



Swarming behaviour associated with group cohesion in tree-dwelling bats



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ABSTRACT

Group living of social species increases the individual survival rate and enhances optimal exploitation of resources within their environment. Groups of cryptic tree-dwelling bats perform frequent roost switching on relatively long distances, whereas groups are temporarily disintegrated during foraging that precedes moving into new roost. In this study, we attempted to elucidate a mechanism in which group members can select new roost from a large set of potential roosting sites without disintegration of the whole group. Exploring the activity at the front of the tree hollows, recorded by automatic infrared monitors, we found that the swarming activity of Leisler's bats was performed during the whole night and was concentrated before the civil twilight at occupied roosts. A generalized linear model revealed significant positive association between the group size and swarming activity while season had negative but smaller effect. As bats swarmed the whole night also at sites that were less occupied or even unoccupied, we suggest that members of a bat colony selected new roost from a potentially larger set of available roosting sites. Thus, we propose a possible signalling role of swarming as a threshold behaviour that ensures group cohesion during roost switching.

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1. Introduction

In many animal species, optimal exploitation of resources depends on maintaining constant movement within the environment (Boinski and Garber, 2000). This task could be considered difficult for solitary living animals; however, it is exceptionally difficult for group-living species where divergent interests are very likely to occur among group members. In such species, it is of vital importance to establish some form of decision-making mechanism, which would be able to filter information from various individuals and make the unambiguous decisions where and when to move and thus prevent the group from disintegration (Frank, 1996; Couzin et al., 2005). The characteristic of decision-making mechanism varies across species but there exist generally two distinct concepts. First, in species where group members are able to suppress each other's reproduction (Clutton-Brock et al., 2010), a hierarchical social structure evolves, and only the dominant individual makes decisions, while other subordinate individuals are forced to copy its choices or leave the group and thus, lose the advantages of group living (e.g. wolves, Peterson et al., 2002; elephants,

Wittemyer and Getz, 2007; mongooses, Creel and Waser, 1991). In the second concept, where reproduction control is impossible, the egalitarian system is formed and all group members should equally contribute to the decision-making process (e.g. lions, Packer et al., 2001).

Tree-dwelling bats possess behavioural characteristics according to which one can expect the presence of very effective group movement mechanism. They form relatively large groups (from tens to more than 100 of individuals) consisting of adult females and their offspring, which roost in tree cavities, under loose bark or in some fissures (Kunz and Lumsden, 2003). When the microclimatic conditions of their roost become unsuitable or the group is overwhelmed by parasites or disturbed by a predator, the bats switch into another roost (Kerth et al., 2001; Fenton et al., 1994). Roost switching in many tree-dwelling species can be very frequent (every second or third day) and the distances between two subsequently used roosts may exceed hundreds of metres (Ruczyński and Bogdanowicz, 2008; Barclay et al., 1988). However, bats do not move to another roost in one cohesive flock as they are separated during previous foraging, but they arrive at the new roosting site before sunrise (Altringham and Fenton, 2006). Thanks to the fission-fusion dynamics of such bat societies, they may split into multiple small groups, or the individuals may intersperse with members from other social groups (Metheny et al., 2008;

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Popa-Lisseanu et al., 2008). Regardless of the fact that group size and composition may change during such roost switching, bats are able to maintain long-term social relationships (Kerth et al., 2011).

Previous field experiments suggested that a bat group operates under the ‘majority rule’ (Kerth et al., 2006). Individuals copy the choice of majority when their preferences are not strictly different and thus, they are able to form a group. However, in the case of strict difference in individuals’ preferences, the bat group may temporarily split into several smaller groups occupying multiple roosting sites. The majority rule could be a plausible mechanism of maintaining the fission–fusion dynamics of bat groups; however, an important question remains unanswered: How do individuals sharing similar preferences select new roost from a large potential set of roosting sites without disintegration of the whole group? Thus, the roost switching could be a more entangled process than expected. As a possible clue for explanation, one could propose bat swarming, a set of behavioural displays (overflights around the roosting tree followed by multiple landings and leaps from the roost entrance before final enter) performed by bats mostly during dawn prior to sunrise (Naďo and Kaňuch, 2013; see video in Supplementary material). Such swarming activity of bats at the vicinity of roost can be accompanied by vocalisation, where various social calls or calls with long-distance propagation attributes are suspected of roost-mate recruitment (Chaverri et al., 2010; Gillam and Chaverri, 2012; Gillam et al., 2013). This behaviour has long been overlooked by researchers, although it was occasionally mentioned in the literature (Vaughan and O’shea, 1976; Kunz, 1982; Russo et al., 2005; Kaňuch, 2007). Recent observations revealed an apparent wave-like pattern in the intensity of bat activity at the roost with very similar behavioural sequences among participating bat individuals (Naďo and Kaňuch, 2013).

In this investigation, we aimed to elucidate the mechanism of roost-switching in a cryptic tree-dwelling bat species and propose the role of swarming in this process. Based on the extensive spatiotemporal data on roosts’ occupancy and swarming activity at the set of tree roosts of a colony of Leisler’s bat, *Nyctalus leisleri*, we tested the hypothesis that higher level of swarming activity is propagated at roosts which are afterwards occupied by more bats thus swarming maintains group cohesion. An alternative hypothesis would be that this behaviour is not related to sociability of bats but to some extrinsic factors (e.g. weather, season).

2. Materials and methods

2.1. Study area

Data collection was conducted in Gavurky Protected Area, central Slovakia (Pliešovská kotlina Basin; E19°08’, N48°27’; 470 m a.s.l.). The study area is the pastured woodland of 70 ha, characterised by 200- to 300-year-old oaks (*Quercus robur* group, *Quercus cerris*) with an open canopy closure. The whole area could be considered homogenous with respect to tree species composition, their age and density of available tree roosts. Massive oaks provide plenty of roosting opportunities in comparison to the surrounding managed forests. Different animal species have refuges and breeding sites in this protected woodland. Among the vertebrates, besides several primary and secondary cavity-nesting birds (e.g. *Dendrocopos major*, *D. medius*, *Picus viridis*, *Sitta europaea*, *Jynx torquilla*, *Parus major*, *Cyanistes caeruleus*, *Ficedula albicollis*, *Sturnus vulgaris* and *Passer montanus*), it also hosts altogether 12, primarily tree-dwelling bat species (e.g. *Nyctalus noctula*, *Myotis nattereri*, *N. leisleri*, *M. bechsteinii* and *Barbastella barbastellus* (Kaňuch and Cel’uch, 2007).

2.2. Study species

The Leisler’s bat is a medium-sized species distributed across most of Europe and roosts almost exclusively in tree cavities, except in Ireland where it inhabits attics due to the loss of natural habitats (Ruczyński and Bogdanowicz, 2005; Spada et al., 2008). Similar to most of the temperate zone bats, this species exhibits strong sexual segregation (Kunz and Lumsden, 2003). Adult males roost solitarily or in small groups away from large maternity groups of females and their offspring, which often exceed 50 individuals (Dietz et al., 2009). Leisler’s bat is an opportunistic aerial-hawking forager feeding mostly on ephemeral insects (Kaňuch et al., 2005) on large distances exceeding several kilometres away from the roost (Shiel et al., 1999). Echolocation with mean pulse duration of 9.4 ms and frequency of peak energy at 27.4 kHz (Obriest et al., 2004) produces only weak echoes from very small targets (Pye, 1993), but such signals are capable to spread on large distances in comparison to higher frequencies which are severely affected by atmospheric attenuation (Lawrence and Simmons, 1982). The Leisler’s bats exhibit long-distance migratory flights of more than 1000 km and their expected average longevity is less than 10 years (Gaisler et al., 2003). Increased mortality during these long-distance migratory flights may have a substantial impact on the genetic composition of *N. leisleri* maternity groups, where relatively low genetic relatedness among females was found (Boston et al., 2012). Banding recovery data (bats were occasional harp-trapped during their evening emergence from the roost) confirmed that our study area was inhabited by a single colony of *N. leisleri* (Kaňuch and Cel’uch, 2007; Naďo and Kaňuch, 2013). This colony consists exclusively of maternity groups that were found to occupy from one to three roosts simultaneously and at least 30 tree roosts in total during the whole study period (Fig. 1a).

2.3. Recording and analysing of bat activity

During two seasons, between 8 June and 21 September 2013 and between 7 May and 29 August 2014, we tracked and monitored the activity of maternity groups of *N. leisleri* by mounting six automatic TM550-8K infrared [IR] monitors (Goodson & Associates Inc., USA) primarily at the sites of the most often occupied roosts whose locations were known from radio-tracking of bats and mapping of tree roosts during the years 2011–2014 (Fig. 1b) of which results were partly published (Kaňuch and Cel’uch 2007; Naďo and Kaňuch 2013). Monitored roosts were at least 150 m apart from each other (median = 308 m; range = 154 – 714 m). Each monitoring device was placed above the roost entrance, focusing downwards with the area of sensitivity optimally adjusted to narrow space in front of the roost (Fig. 1c). Such adjustment allowed to monitor bats either emerging/entering the roost or landing/overflying in very close proximity to the roost entrance (up to 50 cm). The IR monitors used in this study were able to detect the movement of warm-blooded animals even in complete darkness and record their activity in minimum intervals of 6 s (i.e. maximum one event per 6 s). We used the number of recorded events as the relative measure of swarming activity performed by bats at each roost. Events recorded during evening departure of bats were used to estimate the group size. For example, if an IR monitor recorded five events before dusk, it indicated that at least five individuals emerged from the roost. As such automatic method did not allow us to estimate group sizes precisely (max. 32 individuals recorded), we defined two categories of bat groups: a small group (up to 5 individuals) and a large group (more than 5 individuals). On a regular basis we did also direct observations at roosts during evening departure to verify this in the field. IR monitors were not able to discriminate whether the trigger was activated by the movement of bat or other nocturnal animal. To make sure that IR monitors provide reliable information

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