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Highly structured fission−fusion societies in an aerial-hawking, carnivorous bat

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In some group-living animals, societies are far from being static but are instead dynamic entities encompassing multiple scales of organization. We found that maternity colonies of giant noctule bats, *Nyctalus lasiopterus*, form fission−fusion societies, where group composition in single tree roosts changes on a daily basis but social cohesion in the larger group is preserved. The population inside a small city park was comprised of three distinct but cryptic social groups coexisting in close proximity. Each social group used a distinct roosting area, but some overlap existed in the boundaries between them. Social groups were stable at least in the mid term because adult females were loyal to roosting areas and young females returned to their natal social groups in successive years. Our results suggest that distinct social groups with separate roosting areas may have existed for at least 14 years. The findings described support the hypothesis that roost-switching behaviour in forest bats permits the maintenance of social bonds between colony members and enhances knowledge about a colony's roosting resources. Fission−fusion societies in forest bats might have evolved as a mechanism to cope with changing conditions in the environment by restructuring subgroups or adjusting subgroup size, to maximize the amount of information that can be transferred between colony members, or as a consequence of territory inheritance by philopatric female offspring. Other factors such as resource competition or kin selection could limit the size and composition of fission−fusion societies and promote strong social structuring within populations.

The tendency of conspecifics to aggregate is widespread in both plants and animals. Essential resources might be patchily distributed in space and time, forcing individuals to come together. Other selective pressures can favour group living, including predator avoidance (Hamilton 1971), increased foraging efficiency (Beauchamp 1999) and cooperative breeding (Emlen 1984). Conversely, living in groups can impose fitness costs, leading to direct competition for resources between group members (West-Eberhard 1979), facilitating the spread of parasites and diseases (Davies et al. 1991; Van Vuren 1996),

requiring common decisions necessary for group coordination which can generate conflict of interest (Conradt & Roper 2000, 2005), and occasionally producing altruistic behaviours, which benefit apparently only the recipient but not the donor (West et al. 2006).

Social animals must continuously balance the trade-off between the costs and benefits of group living (Alexander 1974). Sociality can thus be a dynamic process (Couzin 2006) in which groups might assemble or split in response to a variety of intrinsic factors (such as age or reproductive status) and extrinsic factors (such as food availability or landscape complexity). Some examples of animals having this flexible, 'fission−fusion' social behaviour are lions, *Panthera leo* (Packer et al. 1990), primates such as chimpanzees, *Pan troglodytes*, or spider monkeys, *Ateles* sp. (Symington 1990), dolphins, *Tursiops* sp. (Lusseau et al. 2006), elephants, *Loxodonta africana* (Wittemyer et al. 2005; Archie et al. 2006), red deer, *Cervus elaphus*

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(Albon et al. 1992), spotted hyenas, *Crocuta crocuta* (Holekamp et al. 1997) and orange-fronted parakeets, *Aratinga canicularis* (Cortopassi & Bradbury 2006). The pattern of temporal associations within these fission—fusion societies is not random, but appears to be tied to individual preferences, in some cases mediated by kinship, resulting in complex social structures (Wittemyer et al. 2005; Archie et al. 2006; Lusseau et al. 2006). Although it is accepted that fission—fusion behaviours allow animals to adapt to changing conditions in their environment by adjusting group size, the ultimate forces shaping the evolution of this type of social organization are still poorly understood (Chapman et al. 1995; Lehmann & Boesch 2004).

Temperate bats offer a good model system to assess the adaptability of group living at several scales, because of their complex life history related to the seasonality of food resources, roost requirements and energetic constraints imposed by flight. Most temperate bat species have 'seasonally variant' social interactions (Bradbury 1977), with sexually segregated units during the breeding season (females forming relatively large maternity colonies and males roosting solitarily or in small groups) and many different grouping patterns during mating and hibernation, including solitary and colonial roosting. It has recently been suggested that maternity colonies of tree-dwelling bats form fission—fusion societies (Kerth & König 1999; O'Donnell 2000; Willis & Brigham 2004), where group members are spread among multiple roosts on a given day with the composition of subgroups varying from day to day. Single bats, or sometimes whole groups, switch roosts regularly (Lewis 1996; Kerth & König 1999; O'Donnell & Sedgeley 1999; Willis & Brigham 2004; Russo et al. 2005). Several hypotheses have been proposed to explain roost switching including avoidance of predators, antiparasite strategy (i.e. roosts are left vacant to interrupt ectoparasite life cycles), minimization of distance to foraging areas, ephemerality of roost trees, and specific thermoregulatory requirements in relation to variable microclimatic conditions (reviewed in Lewis 1995; Lewis 1996; Kerth & König 1999; Kunz & Lumsden 2003). In the latter case, we expect that individuals with different thermoregulatory requirements, for example lactating versus pregnant females, might differ in their roost-switching patterns (Willis & Brigham 2004). Recent studies best support two alternative hypotheses: (1) roost switching could be a way of maintaining social bonds between bats belonging to a colony which is spread over large areas of forest (O'Donnell 2000; Willis & Brigham 2004; O'Donnell & Sedgeley 2006); or (2) roost switching could serve to enhance and share knowledge about a large pool of roosts (Kerth & Reckardt 2003; Russo et al. 2005; O'Donnell & Sedgeley 2006). Even if forest bats change roosts often, they nevertheless appear to be loyal to roosting areas (Brigham et al. 1997; O'Donnell & Sedgeley 1999; Cryan et al. 2001) and even to specific trees, over the mid, and possibly the long term (Willis et al. 2003).

The giant noctule, *Nyctalus lasiopterus*, is the largest and one of the rarest European vespertilionid bats (body mass = 50 g; forearm = 65 mm; wing span = 450 mm). It has a Circum-Mediterranean distribution (Ibáñez et al. 2004), possibly related to its dietary specialization: it is the sole predator known to catch nocturnally migrating songbirds which concentrate in Mediterranean regions in spring and autumn (Bruderer & Liechti 1999), while itself on the wing (Ibáñez et al. 2001, 2003; Popa-Lisseanu et al. 2007). During summer, it hunts insects in the open like other aerial-hawking bats. Individuals roost sexually segregated, in trees (Ibáñez et al. 2004): most adult males appear to be solitary throughout the year whereas adult females and their young aggregate in breeding colonies during spring and summer, joining males in the mating season in autumn. In some localities, only one of the two, either female and young breeding colonies or all-year male populations (females arriving only in autumn from unknown areas) have been found, suggesting that sexes might also show local and/or altitudinal segregation apart from roost segregation, with breeding colonies located in the lower or warmer areas (C. Ibáñez, A. Guillén, P. Agirre-Mendi, J. Juste & A. Popa-Lisseanu, unpublished data; cf. Barclay 1991). No data on hibernation exist.

We studied social structure and roost use by individuals in a giant noctule breeding population, located in a small urban park in southwestern Spain. The south of the Iberian Peninsula, which is a main confluence of bird migratory routes, is the most intensely deforested region in the Mediterranean basin (Arribas et al. 2003). Few natural roosts are available for forest-dwelling bats, and some historic urban parks constitute 'roosting islands' for giant noctules in an otherwise treeless agricultural or urbanized landscape. We report patterns of roost use by giant noctule bats from an urban park across several years, with the following aims: (1) assess whether maternity colonies of giant noctule conform to the fission—fusion society model, as has been proposed for smaller tree-dwelling bat species. (2) Define population structure and the limits of 'colony' or 'social group', considered ambiguous concepts for forest bats (e.g. Lewis 1996). More specifically, we question whether each tree contained one social group, whether all bats in the park belonged to a single social group scattered in many different tree roosts, or whether a few social groups, with members scattered in several tree roosts, coexisted within the park. (3) Test whether single trees are used over multiple years and if bats are loyal to roosting areas over time. (4) Test whether roost-switching patterns, in particular frequency of roost switching, differ between individuals or between different reproductive periods. (5) Evaluate the hypotheses proposed to explain roost-switching behaviour in forest bats.

METHODS

Study Area

The study was conducted in María Luisa Park, situated in Seville, Andalusia, Spain (37°24′N, 5°59′W, altitude 10 m asl). This 23-ha park was established in 1850 and has a dense subtropical vegetation, mostly exotic species including large specimens of *Platanus* sp., *Gleditsia triacanthos* and *Sophora japonica*, and tall palm trees, for example *Washingtonia filifera*. A breeding population of c. 500 giant noctules use the cavities and hollows of these mature trees

and roost under the dry leaves of *Washingtonia* (Ibáñez et al. 2004).

The area has a typical Mediterranean climate, with hot dry summers and precipitation occurring mostly in autumn and winter. Average annual rainfall is ∼550 mm, mean annual temperature 18.6°C and there are almost 3000 hours of sunshine per year. The land surrounding the city of Seville is mostly devoted to agriculture, with a few fragmented natural vegetation (mostly shrubs) patches.

The giant noctule population is comprised primarily of females and their young who are born in late May–early June and start flying in July. Adult females lactate until early August (Ibáñez et al. 2004). Most bats abandon the roosting area from August to November, and females begin aggregating at roosts in March.

Capture, Monitoring and Radiotracking

Bats were netted when emerging from or returning to several trees with accessible roosting cavities in 1999–2006. Netting was conducted regularly (but never more frequently than once per month to minimize disturbance). Exit counts were also performed at some of these roosts. Tree cavities were occasionally inspected with a small infrared video camera after adults had emerged, to determine the timing of parturition.

Bats were individually marked with 5.2-mm aluminium alloy rings (Porzana, Ltd, Icklesham, U.K.), and beginning in 2003, also with subcutaneously implanted transponders (ID100, Trovan, EID Ibérica, Spain). Transponders (2.2 × 11.5 mm) were inserted between the shoulder blades using a Trovan robust applicator with a 12-gauge needle (EID Ibérica, Spain). Transponders have been successfully used to mark smaller bats, for example *Myotis bechsteinii* (8–14 g) and *Eptesicus fuscus* (15–20 g), with no apparent adverse effects (Kerth & König 1996, 1999; Kerth & Reckardt 2003; Wimsatt et al. 2005). Bats were classified based on age, sex and reproductive status. Lactating females had enlarged nipples surrounded by hairless skin. Juveniles had cartilaginous plates in the metacarpal–phalangeal joints (Anthony 1988). During 2003, we caught 11 bats at several tree roosts and equipped them with collared radiotransmitters (Pip Ag392, Biotrack, Dorset, U.K.). Owing to transmitter failure, no data were collected for one individual (Table 1). In April 2004, we attached radiotransmitters to 15 different individuals captured at three different sites inside the park (Table 1). All tagged bats were adult females with average or above body mass. To affix transmitters, the ends of a Teflon collar were glued together around the neck of the animal. The collar was also attached to the back of the neck with surgical cement (Skin-Bond, Smith and Nephew United, Largo, FL, U.S.A.), after clipping the fur to prevent the transmitter from rotating around the

Table 1. Roost-switching behaviour of radio tagged giant noctules

Bat ID	Radiotracking period	No. of days tracked	No. of trees used	FR prelact.	FR lact.	FR total	Social group
92.1	July 1992	13	3	—	—	4.33	I
92.2	July 1992	16	7	—	—	1.86	I
1	April–June 2003	47	16	—	—	—	III
2	April–June 2003	46	11	—	—	—	III
3	April–May 2003	17	6	—	—	—	III
4	April–May 2003	13	7	—	—	—	III
5	July 2003	16	6	—	—	—	I
6	July 2003	15	5	—	—	—	I
7	July 2003	9	3	—	—	—	I
8	Oct–Nov 2003	16	3	—	—	—	II
9	Oct–Nov 2003	14	4	—	—	—	I
10	Oct–Nov 2003	11	2	—	—	—	II
11	April–July 2004	68	14	1.54	3.75	2.09	II
12	April–July 2004	68	8	3	6	3.88	II
13	April–May 2004	12	3	—	—	—	I
14	April–May 2004	26	7	2.08	—	2.08	I
15	April–June 2004	70	8	4.45	4.67	4.53	I
16	April–July 2004	72	19	1.86	3.11	2.23	I
17	April–June 2004	41	11	2.35	—	2.35	I
18	April–May 2004	29	4	2.25	—	2.25	II
19	April–May 2004	27	3	2.33	—	2.33	II
20	April–May 2004	23	8	1.83	—	1.83	II
21	April–June 2004	66	8	2.47	2.33	2.41	III
22	April–May 2004	34	8	2.75	—	2.75	III
23	April–June 2004	55	15	2.85	1.78	2.41	III
24	April–June 2004	60	7	3.00	7.00	3.69	III
25	April–May 2004	25	4	—	—	—	III
27 (no. of bats)		909 (total days)	73+4* (no. of trees)	2.52±0.74 (mean±SD)	4.88±1.91 (mean±SD)	2.68±0.82 (mean±SD)	

Frequency of roost switching (FR) = days/roost before moving to another roost for the prelactation (prelact.) and lactation (lact.) periods. Social group = the cluster-defined group that each bat was assigned to, according to site of capture and cluster analysis reported in the text. Data on FR for bats tracked in 1992 were not considered for the calculation of mean ± SD total FR.
*Trees used only in 1992.

neck. The thin teflon collar was designed to fall off after 1–6 months. The total mass of transmitter, collar and glue was ∼1.85 g, representing less than 5% of body mass (Aldridge & Brigham 1988). Specifically, radiotransmitter mass represented 3.0% and 4.4% of the mass of the largest (61.8 g) and smallest (42 g) tagged bats, respectively. Capture and marking of bats were approved by the Environmental Council of the Junta de Andalucía.

In 2003, we located radiotagged bats using handheld telemetry receivers (FT-250 RII, Yaesu Musen Co., Ltd, Sapporo, Japan; Falcon V, Wildlife Materials International, Inc., IL, U.S.A.) and three-element Yagi antennae (AF Antronics, Inc., IL, U.S.A.), approximately four times a week. In 2004, the bats were tracked to tree roosts every day, until the signal was lost. Transmitter life was approximately 2 months.

Emergence by marked bats was continuously monitored using two automatic transponder readers (LID 650, Trovan, EID Ibérica, Spain) installed at two roost trees located 265 m apart, from January 2004 to August 2006. While entering or leaving the tree cavity, the bats flew through a circular antenna around the entrance so that their individual code, the date and time were recorded.

Effect of Transponder Marking and Radiotagging on Bats

Transponder injection caused no bleeding and the small hole created by the needle healed within a few days. None of the recaptured transponder-marked bats ($N = 58$) showed evidence of scabs or scarring, and transponders remained positioned between the shoulder blades. We did not detect any adverse effect of radiotagging on the bats. We recaptured and removed tags from only three individuals. However, two transmitters with detached collars were found on the ground near roosts (1 and 2 months after tagging, respectively). Another two bats, no longer carrying transmitters, were recaptured 1 and 2 years, respectively, after tagging. Their body mass had not declined and they showed no outward sign of having carried a transmitter. In addition, 10 out of 13 radiotagged bats (76.9%) belonging to the two social groups monitored with transponder readers (excluding bats for which radiotransmitters were recovered) were detected in successive years, a similar proportion to transponder-marked bats of these two social groups detected at the readers (76.8%; Table 2), suggesting that radiotagging did not affect survival.

Group Structure

The existence of an organized versus random structure in the giant noctule population of the María Luisa Park was assessed using two approaches: (1) the similarity in the use of different tree roosts by individual bats; (2) the degree of association between pairs of bats.

In the first approach, a cluster analysis was conducted based on the similarity in the use of roost trees. The similarity, or overlap, was calculated using the Freeman–Tukey statistic

Table 2. Number of giant noctules detected by transponder readers 1 and 2 and assigned to their individual social groups, January 2004–August 2006

	No. of bats belonging to each social group		
	Social group I	Social group II	Social group III
No. of bats marked	81	61	114
No. of bats registered at reader 1	61 (2904)	1 (1)	0 (0)
No. of bats registered at reader 2	0 (0)	48 (1919)	6 (8)

Numbers in parenthesis indicate bats visits∗days (the sum of the number of days that bats of each social group were registered at each device).

(Matusita 1955; Krebs 1989) as follows:

$$\text{FT}_{ij} = \sum_{r=1}^{k} \left(p_{ir} \cdot p_{jr} \right)^{1/2}$$

where FT_{ij} is the overlap, or similarity, in the use of available roost trees by individuals i and j, and p_{ir} is the proportion of days, from the total number of radiotracking days, that bat i was found in tree r (idem for bat j). This allowed us to identify groups of bats showing similar roost use. A dissimilarity index was then entered for the calculations, defined as 1-overlap.

We created hierarchical groupings using four different clustering methods (UPGMA or unweighted pair-group average, Ward's weighted method, SLINK or single linkage method, and CLINK or complete linkage method), as agreement between the outcome of different clustering algorithms is usually a sign of a pronounced structure in the data.

In the second approach, we relied again on hierarchical clustering (UPGMA, Ward's method, SLINK and CLINK), now based on a matrix of associations between all possible pairs of bats. The association index for a given pair was calculated by dividing the number of days that two bats roosted together in a particular roost by the number of days both bats were radiotracked. In this analysis we only used data for the 15 bats tracked in 2004, as they were monitored simultaneously but had been captured at three different sites within the park (five bats at each site). To assess the integrity of the groups, we compared the outcome of the four clustering methods.

The trees used by bats were assigned as belonging to one (or, rarely, to several) of the three groups identified by cluster analysis, according to which group used them. For all recaptured bats, we noted whether the tree where each individual was recaptured belonged to the same group as the tree where it had been captured previously. Given that bats switch frequently from one tree to another, in the absence of a population substructure all bats would have the same probability of recapture in all three subsamples of trees.

Likewise, if there was no population substructuring and bats switched randomly between roosts throughout the park, the two automatic reading devices installed at two different trees should with equal probability detect bats captured at any site within the park. We assigned each bat to the group where it was first captured. We evaluated using a χ^2 test whether bats belonging to each of the three groups were detected with equal probability, that is if they roosted at random, in the two trees equipped with transponder readers. The number of individuals from each group that were detected by each device was compared with the expected frequency calculated from the number of bats marked with transponders in each group assuming that they all had the same probability to be detected at each reader. Additionally, we recorded the number of days that bats from each group were detected at each reader, to distinguish frequent from rare events (i.e. if a bat visited a 'foreign' group regularly or only occasionally).

The overlap between the roosting areas of each cluster-defined group of bats was depicted graphically using ArcView GIS 3.2 (Environmental Systems Research Institute, Inc., CA, U.S.A.) and spatial analysis performed with the Animal Movement extension (Hooge & Eichenlaub 1997). Coordinates of all roost trees were plotted in a digital orthophoto of the María Luisa Park with 0.5-m resolution (Ortofotografía digital de Andalucía, Junta de Andalucía 2004). We superimposed on to the photographs detailed digital maps of the park (Servicio de Parques y Jardines, Ayuntamiento de Sevilla 2002) to precisely locate trees. As not all trees were used by all bats, and not all trees were used with the same intensity, we identified 'core roosting areas' of each cluster-defined group of bats by drawing 50% contour lines using the fixed kernel estimation method (Worton 1989). We counted the number of days that each bat roosted in each tree, which is equivalent to weighting by intensity of use. The 95% kernel use distribution was used to describe the overall roosting range. The smoothing parameter (h) was fixed to a value of 15 m.

Loyalty to Roosting Areas

Using recapture and transponder data, we assessed whether adult females were loyal to their roosting areas between years and if young females returned to their natal roosting areas in subsequent years.

Data collected in a preliminary study in 1992 were used to assess the long-term stability of roosting patterns. In July 1992, two adult female bats captured emerging from a tree roost in the María Luisa Park were fitted with transmitters and followed to their roosts for 13 and 16 days, respectively. Several other trees were checked in 1992 and in subsequent years for the presence of bats.

Roost Switching

Ninety per cent of adult females breed in the study area but reproductive status was not apparent at the end of April when bats were captured and tagged (see Results).

Based on the timing of parturition in the study area (see Results), we calculated roost-switching frequency for the prelactation period (from when bats were tagged until 31 May), and for the lactation period (from 1 June until the signal was lost). We used a paired t test to assess differences in roost-switching frequency between reproductive periods, for individuals that were continuously tracked (i.e. every day) during both periods in 2004. The power of the test was calculated using Power and Precision Version 2.0 (Borenstein et al. 2000). Nonsignificant deviation from normality and homogeneity of variances were evaluated using Kolmogorov–Smirnov and Levene tests. To assess if some individuals switched roosts at a different rate than others, we used a Friedman test (for repeated measures) with individuals as a factor and the number of consecutive days they remained in each successive tree before each roost-switch as the repeat level factor. For this calculation, only data from the prelactation period were used, and to obtain a balanced design, we only tested a subsample of 10 individuals with equal numbers of repeat levels ($N = 12$).

RESULTS

Three-hundred and twelve individuals were captured and marked between 1999 and 2006, of which only 16 were adult males. Parturition took place between late May and beginning of June, and 90% of adult females captured during June and July ($N = 244$) were lactating. Tagged bats switched roosts frequently and used 73 different trees (Fig. 1, Table 1). They nearly always returned to the park for day roosting (only in 5 of 885 attempts did we fail to find the signal for a bat). Night roosting inside the park was also observed, but we did not attempt to locate night roosts precisely. The number of bats emerging from counts at five roosts varied from 14 to 60 (mean = 27, $N = 13$) in the breeding season.

Social Groups and their Roosting Areas

All clustering methods separated the 25 bats into three main groups based on roost use (Fig. 2). Hereafter, we designated these as social groups I, II and III (Fig. 2, Table 1). The four methods grouped bats in the same way (clustering following Ward's method is shown; Fig. 2): all bats that were captured at the same or at very nearby trees were assigned to the same cluster, except for bat 17 which was captured together with members of social group I, but cluster analysis placed it in social group II.

Based on pairwise associations, all hierarchical trees also revealed three main assemblages (clustering following Ward's method is shown; Fig. 3). All 15 bats were distributed in the same clusters as the previous approach, again with the exception of bat 17, which was placed into all three social groups depending on the clustering method.

All roost trees were identified and mapped allowing us to assign each of the 312 bats captured in 1999–2006 to one of the three social groups, depending on the tree where it was first captured. Of 60 recaptured individuals, only one (a juvenile) was recaptured in a tree belonging to a different group from where it was first caught, and it is
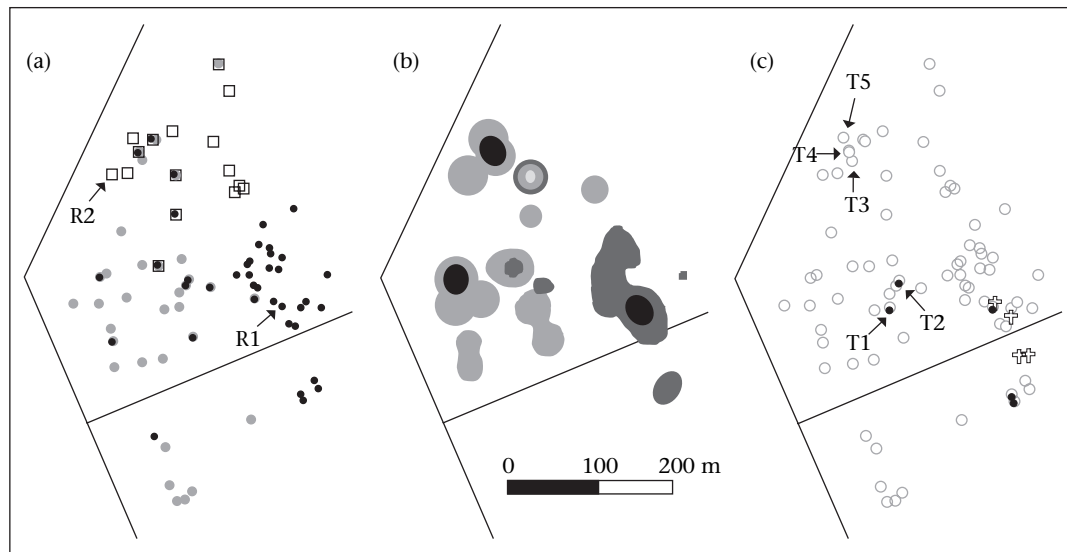
Figure 1. Distribution of roosts in the María Luisa Park (Seville, Spain). (a) Trees used for roosting by three social groups; black dots: social group I; black squares: social group II; grey circles: social group III. Arrows indicate the position of the two automatic reading devices. (b) Roosting areas of the three groups. Dark grey: 95% kernel of group I; middle grey: 95% kernel of group II; light grey: 95% kernel of group III; black: 50% roosting areas of each group. (c) Trees used for roosting by two bats radiotracked in 1992. Black dots: trees still used in 2003−2004; crosses: trees that have been felled. Roost trees characterized in 2003−2004 are shown as grey dots for comparison. T1 and T2 represent trees later used by social group III (see text). Roads are marked as lines for aiding comparison between subfigures.

unclear whether this individual actually emerged from the roost or merely got entangled on the net while passing by (unlike most bats, this individual was not seen emerging from the cavity). The automatic readers detected 116 of the 256 bats marked with transponders. Based on our cluster analysis, readers were located in trees used by social groups I and II, respectively, and we designated them as readers 1 and 2 (Fig. 1a). Reader 1 detected 61 bats belonging to social group I (75% of all marked bats in this group) and only one outsider, an adult female assigned by capture site to group II (Table 2). Reader 2 detected mostly bats marked at roosts of social group II (48 bats, i.e. 79% of bats marked from this group; Table 2), and only six 'foreign' bats, five adult females and one adult male,

assigned by capture site to social group III (5% of all marked bats from social group III). This pattern is significantly different from random (Chi-squared test: $\chi^2_5 = 249$, $P < 0.001$), that is bats from all three social groups did not have the same probability of being detected at readers 1 and 2: bats from social group I were detected at reader 1, bats from social group II were detected at reader 2, and bats from social group III, with no reader located at their roosts, were negligibly detected.

To compare activity patterns of 'native' versus 'foreign' bats visiting the reader-equipped trees, we counted the number of days each bat was detected (Table 2). For reader 1, 'native' bats (those assigned to social group I) visited the roost an average of 47 (±45 SD) days per bat
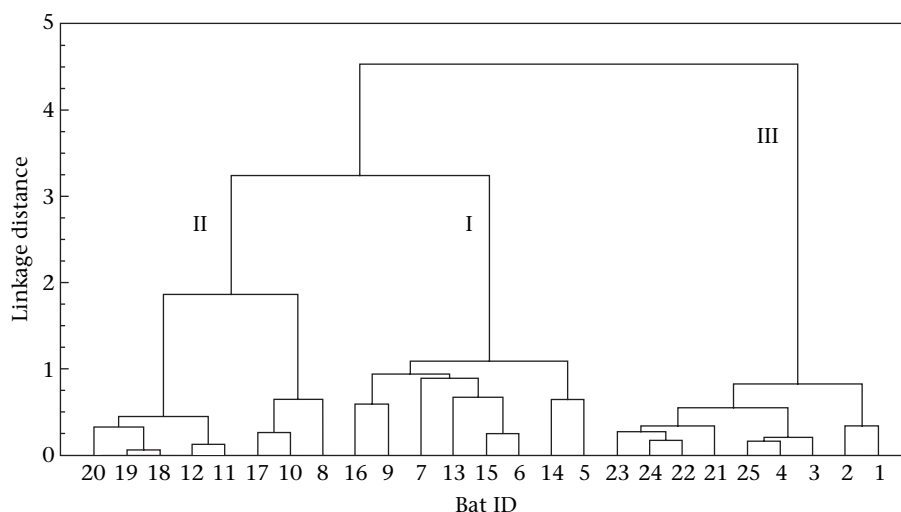

Figure 2. Results of cluster analysis (Ward's method) for the 25 bats radiotracked (2003−2004) revealing three main subunits (social groups I, II and III). Bats are assembled together depending on the degree of similarity in their roost use.
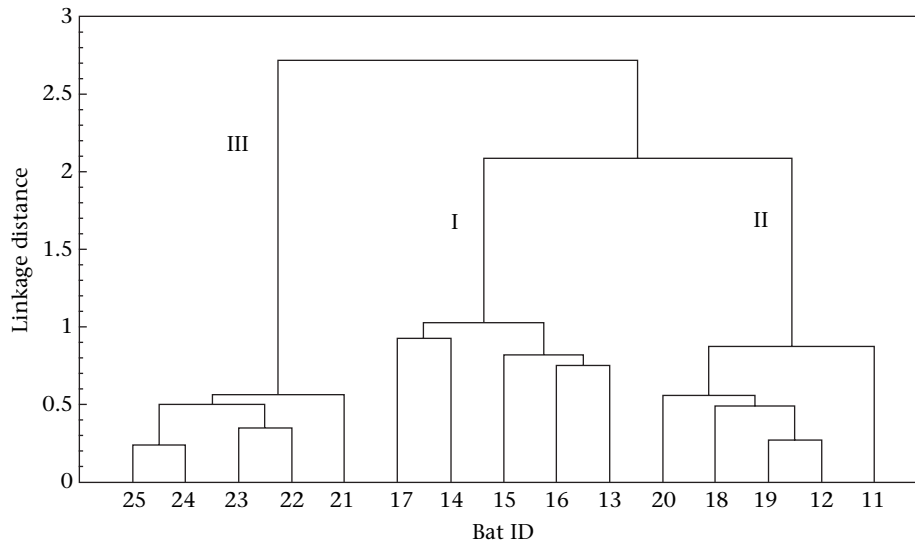
Figure 3. Results of cluster analysis (Ward's method) for the 15 bats radiotracked in 2004. Aggregations are based on pair-wise associations between all bats.

(noncontinuous days, as the bats left the roost and returned to it several times), resulting in 2904 bat visits∗ days. Although individual variation was large, only five bats (∼8%) were detected on fewer than 3 days. For reader 2, 'native' bats used the tree on average 40 noncontinuous days (±48 SD) for a total of 1919 bat visits∗days. Only five bats (∼10%) were detected on less than 3 different days. Bats emerged soon after sunset but activity by bats entering and leaving usually continued for the whole night. Some individuals made more than one emergence-return event. In contrast, 'foreign' bats had only one record each, mostly between 0500 and 0600 hours, except one bat that was detected on each of two consecutive nights. Except for this case, in which the bat presumably day-roosted in the tree, there was no evidence that the 'foreign' bats roosted in the tree. They could merely have sat in the entrance to explore the cavity, as a bat roosting in a tree should have at least two records (entrance and emergence).

Roost trees were assigned to the social group where the bats that used them belonged (Fig. 1a). Bats from social group I roosted in 39 trees; social group II used 27 trees; and social group III used 34 trees. Each social group generally roosted in a spatially distinct area of the park, although 14 trees (19% of all 73 used trees) were used by bats from several social groups (two trees shared by social groups I and II, 7 by social groups I and III, two by groups II and III and three shared by all social groups; Fig. 1a). These shared trees were either located in the core roosting area of one social group and only occasionally some 'foreign' bat roosted in them, or they were located at the boundaries between roosting areas and used occasionally by one or a few bats of each social group (Fig. 1b). Core roosting areas of each group, designated by 50% kernel use distributions, did not overlap (Fig. 1b). These areas contained few roost trees, but these trees were the most important (i.e. most used) by the different social groups. When spatial overlap between social groups took place, one or all of them used the area only marginally (95%

kernel; Fig. 1b). Percentage surface area of roosting ranges of each social group (designated by 95% kernels) shared with other social groups was 15% for social group I, 17% for social group II and 9% for social group III (Fig. 1b).

Loyalty to Roosting Areas and Trees

Sixty bats were recaptured, all of them in their distinct roosting areas, some 1 year ($N = 15$), 2 years ($N = 15$), 3 years ($N = 13$) or 4 years ($N = 1$) after their first capture. Bats were also found repeatedly in their roosting areas across different seasons. At least 32 out of 49 adult females (65%) carrying transponders from social groups I and II (with one reader each) before 2006, returned in subsequent years to their roosting areas. At least 17 females returned to their natal roosting areas based on detections at the readers, out of 27 juvenile females marked from social groups I and II before 2006 (55%).

The two individuals radiotracked in 1992 were followed to their roosts for 13 and 16 days, respectively, and used nine different trees. Some trees including the one where they were captured, no longer exist but were situated inside the main roosting area of social group I. Three other trees used in 1992 were still used in 2003 and 2004 by bats from social group I. One tree where reader 1 was located has been checked every year since 1992 and has been occupied by giant noctules every year. Another tree occupied in 1992 (T1; Fig. 1c) was reused in 2003 and 2004 by bats from social group III, and roost T2 was shared in 2003 and 2004 by both social groups I and III (Fig. 1a). These two last roosts, which were not checked every year, are near the boundary between the current core areas of groups I and III. Although the park was not intensively surveyed for giant noctules in 1992, several other trees with bats were detected. Specifically, trees T3, T4 and T5 (Fig. 1c), which in 2003–2004 belonged to the core area of social group II (Fig. 1b), were occupied in 1992 but not used by the two radiotagged bats.

Roost-switching Behaviour

Bats spent an average of 2.68 ($\pm$ 0.82 SD; range: 1–31; mode = 1; $N = 13$ bats) days in a given tree before moving to another roost (Table 1). Most roost trees were reused during the study period (less than 30% were used only once). Only seven bats provided data during the lactation period because transmitters failed or fell off before June (Table 1). Average roost-switching frequency was not significantly different before (2.52 days/roost $\pm$ 0.74 SD) versus during lactation (4.88 $\pm$ 1.91 SD; paired t test, $t_6 = -1.97$, $P = 0.096$). Power of the test was 0.38. Roost-switching rate (counted as the number of consecutive days that each bat roosted in each successive tree) did not differ significantly between individuals (Friedman test: $\chi_9^2 = 7.06$, $N = 12$, $P = 0.63$).

Although group composition in a particular tree varied from day to day, roost mates rarely switched to another tree simultaneously. Thus, bats did not seem to move as a group. On 22% of the days that we located bats in their roosts (excluding date of capture), all tagged bats belonging to a social group were scattered in different trees. On only 19% of days did all tagged bats from a social group roost in the same tree. Mean number of different trees used simultaneously per social group (considering days when all five radiotagged bats of a social group could be located) was 2.76 (range = 1–5 trees; $N = 45$ observations). These represent minimum values (i.e. minimum number of trees used simultaneously per social group), as we radiotracked only a small subsample of each social group (five bats out of an estimated 80–100 adult females per social group). Values varied with social group; for social group I (the group that used the largest number of tree roosts), all tagged individuals roosted separately on more than 40% of days and were together in the same tree only on the day of capture. Five trees were used continuously throughout the radiotracking period: two of which were the trees equipped with automatic transponders readers (Fig. 1a), where continuous bat activity was recorded from March until November.

Bats radiotracked in 1992 showed a similar roosting behaviour to that described above, with frequent roost switching (Table 1, Fig. 1c).

DISCUSSION

Giant noctules formed fission–fusion societies similar to those of chimpanzees, elephants, dolphins and some forest bats. Group members were spread between several roost trees on a daily basis with frequent remixing through roost switching. Colonies were thus dynamic entities exceeding the limits of single trees.

Cryptic, Stable Social Groups: Close Together… but Still Apart

Giant noctule colonies were not restricted to a single tree; however, all bats in María Luisa Park did not belong to a single colony. Three clearly defined social groups coexisted in close proximity. The absence of apparent barriers between the social groups and the fission–fusion behaviour, with frequent roost switching and remixing of individuals, would make this population structure difficult to detect through roost monitoring and checking group size. Roosting areas of the three social groups were generally distinct but with some degree of overlap (9–17%). Distinct forest patches used by different social groups have been identified for several forest bat species (Kronwitter 1988; O'Donnell 2000; Willis et al. 2003). Roosting areas for these species are typically nonoverlapping and occupy several hundred hectares. For giant noctules, overlapping roosting areas inside 20 ha can probably be explained by the high density of roosting opportunities within an otherwise barren landscape.

According to the definition of maternity colony (i.e. a group of reproductive females roosting together), the giant noctule population of María Luisa Park consists of three distinct maternity colonies. Our results suggest that these are stable over time, as adult females remained in their roosting areas and returned to them year after year for at least 5 years. Juvenile females also returned to their natal roosting areas in subsequent years. Female philopatry is common in social mammals (Greenwood 1980). In bat societies, including those using fission–fusion, female philopatry can restrict female-mediated gene flow between nearby social groups, creating matrilineal societies; male dispersal is usually the rule, preventing genetic isolation between social groups and populations (Petit & Mayer 1999; Kerth et al. 2000, 2002a; Castella et al. 2001; Metheny 2006). Fission–fusion maternity colonies of Bechstein's bat, *M. bechsteinii*, are closed matrilineal societies with extreme female natal philopatry and practically no immigration (Kerth et al. 2000, 2002b). In contrast, social groups of *E. fuscus* are more lax and there is immigration of females (Metheny 2006). Although giant noctules occasionally visited roosts of neighbouring colonies, we did not detect permanent changes of roosting area by any bats. It remains unknown whether immigration and genetic mixing between social groups occur.

Separate social groups and roosting areas have potentially existed in the park since at least 1992, with specific trees reused over the long term (up to 14 years).

Why do Forest Bats Switch Roosts?

Before lactation, giant noctules switched roosts on average every 2.52 days, a value similar for all-year male and autumn mixed populations of the similar species *Nyctalus noctula*, the common noctule, in Germany (2.57 days/roost; Kronwitter 1988). In our study, reproductive period did not influence significantly the rate of roost switching, contrary to barbastelle bats *Barbastella barbastellus* in forests (Russo et al. 2005). However, a tendency towards slower rates during lactation was observed, and the low power of the test (0.38) for the small sample size ($N = 7$) may have prevented significance. Roost-switching frequency did not differ significantly between individuals. Such as in *B. barbastellus*, for which roost switching was not influenced by age, sex or body condition (Russo et al. 2005), our results thus do not support that variable

requirements (e.g. thermoregulatory) are a major force shaping roost-switching behaviour by giant noctules.

Parasite load poses energetic costs for bats, partly expressed by extra time spent in grooming (Giorgi et al. 2001). Costs might be more pronounced for individuals in maternity colonies, as decreased immunocompetence in gestating females and in juveniles is linked to increased parasite infestation (Christe et al. 2000). Roost switching could thus function as an antiparasite strategy (Lewis 1995, 1996; Reckardt & Kerth 2006). However, giant noctule subgroups rarely abandoned the roost trees simultaneously. This situation, also observed in populations of *N. noctula* (Kronwitter 1988), differs from other forest bats (Lewis 1996; O'Donnell & Sedgeley 1999; Russo et al. 2005). At least the two trees equipped with automatic readers were used continuously from March, when females start congregating at roosts, until September–November. If avoidance of parasites was driving roost switching, tree cavities should remain vacant for enough time to disrupt parasite life cycles (Lewis 1996), at least for parasites that do not accomplish their entire cycle on hosts. Although the effectiveness of this behaviour has been shown for some forest bats (Reckardt & Kerth 2006), it does not seem the case in giant noctules. Likewise, continued use of tree roosts does not support the hypothesis that escape from predators learning about bat emergence is the main cause of roost change.

Rather, our results support the hypothesis that roost switching is a means of maintaining social bonds between colony members spread over multiple roosts − which is consistent with other studies (O'Donnell 2000; Willis & Brigham 2004; O'Donnell & Sedgeley 2006). In addition, we suggest that this behaviour may serve to retain and transfer knowledge about a large number of roosts (Kerth & Reckardt 2003; Russo et al. 2005). The hypothesis that forest bats switch roosts because trees are ephemeral does not contradict this view, as the knowledge and preservation of a pool of roosts would make the colony less vulnerable to roost losses due to natural processes or human management.

Why do Forest Bats form Fission–Fusion Groups?

Several reasons might promote sociality in breeding females, for example better thermoregulation in larger groups, increased protection from predators or cooperative breeding (Kalcounis & Brigham 1994; Kerth et al. 2001; Kunz & Lumsden 2003). Obviously these direct benefits of group living would only concern bats sharing the same roost simultaneously. What then is the advantage of belonging to a group larger than the cluster that is actually roosting together, and that needs roost switching to maintain cohesion?

The fluidity of fission–fusion social systems allows animals to counterbalance resource competition by splitting in small groups and yet aggregate when it is beneficial. Wild chimpanzees, for example, live within a large 'community' but form smaller 'parties' of variable size according to environmental, social or demographic conditions which also vary in time and space (e.g. Chapman et al. 1995; Lehmann & Boesch 2004). The existence of the 'community' allows chimpanzees to respond effectively to changes that alter their finely tuned balance between costs and benefits of group living. In elephant populations, 'core' social groups ('families') fuse in response to variable levels of food competition or risk of predation on calves, forming larger, 'bond' groups, which can also aggregate into 'clans' (Wittemyer et al. 2005). If direct benefits of group living for forest bats also depend on subgroup size (such as thermoregulation or protection of young), or if optimum subgroup size varies in response to factors such as climate or roost characteristics, then sudden changes in the environment (e.g. roost alterations, roost losses or climatic changes) or in the composition of subgroups (e.g. death, dispersal or immigration) might compromise these benefits. As in primate and elephant fission–fusion societies, belonging to a larger group allows restructuring bat subgroups in response to these changes, and in the long term, this would benefit all members of the group.

A further potential direct benefit of group living, that goes beyond the limits of subgroups, is information transfer. The amount of information that can be retained and preserved depends on number of individuals composing a group, but not necessarily on number of individuals roosting together (even if transmission of this information at a given time is more likely to occur between individuals that are roosting together). Social animals, from insects to birds, might gain information from other colony members about their environment, specifically about the location of food patches (Ward & Zahavi 1973; Danchin & Wagner 1997; Chittka & Leadbeater 2005). These mechanisms have been poorly studied in bats, but information transfer both about foraging areas (Wilkinson 1992) and about new roosts (idem; Kerth & Reckardt 2003) have been shown for some species.

Finally, large groups spread across several roosts might be a consequence of female philopatry in forest bats. If roosts are a limited resource, territory inheritance would be beneficial for female offspring, which are unlikely to find better roosts away from 'home', and for their mothers, that by allowing daughters to remain in high-quality roost areas, increase the probability that their genes will be passed on (Lindström 1986). Giant noctules, like all other temperate bats, have low reproductive rates, giving birth to one or two pups per year. However, bats are long lived and thus many generations overlap. This can eventually lead to the formation of larger groups than can fit into the limited volume of a tree cavity. Sharing multiple roosts might be more beneficial than splitting colonies whose members are familiar to each other and would thus be more likely to perform cooperative behaviours.

If Larger Groups are Advantageous, Why do not Cryptic Social Groups Mix?

The fact that giant noctules, like other forest bats, form fission–fusion societies suggests that living in larger

groups among several roosts provides fitness benefits. In this case, we could also expect social groups living in adjacent roosting areas to mix, eventually forming one single group, but the three distinct giant noctule groups were stable at least over the medium term (5 and possibly up to 14 years). This is surprising given that no physical or geographical barriers exist between roosting areas, which even overlapped to some extent, and giant noctule bats foraged up to 40 km away from their roosting areas (A. Popa-Lisseanu, F. Bontadina & C. Ibáñez, unpublished data). The overall foraging areas of the three social groups overlapped almost completely (idem); moreover, visits of bats to roosts of neighbouring social groups took place occasionally. Persistence of this social separation could be explained if the advantages of group living for giant noctules depend on associating with kin, and if female philopatry generates significant levels of relatedness among group members. However, colony members of other forest bat species, including those showing fission—fusion behaviour, differ greatly in their levels of relatedness and do not associate preferentially with kin. Average relatedness within colonies is low as a result of male dispersal, suggesting that kin selection does not explain group living (Burland et al. 2001; Kerth et al. 2002b; Metheny 2006). This remains to be tested in giant noctules. Alternatively, the costs of group living, in particular resource competition, could limit the size of the larger group. If roosts are a limited resource, and in addition, if keeping track of roosts and transferring information between group members that cooperate is costly, xenophobic behaviours could be expected (Kerth et al. 2002b), contributing to the maintenance of the observed high structuring in the giant noctule population.

Conservation Implications

Defining population boundaries in a metapopulation system is a basic step for developing sound conservation plans. The consequences of loss of resources may be very different if distributed between all population subgroups versus the impact falling on one group. Giant noctules living in María Luisa Park are at risk because of regular felling of trees in response to incidents of limbs falling on tracks where people walk. The population will be more likely to recover if tree losses are partitioned between the subgroups than if all removed trees fall inside the roosting area of one colony.

Our results confirm that a large number of roosts are needed to preserve colonies of forest bats (cf. O'Donnell 2000; Willis & Brigham 2004; Russo et al. 2005). Based on our results, we suggest that a minimum number of 30 roost trees per colony of ∼100 adult females should be preserved to enhance the chances of subpopulation survival. We detected roosts which are exceptionally important for colonies, defined by their location in core roosting areas. Colonies of other forest bat species might also make preferential use of specific roosts within their roosting areas. For example, common noctules *N. noctula* in Germany used many trees but spent almost half of their time in the centre of their roosting areas (Kronwitter 1988). We recommend that for tree-dwelling bat species living in managed woodlands, special care is given to identify core roosts and to determine if cryptic social groups exist, to ensure that core roosts and a minimum number of roosts per social group (estimated from monitoring roost-switching behaviour) are preserved.

Supplementary Material

Supplementary data can be found, in the online version, at doi:10.1016/j.anbehav.2007.05.011.

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