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Information transfer about roosts in female Bechstein's bats: an experimental field study

Gerald Kerth* **and Karsten Reckardt**

Zoologisches Institut, Universität Zürich, Verhaltensbiologie, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

Information transfer among group members is believed to play an important part in the evolution of coloniality in both birds and bats. Although information transfer has received much scientific interest, field studies using experiments to test the underlying hypotheses are rare. We used a field experiment to test if communally breeding female Bechstein's bats (*Myotis bechsteinii*) exchange information regarding novel roosts. We supplied a wild colony, comprising 17 adult females of known relatedness, with pairs of suitable and unsuitable roosts and monitored the arrival of individuals marked with transponders (PIT-tags) over 2 years. As expected with information transfer, significantly more naive females were recruited towards suitable than towards unsuitable roosts. We conclude that information transfer about roosts has two functions: (i) it generates communal knowledge of a large set of roosts; and (ii) it aids avoidance of colony fission during roost switching. Both functions seem important in Bechstein's bats, in which colonies depend on many day roosts and where colony members live together for many years.

Keywords: Chiroptera; communal roosting; cooperation; information transfer; social behaviour

1. INTRODUCTION

An important advantage of sociality is the ability to learn from conspecifics about the environment. Information transfer among group members is widespread and occurs in eusocial insects (see, for example, Hölldobler & Wilson 1990) and various vertebrates (see, for example, Brown 1986; Galef 1991; Reebs 2000). Information transfer (about food) is believed to be an important factor in the evolution of coloniality in birds and bats (see, for example, Ward & Zahavi 1973; Wilkinson 1992).

Three main hypotheses have been proposed to explain how information transfer can lead to communal roosting and breeding (reviewed in Richner & Heeb 1996). The 'information centre hypothesis' assumes communal roosting is beneficial because all group members profit from information transfer at the roost (Ward & Zahavi 1973). In contrast, the 'two-strategy hypothesis' proposes that inferior foragers profit from information transfer at the roost while superior foragers profit from other benefits of communal roosting correlating with group size, such as safety from predators (Weatherhead 1983). Finally, the 'recruitment centre hypothesis' presumes that successful foragers transfer information at the communal roost to group members that do not reciprocate in transferring information, as recruiters profit from the presence of conspecifics in the foraging habitat (Evans 1982; Richner & Heeb 1996).

To evaluate the hypotheses about information transfer empirically, field experiments are required to test their predictions (Weatherhead 1987). Although information transfer has received much scientific interest, field studies using experiments to test the underlying hypotheses are rare (Galef & Giraldeau 2001) and are primarily restricted to studies of birds exchanging information about food (Weatherhead 1987; Prior & Weatherhead 1991; Marzluff *et al.* 1996; Buckley 1997).

Here, we present a field experiment in which we tested whether communally breeding female Bechstein's bats (*Myotis bechsteinii*) exchange information about novel roosts. Because colonies of this species use up to 50 day roosts during one reproductive season, information transfer among colony members could aid the acquisition of knowledge about suitable roosts (Kerth *et al.* 2001*a*). Bechstein's bat colonies are matrilineal societies of stable composition, comprising 15–40 females of different relatedness (Kerth *et al.* 2000, 2002). Thus, information transfer about roosts, if present, could be based both on reciprocity among long-term associated colony members and on kin selection among closely related females.

Owing to the biology of Bechstein's bats, our study differs from the existing experimental field studies on information transfer in three ways. First, we observed a species that forms stable colonies. Second, we provided novel roosts instead of food. Finally, we investigated the effect of kinship that is often ignored in studies of information transfer because of the transient nature of groups in most species studied so far (Dall 2002).

We provided a wild Bechstein's bat colony with pairs of suitable and unsuitable bat boxes. If females transfer information, we expected them to recruit each other to suitable boxes. In this case, we had four predictions: (i) if information is transferred at the day roost, the information centre hypothesis should apply if bats reciprocate in recruiting and following; (ii) if some females consistently explore and recruit more than others, the two-strategy or the recruitment centre hypothesis should apply if recruitment at the roost is independent of relatedness; (iii) if relatives are preferentially recruited, kin selection could explain why information is transferred to colony mates that do not reciprocate; and (iv) if bats recruit each other at the novel box ('local enhancement' (Thorpe 1963 in Galef & Giraldeau 2001)), day roosts do not serve as information or recruitment centres.

* Author for correspondence (kerth@zool.unizh.ch).

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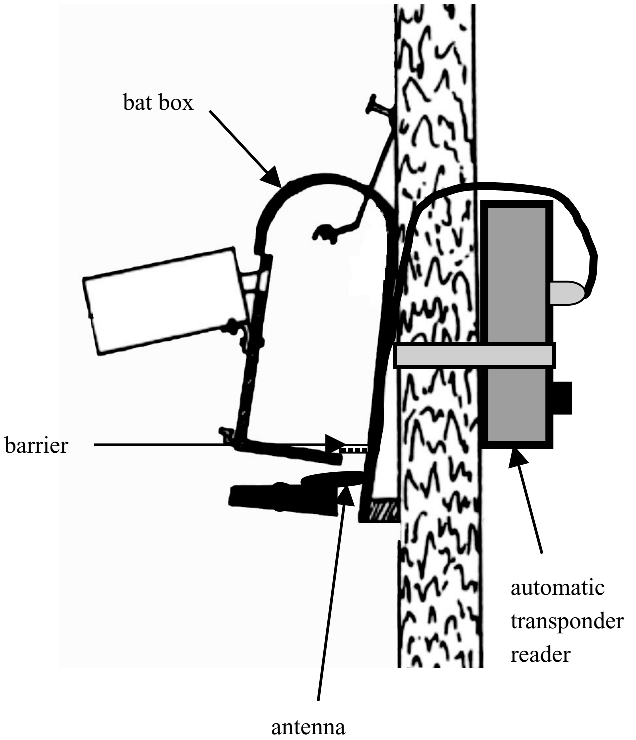

Figure 1. 'Unsuitable' experimental box: bat box equipped for continuous monitoring with an automatic transponder (PIT-tag) reader. A barrier blocking the interior entrance makes this box unsuitable for roosting (see text for details).

2. METHODS

(a) *Study site, animals and monitoring of day roost occupation*

We conducted our study from 27 July to 3 October 2000 and from 24 April to 21 September 2001 in the home range of the Bechstein's bat colony 'Blutsee' (Kerth 1998). This colony occurs in a deciduous forest near the city of Würzburg (northern Bavaria, Germany) and has been continuously studied since 1993 (Kerth 1998, 2004). All adult females (19 in 2000 and 18 in 2001) were individually marked with transponders (PIT-tags) (Kerth & König 1996). Furthermore, degrees of relatedness among 17 females, present in both years, were determined in a previous study (Kerth *et al.* 2002). The Blutsee colony roosts mainly in bat boxes ('2FN', Schwegler, Germany). We checked several times a week for the presence of bats in 118 boxes distributed in the centre of the colony's home range (*ca.* 0.5 km^2). Experimental boxes were checked daily. If bats were observed in a box, we identified individuals using mobile PIT-tag readers (Kerth & König 1996, 1999).

(b) *Field experiment*

We placed 20 pairs of new bat boxes within 300 m of day roosts used by the Blutsee colony in previous years. All experimental boxes were of the same type used by colony members since 1993 (Kerth 1998). Each new pair consisted of a 'suitable' and an 'unsuitable' box, hanging side by side at the same tree. The boxes had two entrances located after each other. Within each box pair we randomly created an unsuitable box by blocking the interior entrance with a mesh wire. In manipulated boxes bats could still enter the entrance area through the first entrance, but roosting was prevented because bats could not pass through the interior entrance (figure 1). This manipulation mimicked a box that cannot be used by bats because it is occupied by nesting birds or dormice, which is a common situation (G. Kerth, personal observation).

Each experimental box was equipped for continuous monitoring with an automatic reading device (figure 1). Reading devices consisted of a reader (EURO 8100, Usling, Germany), an oval antenna (6 cm × 4 cm) and a battery (12 V/3.6 Ah). Readers recorded and stored PIT-tag numbers, times and dates of bats passing the antenna in the box's entrance area. Data were regularly transferred to a laptop computer. All experimental boxes were monitored every night, beginning from the day they were established. We regarded a single experiment (monitoring of one box pair) as completed when all females had visited one box, or when the suitable box had been used as a day roost for the first time. In the autumn of 2000 we stopped the experiments when the females left for hibernation, resuming them when the bats reappeared in the spring of 2001. In addition to the experimental boxes, we monitored all day roosts in 2001 (30 bat boxes and one tree hole) for as long as bats occupied them.

(c) *Data analysis*

Monitoring bat boxes with automatic PIT-tag readers is new. Thus, we first tested the efficiency of our method. We determined the percentage of bats recorded in boxes during the day with mobile readers that were also recorded by automatic readers when departing the day roosts the following night.

If information transfer occurs, we predicted females recruit each other to suitable boxes. In this case, more colony members should be recorded in suitable than in unsuitable boxes. For this prediction to hold females must not enter unsuitable boxes *a priori* (without information transfer) less than suitable boxes. We tested this by assessing for any bias in initial box preferences. Subsequently, we tested whether the number of naive bats, defined as new individuals that entered a box after the visit of the first bat, differed between suitable and unsuitable boxes. In 14 experimental pairs, single readers failed to record in some nights owing to occasional power loss. Therefore, we only included readings from nights where we had been able to monitor both boxes. For comparisons within box pairs (suitable versus unsuitable boxes) we used Wilcoxon's matched-pair tests.

To quantify individual recruitment we compared the time between consecutive readings of bats in a box. We defined recruitment of a naive bat to a new box as the visitation of a naive bat to a box within no more than 3 min of an 'experienced' bat (an individual that had entered the box on a previous visit). We allowed for a 3 min delay between readings as females do not enter a box immediately upon arriving at it: females returning at night to a day roost usually encircle it for some time before entering it (G. Kerth, personal observation). For the same reason we included events of a naive bat entering a novel roost up to 3 min before the experienced bat. When analysing individual recruitment, we included only readings from a box before the first power loss. Thus we avoided misinterpretation of individual arrival patterns that could also be attributed to occasional power losses. χ^2-tests and a Mann–Whitney *U*-test were used for independent data; Spearman's rank correlations for comparisons of individual behaviour.

For each of the 17 bats present in both study years we quantified the following parameters: (i) number of experimental boxes it discovered (i.e. how often it was the first bat to enter); (ii) how often it recruited a colony mate; (iii) how often it was recruited; (iv) how often it entered a new box without being recruited.

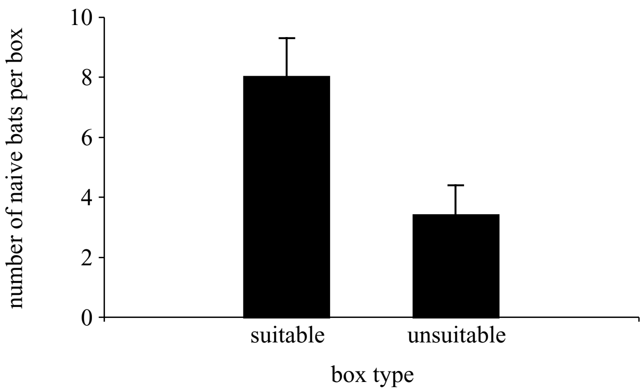

Figure 2. Number of naive bats (mean ± s.e.m.) in suitable versus unsuitable bat boxes (see text for details).

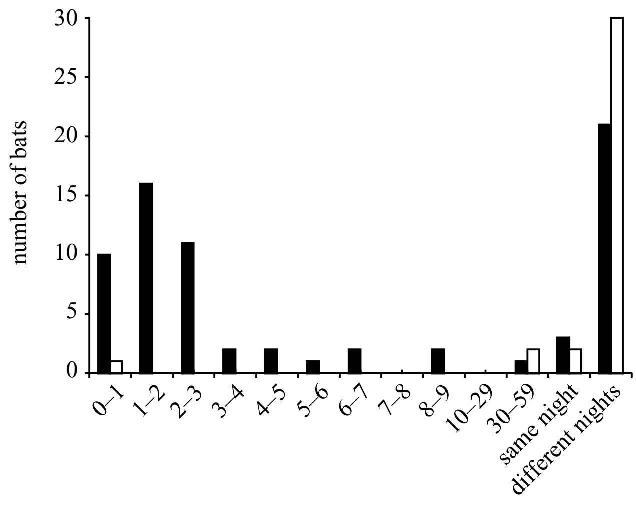

Figure 3. Time between experienced and naive bats arriving at experimental bat boxes. Filled bars, suitable boxes; open bars, unsuitable boxes. (See text for details.)

3. RESULTS

(a) *Efficiency of the automatic box monitoring*

The automatic readers confirmed 1508 of 1548 individual readings obtained during the day in 2001. Thus, their efficiency was 97%. Although occasional battery failure caused some gaps in our automatic box monitoring, on average we were able to monitor both boxes of a pair in 91% of its observation nights (range: 63–100%).

(b) *Discovery and occupation of experimental boxes*

Females discovered 19 of the 20 experimental pairs. On average a box was entered for the first time 29 nights after it was introduced (range: 0–118 nights, excluding the time between October 2000 and April 2001 when bats were absent). Fourteen of the 19 suitable boxes discovered were used as day roosts. Time between discovery of a suitable box and its first use as a day roost ranged from 3 to 151 days (the mean was 88 days).

(c) *Number of naive females recorded in suitable versus unsuitable boxes*

The first recorded bat entered the suitable box in 11 and the unsuitable box in 8 of 19 cases ($\chi^2 = 0.5$, n.s.). Of the 9 box pairs that had no observation gap before the arrival of the first bat, this ratio was 5 : 4. After a box had been discovered by the first bat, the number of naive bats recorded was significantly higher for suitable than for unsuitable boxes ($n = 19$ box pairs, $Z = -3.46$, $p < 0.001$; figure 2). We obtained a similar result when comparing numbers of naive bats in the two box types before the first monitoring gap ($n = 9$ box pairs, $Z = -2.37$, $p < 0.02$).

Furthermore, the ratio of recruited to not-recruited bats was significantly higher in suitable boxes (data before the first observation gap). In suitable boxes, 37 out of 71 naive bats were recorded within 3 min of an experienced bat. In unsuitable boxes this ratio was only one out of 35 ($\chi^2 = 24.7$, $n = 106$, $p < 0.0001$; figure 3). Most recruitment events (84%) occurred between 22.30 and 03.30 and recruitment followed a bimodal distribution with one peak at 23.30 and the other at 01.30.

(d) *Individual box visiting behaviour*

We obtained 3101 individual readings at 56 bat boxes and one tree hole (experimental box pairs and day roosts) during 201 nights. We found a significant positive correlation between the number of new boxes a bat discovered, the number of colony mates it recruited, and the number of its independent (not-recruited) box visits as a naive bat (table 1). By contrast, the number of times a bat was recruited by its colony mates was not significantly correlated with any of the other parameters (table 1).

Recruited bats often arrived in a group. In 12 of the 38 recruitment events the recruited bat entered a box with more than one experienced female within 3 min. In 12 other instances only one experienced bat was recorded within 3 min of the naive bat, but further experienced bats were observed a few minutes later. For further analysis we aimed to unambiguously identify single individuals as recruiters. We included only recruitment events, in which no other experienced bat was observed within 20 min of the recruiter (the experienced bat that was recorded within the 3 min period). Confirmed single recruiters did not recruit colony mates depending on their relatedness. Pairwise relatedness between recruiters and recruited bats (14 pairs) did not differ from pairwise relatedness among all 17 females present in both years (median $r = 0.02$ in both cases; $n_1 = 14$, $n_2 = 136$, $U = 904$, n.s.).

4. DISCUSSION

(a) *Information transfer about novel roosts*

Our data show that female Bechstein's bats recruited naive colony mates to suitable roosts. To the best of our knowledge, this is the first experimental evidence that bats transfer information about novel roosts. Although there is also some indication of information transfer about roosts in evening bats (Wilkinson 1992), little is known whether this behaviour occurs in other bat species. However, we do not think that female Bechstein's bats are exceptional in exchanging information about roosts. Instead, we assume that such cooperation is common in bats. Many bat species frequently switch roosts (Lewis 1995) and information transfer could help them to avoid colony fission during roost switching, as has been shown for ant colonies (Pratt *et al.* 2002).

Table 1. Spearman's rank correlation coefficients (r_s) and p values, resulting from comparisons between the box visiting behaviour of 17 female Bechstein's bats belonging to one maternity colony. We compared: (i) how many new boxes a bat discovered; (ii) how often a bat entered a new box without being recruited (independent visits); (iii) how often a bat was recruited to a new box; and (iv) how often a bat recruited a colony mate to a new box (see text for details).

	(i) discovered boxes	(ii) independent visits	(iii) times recruited
(ii) independent visits	$r_s = 0.51$ $p = 0.035$		
(iii) times recruited	$r_s = 0.16$ $p = 0.539$	$r_s = -0.09$ $p = 0.737$	
(iv) times being a recruiter	$r_s = 0.55$ $p = 0.023$	$r_s = 0.76$ $p < 0.001$	$r_s = -0.10$ $p = 0.692$

Furthermore, information transfer might generate communal knowledge of roosts. On average it took about three months between the discovery of a suitable box and its first use as a day roost. This indicates that females build up knowledge of a large set of roosts, from which they select appropriately. Because female Bechstein's bats depend on many different roosts (Kerth *et al.* 2001*a*) communal knowledge of day roosts could be an important resource for a colony.

(b) *Local enhancement versus recruitment at the day roost*

Naive females could have been recruited to suitable boxes via local enhancement due to scent marks, or by calls of bats visiting a suitable box. Local enhancement using scent marks seems unlikely because most naive bats entered a novel box in the company of experienced bats. Our data indicate that colony mates had to be present to attract naive females. Because we did not record sound, we cannot completely exclude the possibility that calls of females visiting a suitable box recruited naive bats (see Barclay 1982). However, this does not explain why naive bats often arrived within a group, unless we assume that several bats heard a call at the same time. This seems unlikely as female Bechstein's bats generally forage apart from each other (Kerth *et al.* 2001*b*).

Instead, the individual arrival pattern of bats is probably best explained as recruitment at the day roost. In nights where we monitored the day roost, naive bats entered the day roost less than 1 h before in 6 out of 25 recruitment events. In three cases the recruiter was recorded in the day roost within 10 min of the recruited bat. Furthermore, our data probably underestimate the degree of recruitment at the day roost. Females that recruited while flying around the day roost, analogous to the aerial displays of communally roosting birds (e.g. Richner & Heeb 1996), could not be detected with our method. Recruitment at the day roost has also been found in evening bats that transfer information about food (Wilkinson 1992).

(c) *Evaluation of the different hypotheses explaining information transfer*

The information centre hypothesis (Ward & Zahavi 1973) requires that colony members alternate when recruiting each other. Such reciprocity has been found in cliff swallows (Brown 1986), ravens (Marzluff *et al.* 1996) and evening bats (Wilkinson 1992). However, like most other studies on information transfer (Galef & Giraldeau 2001) we found no evidence for reciprocity in Bechstein's bats. Females that explored and recruited intensively were not more often recruited than bats that explored and recruited little. Thus, the information centre hypothesis seems not to apply to female Bechstein's bats.

One explanation for the absence of reciprocity during recruitment would be kin selection. However, kin selection is unlikely to explain information transfer about roosts in Bechstein's bats because females did not preferentially recruit relatives.

Instead, both the two-strategy and the recruitment centre hypothesis can explain why bats transfer information to unrelated colony mates that do not reciprocate. Both hypotheses assume that recruiters receive grouping benefits (Richner & Heeb 1996). The recruitment centre hypothesis predicts grouping benefits at the novel resource, whereas the two-strategy hypothesis expects benefits to occur at the communal roost. In Bechstein's bats, social thermoregulation could be such a grouping benefit. By recruiting colony mates, females probably raise the roost temperature, which appears to be important for successful reproduction (Kerth *et al.* 2001*a*). Because the same grouping benefits apply to the day roost and the novel box, we cannot discriminate between the recruitment centre and the two-strategy hypothesis in our study.

5. CONCLUSION

Communal roosting provides female Bechstein's bats with the ability to exchange information about novel roosts, a resource on which they strongly depend. However, colony members probably differ in what they gain from coloniality. Females, which explore little, are likely to benefit directly from information transfer, whereas individuals that explore and recruit intensively probably augment their colony by generating communal knowledge. We expect that such cooperation is stable, because females serving as 'scouts' receive grouping benefits such as social warming (see Clutton-Brock 2002).

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