ANIMAL BEHAVIOUR, 2008, **75**, 471–482
doi:10.1016/j.anbehav.2007.05.011

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

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*(Received 20 December 2006; initial acceptance 21 January 2007;
final acceptance 28 May 2007; published online 29 October 2007; MS. number: 9222R)*

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.

Keywords: fission–fusion; giant noctule bat; *Nyctalus lasiopterus*; radiotracking; roosting behaviour; roost-switching; sociality; transponders

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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0003–3472/08/$34.00/0

(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