001	2003	2004	2005	2006	2007
n of resident males	26	32	13	23	15	17	20
total n of all present males	27	37	19	28	27	23	27
n max MC 8 (May–June)	90	40	10	25*	20	20	30
n max MC 22 (May–June)	120	145*+	80	85	70*	70*	95*

were tree holes or crevices (35–62%) and crevice-roosts in buildings (27–50%), less commonly boxes (4–18%), and occasionally also covered deer-stands (0–9%).

During the study period (1999–2007) we recorded 17 cases of a replacement of an original resident male by another male, by which the new males colonized both the specific vocalization sites and day roosts of the original males. All these cases were associated with the definite disappearance of a former male. Furthermore, five vocalization sites were abandoned by their residents and were not recolonized. In total, 17 roosts in active vocalization sites became abandoned, mostly due to the destruction of the roosts. At the same time, 13 roosts of resident males were newly established during the course of the study, mostly in areas of existing vocalization sites. Five of them appeared in newly established vocalization sites.

Dynamics of Advertisement Behaviour and Night Activity

The advertisement calls were recorded on regular transects from May until mid-September during 2000–2007, except for the earliest incidence of advertisement calls on April 18 (in 2004) and the latest record on September 20 (in 2005). The number of advertising males recorded on a single transect changed considerably during the season in a similar way regularly repeated on each of the nine seasons of the study. A slight peak in the number of advertising calls was recorded in May, while the main peak was always in August (Fig. 3).

During the study we observed the vocalization activity of chosen resident males and recorded the amount of advertising activity (sedentary display, SD and songflight, SF) and echolocation calls. Unlike advertisement calls, echolocation calls did not allow for such individual recognition, so that the amount of echolocation activity recorded refers to both resident males and unknown individuals. In most instances the observed songflight performances corresponded to just one of the following contrasting types: (a) close SF — resident male performed a slow flight close to the roost (5 m) usually over a circular route, and approached the roost with a few advertisement calls. Echolocation calls were sometimes absent. This type was usually observed in the morning; (b) near SF — resident males performed flight along a regular relatively short route (10–40 m), and emitting of advertisement calls was regular. Echolocation calls were sometimes absent;

(c) regular remote SF – resident males returned to the roost at regular intervals with advertisement calls; (d) irregular remote SF — sporadic passes with advertisement calls. This type was usually produced by males identified as aliens by acoustic analysis.

Whole night observations of resident males *1*, *4*, *12a*, *12b*, *17b* and *17* during 2003–2007 revealed that at the beginning of each season advertisement calls were performed almost exclusively as SF and comprised only 5% of whole night activity. The vocalization records of that period are predominantly composed of echolocation calls. In contrast, during the peak of the mating season in August, advertising activity composed 58% of whole night activity. Most advertisement calls were emitted at the entrances of roosts as SD (76% of vocalization recorded — Fig. 4). Prior to the mating season (May–June), when resident males do not spent much time in advertising their vocalization sites, we also recorded their social calls far from their roosts. In 2003–2005, when continuous observation in maternity colonies 8 and 22 was undertaken, besides juvenile and female social calls we also recorded irregular songflight calls of 13 male individuals in the near vicinity of both maternity roosts (16–359 advertisement calls containing the motif ABC per night). Five of these males were recognized as individuals: resident males occupying a moderately-distant vocalization site (distances of their roosts to the nearest maternity colony are in parentheses) — maternity colony 8: *6a* (250 m), *6b2* (246 m), *7c* (124 m); maternity colony 22: *17b* (530 m), *21* (100 m).

During the mating season in August and September, we radio-tracked five males (three resident males: *4*, *12b*, *12c* and two non-residents captured at vocalization sites *4* and *12*) and two females (adult and juvenile) for two to five nights with a precise location of bat position. Because the number of bats was low, our results are only descriptive in character. The ratio of unknown activity of resident males *4*, *12b*, *12c* was very low (7.5%, 4.5% and 14%) in comparison to non residents (72 and 57%) and females (16% adult and 83.5% juvenile). Resident males spent most of the night at their vocalization sites (78–83% of their whole night activity) and used relatively small areas: 27.0 ha, 16.4 ha, 2.6 ha (observations over two nights only). The longest recorded distance from the resident day roost was 700 m. These resident males temporarily alternated their vocalization roosts within a vocalization site during a single night (1–4 switches at an average distance of 16.5 m). In all instances, the vast
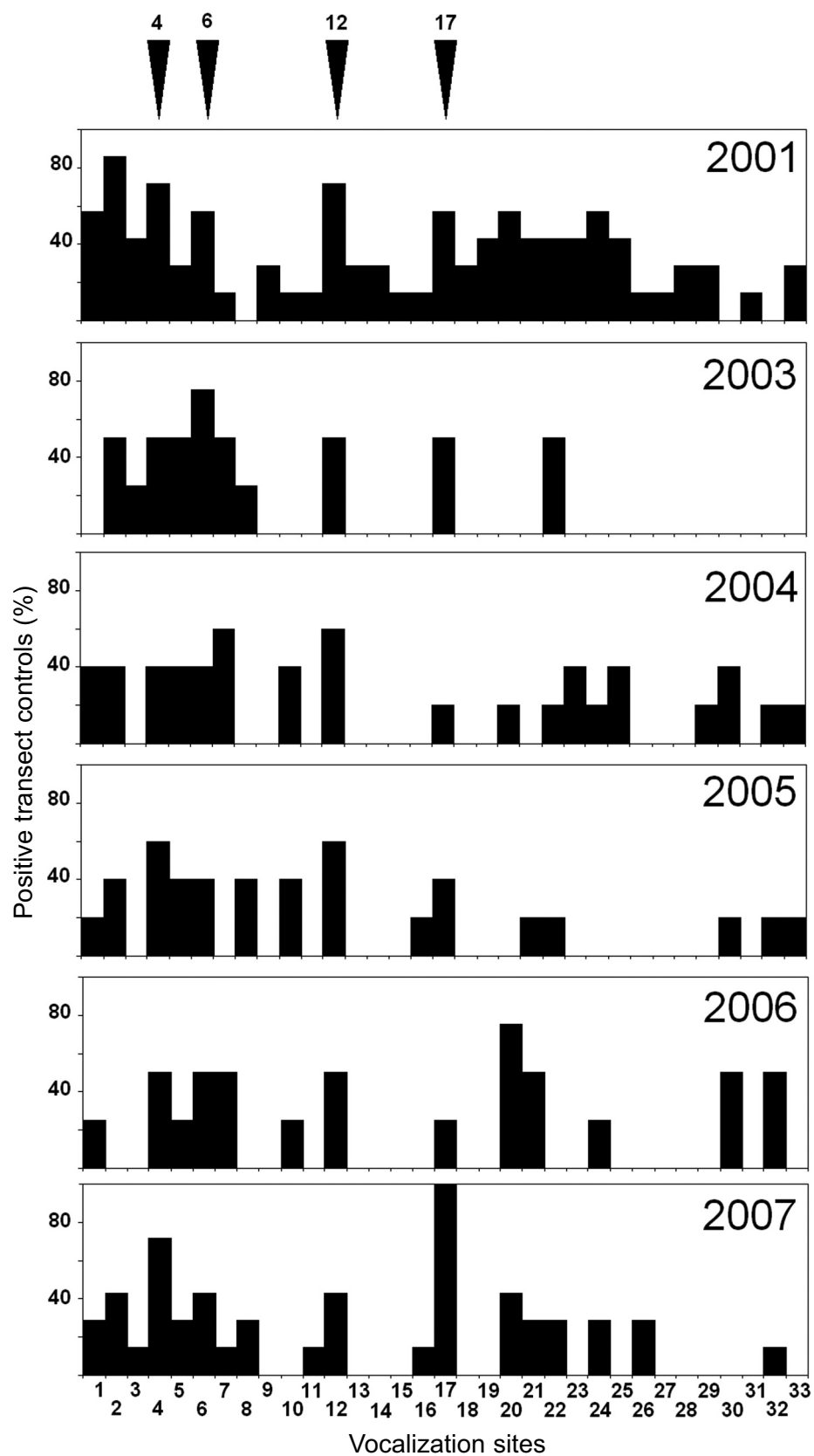
FIG. 2. Percentages of positive transect controls from regular vocalization sites 1–33 in the peak of the mating period. The arrowheads indicate the vocalization sites with steadily high activity throughout the study period. The data of year 2002 are not presented due to incomplete records (two controls only)
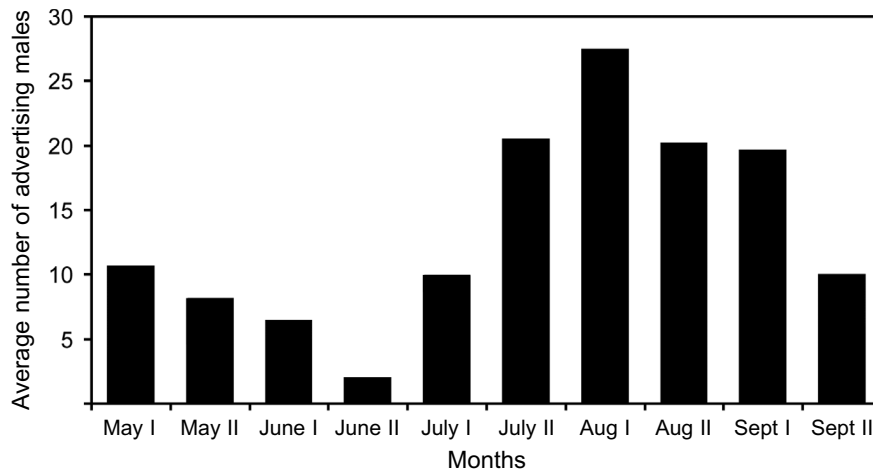
FIG. 3. Seasonal course of mean number of vocalizing males on transect during the seasons 2000–2007 together with other vocalising males recorded during continous whole-night observations at sites situated on the transect. I and II refer to the first and second half of particular months

majority of calls were produced from the resident's day roosts. By contrast, two non-resident males with regressed testes captured in the territories of resident males exploited at least five times a larger area during the night (116.2 ha, 171.2 ha) and were found at remote distances from the mist-netting site, where they had their day roosts (1050 m and 1500 m, 2900 m), which they switched daily. One juvenile female captured from the harem of male *1* also used a large area (273.9 ha) and spent most of the night far from her day roost. She switched roost only once (150 m). An adult female in the post-lactation period which roosted separately in the territory of male *4*, spent 76% of the night close to her day roost or within it. This female was once recorded in the roost

of male *4* (10 minutes), and once she visited the roost of male *1d* at a distance of 950 m, spent there approximately 40 minutes, and then flew back to her day roost.

Male Groups

In species with resource defence-polygyny, where the resource is a roost with adjacent territory, we would expect a relatively uniform distribution of resident advertising males. Nevertheless, the observed spatial distribution revealed a nested aggregation which clearly contradicted this assumption.

While the average distance between roosts of resident males in the study area fitted a normal distribution with a mean value of 1192.6 ± 181.2 m (median: 1144.7 m, min–max: 899.2–1764.2 m, skewness: 0.99, kurtosis: 0.7), the distance to the nearest roost showed a markedly skewed exponential-like distribution with a distinct peak at 0–20 m (Fig. 5). Less distinct peaks appeared also at distances of 80–100 m, 140–160 m and 200–220 m in years with a high number of recorded males (2000: *n* = 26 and 2001: *n* = 32), whereas in other years such peaks were indistinct.

Effect of colony distance

The spatial distribution of males' vocalization sites showed a clustering tendency in relation to the position of maternity colonies. Thus 48% of males performed advertisement display in moderate vicinity (50 to 500 m) to either one of the maternity colonies. In resident males, which roosted in moderate vicinity to the maternity colony, the average
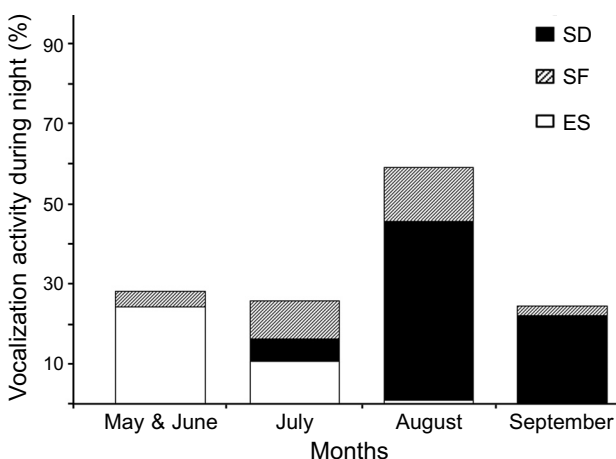

FIG. 4. Vocalization activity of resident males (*1, 4, 12a, 12b, 17a, 17*) during whole night observation during 2003–2007. Non-vocalization activity included silence in the roost, foraging beyond reach of bat detector and unknown activity. SD = sedentary display, SF = songflight, ES = echolocation call
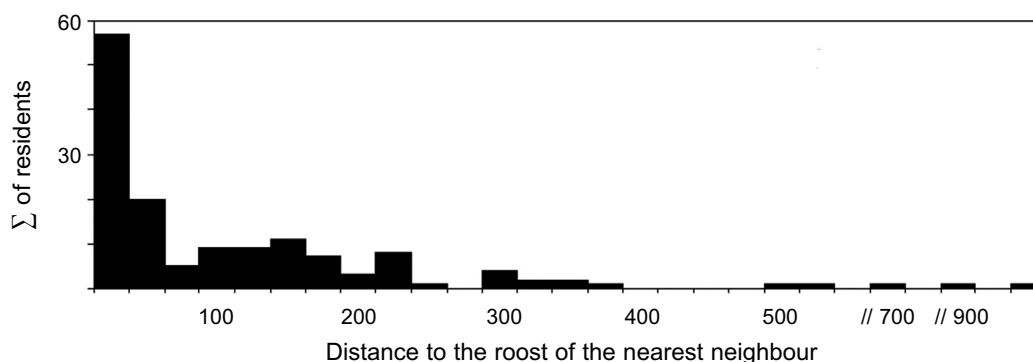
FIG. 5. Sum of all resident advertising males' distances to the nearest neighbour male roost in the peak of the mating period 2000–2007 (from mid-July to mid-September)

distance to a roost of the nearest resident male was 21.9 m and 23.7 m, respectively. Besides this, a significant number of vocalization sites were situated at a considerable distance from the maternity roosts and males had their vocalization roosts at greater distances from one another and the average distance to the roost of the nearest male was 96.5 m (Fig. 6). In the total sample, which includes also non-residents, distance to the nearest neighbour and distance from the nearest maternity roost were significantly correlated (Spearman, $r = 0.49$, $n = 62$, $P < 0.001$).

Aggregation of male roosts

In general, 28 of 46 resident males recorded during the study period (i.e., 61%) roosted at least for one season in close vicinity (1–29 m) to the roost of another resident male. Such groups were composed of two (five vocalization sites) or three resident males (three vocalization sites). We did not document continuous joint occupancy of the same roost by two or more males (even if they shared the same vocalization site).

The number of males in a group and the presence of particular individuals changed during the study period as some males disappeared and new males arrived. The average duration of a dyadic association of two males was 2.60 ± 1.89 years. The longest duration was observed in males *12a* and *12b* (seven years), which occupied the vocalization site relatively distant from both maternity roosts. We found no relation between the duration of dyadic occupation of a vocalization site and its distance from both maternity roosts.

At all vocalization sites that were at a moderate distance to maternity colonies (50–500 m), disappearance of a resident male did not result in the disappearance of other group members, and the

respective roost was soon colonized by another male. In the vocalization sites of dyadic and triadic residents, alien males also appeared relatively regularly (both sexually active and inactive individuals), including those which performed temporarily advertisement displays (Table 2). In such instances, we observed apparent agonistic behaviour of the resident male, including chasing of intruders, which resulted in one case in direct attacks that even continued in a struggle on the ground. In contrast, we did not record such aggression among dyadic and triadic residents. To avoid misinterpretation of behaviour data, we chose from our behavioural and acoustic material only a flight-out reaction of the resident male performing sedentary display to songflight of his dyadic/triadic partner or alien male close resident's roost (n situations with alien male = 18; n situations with dyadic/triadic partners = 31). Resident males flew out from their roost in 89% of cases as a response to alien males' songflight and stayed in roost in 11% of them, whereas the reaction to dyadic/triadic partners was just the reverse: in 6% of cases resident males flew out and in 94% of cases did not abandon the vocalization roost and continued in sedentary display.

The resident males roosting in close vicinity and sharing the same vocalization site tended to synchronize their vocalization activity pattern (Fig. 7). Those male dyads associated for more years (*12a*, *12b*; *17a*, *17b*; *6a*, *6b*) exhibited synchronized vocalizations quite regularly throughout each season of the study. From the three vocalization sites where we observed triadic displays, two of them repeated for two and four successive years, respectively (males *12a*, *12b*, *12c* in 2003–2006, males *17a*, *17b*, *17c* in 2001, *6a*, *6b*, *6c* in 2000–2001).

Between-individual differences of individual specific parameters of advertisement calls of dyadic
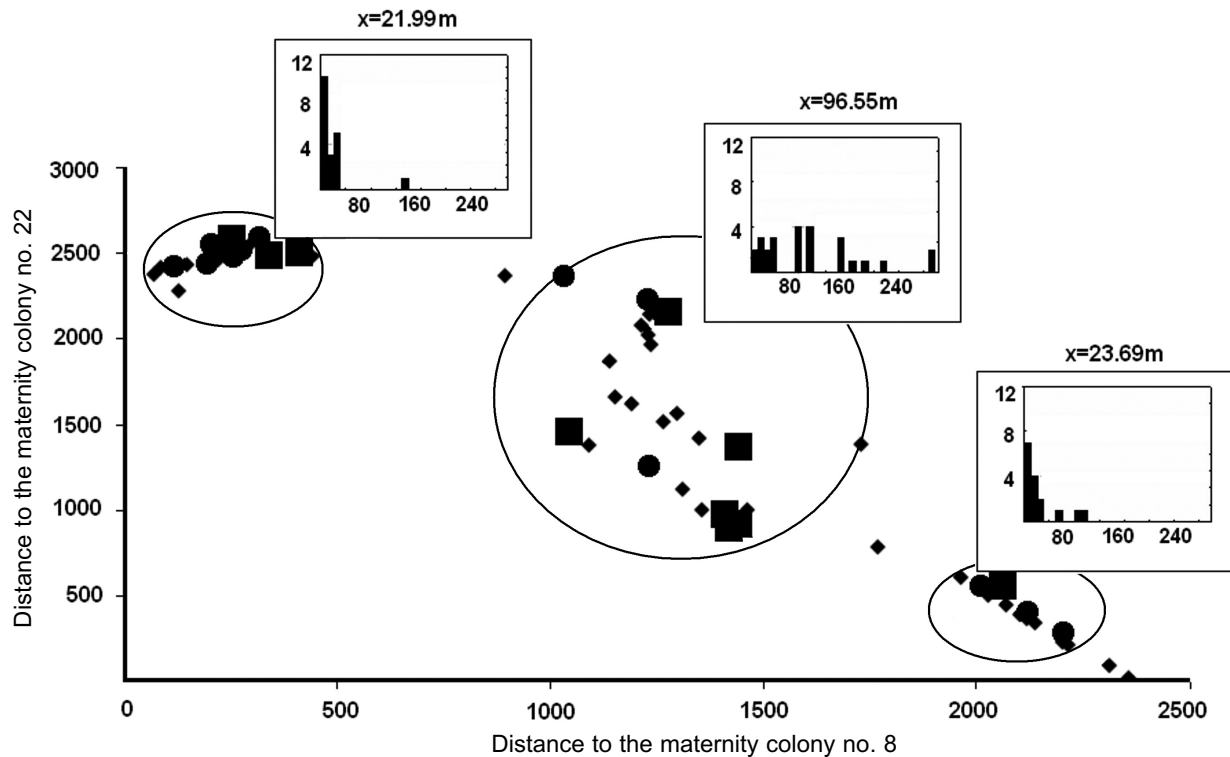
FIG. 6. Distribution of all records of advertising males with respect to their distance to both maternity colony 8 and maternity colony 22. The records clearly split in three clusters, encircled here, which differ also in distances to the nearest male neighbours shown at histograms (abscissa — distance to the nearest male neighbour in metres, ordinate — number of cases). The average distance to the roost of the nearest male (x) for each encircled group is above each histogram. Diamonds = males regularly advertising in a single season and irregularly vocalizing males (mainly songflight), circles = males regularly advertising for two or three seasons, squares = males regularly advertising in four or more seasons

males did not show any clear pattern. The differences in one of important parameter, the lowest frequency of the third note of motif C — lof C3 (Jahelková *et al.*, 2008), fell into a range from 0.93 kHz (males *12a* and *12b*: association 7 years, $n_{lofC312a} = 225$, $n_{lofC312b} = 78$ — Figs. 7 and 8) up to 20.43 kHz (males *17* and *17b*: association 1 year, $n_{lofC317} = 21$, $n_{lofC317b} = 23$). No clear relation between the proportion of between-individual difference of advertisement calls among dyadic or triadic males, and duration of their association, was found.

Significant differences in vocalization between the group resident and solitary resident males were found only in July and reflected rather the individual pattern of display: solitary males performed more sedentary displays (Mann-Whitney *U*-test, $z = -2.32$,

TABLE 2. A survey of the situation in the vocalization sites (VS) regularly occupied by males throughout study period (1999–2007). (i) VS = vocalization site, (ii) MC distance = distance (in m) to maternity colonies 8 and 22, (iii) type of the roost (T = tree hole/crevice, B = box, H = crevices in house), (iv) group size: mean (minimum–maximum) numbers of males recorded at a single control, (v) ReM = number of resident males recorded in a vocalization site, (vi) SAM = total number of sexually active males captured in the site (vii) SIM = total number of sexually inactive males captured in the site, (viii) F = total number of females captured in the site; (ix) M SD/SF = number of individually specific sedentary or songflight display records in the site, i.e. number of males performing advertising calls, sneaks included, (x) Behaviour observed in the site: SD = sedentary display, SF = songflight, SF-G = slow songflight with gliding, FL = false landings, CH = chasing, G = struggle on the ground, TF = tandem flight, MS = morning swarming, SV = record of regular synchronous vocalization

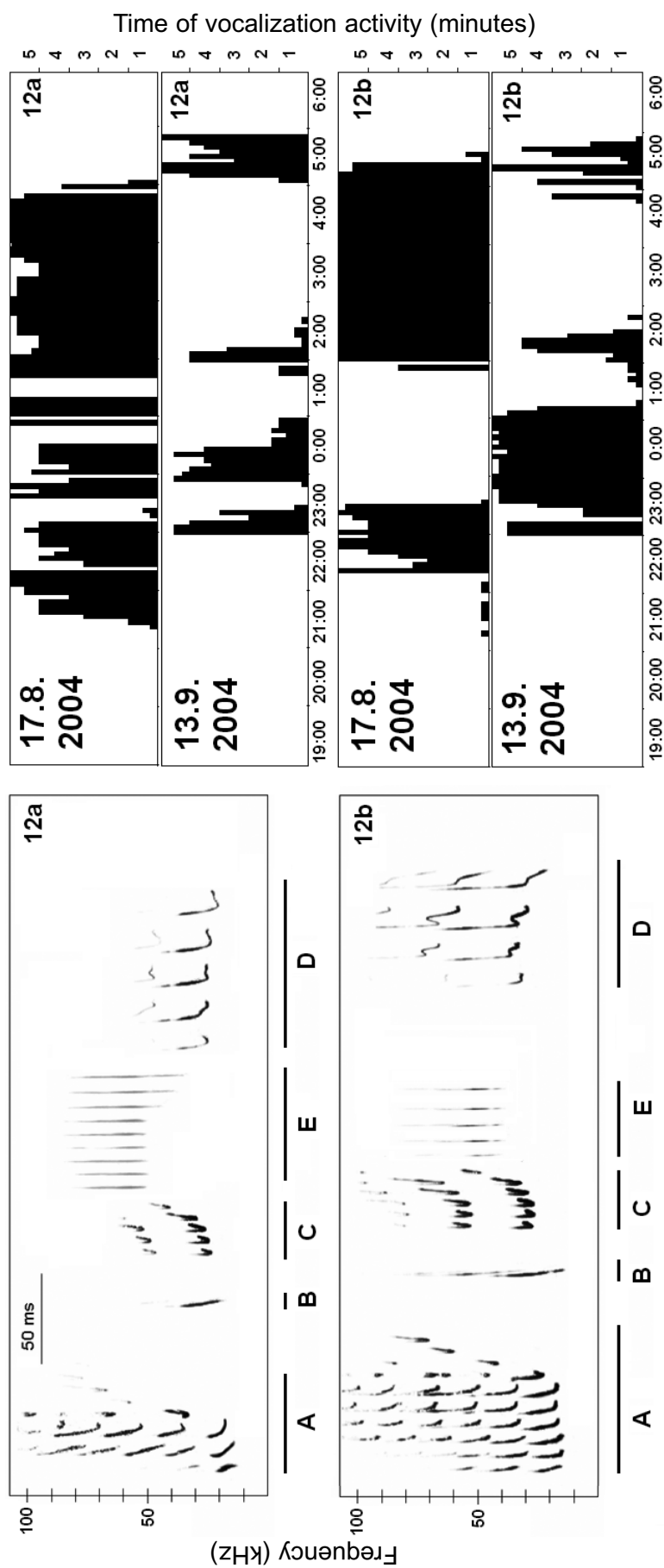| VS	MC distance	Roost type	Group size	ReM	SAM	SIM	F	MSD/SF	Behaviour
1	1250, 2180	H, T, T	1.44 (1–2)	4	9	5	12	5	SD, SF, FL, CH, G, SV
4	420, 2500	H, T	1.14 (1–2)	2	3	4	2	5	SD, SF, SF-G, FL, CH, MS
6	250, 2520	T, B, B	2.43 (2–3)	5	19	7	9	10	SD, SF, SF-G, FL, CH, TF, SV
12	1430, 930	H, H, T	2.71 (2–3)	4	3	2	6	5	SD, SF, SF-G, FL, CH, MS, SV
17	2040, 520	H, H, B	2.00 (2–2)	5	10	1	5	6	SD, SF, SF-G, FL, CH, TF, MS, SV

Fig. 7. Left: Sonograms of males' advertising calls (*12a* and *12b*) with distinguished motifs A, B, C, D, E. Right: two examples of continuous records of their vocalization activity during whole-night observations on 17 August and 13 September 2004. Note apparent synchronization both in the timing of the major burst of vocalization and the amount of vocalization activity

n = 12, *P* < 0.05). The higher proportion of echolocation calls at group resident vocalization sites (Mann-Whitney *U*-test, *z* = 2.04, *n* = 12, *P* < 0.05) suggests an increased flight activity in the sites either in the resident or alien bats. At the peak of the mating season (August), no statistically significant differences were found.

DISCUSSION

The concept of resource-defence polygyny expects a close connection among territoriality of males, specific resource, and males' capability to defend the resources which affects males' mating success (Krebs and Davies, 1993). In *P. nathusii*,
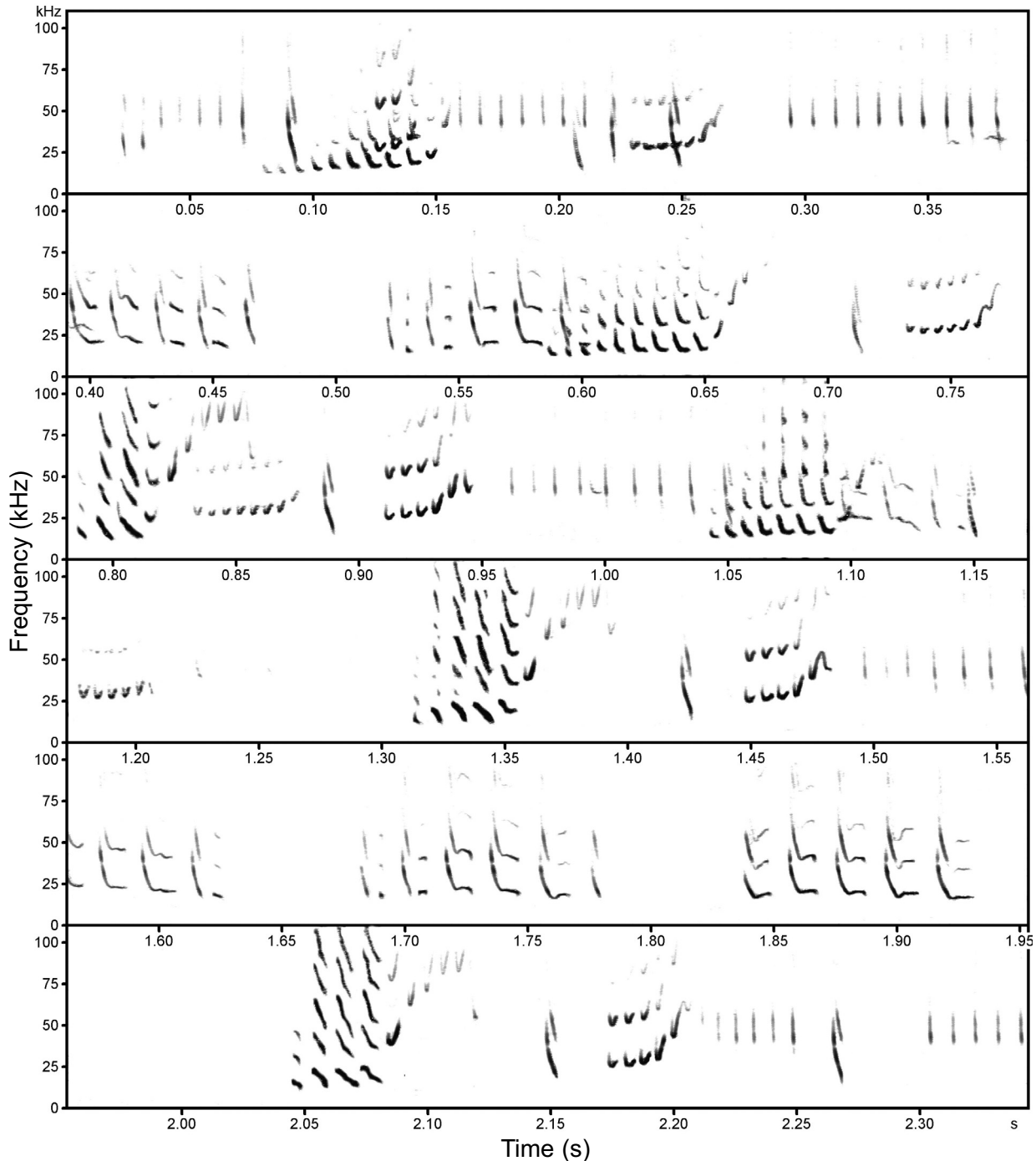

FIG. 8. A sonographic record of synchronous vocalizations of male *12a* which performed sedentary display and *12b* which performed songflight. Motifs of advertisement calls are as follows: 1st line – *12a*: EBEBE, 12b: ABC and faint D; 2nd line – *12a*: D, *12b*: faint D and ABC; 3rd line – *12a*: ABCED, *12b*: C and AB, echolocation call; 4th line – *12a*: ABCE, *12b*: C, echolocation call; 5th line – *12a*: D; 6th line – *12a*: ABCEBE

a long-distant migrant, meeting a mating partner might present a very hard task. Behavioural adaptations which make possible meeting of both sexes are conspicuous: males exhibit excessive advertisement vocalization asso-ciated with protection of specific site which can be considered as the defended resource (Gerrell-Lundberg and Gerrell, 1994). Our study demonstrated that strict resource-defence polygyny do not have to concern all males and that behavioural performance of territoriality can be modified.

During the course of a season, the advertising activity of males increased in July and reached its peak in August, i.e., synchronously with disintegration of the local maternity colonies and disappearance of adult females from maternity roosts. A small peak of advertising activity also appeared in May. In most cases the May advertisement vocalization was produced by the resident males which further occured throughout the season. We hypothesize that the May peak of advertising activity is related to reestablishing territories of resident males at that time. Their advertising vocalization is supposedly intended to repel the males arriving from migration and/or to advertise a male's presence to females occupying neighbouring maternity roosts. The songflight of the resident males recorded close to maternity roosts at that time may support such a possibility, as well as differences in complexity of acoustic repertoire of males between late summer and spring (Jahelková *et al.*, 2008).

The epidydimis of males from the winter and spring period may contain active sperm similar to that during the mating season (Braun, 2003), which suggests that *P. nathusii* may mate even during time of spring migration. The fact that parturitions in *P. nathusii* are not very synchronous and take place over a period of about three and half to five weeks (so that both weaned and newborn pups can occur together in one roost — cf. Heise, 1984; Schmidt, 1985; authors' own data) provides indirect support for such a possibility as well. As in other pipistrelles, parturitions in one year old females are no exception (Hackethal and Oldenburg, 1984; Schmidt, 1984; Haensel, 1985). The above mentioned indirect evidence can not exclude that females may mate also during the spring migration period, and that in consequence of spring mating the maternity colonies are assembled in the vicinity of traditional males' roosts far away from the original breeding areas. Based on behavioural observation, Russ *et al.* (1998) also discussed the possibility and importance of spring mating in a dynamic Irish population

which continuously adapted its range in response to climate changes (Lundy *et al.*, 2010).

We stress this possibility particularly in respect of the history of the population under study: although the males of *P. nathusii* were recorded in that intensively studied area since 1968, the maternity colonies and regular presence of males throughout the breeding period had not been recorded except for the most recent decade (Jahelková *et al.*, 2000). The appearance of the resident population in the region, where the presence of the species was previously restricted mainly to the period of migration, is obviously a result of the recent expansion of the species (Lundy *et al.*, 2010). In any case throughout the study period the resident population of *P. nathusii* was enriched by migratory individuals (both males and females) during mating season. The numbers of resident males have varied annually, the lowest number of resident males appeared in years when also the size of maternity colonies diminished. The mean duration of roost occupancy by particular males was slightly lower than in Germany, 2.05 years versus 2.47 years (cf. Schmidt, 1994*a*, 1994*b*), although four males occurred at the same vocalization sites throughout for at least seven or eight years. Their age was thus at least eight or nine years, which approaches the highest age documented for males of Nathusius' pipistrelle from the wild, i.e., 11 years (Haensel, 1994).

According to the predictions of the resource defence model with an active defence of the roost and adjacent territory, which is assumed to correspond to the mating system of pipistrelles (Gerrell-Lundberg and Gerrell, 1994), we should expect a relatively even distribution of advertising males. Yet, the spatial distribution of resident males of *P. nathusii* in our study area contradicted this assumption in being largely uneven and clumpy, with the aggregation of vocalizing sites and male roosts in the vicinity of maternity colonies. Moreover, several male roosts were also aggregated far away from the maternity roosts.

In general, four hypotheses have been proposed to explain male aggregation during the mating period: (a) males are concentrated on hotspots whose qualities exceed other places; (b) males increase the attraction of females by amplification of their advertising stimulus; (c) male aggregations themselves are preferred by females; and d) males aggregate to reduce the risk of predation (Bradbury and Gibson, 1983). The last explanation seems quite improbable in our case, but the other three can not be excluded. It seems greatly probable that the simultaneous

occupancy of vocalization sites by two or three resident males (quite regular in the study area) and observed simultaneous vocalization from their neighbouring roosts could magnify the advertising effect and attractiveness of the sites, particularly for alien females passing through during autumn migration. Maybe such a setting promotes a reduction of territoriality of the long-term dyadic or triadic aggregations of particular males, who repeatedly colonized the same vocalization sites and the same roosts for several consecutive seasons — in our case for up to seven years.

A regular appearance of non-resident and non-territorial adult males in busy vocalization sites is another phenomenon deserving special attention. Alien individuals were recorded both by netting and by analyzed acoustic display (sequences of ABC motifs). Busy mating sites might also attract less successful males, who can perform a strategy of satellites or sneaks. Such an alternative strategy for non-territorial males in pipistrelles has been suggested already by Lundberg (1989).

During whole night observations we recorded aggressive reactions of resident males to the song-flights of non-residents and the chase of intruders, but obviously no such reaction occurred towards their own dyadic partners. The acoustic reaction of residents to the echolocation calls of other individuals (both male and female) was positive in 70% of cases and included changes in syntax and apparent increase of notes in motifs C and A of the advertisement call (Jahelková *et al*., 2008). No acoustic change in advertisement calls was observed in reaction to echolocation calls of the dyadic partner.

These observations may suggest a mutual tolerance among equivalent males at a hotspot which put all their energy to advertising display instead of agonistic interaction (chasing, struggles, etc.). The differences in reactions towards alien males and dyadic partner suggest together with the long-term persistence of dyadic associations and/or synchronized vocalization of dyadic males that the possibility of a cooperation within the dyadic association can be taken in account. It should be remembered that aggression of sexually active males of *P. nathusii* towards the same sex can be reduced and some males tolerate the presence of one or two juvenile males even within their harems (Kuthe and Ibisch, 1994; Fiedler, 1998; Haensel and Tismer, 1999; authors' personal observations). Interestingly the sharing of the same bat box by two sexually-active males has been reported (Fiedler, 1998; Haensel and Tismer, 1999).

In any case, the results discussed above suggest that the mating system of *P. nathusii* may differ in more respects from the state predicted by the resource-defence polygyny model. In its aggregation of males and synchronous advertising vocalization it might remind one of a lek system, but from which it differs, for example, by its small size and long-term stability of the multi-male aggregations.

Moreover, within the study population we can identify males whose tactics correspond to either the former or latter model, but also a number of those who behave in the way contradicting the prediction of both the models. The mating system of *P. nathusii* can thus be looked upon rather as a dynamic entity controlled by female choice and diverse strategies of males. Three major alternatives were observed: (1) resident males, which occupy roosts and start their production of social calls in April to September with the peak of the mating season being August; these males can be associated in long-term stable dyadic or triadic groups; (2) migratory males, for which vocalization is annually recorded at the end of August and in September at the same sites, often near or inside busy vocalization sites; (3) males which occur sporadically at the vocalization sites of resident males and which may play a role of satellites or sneaks.

Alternatively, all these specificities and broad variation in the reproductive tactics of males can be regarded as functional adaptations related to the spatial dynamics of a species whose seasonal dynamics is indexed by long-distance migrations. We would thus expect that the mating system of *P. nathusii* is not unique among European bat species. More likely it seems that in other species we can also find considerable variation in the mating tactics and behaviour of individual males and, similarly, as in the species under study, the female's choice of individual males presents perhaps the essential role. We should take into account the possibility that the standard definitions of chiropteran mating systems — corresponding to mere 'ready-made' text-book categories — may respond more to a lack of knowledge than to real phenomena (see also Sachteleben and Helversen, 2006; Chaverri *et al*., 2008).

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