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Author for correspondence:
Simon Ripperger
e-mail: simon.ripperger@gmail.com

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Animal behaviour

Proximity sensors on common noctule bats reveal evidence that mothers guide juveniles to roosts but not food

Simon Ripperger[1,2], Linus Günther[1], Hanna Wieser[1], Niklas Duda[3], Martin Hierold[3], Björn Cassens[4], Rüdiger Kapitza[4], Alexander Koelpin[5] and Frieder Mayer[1,6]

[1]Museum für Naturkunde, Leibniz-Institute for Evolution and Biodiversity Science, Invalidenstraße 43, 10115 Berlin, Germany
[2]Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Republic of Panama
[3]Institute for Electronics Engineering, Friedrich-Alexander University of Erlangen-Nürnberg, Wetterkreuz 15, 91058 Erlangen-Tennenlohe, Germany
[4]Carl-Friedrich-Gauß-Fakultät, Technische Universität Braunschweig, Mühlenpfordstraße 23, 38106 Braunschweig, Germany
[5]Chair for Electronics and Sensor Systems, Brandenburg University of Technology, Siemens-Halske-Ring 14, 03046 Cottbus, Germany
[6]Berlin-Brandenburg Institute of Advanced Biodiversity Research, Altensteinstr. 34, 14195 Berlin, Germany

SR, 0000-0003-1527-8657; LG, 0000-0001-9181-4621; ND, 0000-0001-7846-353X; AK, 0000-0002-9071-5661

Female bats of temperate zones often communally rear their young, which creates ideal conditions for naive juveniles to find or learn about resources via informed adults. However, studying social information transfer in elusive and small-bodied animals in the wild is difficult with traditional tracking techniques. We used a novel 'next-generation' proximity sensor system (BATS) to investigate if and how juvenile bats use social information in acquiring access to two crucial resources: suitable roosts and food patches. By tracking juvenile–adult associations during roost switching and foraging, we found evidence for mother-to-offspring information transfer while switching roosts but not during foraging. Spatial and temporal patterns of encounters suggested that mothers guided juveniles between the juvenile and the target roost. This roost-switching behaviour provides evidence for maternal guidance in bats, a form of maternal care that has long been assumed, but never documented. We did not find evidence that mothers guide the offspring to foraging sites. Foraging bats reported brief infrequent meetings with other tagged bats that were best explained by local enhancement. Our study illustrates how this recent advance in automated biologging provides researchers with new insights into longstanding questions in behavioural biology.

1. Background

Social information should be of particular importance for juveniles during the early period of their lives [1]. The presence of parents and other adults gives plenty of opportunities to socially acquire information [1,2] that would otherwise be more costly to acquire through trial-and-error learning [3,4]. Social information can enable better decisions in contexts such as predator avoidance, reduction of parasitism, habitat choice and foraging [5]. While the value of social information for the young of most mammalian species is widely accepted, the empirical evidence is highly biased towards tractable species and captive experiments. A great challenge has been the study of social information transfer in small and elusive species in nature.

The role of social information between mother bats and their juveniles has been a longstanding topic. Juvenile bats can relocate with their mothers to a new roost after being excluded from their current roost [6], and home ranges in mothers and their offspring show spatial association in at least three species [7]. These observations suggest the possibility of following and guidance by juveniles and their mothers. However, studies should analyse the spatial proximity among mothers and offspring at high temporal resolution during foraging and roost switching in order to clearly demonstrate guidance by mothers or following behaviour by juveniles.

During the past decade, several emerging technologies have revolutionized the field of bio-logging and in turn our understanding of the behaviour of wild animals. However, studies on small vertebrates still lag behind due to the scarcity of fully automated lightweight tracking devices [8]. For studying most small animal species in the wild, old-fashioned tracking technologies such as VHF-telemetry and PIT-tagging still represent the state-of-the-art, but the data obtained typically lack the accuracy and resolution to observe processes like information transfer in detail.

Proximity loggers, which sense dyadic associations by communication among animal-borne tags, represent a powerful tool for the study of information transfer [9,10]. Yet, the first generation of proximity loggers suffered from performance problems [11], newer versions have faced a trade-off between weight [12] and runtime [13]. In the present study we used the newly developed miniaturized proximity sensor system 'BATS', a fully automated system for documenting associations among individuals at a tag weight of 1–2 g and runtimes of at least one to two weeks [14–16]. In addition to logging encounters, we could localize many encounters to a particular site by placing stationary base stations below known roosts. Here we report on the first extensive study to apply our system.

We investigated the use of social information in acquiring access to two types of resources that are crucial in the life of a juvenile bat: suitable roosting sites and food patches (e.g. tree holes or bat boxes and insect-rich foraging grounds). Frequent roost switches may help to maintain favourable microclimatic conditions [17] or to avoid parasites [18], while food supply during early development may have lasting fitness consequences [19,20]. Behavioural experiments demonstrated the benefits of social information in both contexts. Social information may facilitate roost finding [21,22] and support the learning of novel foraging behaviours [23,24]. We hypothesized that fledging offspring would use social information by following their mother or other adults in the social groups to roosts or foraging sites. Accordingly, juveniles that successfully switch roosts should be associated with at least one individual from the roost group when leaving the first roost and also when arriving at the second roost. If social information is used for finding foraging grounds, we expect the same pattern when starting a foraging bout. Additionally, we expect repeated associations during the several minutes while bats commute to a foraging ground, and possibly, but not necessarily, when returning to the roost.

2. Material and methods

This study was conducted in 'Königsheide Forst', a mixed forest in the city of Berlin, Germany, from June to August in 2016 and 2017.

The area comprises many natural roosts in tree holes and roughly 130 bat boxes. We studied maternity colonies of the common noctule bat (*Nyctalus noctula*), seasonal aggregations where females jointly give birth and rear their young. Maternity colonies involve fission–fusion dynamics where females and their offspring (often twins) move among several roosts, with temporary groups of up to *ca* 50 individuals [25]. We captured entire social groups from bat boxes during the period when around two-thirds of offspring have already fledged. After fledging, juvenile noctule bats still nurse from their mothers for a few weeks [26]. This should be the most likely time for our study to observe information transfer. We tracked a total of 60 bats (2016: 10 juveniles and 16 adult females; 2017: 19 juveniles and 15 adult females).

The fully automated BATS tracking system includes field strength-related distance estimation between animal-borne mobile nodes (hereinafter 'proximity sensors', figure 1), and automated remote data download by stationary nodes (hereinafter 'base stations'). The proximity sensors weigh 1.1–1.9 g depending on battery size and housing. Runtime is at least 1 week. The proximity sensor broadcasts a signal every 2 s. When other proximity sensors are within reception range of max. 10 m [27], the start of a 'meeting' is created. As soon as no signal has been received by the respective meeting partner for 10 s, the proximity sensor closes the meeting and stores it in the on-board memory along with the ID of the meeting partner, a timestamp, the total meeting duration, and the maximum received signal strength indicator (RSSI). The signal is simultaneously received by any base station within range. We positioned base stations near potential roosts to detect tagged bats arriving or departing. We therefore termed a signal from a bat to a base station as a 'presence signal'. Base stations remotely downloaded and locally stored all data. For an in-depth description of the BATS tracking system design see [15].

We detected unambiguous roost switches and foraging bouts using the presence signals of tagged juveniles at base stations. During these events, we screened for individuals that jointly depart from a roost and also jointly arrive at the target roost (indicated by meetings upon departure and arrival). We also detected meetings during the entire time of a foraging bout by a juvenile (see electronic supplementary material, figure S1 for details). To test whether juveniles preferably associate with their mothers, we used Mantel tests (ade4 R package, 9999 permutations) to test whether the matrix of mother–offspring (1) and non-mother–offspring relationships (0) predicted matrices based on unweighted networks of association during roost switching and foraging. We tested the years 2016 and 2017 separately (see electronic supplementary material for details on microsatellite-based kinship analysis).

3. Results

Proximity sensors successfully documented associations among tagged juvenile and adult bats while switching roosts. Juveniles were associated with adults during 16 roost-switching events by 12 different juveniles. In 2016, seven juveniles were observed 10 times to associate with an adult during roost switching. All 10 roost-switching dyads were mothers and their offspring. In 2017, five juveniles switched roosts twice in association with their mother and in four cases with another adult female. Mothers and juveniles were observed switching roosts together more than expected by chance (2016: $r = 0.88$, $p < 0.001$; 2017: $r = 0.21$, $p < 0.01$).

Some juveniles switched directly among two roosts; such events took only seconds to minutes (table 1). During other events, bats used stopover sites and movements show that mothers made several attempts to re-associate with their

Figure 1. Unpackaged proximity sensor (*a*) and tagged adult common noctule bat (*Nyctalus noctula*) ready for take-off (*b*).

Table 1. Summary of joint roost-switching events by juveniles and associated partners. Roost-switching durations and distances were only determined when both roosts were known and equipped with base stations. Switching mode: 1 switch among two known roosts; 2 switch among two known roosts including a joint stopover at an unknown site indicated by stable meetings; 3 switch between a known and an unknown roost (indicated by stable meetings, see electronic supplementary material, figure S1c).

season	juvenile ID	sex	partner ID (mother)	distance (m)	duration (hh:mm:ss)	switching mode
2016	9311	f	9330 (m)	307	01:48:44	2[a,b]
2016	9318	f	9330 (m)	307	00:01:54	1[a,b]
2016	9311	f	9330 (m)	297	00:00:56	1[a]
2016	9318	f	9330 (m)	297	00:00:35	1[a]
2016	9323	m	9340 (m)	307	01:38:41	2
2016	9325	m	9336 (m)	307	01:06:48	2
2016	9307	f	9338 (m)	—	—	3
2016	9319	f	9327 (m)	—	—	3
2016	9312	f	9334 (m)	—	—	3
2016	9323	m	9340 (m)	—	—	3
2017	9376	f	9383	179	00:00:20	1
2017	9373	m	9412	248	00:00:26	1
2017	9376	f	9383	—	—	3
2017	9370	f	9368 (m)	—	—	3
2017	9380	m	9413	—	—	3
2017	9391	f	9385 (m)	—	—	3

[a]Roost switch of mother and twins including repeated commuting flights.
[b]See figure 2 for a schematic representation.

young before both arrive at the new roost (figure 2). Such attempts of re-association suggest that (i) the offspring was actively flying and not carried by the mother, and (ii) the observed behaviour was not simply a juvenile following its mother, but rather some form of guidance by the mother. For example, figure 2 illustrates one case of a mother, which was attending to its twins that were separated, and appeared to herd them while moving from one roost to another.

When starting a foraging bout, juveniles never associated with their mothers and rarely encountered other tagged adults. In total we detected 42 foraging bouts of juveniles (2016: four juveniles, eight bouts; 2017: nine juveniles, 34 bouts). Whenever a juvenile and its mother were co-roosting before both started individual bouts ($n = 13$ events), the mother left the roost at least 4 min earlier than the juvenile (4:31 to 86:02 min). During six of the 42 foraging bouts of juveniles (14%, $n = 7$ juveniles), we detected 21 encounters
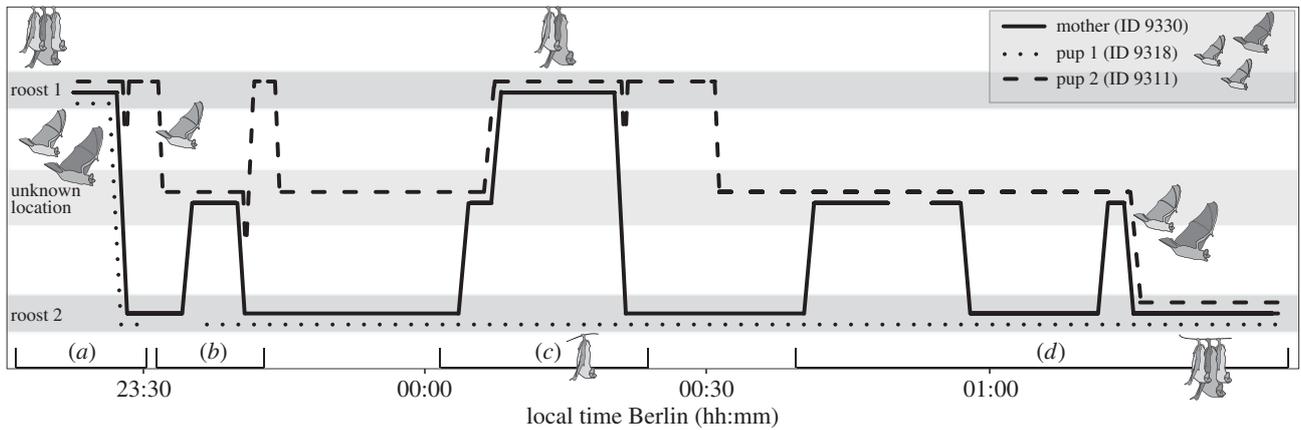
Figure 2. Schematic representation of a mother and its twins switching roosts together (based on meeting data and presence signals). Repeated commutes back and forth indicate guidance behaviour of the mother. (a) A mother and its twins jointly leave roost 1 and the mother successfully moves 307 m distance to roost 2 with juvenile 1. The association between mother and juvenile 2 aborts and juvenile 2 flies back to roost 1. (b) Juvenile 2 moves from roost 1 to an unknown location where it is later joined by its mother after a few minutes. Both fly together towards roost 2, but juvenile 2 flies back to roost 1 while the mother encounters juvenile 1 at roost 2. (c) The mother joins juvenile 2 in an unknown location and they jointly switch to roost 1. They jointly leave roost 1, but only the mother arrives at roost 2 starting a meeting with juvenile 1; meanwhile, juvenile 2 flies back to roost 1. (d) The mother joins juvenile 2 at an unknown location. At around 00:50 the meeting is interrupted for several minutes possibly because at least one individual left, before the mother commutes twice between its two juveniles. Finally, around 01:15 the mother successfully switches with juvenile 2 to roost 2. All three bats stay at roost 2 until shortly before 02:00.

with 11 individuals, which lasted between 1 and 30 s. Three of these meetings occurred within less than 90 s after the two co-roosting individuals left their roost, but no further meetings were observed during these foraging bouts. All remaining meetings occurred at least 7 min after roost departure. The meeting partners included eight other juveniles, two adult females, and only one identified mother, which is not different from chance (2017: $r = 0.08$, $p = 0.19$; 2016: no mother–pup dyad among three observed dyads and therefore not tested).

4. Discussion

Studying the wild social behaviour of small nocturnal animals is challenging. Our newly developed proximity sensor system enabled us to detect a novel behaviour consisting of brief, hard-to-observe events: coordinated roost movements by mothers and young. In some cases, mothers repeatedly commuted back and forth until offspring moved to the new roost (figure 2). The most parsimonious explanation for this pattern of behaviour is maternal guidance of juveniles, a form of maternal care that has been suspected but never previously demonstrated. Young bats are highly dependent on maternal care for food, protection, and warmth [28]. Maternal care in bats is known to include nursing, post-weaning food provisioning [29,30], grooming [31–33], and pup guarding [34]. In some species, mothers often carry young in flight, possibly to other temporary roosts or feeding grounds [35]. However, this is the first study to provide empirical evidence that mothers guide volant young to roosts.

Anecdotal evidence from other bat species suggest that mothers and young maintain contact during the initial foraging flights of juveniles [36]. However, we did not find evidence for coordinated mother–young foraging in noctule bats. Instead, juveniles started foraging considerably later than their mothers and only occasionally encountered other tagged colony members. Insectivorous bats often eavesdrop on the 'feeding buzzes' of conspecifics, a form of local enhancement at feeding grounds, which may explain the juvenile encounters with others [37–39].

Why does mother–offspring guidance occur during roost switching but not foraging? One possible explanation is that mother–young associations are crucial for social thermo-regulation and lactation, which lasts for three weeks to two months depending on the species (reviewed by Kerth [40]). In noctule bats, nursing continues after fledging [26] and can last for up to two months in captivity [31]. Another factor is that noctule bats feed on diverse insect prey [41], which may enable juveniles to forage opportunistically. Compared to food, suitable roosts of high quality may be harder to find without social cues and roost quality might also require more assessment. Prey patches are ephemeral and any conspecific might provide social cues about prey location. In contrast, social information about roosts is stable enough to accumulate disproportionately among philopatric adult females. Finally, although noctule bats can find new roosts by eavesdropping on social calls [42], this behaviour would not allow for finding specific individuals at distances observed in our study.

Our study shows a further step forward in the current revolution in tracking technology enabling to address long-standing biological questions. Twenty years ago, Wilkinson & Boughman [43] speculated that young bats follow adults in situations such as roost switching, and modern technological innovations have now allowed us to unequivocally track mother–juvenile associations during roost-switching movements. The integration of smart power management and multiple sensors has reduced the size and energy consumption of sensors, allowing for the collection of high-resolution datasets that can reveal how social networks change over time [44] and the existence of rare, but biologically important, behaviours.

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