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Group decision making in fission–fusion societies: evidence from two-field experiments in Bechstein's bats

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Group decisions are required when group coordination is beneficial, but individuals can choose between alternatives. Despite the increased interest in animal group decision making, there is a lack of experimental field studies that investigate how animals with conflicting information make group decisions. In particular, no field studies have considered the influence of fission–fusion behaviour (temporary splitting into subgroups) on group decisions. We studied group decision making in two wild Bechstein's bat colonies, which are fission–fusion societies of stable individual composition. Since they frequently switch communal roosts, colony members must regularly make group decisions over where to roost. In the two-field experiments, we provided marked individuals with conflicting information about the suitability of potential roosts. We investigated whether conflicting information led to group decisions that followed a 'unanimous' or a 'majority' rule, or increased colony fission. Individual behaviour suggests that bats considered both their own information and the behaviour of others when deciding where to roost. Group decisions about communal roosts reflected the information available to a majority of the bats roosting together, but conflicting information led to an increased fission in one colony. Our results suggest that fission–fusion societies allow individuals to avoid majority decisions that are not in their favour.

Keywords: group coordination; information transfer; *Myotis bechsteinii*; roost selection; social behaviour

1. INTRODUCTION

Animals profit most from sociality if they coordinate their behaviour, e.g. during movement, baby sitting, sentinel behaviour and foraging (Whitehead 1996; Clutton-Brock *et al.* 1999; Wilson 2000; Franks *et al.* 2002; Couzin & Krause 2003). Since group coordination often requires group decisions, group decision making is likely to be important in most animal societies, as it is in human societies (List 2004; Conradt & Roper 2005). Several recent theoretical models have investigated how group members should make group decisions to optimize their fitness (Conradt & Roper 2003; List 2004; Couzin *et al.* 2005), but surprisingly little is known about how group decisions are actually made in natural situations. Group decision making in animals is probably best documented in social insects in the context of group movements (Franks *et al.* 2002; Lioni & Deneubourg 2004). However, with the exception of honeybees (*Apis mellifera*; Seeley & Buhrman 1999, 2001) and African elephants (*Loxodonta africana*; McComb *et al.* 2001), we are unaware of field studies that have manipulated individual information and investigated the effect on group decision making. Moreover, most theoretical models and empirical studies dealing with group decisions have focused on consensus decisions, where the group stays together (Conradt & Roper 2005). In fission–fusion societies, found in various mammals (Kerth & König 1999), individuals could avoid group decisions that are not in their favour by temporarily splitting into subgroups. How this possibility affects group decisions in animal societies is largely unknown.

Here, we present an experimental field study on group decision making in female Bechstein's bats (*Myotis bechsteinii*), which live in fission–fusion societies. Bechstein's bats rear their offspring communally in colonies consisting of 10–45 adult females. Benefits of sociality include social thermoregulation and opportunities for cooperation (Kerth 2006). Colony members frequently switch communal roosts (tree cavities and bat boxes) and transfer information to each other about suitable roosts (Kerth & König 1999; Kerth & Reckardt 2003). Roost switching probably allows females to avoid parasites and select optimal roosting temperatures (Kerth *et al.* 2001; Reckardt & Kerth 2006). Despite their stable individual composition (Kerth *et al.* 2002), colonies regularly split into subgroups using separate roosts (Kerth & König 1999). Switching communal roosts requires the members of a colony to decide every night whether or not to abandon a roost and, if so, where to roost next. Bechstein's bat colonies therefore face similar challenges to honeybee and ant colonies moving to a new nest site (Franks *et al.* 2002), but at a much higher frequency.

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We manipulated the information the Bechstein's bats have about the suitability of a roost and studied how conflicting information affected group decisions about communal roosts. We predicted that if group decisions follow a 'unanimous rule' and require the agreement of all individuals, colonies should not use roosts that some of their members have experienced as unsuitable. If group decisions follow a 'majority rule', we predicted that even bats with the information 'unsuitable' would use a roost if most of the bats roosting there had found it to be suitable. Finally, if the individuals follow their own information instead of seeking a group agreement (consensus), we predicted increased colony fission when some bats chose a roost found unsuitable by others. Permanent roost monitoring using automatic readers allowed us to record the following and the roosting behaviour of individual bats implanted with microchips (passive-induced-transponder (PIT)-tags; Kerth & Reckardt 2003). In our first experiment, we provided individuals with conflicting information about the suitability of new roosts (bat boxes) placed in the home ranges of two colonies. In our second experiment, we provided members of one colony with conflicting information about the suitability of their current roost.

2. MATERIAL AND METHODS

We conducted our study in the home ranges of two Bechstein's bat colonies (Blutsee and Guttenberg2) that are found in adjacent deciduous forests, near the city of Würzburg (Germany). Adult females in both the colonies were individually marked with PIT-tags (Kerth & Reckardt 2003). The number of marked bats present throughout the study period was 10 for Blutsee and 34 for Guttenberg2. From 1 May to 27 August 2004, we checked daily for the presence of bats in 126 bat boxes ('2FN', Schwegler, Germany) distributed in Blutsee's home range and 74 boxes distributed in Guttenberg2's home range (both the areas are about 0.5 km^2). All the boxes were checked once more on 2 days in mid-September. Since the entrances of the bat boxes face the ground, roosting bats can be seen with a torch without opening the box. If bats were observed in a box, we identified individuals during their emergence in the evening using automatic PIT-tag readers. Readers recorded and stored PIT-tag numbers, times and dates of bats passing the antenna in the box's entrance area (Kerth & Reckardt 2003).

In our first experiment, we placed new bat boxes (22 for Blutsee; 17 for Guttenberg2) in the home range of each colony 20–50 m away from boxes used in the previous years. All new boxes were of the same type used by the colonies for many years. To provide individuals with different information about the suitability of the same box, we established the following procedure for 16 of the 39 new boxes (10 for Blutsee; 6 for Guttenberg2; figure 1). After positioning a box, its interior entrance was initially left open, making the box suitable for roosting. After 2–4 colony members had visited at night, the interior entrance of the box was blocked with wire mesh. This manipulation mimicked a roost that cannot be used by bats owing to nesting Hymenoptera, birds or rodents. Each box remained unsuitable until 1–4 colony members had visited it at night, whereupon the wire mesh was removed, making the roost suitable again. Depending on their arrival time at a box, bats could gain the information 'suitable' or 'unsuitable'. The remaining 23 new boxes served as controls and were never blocked. Activity at new boxes was monitored every night, from the day of their establishment. We defined a single trial (monitoring of one box) as completed when the box had been used as a day roost for the first time. After the bats had abandoned the box, we removed the reader and attached it to a newly placed box. This procedure resulted in different numbers of new boxes in the two colonies.

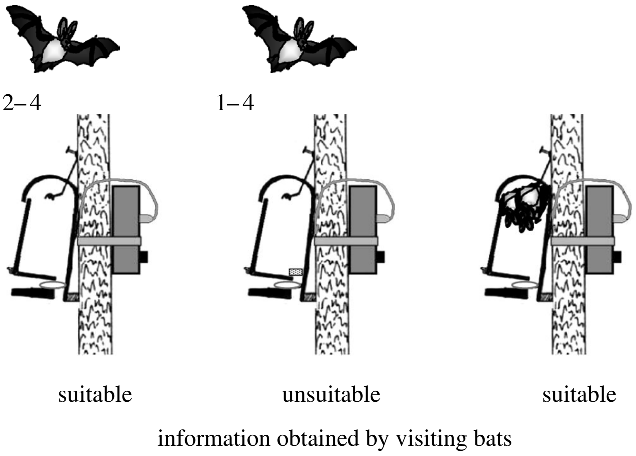

Figure 1. Treatment of 'blocked' boxes in experiment 1 (see text for details). The interior entrance of the box was temporarily blocked with a wire mesh (dotted bar). Antennae (grey loop) placed in the entrance area and connected to automatic PIT-tag readers (grey box) allowed identification of arriving bats.

We determined the information status of all the bats roosting in a new box based on the information they had obtained on their last nightly visit before using the box as a day roost. We also noted how often bats used a new day roost naively, without visiting it before on at least one night. To quantify the information transfer, we determined when experienced individuals returned at night with a naive colony mate to a new box. We defined information transfer as the visit of one or more naive bats to a box within not more than 3 min of a bat that had entered the box on a previous visit (Kerth & Reckardt 2003). A colony can only learn that a given box is unsuitable if at least one bat attempts to enter it while blocked and subsequently transfers this information. In analysing the effect of conflicting information, we therefore excluded those boxes that received no visits during the blockage.

In our second experiment, we provided the females of Guttenberg2 with conflicting information about the suitability of their current roost. During the nightly emergence of the bats, we briefly disturbed those individuals that had not left the box yet, by making scratching and rustling noises (including ultrasound) on the outer surface of the box using aluminium foil attached to a stick. Over 12 nights, we disturbed varying proportions (27–100%) of bats that roosted together during the previous day. As the boxes had been monitored with PIT-tag readers the previous night, we knew how many marked bats were present before they started to emerge on the night we carried out a trial. During the emergence, we counted the leaving bats with a night-vision scope and disturbed the box when a previously defined proportion remained, alternating between disturbing a majority and a minority. From the PIT-tag reader, we later determined which bats had experienced the noise and which reused the box the next day. To minimize any costs due to induced roost switching, all trials were performed outside the nursing season and at the most twice a week, which is less than the normal roost-switching frequency.

We used Mann–Whitney U-tests, χ^2-tests and Spearman's rank correlations for independent data and Wilcoxon matched-pair tests for related data. All p-values are two tailed and we provide medians or ranges. The small sample sizes in Guttenberg2 sometimes allowed only descriptive statistics. In these cases, we focused on Blutsee for statistical tests or pooled the data for both the colonies if they showed the same range and direction.

3. RESULTS

(a) *Group decisions about new communal roosts (experiment 1)*

(i) *Fission–fusion and roosting behaviour*

Both the colonies frequently switched roosts and regularly split into subgroups. Blutsee females ($n=10$) stayed a median of 3.2 days in a roost while Guttenberg2 females ($n=34$) stayed 1.8 days (Mann–Whitney U-test: $U=0.0$, $p<0.001$). During the roost switching, Blutsee split less often than Guttenberg2 (on 30 out of 104 days versus on 45 out of 72 days; χ^2-test: $\chi_1^2=19.7, p<0.001$) and formed fewer subgroups (range: 2–3 versus 2–4; $U=445.0$, $n_1=30$ days, $n_2=45$ days, $p<0.01$).

The colonies found 35 of the 39 new boxes, using 30 as day roosts (Blutsee, 18 out of 22; Guttenberg2, 12 out of 17). Females needed a median of 1–2 weeks to find a new box and another 1–3 weeks to use it as a day roost. Continuously monitored blocked and unblocked boxes did not significantly differ in the number of days between discovery and first use as a roost (Blutsee: 9 versus 6; $U=20.5$, $n_1=6$, $n_2=9$, $p=0.44$; Guttenberg2: 21 versus 18, $n_1=3$, $n_2=4$; excluding days on which boxes were blocked and thus could not be used as roosts). Each of the colonies also roosted in 24 old boxes, introduced in the previous years. After choosing a roost, individuals spent significantly more days in new than old boxes (Wilcoxon matched-pair test; Blutsee: 4.0 versus 2.2, $n=10$, $Z=2.8$, $p<0.01$; Guttenberg2: 3.0 versus 1.9, $n=34, Z=4.8, p<0.001$).

(ii) *Individual nightly visiting behaviour at temporarily blocked boxes*

Individuals often visited boxes on several nights before using them as day roosts. The visiting behaviour of the bats depended on the information they obtained on an earlier night. Individual bats returned somewhat more often (in 83% versus 63% of the cases; $U=145.5$, $n_1=27$, $n_2=14$, $p=0.23$) and significantly earlier (after 2 versus 3 days; $U=53.0$, $n_1=23$, $n_2=9$, $p=0.03$) after obtaining the information 'suitable' than 'unsuitable'. As a result, 79% of the 101 visits with the information 'suitable' resulted in a revisit on a later night, but only 54% of the 26 visits with the information 'unsuitable' ($\chi_1^2=6.9, p<0.01$; visits that occurred on the night immediately before a box was used as a day roost were excluded, as no further night was available for a revisit).

We identified 27 information-transfer events at temporarily blocked boxes (arrival of a naive bat within 3 min of an experienced bat). The number of such events per box did not significantly differ between blocked and unblocked boxes (Blutsee: 2.0 versus 3.0; $U=21.5$, $n_1=6$, $n_2=9$, $p=0.51$; Guttenberg2: 5.0 versus 2.0; $n_1=3$, $n_2=4$). In 24 cases, a naive bat arrived with an experienced bat with the information 'suitable'. Of the remaining three cases, two (one in each colony) involved a naive bat following an experienced bat with the information 'unsuitable', while in the remaining case, the naive bat followed two experienced bats with conflicting information. The 11 bats that obtained both the types of information and returned with at least one naive colony mate were followed to a box significantly more often when they had the information 'suitable' than 'unsuitable' (1 versus 0; $Z=2.4$, $p<0.02$). This effect remained after we had corrected for differences in the number of nights for which each bat had the information 'suitable' and 'unsuitable' (n information transfer events/n nights with the respective information: 3% versus 0%; $Z=2.0$, $p=0.05$).

(iii) *Group decisions about communal day roosts*

Members of the two colonies roosted in 11 of the 15 boxes visited while they were blocked (including the two boxes that were occupied in September, after we had stopped our continuous box monitoring). This ratio is not significantly different from 16 boxes used out of the 17 that were never experienced as unsuitable ($\chi_1^2=2.6$, $p>0.10$; three boxes were excluded because they were occupied by other animals and thus unavailable to the bats).

Fewer Blutsee females roosted in previously blocked than unblocked boxes (3.5 versus 9.0; $n_1=6$, $n_2=9$, $U=11.0$, $p<0.06$), while in Guttenberg2 more bats roosted in previously blocked than unblocked boxes (12.0 versus 5.0, $n_1=3$, $n_2=4$). To correct for the seasonal effects on box occupation (Kerth *et al.* 2001), we compared group sizes in the previously blocked and unblocked boxes with average group sizes in roosts occupied 5 days before and after a new box was occupied. Significantly fewer Blutsee females roosted in previously blocked boxes when compared to the average group sizes (3.5 versus 7.1; $Z=2.2$, $n=6$, $p<0.03$), while group sizes in unblocked boxes were similar to that of the average (9.0 versus 8.2; $Z=0.5$, $n=9$, $p=0.59$). In Guttenberg2, group sizes in the three previously blocked boxes were slightly higher than average group sizes (12.0 versus 10.2). The difference between the colonies was also evident in the roosting behaviour of bats that had visited temporarily blocked boxes at night. Among those females, the ratio of roosting to non-roosting bats was significantly smaller in Blutsee than in Guttenberg2 (21–25 versus 26–6; $\chi_1^2=10.0$, $p<0.001$). In the Blutsee colony, this ratio was similar for bats with the last information 'unsuitable' and 'suitable' (previously blocked boxes: 3–5 versus 18–20; $\chi_1^2=0.3$, $p>0.5$), but significantly smaller in previously blocked than in unblocked boxes (21–25 versus 51–16; $\chi_1^2=11.0, p<0.001$).

In both the colonies, we regularly observed bats using a new communal roost naively, without having visited it previously at night. The proportion of experienced bats present on the first day of roosting was similar in previously blocked and unblocked boxes, but higher in Blutsee than in Guttenberg2 (83% versus 67%; $U=25.0$, $n_1=15$, $n_2=7$, $p=0.05$). In both the colonies, more bats roosting in previously blocked boxes had obtained the information 'suitable' than 'unsuitable' on their last visit (5 versus 1 bat; $n=9$ boxes, $Z=2.5$, $p<0.02$). However, this ratio was similar in roosting bats and those that had visited the temporarily blocked boxes at night, but did not roost in them (41–6 versus 26–6; $\chi_1^2=0.5$, $p=0.50$).

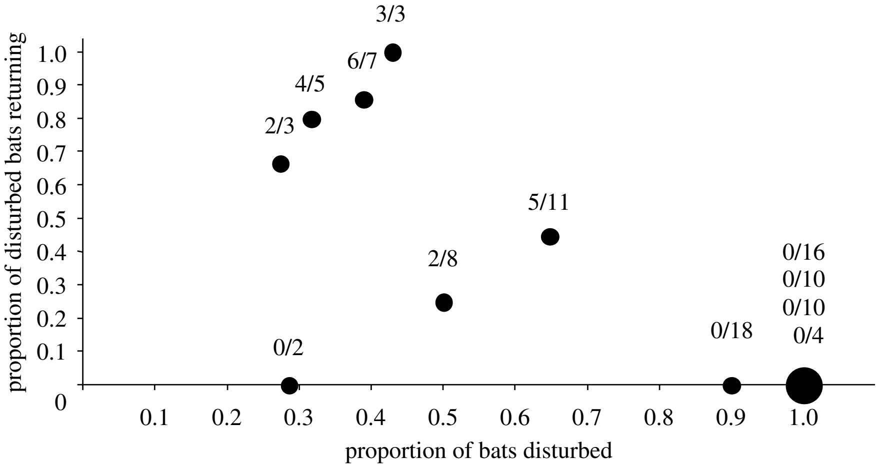

Figure 2. Proportion of disturbed bats reusing a day roost in relation to the proportion of bats that had been disturbed during their emergence from the roost the evening before. The large point represents four nights, where all the bats had been disturbed. The ratio given above each point shows the number of disturbed bats that returned to that box in relation to the total number of disturbed individuals.

(**b**) *Group decisions about abandoning an established communal roost (experiment 2)*

In five of the six cases in which we had disturbed most or all (65–100%) of the bats that had not yet left their roost during the nightly emergence, none of the disturbed bats returned the next day. In contrast, in five of the six cases in which we disturbed not more than half (27–50%) of the bats, several or all of the disturbed bats returned. Twenty-six bats experienced both a disturbance and no disturbance on different nights. These females returned significantly less often to the roost after being disturbed than after not being disturbed (in 0% versus 58% of the cases; $Z=3.7$, $n=26$, $p<0.001$). This shows that our acoustic disturbance was effective. Moreover, the bats did not habituate to the disturbance, as the proportion of returning bats did not increase during the 12 successive tests (Spearman's rank correlation: $r_s=0.04$, $n=12$, $p=0.91$).

Individual information did not completely explain the behaviour of the bats. A significantly higher proportion of disturbed bats abandoned a roost when a majority or all bats in the roost experienced the disturbance, compared to cases when at most 50% had been disturbed (77% versus 0%; $U=4.5$, $n_1=6$, $n_2=6$, $p<0.03$). Overall, when a bigger proportion of the bats in a roost were disturbed, fewer of the disturbed bats returned to the roost ($r_s=-0.65$, $n=12$, $p<0.03$; figure 2). In the eight cases, where individuals differed in their information since we had disturbed only some of them (27–90%), this correlation was still negative but no longer significant ($r_s=-0.26$, $p=0.53$). However, significantly more disturbed bats returned when more undisturbed bats also returned ($r_s=0.90$, $n=8$, $p<0.01$). During our tests, some individuals had been disturbed more often than others. To correct for individual effects, we analysed the behaviour of the 17 bats that had been disturbed both with a majority and a minority of their roost mates on different nights. These bats returned significantly more often to the roost when a minority of their roost mates had also been disturbed, compared to a majority (in 66% versus 0% of the cases; $Z=3.1$, $n=17$, $p<0.01$).

4. DISCUSSION

Our two-field experiments suggest that female Bechstein's bats considered both their own information and the behaviour of their colony mates when deciding where to roost. This was particularly evident in our second experiment. When disturbed, the same individuals that typically abandoned a roost if the majority of their roost mates were also disturbed tended to return if only a minority were disturbed. This confirms that female Bechstein's bats make group decisions (Conradt & Roper 2005). Moreover, the frequent roost switching in combination with the fast discovery of, and preference for, new boxes observed in our first experiment underline the importance of frequent group decisions about communal roosts.

(**a**) *Which rules are used in decisions about communal roosts?*

Our data are consistent with group decisions following a majority rule, but not a unanimous rule. In our first experiment, the majority of bats roosting for the first time in a new box had the prior information that the box was suitable. Nevertheless, we regularly observed bats using a new communal roost naively, without having visited it previously at night, and in five out of nine previously blocked boxes, one or two bats moved in even though their last information was that the box was unsuitable. Unfortunately, in the first experiment, we could not test whether a majority of bats are required to make group decisions about communal roosts. For practical reasons, we could only provide a minority of bats with the information that a box was unsuitable. Waiting until a majority experienced a box as unsuitable would have taken too long a period to allow that box to be occupied before the bats left our study site in autumn. Revisits of bats to previously blocked boxes, once those boxes became suitable again, further reduced the number of bats with the last information 'unsuitable'. Despite this, our second experiment provides strong evidence for majority decisions, since disturbed bats were more likely to return to a roost if a majority of their roost mates had not been disturbed.

Our first experiment suggests that temporary group fission allows individuals even in a stable society to avoid majority decisions that are not in their favour. The smaller group sizes observed in the previously blocked boxes in the Blutsee colony may reflect that individuals resist the group decision to use a roost if their own experience tells them it is unsuitable. The generally higher degree of colony fission in Guttenberg2 may be the reason why such an effect was not observed in this colony. Increased fission could be an adaptive response of Guttenberg2 females to the large size of their colony, if the optimal number of bats per roost is similar for both the colonies. Alternatively, it might reflect greater difficulties in reaching an agreement on a single roost when there are more bats in a colony. In ants and other arthropods, the tendency to form more than one foraging chain or to aggregate at more than one resource presented in an experimental arena is often a function of group size and can be explained by simple aggregation rules and self-organization principles (Lioni & Deneubourg 2004).

(**b**) *How many bats are involved in the decision about a communal roost?*

Two pieces of evidence suggest that in our first experiment, most of the bats roosting together were involved in the decision-making process. First, most of the females roosting in a new box had visited it before. Second, 80% of Blutsee females revisited a box with a naive colony mate. The percentage of experienced females that returned with a naive colony mate was much smaller in Guttenberg2 (24%), but this may be largely a consequence of the low number of occupied boxes in relation to the large size of this colony. In contrast, in honeybee and ant colonies, only a small subset of the members inspect a new nest site and are involved in the decision-making process (about 5% in honeybees and one-third in ants; Seeley & Buhrman 1999; Pratt *et al.* 2002). In African elephants, a single old female leads a group and decides with which non-group members to interact (McComb *et al.* 2001). Group decisions in primates (Byrne 2000) and fishes (Couzin & Krause 2003) may also involve only a small part of the group, whereas in some ungulates, they may involve all the group members (Wilson 2000; Conradt & Roper 2005).

Two reasons could explain why most bats visited a box before they used it as a roost. First, conflicting interests may prevent bats from relying entirely on social information, as this only makes sense if the requirements of individuals are similar (Danchin *et al.* 2004). Unlike in most eusocial insects, individual interests can differ in Bechstein's bats due to the genetic and demographic heterogeneity of their colonies (Kerth *et al.* 2002). For example, lactating females prefer warmer roosts than non-reproductive ones (Kerth *et al.* 2001). Second, by relying on many inspecting individuals, a colony may ensure that the best roost is chosen (Franks *et al.* 2002, 2003; Conradt & Roper 2003; Seeley & Visscher 2003; List 2004; Simons 2004). Since Bechstein's bat colonies are small compared to ant and honeybee colonies, more colony members may be required to make an optimal decision (Couzin *et al.* 2005). This would also explain why higher fractions of the colony inspected a roost and transferred information in the Blutsee colony than the three-times larger Guttenberg2 colony. Our limited sample size prevented us from further investigating the influence of colony size and structure on group decision making. Future studies with more Bechstein's bat colonies are necessary to understand how individual bats and colonies as a whole differ in their decision making about communal roosts. Bats in general provide challenging opportunities for studies on group decision making, since the diversity of their social systems allows comparative analyses.

As a consequence of the nocturnal activity of bats, we know little about the mechanisms involved in the group decision making about communal roosts. However, following each other to potential roosts at night (Kerth & Reckardt 2003) and copying the choices of others (Laland 2004) while flying in a group around a roost in the morning (swarming) are likely mechanisms by which group decisions could be made. Faster and more frequent revisits by the experienced females to suitable boxes, as observed in our first experiment, could provide a simple mechanism leading to increased arrival rates of naive colony members whenever a suitable roost is found. Such a mechanism would work regardless of whether the information transfer is an active process or based on passive following.

5. CONCLUSIONS

Our experimental field study shows that even in situations where individuals have conflicting information, group decisions can reflect the preferences of a majority as predicted by models of group decision making (Conradt & Roper 2003; Couzin *et al.* 2005). However, we have to keep in mind that such models may not completely apply to Bechstein's bats, since they typically do not allow splitting into subgroups, or do not consider temporary fission as an adaptive outcome of group decisions. Temporary splitting into subgroups is widespread among social animals and can be adaptive (Kerth & König 1999). Hence, fission–fusion societies deserve a closer look, both by empiricists and theoreticians, if we are interested in understanding the evolution of group decision rules across a wide range of taxa.

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