

# Social structure of three sympatric bat species (Vespertilionidae)

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## Abstract

The social structure of three sympatric bat species occupying bat boxes in woodland in southern England was studied: *Pipistrellus pipistrellus* (pipistrelle), *Plecotus auritus* (brown long-eared bat) and *Myotis nattereri* (Natterer's bat). Before parturition, *P. pipistrellus* populations were heavily skewed towards solitary males. After parturition, the sex ratio was closer to unity. Recaptures of marked bats suggested that after parturition a resident male population of *P. pipistrellus* is invaded by a transient female population. The sex ratios of populations of *P. auritus* and *M. nattereri* were very close to unity, both pre- and post-parturition. The numbers of recaptures of individual bats were similar for both sexes in *P. auritus* and slightly higher for females in *M. nattereri*. In the mating season (August–October), solitary male *P. pipistrellus* were found with small groups (1–9) of females. In contrast, in both *P. auritus* and *M. nattereri*, mixed sex groups were found pre- and post-parturition, and roosting groups in the mating season contained up to 20 females and up to 10 males. The stability of female groups in *P. auritus* appeared to be higher than *M. nattereri* and *P. pipistrellus* as known females were found together more frequently. These patterns are discussed with reference to the possible differences in foraging and social behaviour.

**Key words:** bat boxes, roosting, social organization, Chiroptera, behaviour

## INTRODUCTION

Mating behaviours vary widely between and within species owing to individual variation and differences between male and female ecology and behaviour (Clutton-Brock, 1989). Emlen & Oring (1977) developed a classification of mating strategies based on the ecological and behavioural potential to monopolize mates, and the mechanism by which such a process takes place. In a comparative study of mating systems in bats, Bradbury & Vehrencamp (1976a, b, 1977) suggested that social systems are based on social dispersion (defined by group and territory size) which is primarily determined by food supply. The subsequent evolution of mating systems can only occur within the limitations imposed by social dispersion, in particular by female dispersion.

Bats are extremely diverse in their mating strategies. Territorial defence of roost sites by males has been described in both temperate and tropical species, for example *Nyctalus noctula* (Sluiter & van Heerdt, 1966) and *Pipistrellus pipistrellus* (Gerell & Lundberg, 1985) in Europe, *Pipistrellus nanus* in Kenya (O'Shea, 1980), *Myotis adversus* in Australia (Dwyer, 1970), *Cynopterus*

*sphinx* in India (Balasingh, Koilraj & Kunz, 1995) and *Artibeus jamaicensis* in the New World (Morrison, 1979; Kunz, August & Burnett, 1983). Male defence of female groups has been found in *Phyllostomus hastatus* (McCracken & Bradbury, 1981), and *Rhynchonycteris naso* (Bradbury & Vehrencamp, 1977) in Central America, and a lekking system has been described for *Hypsignathus monstrosus* in Africa (Bradbury, 1977b). In contrast, some bats form mating aggregations ('swarming') where both sexes are promiscuous and there is little or no sexual selection, e.g. *Myotis lucifugus* in North America (Fenton, 1969; Thomas, Fenton & Barclay, 1979), although DNA fingerprinting of young of this species has shown fertilization success is skewed towards individual males or male lineages (Watt & Fenton, 1995).

*P. pipistrellus* and *N. noctula* have been described as resource defence polygynists: both defend roosts, and mating groups invariably consist of a male and one or more females (Sluiter & van Heerdt, 1966; Gerell & Lundberg, 1985; Lundberg & Gerell, 1986). Studies of social structure and mating behaviour can be facilitated by providing artificial roost boxes, which many species will readily recruit into their pool of natural sites (e.g. Stebbings, 1966; Gerell & Lundberg, 1985; Heise & Schmidt, 1988; Benzal, 1991).

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It has recently been discovered that there are two distinct types of *P. pipistrellus* that echolocate at different frequencies (Jones & van Parijs, 1993). Some echolocate with a frequency of maximum amplitude averaging 46 kHz and some at 55 kHz, and it was suggested that these two phonic types were cryptic species. Park, Altringham & Jones (1996) found evidence for reproductive isolation between the two phonic types as only individuals of the same phonic type roost together during the mating season.

We have looked at the social structure of three sympatric species occupying woodland in southern England: pipistrelle, (*P. pipistrellus*), brown long-eared bat, (*Plecotus auritus*) and Natterer's bat, (*M. nattereri*). The differences in social organization observed are discussed in relation to current ecological theories of mating system evolution.

For the purpose of this study, we have used the term mating group to describe roosting groups of reproductively mature males and adult females found in the same box during the mating season.

## METHODS AND MATERIALS

### Study area

The study area consisted of 20 sites in an area covering 360 km<sup>2</sup> on the south coast of England (near Wareham, Dorset), managed by the Forestry Commission. This area is a patchwork of semi-natural deciduous woodland and heathland, dominated by plantations of non-native coniferous species. Bat boxes have been erected throughout this area since 1976 and there are now approximately 500 boxes. Distances between adjacent sites varied from 0.5 to 2.5 km, with a mean ( $\pm$  S.D.) separation of  $1.6 \pm 0.5$  km. Many of the sites were joined to adjacent sites by areas of woodland, though some were more isolated. With one exception, each site consisted of 6 trees with 3 boxes per tree, approximately 2.5–3 m up the tree, facing north, south-east and south-west. One site began with 60 trees in 1976, each tree having 8 boxes, facing north, south, west and east. Boxes were situated on 2 levels, 3 and 5 m from the ground. Forty of these trees were felled in 1984. Boxes were made of timber, to a design described by Stebbings & Walsh (1988). Areas covered by each site varied; the largest site, using 60 trees, originally covered 25 acres, and 1 site was situated on 2 sides of a 110 m wide ride. However, at most sites the cluster of 18 boxes was contained within a circle of radius 55 m.

Surveys were generally carried out between March and October. The number of surveys carried out each year varied, with approximately 4 surveys a year. Surveys for each site were completed in one day so that bats could not move between boxes within a survey period. Regular inspections did not appear to cause undue disturbance; in this and other studies, bats were repeatedly found at the same site for many years. Bats found were removed from the box (the box lids were

removable for easy access), identified, sexed, aged (immature or adult, see social grouping) and ringed with aluminium alloy rings (Mammal Society). All bats were ringed under licence from English Nature. They were then returned to the box or released if active. Released bats frequently entered nearby boxes within a few minutes. This paper analyses data collected between 1977 and 1993. Where required, data were tested for normality (Kolmogorov–Smirnov) and equal variance (Levene Median) and non-parametric methods were adopted where data violated the assumptions of normality. All data are presented as means  $\pm$  standard deviations. Analysis was carried out on Sigmastat (Jandel Scientific).

For analysis purposes, the main period of bat activity (April to October) was divided into pre-parturition (April to June) and post-parturition (August to October) periods. The females of the species form maternity colonies in May and June and the young are born in July. The main mating period for these bats is August to October, although there have been observations of matings during the hibernation period. For each of the three species, the following analyses were made:

### Population statistics

#### *Movement between sites*

Bats recorded at more than one site were examined with respect to species, sex and age and whether the move appeared to be made by a solitary bat or by a group.

#### *Sex ratios*

These were determined by examining total numbers of males and females caught from all sites each year within pre- and post-parturition periods. Individuals found multiple times within a period (i.e. pre- or post-parturition) in the same year were counted only once.

#### *Recaptures*

The number of times individual bats were caught was calculated across all sites and variation between sex and species examined.

### Social organization

#### *Group size*

The total number of groups (group size is defined by the number of bats found in the same box) over the survey period (i.e. 1977–1993) across sites were collated and variation in group size between pre- and post-parturition periods and species was examined.

### *Social groupings*

To analyse social organization, each group found was classed as 1 of 7 social categories. These were defined as follows: single female, single male, groups of females, groups of males, mixed-sex groups containing 1 adult male, mixed-sex groups containing more than 1 adult male, and juvenile groups (juveniles on their own or with adults of 1 sex). Visible cartilaginous epiphyseal plates in finger bones of bats under a few months old allowed young bats to be distinguished from adults (Anthony, 1988). Males of most small vespertilionid bats achieve sexual maturity in their first full season of food abundance following birth, and in some species females may become receptive to males in their first autumn (Racey, 1988). Age at sexual maturity is dependent on body condition, e.g. nutritional status (Speakman & Racey, 1986). Sexual maturity in *P. auritus* is reached at approximately 16 months in both sexes (Stebbing, 1966). Where relevant, it has been assumed that all juveniles in the post-parturition mating season were sexually immature. Combining data for all years across sites, social structure in the pre- and post-parturition periods was examined.

### *Mating group structure*

Roosting groups of reproductively mature males and adult females found in the same box during the mating season (August–October) were examined. Some sites contained many mating groups so, to avoid pseudoreplication (Hurlbert, 1984), it was necessary to ensure that no individuals appeared in more than one group. A list of mating groups was compiled and one group chosen at random. Each group was examined to ensure no individuals had been represented in the other groups previously chosen. The group was discarded if an individual had already been included. Each point represents a mating group containing individuals unique to that group. We have assumed that all adult males were sexually mature. Although this was not always determined, when documented by the examination of testes and epididymis (following Racey, 1988), adult males were reproductively mature.

### *Female group stability*

This was assessed by examining the associations of individuals with others of the same sex recorded over time. Only the post-parturition period was investigated here as it is the females' behaviour in the mating season that determines the mating strategy adopted by the males. For each species, females found with another female were categorized according to the number of times they had been found together in the same box. Six females of each species that had been captured 4 times in the post-parturition period were analysed. Although some female *P. auritus* had been found more often, this

was the maximum number of recaptures for female *P. pipistrellus*. It was not possible to analyse these associations statistically as the long time period over which ringing occurred meant that it was impossible to establish which females were concurrent within the study area, hence pair-wise comparisons of association indices may be biased to an unknown extent. For example, if association indices were to be made for all combinations of pairs of female *P. auritus* at one particular site, more information would be needed on the life expectancy of those females. If one bat was ringed in 1980 and another in 1985, it was not possible to calculate how long both those females might be expected to be at that site at the same time and therefore have the opportunity of associating with each other.

## RESULTS

A total of 1662 bats were ringed at these sites between 1976 and 1993, including 976 *P. auritus*, 355 *P. pipistrellus*, and 286 *M. nattereri*.

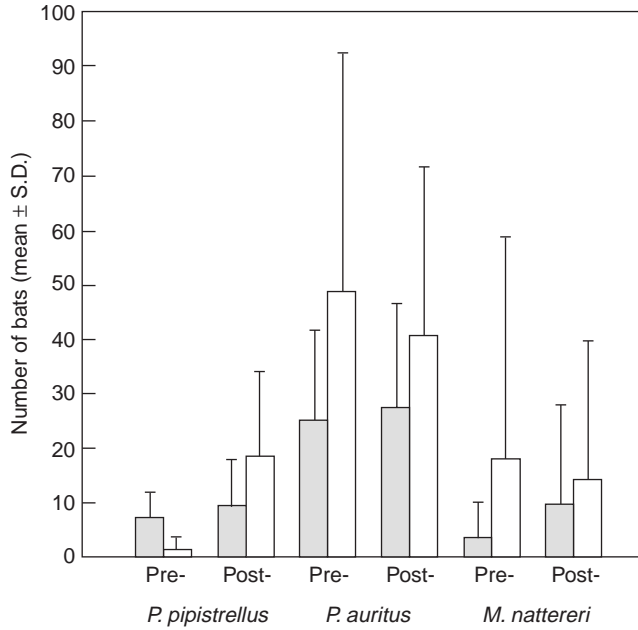
### *Population statistics*

#### *Movements between sites*

Distances between any two sites varied from 0.5 to 15 km. One male and one female *P. pipistrellus* were found in a box at more than one site (64 males and 74 females have been found at least twice). Both movements appeared to involve solitary bats, i.e. neither of the bats were found together before or after the move. In each case, the two sites were 1.5 km apart. Three male and three female *P. auritus* were found in boxes at more than one site (207 males and 326 females have been found at least twice). Two of the movements were made by single bats between sites 1.75 and 1.5 km apart. The other movements between sites appeared to be undertaken by two female bats together: the bats were found together before and after changing sites. These two individuals moved twice between two sites 2 km apart. One male and four female *M. nattereri* were found in boxes at more than one site (47 males and 123 females have been found at least twice). Two of the movements were made by single bats between two sites 2.75 km apart. The other movements between sites were undertaken by a group of three bats between two sites 2.75 km apart. There were insufficient data to test for differences in site fidelity between species and sexes.

### *Sex ratio*

Owing to unbalanced numbers of surveys during the pre- and post-parturition periods, it was not possible to analyse sex-ratio data using Kruskal–Wallis one-way analysis of variance by ranks and multiple comparison tests. Analysis has been confined to examining variation



**Fig. 1.** Mean ( $\pm$  S.D.) number of male and female *P. pipistrellus*, *P. auritus*, and *M. nattereri* found in bat boxes during each pre- and post-parturition period ( $n = 16$  years):  $\blacksquare$  males,  $\square$  females.

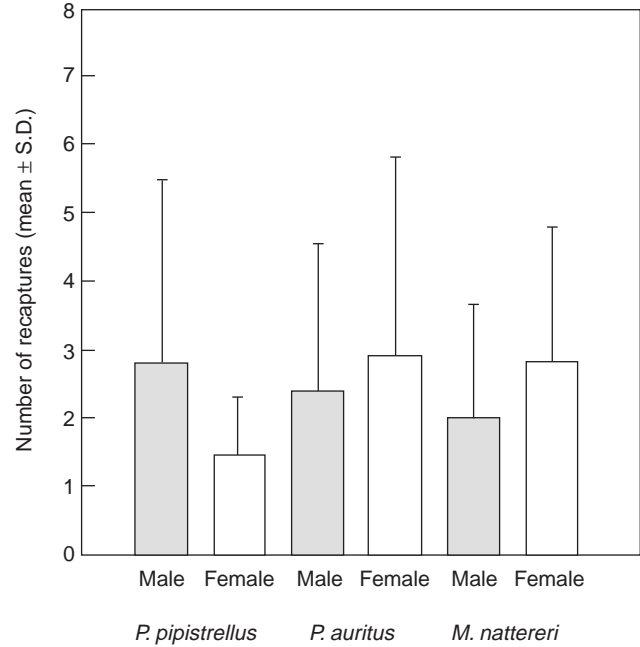
**Table 1.** Mann–Whitney  $T$  comparisons between numbers of males and females during the pre- and post-parturition periods.  $n_1:n_2 =$  number of pre- and post-parturition periods. \* $P < 0.05$

Comparison	Mann–Whitney $T_{n_1:n_2}$
Pre-parturition period:	
male vs. female <i>P. pipistrellus</i>	366.5 <sub>16:16</sub> *
male vs. female <i>P. auritus</i>	213 <sub>16:16</sub>
male vs. female <i>M. nattereri</i>	231 <sub>16:16</sub>
Post-parturition period:	
male vs. female <i>P. pipistrellus</i>	229.5 <sub>16:16</sub>
male vs. female <i>P. auritus</i>	298.5 <sub>16:16</sub>
male vs. female <i>M. nattereri</i>	278 <sub>16:16</sub>

between sexes (of the same species) within the pre- and post-parturition periods. The pre-parturition box population of *P. pipistrellus* was highly skewed towards males (Table 1, Fig. 1). In the post-parturition period, there was a marked influx of females which brought the sex ratio closer to unity. The mean number of females found during the pre-parturition period each year over the entire study area was  $1.4 \pm 2.6$ , increasing to  $18.6 \pm 15.6$  during the post-parturition period. In contrast, populations of both *P. auritus* and *M. nattereri* had sex ratios which did not significantly differ from unity during the pre- and post-parturition periods (Table 1, Fig. 1).

### Recaptures

The number of recaptures (Table 2, Fig. 2) between species and between sexes differed significantly (Kruskal–Wallis  $H_{df} = 93.9_5$ ,  $P < 0.0001$ ). The mean



**Fig. 2.** Mean ( $\pm$  S.D.) number of recaptures of male and female *P. pipistrellus*, *P. auritus*, and *M. nattereri*:  $\blacksquare$  males,  $\square$  females.

**Table 2.** Post-hoc tests (Dunn's Method  $Q$ ) of numbers of recaptures between males and females within species and between female *P. pipistrellus* and female *P. auritus* and *M. nattereri*.  $n_1:n_2 =$  numbers of bats. \* $P < 0.05$

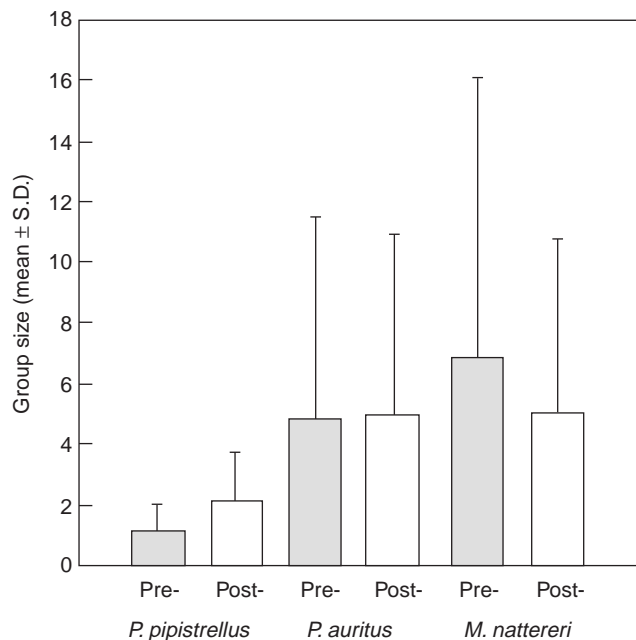
Comparison	Post-hoc test (Dunn's Method) $Q_{n_1:n_2}$
male vs. female <i>P. pipistrellus</i>	5.51 <sub>106:239</sub> *
male vs. female <i>P. auritus</i>	2.92 <sub>407:556</sub>
male vs. female <i>M. nattereri</i>	3.99 <sub>105:187</sub> *
female <i>P. pipistrellus</i> vs. female <i>P. auritus</i>	8.30 <sub>556:239</sub> *
female <i>P. pipistrellus</i> vs. female <i>M. nattereri</i>	8.10 <sub>205:239</sub> *

number of recaptures of male *P. pipistrellus* was  $2.8 \pm 2.7$  compared with  $1.5 \pm 0.9$  found for females. *P. auritus* differs from *P. pipistrellus* in having a similar number of recaptures for males and females and, in *M. nattereri*, females have a higher number of recaptures than males. Female *P. auritus* and female *M. nattereri* had higher numbers of recaptures than female *P. pipistrellus*.

### Social organization

#### Group size

Group size (Table 3, Fig. 3) differed significantly between species (Kruskal–Wallis,  $H_{df} = 81.2_5$ ,  $P < 0.0001$ ). *P. pipistrellus* formed smaller groups than *P. auritus* and *M. nattereri* during the pre-parturition period but there were no significant differences between group sizes during the post-parturition period. In order to compare group sizes between periods, juveniles were removed



**Fig. 3.** Mean ( $\pm$ S.D.) group size of *P. pipistrellus*, *P. auritus*, and *M. nattereri* during pre- and post-parturition periods:  $\blacksquare$  pre-parturition,  $\square$  post-parturition.

**Table 3.** Post-hoc tests (Dunn's Method  $Q$ ) of group size between species within the pre- and post-parturition periods and within species between the pre- and post-parturition periods. n1:n2 = number of groups. \* $P < 0.05$

Comparison	Post-hoc test (Dunn's Method) $Q_{n1:n2}$
Between species, pre-parturition:	
<i>P. pipistrellus</i> vs. <i>P. auritus</i>	7.81 <sub>89:262</sub> *
<i>P. pipistrellus</i> vs. <i>M. nattereri</i>	5.76 <sub>89:52</sub> *
<i>P. auritus</i> vs. <i>M. nattereri</i>	0.31 <sub>262:52</sub>
Between species, post-parturition:	
<i>P. pipistrellus</i> vs. <i>P. auritus</i>	3.42 <sub>189:142</sub>
<i>P. pipistrellus</i> vs. <i>M. nattereri</i>	2.70 <sub>189:47</sub>
<i>P. auritus</i> vs. <i>M. nattereri</i>	0.36 <sub>142:47</sub>
Within species, between periods:	
<i>P. pipistrellus</i>	5.02 <sub>89:189</sub> *
<i>P. auritus</i>	0.64 <sub>262:142</sub>
<i>M. nattereri</i>	0.40 <sub>52:47</sub>

from the analysis of group size in the post-parturition period. Only in *P. pipistrellus* did group size increase significantly following parturition.

### Social grouping

To allow for direct comparisons, social groups are shown as the proportion of all bats of a species found in each social category (Fig. 4). During the pre-parturition period, the great majority of *P. pipistrellus* found in boxes were single males, with small numbers of single females and females in groups. Few bats were found in mixed-sex groups (two groups of one male and one female). In contrast, *P. auritus* and *M. nattereri* were

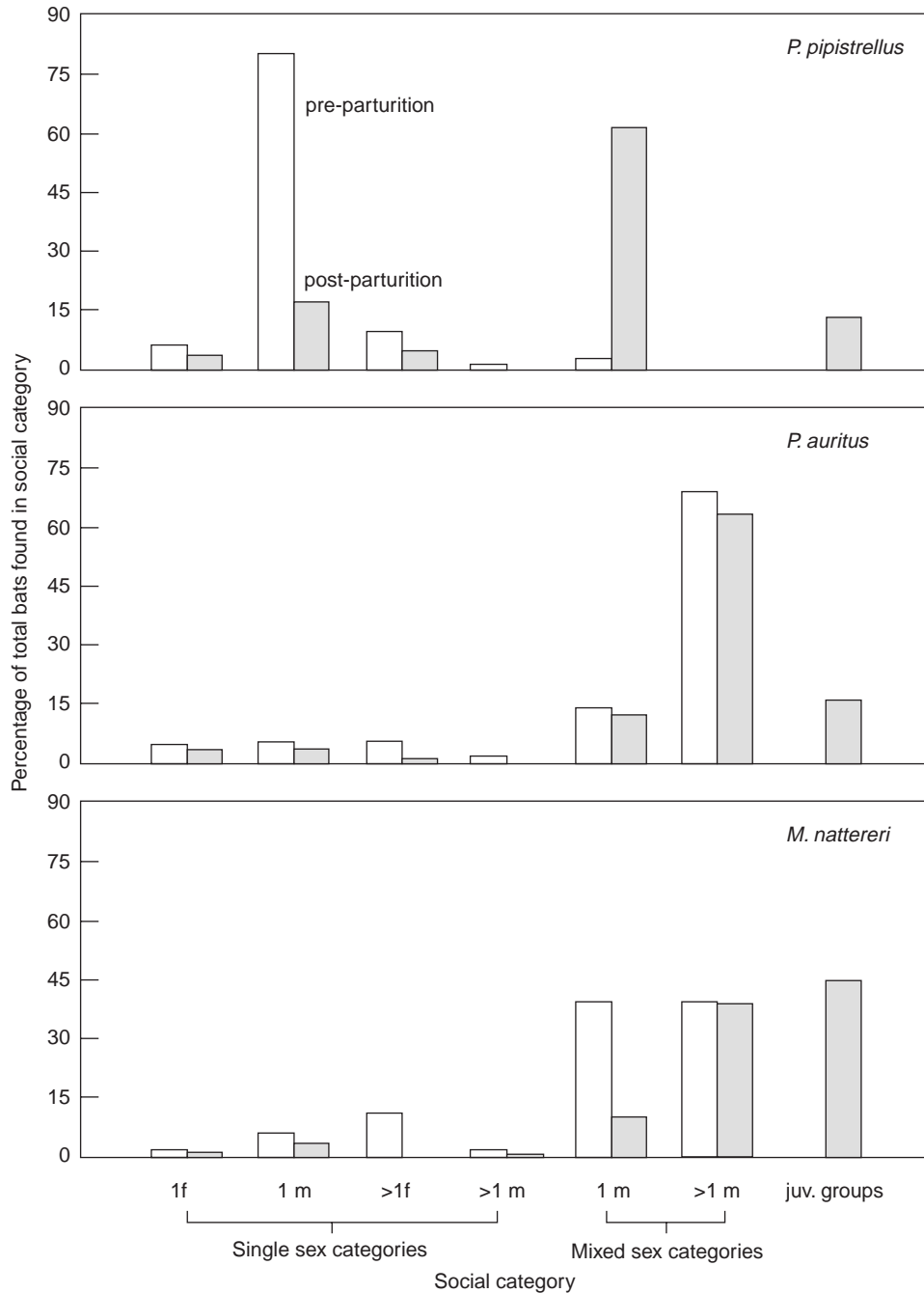
found predominantly in mixed-sex groups (single and multi-male). The social pattern of *P. pipistrellus* changed during the post-parturition period, with a large increase in the proportion of bats found in mixed-sex groups. Combining all years, the proportion of bats found in this group rose from 2.7% in the pre-parturition period to 61.3% after parturition ( $z$ -test,  $z = 12.2$ ,  $P < 0.0001$ ). There was a decrease in the proportion of single males found, from 80.1% in the pre-parturition period to 17.0% after parturition ( $z$ -test,  $z = 14.1$ ,  $P < 0.0001$ ). Some juvenile groups were also found during the post-parturition period. Changes in the social pattern of *P. auritus* and *M. nattereri* after the maternity season were not so marked. The majority of bats found in mixed-sex categories during the post-parturition period were in groups containing more than one male and juvenile groups were also found.

### Mating group structure

Figure 5 shows the number of males and females in each mating group for the three species. In the 36 non-overlapping (see **Methods**) mating groups (chosen at random from a total of 75 groups) of *P. pipistrellus* there was always just one adult male present. Inspection of the remaining mating groups confirmed there were no instances of a mating group containing more than one adult male. Up to nine females were found with a single male, but the majority (29/36) of groups contained three females or less. The mean number of females in each mating group was  $2.4 \pm 1.8$ . For *P. auritus*, 32 mating groups were chosen at random from a total of 66. There was a strong positive correlation (Spearman Rank Correlation,  $r = 0.61$ ,  $P < 0.001$ ) between the numbers of adult male and female *P. auritus* in mixed-sex groups in the period August to October. The majority of mating groups (23/32) were multi-male. The maximum number of females found in the single male groups was five, but up to 15 females were found in multi-male groups (the remaining mating groups included up to seven females in single male groups and up to 21 in multi-male groups). No correlation was found between the numbers of male and female *M. nattereri* in mating groups. Seven mating groups were chosen at random from a total of 16. Four of these groups were multi-male. There were up to six females in the single male groups and up to nine in the multi-male groups (the remaining mating groups included up to nine females found in single male groups and up to 20 in multi-male groups).

### Female group stability

The distribution of female associations in six *P. auritus* (Fig. 6a) showed few associations (called here weak associations) with many females (many females found with other females just once) and more associations (strong associations) with a smaller number of females (females found with the same female three or four times



**Fig. 4.** Percentage of bats (across sites, years combined) found in different social categories during the pre-parturition (□) and post-parturition (▒) periods. Seven categories were defined. Within single-sex categories were single females (1 f), single males (1 m), groups of females (>1 f) and groups of males (>1 m). Within mixed-sex categories were mixed-sex groups containing one adult male (1 m) and mixed-sex groups containing more than one adult male (>1 m). Groups containing juveniles on their own or with adults of one sex were classed juvenile groups (juv. groups). For example, *P. pipistrellus* found in the pre-parturition period included 6.2% single females, 80.1% single males, 9.6% females in female groups, 1.4% males in male groups and 2.7% males and females in mixed-sex groups containing one adult male.

out of a possible four). In contrast, female *P. pipistrellus* were rarely found with the same female more than once (Fig. 6b). Female *M. nattereri* (not shown) appeared to be intermediate between these two patterns, showing a higher number of weak associations and fewer strong associations than *P. auritus* but not to the extent that female *P. pipistrellus* did.

## DISCUSSION

We have assumed that bat boxes represent a subset of tree roosts, and that bats use them in the same way as they do natural roosts. Jones & van Parijs (1993) have shown that there are two distinct phonic types of *P. pipistrellus*, echolocating with peak energy at 46 or 55



males. In the post-parturition period, there was a large increase in the number of females present. This suggests that a resident male population was invaded by a transient female population after the maternity season. Similar observations were reported for large cave-dwelling colonies of the bent winged bat, *Miniopterus schreibersii* (Dwyer, 1966). This is consistent with our findings of high site fidelity, since maternity colonies of female *P. pipistrellus* occur in other roosts, not monitored in this scheme (mostly buildings). The sex ratios of *P. auritus* and *M. nattereri* did not differ significantly from unity, during the pre- or post-parturition periods, and there was little change in the sex ratio or total number of bats between pre- and post-parturition periods, suggesting that there are resident populations of both sexes.

### Recaptures

The conclusions drawn from the sex ratio data are supported by the number of recaptures. Male *P. pipistrellus* were recaptured significantly more often than females. There was no significant difference between the numbers of recaptures of male and female *P. auritus*, and in *M. nattereri* females had a higher number of recaptures. Males and females of *P. auritus* and female *M. nattereri* had a significantly higher number of recaptures than female *P. pipistrellus*, again suggesting a more resident population in each case.

Parallels can be drawn between the sex ratios and numbers of recaptures found in this study and the work of Barclay (1991) who concluded that food availability and foraging style influenced the distribution of two related species. In an area of the eastern slopes of the Rocky Mountains in Canada, over 90% of little brown bats (*M. lucifugus*) captured during the summer months were adult males. In the same region, equal numbers of male and female long-eared bats (*M. evotis*) were found. *M. lucifugus*, like *P. pipistrellus* (Sullivan *et al.*, 1993), feeds mostly on the dusk peak of small aerial insects. Barclay argued that these insects could not meet the energetic requirements of pregnant females, and no female *M. lucifugus* were found between June and August during the three years of the study. *M. evotis* is a gleaner, feeding on moths in a similar way to *P. auritus* (Barclay, 1991; Shiel, McAney & Fairley, 1991). It feeds on a less abundant food source, but one which is available throughout the night. The feeding strategy of *M. evotis* allows them to exploit these insects, enabling females to remain in the woodland throughout the season. *M. nattereri* is also a gleaner, although it feeds primarily on resting diurnal Diptera (see Vaughan, 1997 for review).

*P. auritus* and *M. nattereri* frequently form maternity colonies in roost boxes, but this has yet to be shown for *P. pipistrellus*. It may be that the two gleaning species are able to forage more effectively in the forest, and thus find

it advantageous to breed there, whereas *P. pipistrellus*, which forages only on the periphery of woodland, does not. Alternatively, it is possible that female *P. pipistrellus* have different roosting requirements to *P. auritus* and *M. nattereri* during the maternity season. All three species commonly form maternity roosts in buildings (e.g. Swift, 1980; Swift & Racey, 1983).

### Group size

Bat boxes are unlikely physically to limit group size as they can hold many more bats than are found in them. The largest groups of bats found were 40 (*P. auritus*), 37 (*M. nattereri*), and 12 (*P. pipistrellus*). Bradbury (1977a) noted that in species with annual cycles of social-organization, group size and stability may differ for each stage in the sequence. Group size increased significantly only in *P. pipistrellus* during the formation of mating groups.

### Social grouping and mating group structure

The large increase in group size of *P. pipistrellus* was due to an influx of females and the formation of mating groups (see also Gerell & Lundberg, 1985). The social organization of *P. pipistrellus* is very different from that of *P. auritus* and *M. nattereri*, both of which form large multi-sex groups before, and during, parturition (Fig. 5). The majority of mating groups of *P. auritus* found between August and October contained more than one male, and up to three times the number of females found in single-male groups. A similar pattern was seen in *M. nattereri*. A study on *M. nattereri* in Scotland found a number of single male mating groups in bat boxes (Altringham & Bullock, 1988).

Where females aggregate in large groups, a single male that adopts a mating strategy of female defence may be unable to monopolize breeding access to the whole group and thus multi-male groups may form as a consequence (Clutton-Brock, 1989). In this study, single males of *P. auritus* were unable to monopolize a group in excess of seven females since an increase in the size of the female group was accompanied by an increase in the number of males. Within a multi-male group, mating success may be limited to one dominant, reproductively active male (Clutton-Brock, 1989). There are no data available on the breeding success of male *P. auritus* or *M. nattereri*. The correlation found between the number of male and female *P. auritus* may simply reflect the sex ratio of the population. In contrast to mating groups of *P. auritus* and *M. nattereri*, the size of the female group associated with male *P. pipistrellus*, which are thought to defend mating roosts (Gerell & Lundberg, 1985), was relatively small. In addition to size, the mobility and compositional stability of female groups may determine their defensibility, and hence the number of males found with them (Bradbury & Vehrencamp, 1977).

### Female group stability

Although it was not possible to quantify the level of female group stability during the mating season, the available evidence indicates that there are only weak associations between female *P. pipistrellus*. By contrast, female *P. auritus* appeared to have weak associations with some females and strong associations with others. Some female *P. auritus* that were captured over four times, so not included in Fig. 6, also showed this pattern: LZ7669 has been captured eight times in the post-parturition period. An analysis of females with whom this female associated (41 in total) indicate a large number of weak associations: 46% of the females were found only once with this female, and 24% twice. However, 17% of females were found with this female four or more times. This suggests that fairly small, stable groups of females exist, associating with other females on a more transient basis. Female *M. nattereri* appear to have a lower group stability and female *P. pipistrellus* a lower one still. Heise & Schmidt (1988) claimed that female *P. auritus* formed closed colonies consisting of close relatives, with larger groups usually subdivided into smaller subgroups, but no data were given to substantiate this statement. The relatedness of the females in our study is also unknown. However, the strong associations between certain females, and the very low incidence of movement between sites, suggests the existence of discrete colonies.

The reasons for female gregariousness may be unrelated to reproduction (Emlen & Oring, 1977). The female groups of *P. auritus* observed in the present study exist all year round and from year-to-year. Animals living in groups often suffer higher rates of ectoparasite transmission (Hoogland, 1979; Brown & Brown, 1986) and increased competition for food, mates and other critical resources than they would if they lived alone (Alexander, 1974). Therefore, the benefits of group living (e.g. reduced thermoregulatory costs, increased foraging efficiency, decreased risk of predation) should outweigh these costs for this to be the best strategy (Hamilton, 1971; Alexander, 1974). What factors might promote group living in these bats? One suggested benefit is the transfer of information about the location or quality of food patches (Fleming, 1982). Until recently, supporting data had been mainly anecdotal (Howell & Hartl, 1980; McCracken & Bradbury, 1981; Wilkinson, 1985), but recently Wilkinson (1992) investigated information transfer in the evening bat, *Nycticeius humeralis*. He found that unsuccessful foragers followed previously successful foragers later the same night. The subsequent foraging success of these followers was higher than unsuccessful foragers that departed alone. Wilkinson (1992, 1995) argued that truly unpredictable but rich foraging patches (e.g. some insects) are more likely to lead to information exchange and favour communal roosting than food sources such as fruit and nectar. However, other factors may be important in other species, for example, information

transfer and co-operation while foraging in the case of *Phyllostomus hastatus* (McCracken & Bradbury, 1981) and optimal group foraging in *Leptonycteris sanbornii* (Howell & Hartl, 1980). Wilkinson's (1992) work on *N. humeralis* compliments Bradbury & Vehrencamp's (1977) finding of an inverse relationship between the stability of a group and the duration of use of a foraging site. Bats exploiting an unpredictable, patchy food source need to change foraging sites regularly. For these bats, Wilkinson predicted that information transfer and communal roosting would be advantageous, and in these bats Bradbury & Vehrencamp (1977) found the most stable groups. The behaviour of female groups will in turn influence the behaviour of males, as described below.

### Mating strategy in relation to female behaviour

A concept central to theories of mating system evolution is defensibility, or the cost/benefit ratio for a male controlling a territory or group of females (Bradbury & Vehrencamp, 1977; Clutton-Brock, 1989). When benefits to a male outweigh the costs, the defence of resources (territory or roost site) and/or females is expected to result. The resource defended must be exploitable for long enough (such as roosts defended by male *P. pipistrellus*: Gerell & Lundberg, 1985) or the group of females suitably stable in composition (e.g. *P. hastatus*: McCracken & Bradbury, 1981) for the defending male to gain sufficient benefit. As stated above, social dispersions, which are believed to drive mating systems, are thought to be determined by food supply in many species, although other resources such as roosts may also be important (Kunz & McCracken, 1996). Bats with differing foraging strategies exploit different food sources and may therefore be expected to have different social dispersions and mating systems.

Diet, foraging strategy, wing morphology and echolocation characteristics are intimately linked (Norberg & Rayner, 1987). *P. auritus* has low aspect ratio wings and low wing loading, making it extremely manoeuvrable and able to glean insects from the ground and leaf surfaces (Norberg & Rayner, 1987). Large, sensitive ears allow it to feed using prey-generated sound, in addition to echolocation (Anderson & Racey, 1991). Its diet consists mainly of noctuid moths, Diptera and beetles gleaned from foliage (Shiel *et al.*, 1991; Vaughan, 1997), although they also take insects in flight (Swift, 1991). *M. nattereri* has a similar wing morphology but feeds largely on diurnal Diptera gleaned from their nightly resting places (see Vaughan, 1997). In contrast, *P. pipistrellus* has intermediate aspect ratio wings and a relatively high wing loading, giving it good agility at high speeds (Norberg & Rayner, 1987). *P. pipistrellus* feeds largely on small nematoceran Diptera and Trichoptera (caddis flies) with some Ephemeroptera, Planipennia and Lepidoptera taken in flight and usually eaten on the wing

(Sullivan *et al.*, 1993; Swift, 1991). *P. pipistrellus* often feeds by trap-lining, which involves moving between a number of foraging patches, each of which is visited at the same time each night (Racey & Swift, 1985). Little is known about the dispersion of these different insect species or of their influence on the dispersion of the bats that feed on them. It is possible that the differences between *P. pipistrellus*, *P. auritus* and *M. nattereri* described in this study are, in part, due to the different dispersions of their insect prey.

The postulated stability of the female groups in *P. auritus* may facilitate a mating strategy of female defence. Group stability amongst female *P. pipistrellus* in the mating season appeared to be very low in this study. The benefits of defending transient and unstable female groups are low, so it should be more economical for males to defend resources such as roosts (Gerell & Lundberg, 1985). Female defence and roost defence are not of course mutually exclusive, and an element of both may be involved in all species (Ostfeld, 1987).

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