

Original Article

A call-and-response system facilitates group cohesion among disc-winged bats

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Acoustic signals are important in maintaining group cohesion, particularly in highly mobile species. For these signals to facilitate group cohesion, individuals must be able to recognize, and respond to, calls emitted by group members. In this study, we document the use and recognition of complementary contact calls in Spix's disc-winged bat (*Thyroptera tricolor*), a species known to form very stable social groups despite using an extremely ephemeral roosting resource. This bat uses 2 sets of calls: "inquiry," which are emitted by flying bats that are seeking roosts or group mates, and "response," which are produced in reply to an inquiry call by individuals that have already located a roost. Here, we test if bats are capable of discriminating between the inquiry and response calls of group and nongroup mates using playback experiments. Results show that flying bats can discriminate between the inquiry and response calls emitted by group and nongroup members and can maintain contact preferentially with the former. Roosting bats, however, exhibited no preference for group over nongroup members and thus responded indiscriminately. We argue that differences in how individuals respond to calls from group and nongroup members may be partly attributed to the costs associated with flight and the potential benefits of recruiting roost mates. *Key words:* communication, contact call, disc-winged bat, group cohesion, *Thyroptera tricolor*. [*Behav Ecol*]

INTRODUCTION

Groups of individuals that continuously associate for long periods of time have the highest probability of evolving cooperative interactions (Nowak 2012), and thus could derive the greatest benefits from group living (Mullen and Copper 1994; Huang 2009). To facilitate group cohesion, group members must adopt several strategies that increase the chances of continuously encountering the same set of individuals, such as the use of a small home range (Sugiura et al. 2011; Foster et al. 2012), persistent use of specific foraging or resting areas (Caccamise et al. 1997; Braune et al. 2005), or the use of olfactory and acoustic signals to coordinate movement or announce location (Radford 2004; Kondo and Watanabe 2009; Arnold and Wilkinson 2011; Bousquet et al. 2011). However, communication can only facilitate group cohesion if individuals can recognize, and properly respond to, signals emitted by group members from signals emitted by nongroup members. Recognition of group from nongroup signals becomes more difficult with increasing mobility, overlap of territories, and greater group size, as the number of individuals that need to be identified increases (Bradbury and Vehrencamp 2011). In this case, selection favors the evolution of complex signals that can encode a greater amount of information (Pollard and Blumstein 2011), coupling of signal modalities (Partan and Marler 2005), and the use of various context-dependent, and structurally unique, acoustic signals (McComb and Semple 2005).

Acoustic signals are widely used by a diversity of organisms to maintain contact with their group, family, or mating partner (Marler 2004; Bradbury and Vehrencamp 2011). These so-called "contact calls" encode various kinds of social information, including not only location but also identity and group membership, which allows individuals from the same group to remain cohesive while recognizing potential competitors or intruders (Kondo and Watanabe 2009). In most species, only 1 type of contact call has been identified, but some species exhibit contact calling systems that involve multiple social calls, each emitted in a specific behavioral context. Meerkats constantly emit "close" calls while locating prey within a foraging patch (Townsend et al. 2010), but use "movement" calls when switching to a new patch (Bousquet et al. 2011). African elephants employ a similar calling system in which separated individuals use "contact" calls until rejoined and emit a "let's go" rumble to announce departure from a feeding or resting site (Poole et al. 1988). These 2 types of calls in meerkats and elephants thus appear to complement each other and facilitate group cohesion, as they indicate the position of other group members while providing information regarding a substantial change in location. Playback experiments demonstrate that elephants, but not meerkats, use the information encoded in 1 type of contact call for discriminating group from nongroup members (McComb et al. 2000; Townsend et al. 2010). Similarly, contact calls in other species are sufficiently unique to allow individual or group recognition, and individuals typically respond more strongly to calls of close kin or group members during playback experiments (Kondo and Watanabe 2009).

Bats are a particularly interesting group of mammals for testing hypotheses regarding the use of contact calls for maintaining group cohesion, as they are often very gregarious and extremely mobile and nocturnal, making visual and olfactory communication ineffective for locating group mates

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over relatively long distances (Bradbury and Vehrencamp 2011). In fact, studies show that acoustic communication is a highly developed sensory modality in bats, and many species exhibit a diverse repertoire of social calls that are used in several contexts (Pfalzer and Kusch 2003). Unfortunately, social communication is still a poorly studied aspect of bat social behavior although there is a growing number of studies particularly focusing on the topic of contact calling systems (e.g., Boughman 1997; Wilkinson and Boughman 1998; Goymann et al. 1999; Pfalzer and Kusch 2003; Carter et al. 2008; Chaverri et al. 2010; Schöner et al. 2010; Furmankiewicz et al. 2011; Carter et al. 2012). However, we lack evidence on the role of acoustic communication in social cohesion, the types of social information encoded in contact calls, and the mechanisms responsible for recognition among group members in most species of bats. Studies available on the topic suggest that bats typically use low frequency calls to maintain contact with group members while foraging or during situations of social isolation (Wilkinson and Boughman 1998; Goymann et al. 1999; Carter et al. 2008). In some species, these calls encode information regarding individual and group identity, and individuals can discriminate between group and non-group members based solely on call structure (Boughman and Wilkinson 1998; Carter et al. 2008). Despite this knowledge, we still have very limited information about the behavioral outcomes of producing contact calls and specifically how individuals physically relocate each other with such a communication system.

In this study, we document the use and recognition of contact calls in Spix's disc-winged bat (*Thyroptera tricolor*), one of the few species of bats known to use an extremely ephemeral roosting resource that becomes unsuitable for further use every day. This bat uses the furled leaves of members of the order Zingiberales, such as heliconias, which are available for periods ranging from 5 to 31 h (Findley and Wilson 1974; Vonhof and Fenton 2004). Despite constant roost switching, research has shown that *T. tricolor* forms very stable social groups whose composition remains unchanged for several years (Vonhof et al. 2004; Chaverri 2010). Thus, given the ephemeral and often sparse nature of furled leaves, *T. tricolor* faces the difficult daily task of locating roosting sites while maintaining group cohesion, which suggests that acoustic communication plays a major role in maintaining these long-lasting associations.

Recent studies have demonstrated that *T. tricolor* uses specific vocalizations to help members of a group find a roost site once one has been located (Chaverri and Gillam 2010; Chaverri et al. 2010), and field observations suggest that individuals also emit calls during flight to maintain contact with group mates (Chaverri G, Gillam EH, personal observation). Two sets of calls have been recorded, "inquiry," which are emitted by flying bats that are apparently seeking suitable roost sites or group mates, and "response," which are produced in reply to an inquiry call by individuals that have already located a roost (Figure 1, Chaverri et al. 2010). Inquiry and response calls have strong individual signatures and weak group signatures, suggesting that *T. tricolor* may be able to discriminate between the calls of group and nongroup members based on familiarity (Gillam and Chaverri 2012). Notwithstanding, there is still no evidence that bats use the information in these calls to maintain long-lasting affiliates while avoiding extra-group interactions.

The goal of this study is to determine, using simple playback experiments in a natural setting, if bats are capable of discriminating between the inquiry and response calls of group and nongroup mates, and to address the question of which type of social call, inquiry or response, is responsible for maintaining intragroup cohesion and extra-group segregation. Based

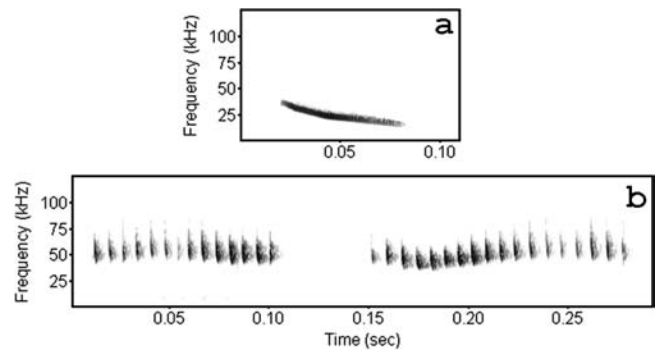


Figure 1
Sonograms that depict the inquiry (a) and response calls (b) of *Thyroptera tricolor*.

on our previous findings of the existence of social calls that apparently facilitate group cohesion (Chaverri et al. 2010) and call signatures that may allow individual recognition (Gillam and Chaverri 2012), this study represents the next step toward understanding how *T. tricolor* constantly relocates the same set of roost mates despite switching roost sites every day. Because response calls appear to function in attracting other individuals to roost sites, whereas inquiry calls allow flying individuals to join other individuals at roost sites and during flight, we predict that 1) roosting bats will produce more response calls when presented with the inquiry calls of group members versus nongroup members; 2) flying bats will more frequently enter leaves from which response calls of group members are being emitted; and 3) flying bats will preferentially approach inquiry calls of group members. To the best of our knowledge, this is the first study to use playback experiments to examine the role of a set of acoustic signals used in different contexts on intragroup cohesion and extra-group segregation.

METHODS

Experiments were conducted from 6 December 2011 through 26 February 2012 at La Gamba, Piedras Blancas National Park, southwestern Costa Rica. During the first month of field work, we surveyed the area for potential roost sites by locating furled leaves with a diameter of opening ranging between 3.5 and 27 cm, as this is the preferred size range of leaves selected for roosting by *T. tricolor* (Vonhof and Fenton 2004). Once a roost was located, we captured bats by pinching the top of the leaf and directed them into a cloth-holding bag; individuals caught in the same leaf were considered to belong to the same discrete, stable social group (Vonhof et al. 2004; Chaverri 2010). Bats were fitted with individually numbered metal wing bands, sexed, aged, and their reproductive condition assessed.

For all individuals and groups captured, we recorded inquiry and response calls within a small portable flight cage (3 × 3 × 2 m). To record inquiry calls, we released a single individual within the cage and kept the rest in a waterproof bag to avoid acoustic interference. Calls were recorded with an Avisoft condenser microphone (CM16, Avisoft Bioacoustics, Berlin, Germany) through an Avisoft UltraSoundGate 116Hm onto a laptop running Avisoft-Recorder software (sampling rate 384 kHz, 16-bit resolution). This process was repeated for all group members.

Because bats only produce response calls after an inquiry call has been emitted (Chaverri et al. 2010), we broadcast previously recorded inquiry calls to elicit and record response

calls. We band-pass filtered these inquiry calls and broadcast them through an UltrasoundGate Player to a broadband loudspeaker (Ultrasonic Omnidirectional Dynamic Speaker Vifa, Avisoft Bioacoustics) to single bats placed inside a furled leaf. To prevent the bats' escape, we placed a circular piece of mesh in the upper portion of the leaf. We placed the microphone near the entrance of the furled leaf, and response calls were recorded onto a laptop computer following the same procedure for recording inquiry calls.

To determine if bats are capable of discriminating between the social calls of group and nongroup mates, we recaptured individuals and conducted 3 sets of playback experiments in a large flight cage ($10 \times 4 \times 3$ m). Experiment 1 allowed us to determine if roosting bats produced more response calls in reply to inquiry calls emitted by group mates versus nongroup mates. Experiment 2 addressed the question of whether flying bats preferentially enter a furled leaf from which a response call from a group member was emitted. Experiment 3 addressed the question of whether flying bats preferentially approach inquiry calls emitted by group members. All bats were maintained in cloth bags in shaded and well-ventilated areas 25 m away from the flight cage while experiments were conducted on other individuals. We provided mealworms (*Tenebrio molitor*) and water to individuals after each experiment and also before releasing them. All protocols for capturing and handling bats were approved by the Costa Rican government (permit # 002-2011-SINAC) and by Boston University's Institutional Animal Care and Use Committee (approval number 11-033).

Experiment 1 was conducted by placing a bat inside a furled leaf and preventing its escape using a circular piece of mesh in the upper portion of the leaf. Once the bat settled in the leaf, we began our experiment by broadcasting 10 inquiry calls in random order, 5 from group members and 5 from nongroup members. One call was broadcasted every 10 s, and each session lasted 100 s. Calls emitted by bats within the roost were recorded onto a laptop computer as described above. If no response calls were recorded, we repeated the experiment once more after a 1-min interval of silence. In our experiments, we counted the number of response calls produced after broadcast of every inquiry call to determine if bats responded more to inquiry calls produced by group members. Because we often did not have 5 calls from different group members and to avoid problems with pseudoreplication (McGregor 2000), we calculated the average number of response calls to inquiry calls from group and nongroup members for each individual. The difference in the number of response calls to inquiry calls from nongroup and group members was assessed using a Wilcoxon signed ranks test in SPSS v. 20 (IBM Corporation, New York).

Experiment 2 presented flying individuals with the choice of entering tubular leaves from which group or nongroup response calls were being broadcast. For this, we placed 2 identically shaped transparent plastic tubes resembling furled heliconia leaves inside the flight cage at a distance of 7 m from each other and 1.5 m from the wall of the flight cage. These artificial structures are readily used by *T. tricolor* (Chaverri G, Gillam EH, personal observation); based on our knowledge of the behavior of this species, we decided that this would be the best way to make roost selection solely based on the broadcasted calls and not on the quality of the available resource (furled leaf). For the experiment, we placed a loudspeaker in a sound-proof box made of fibrolite that was reinforced with plywood and mounted below the tubular structure. The broadcasted sound was channeled through a plastic funnel to simulate a roosting bat's calling behavior as accurately as possible. At the beginning of the experiment, we released the experimental bat at the center of the flight cage

and started broadcasting different bouts of response calls at each artificial leaf (Chaverri et al. 2010). Paired bouts contained the same number of response calls. One loudspeaker repeatedly broadcast a bout of response calls from a group member, whereas the other repeatedly broadcast a bout from a nongroup member. The first and second bouts of response calls were broadcast after a single bat was released and when it was flying in the middle of the cage; subsequent broadcasts were emitted approximately every 5 s after the end of the bout regardless of where the bat was located. A preference for a particular call (group vs. nongroup) was determined by the decision to enter a given roost within 5 min of the beginning of the experiment. After each successful experiment (i.e., bat entered a leaf within 5 min), we replaced the plastic leaves with new ones to avoid problems with preferences based on olfactory cues. After an unsuccessful experiment (i.e., the bat did not enter a leaf within 5 min), we allowed the bat to rest in the cloth bag away from the flight cage while we conducted the experiment on the other group members. We then repeated the experiment on bats that had unsuccessful first attempts, alternating the speaker from which the call from a group member was broadcast. No additional experimental trials were conducted on bats that did not enter a leaf on the second attempt. To determine if there was a significant preference to enter leaves from which a call from a group member was being emitted, we used the 2-tailed exact binomial test of goodness-of-fit assuming an expected proportion of 1:1.

Experiment 3 was conducted to determine if bats flying in the same area while concurrently searching for roost sites would prefer to approach group members. This was done by first placing the flight cage over an area with abundant vegetation, to simulate the understory where bats typically look for roosting sites, and marking the center of the cage with flagging tape. Two speakers were placed at the exact opposite sides of the flight cage on tripods at a distance of 7 m from each other; one speaker broadcast the inquiry call of a group member, whereas the other broadcast the inquiry call of a nongroup member. The broadcast sequence consisted of 1 s silence, call 1 (speaker 1), 1 s silence, call 2 (speaker 2), 1 s silence. Calls 1 and 2 were from different individuals, one being a group member and the other a nongroup member; we randomly selected the order in which calls from group and nongroup members were presented and the speaker from which they were broadcast. Each experiment lasted 1 min; in the first 30 s, we released a single bat in the flight cage and recorded time spent in each side of the flight cage. In the second 30 s, we broadcast the playback sequences and continued to record time spent on each side of the cage. Experiments were considered successful if individuals flew continuously for 1 min; however, if bats landed on leaves or on the side of the cage before the end of the experiment, we repeated the trial once more. At the end of the experiment, we determined if the proportion of time spent on the side of the cage where the speaker was broadcasting a group member call increased once the broadcast began. We used a Wilcoxon signed ranks test to assess significance.

Gillam and Chaverri (2012) assessed the strength of individual and group signatures in the inquiry and response calls of *T. tricolor*. One measure that was not calculated in this study was information capacity (H_s), which quantifies the amount of information that can potentially be encoded in a call type. H_s allows for standardized comparisons across taxa and assessment of how many unique signatures can possibly be constructed for a given signal (Beecher 1989). To better interpret the results of this study, we chose to calculate H_s for inquiry and response calls based on the data set used in Gillam and Chaverri (2012). Information capacity was

calculated based on the results of the Principal Components Analysis (PCA) and nested MANOVA described in Gillam and Chaverri (2012). As described by Beecher (1989), the estimates of variance attributable to differences within bats (S_W^2) and among bats (S_B^2) were used to determine total variance (S_T^2) for each Principal Component (PC) retained in the analysis. The information capacity for each factor was calculated as $H_i = \log 2(S_T/S_W)$. The total information capacity for each call type was obtained by summing the information capacities of each factor ($H_s = \sum H_i$).

RESULTS

The first experiment, which tested if roosting bats preferentially respond to inquiry calls emitted by group mates, was conducted on 74 bats; however, only 45 individuals from 15 groups produced calls during the experimental trial. After broadcasting an inquiry call, bats responded with a bout comprised of a minimum of 1 and a maximum of 47 response calls (mean $2.37 \pm$ SD 4.82). The number of response calls produced per individual was highly stereotyped: very responsive individuals consistently produced more than 5 calls in a single bout, whereas less responsive individuals rarely produced more than 3 calls in a single bout. We found that there was no significant difference in the number of response calls to inquiry calls from group members compared with calls from nongroup members (mean number of response calls to: group members = 2.22 ± 3.67 , nongroup members = 2.44 ± 5.15 ; Wilcoxon signed ranks test: $Z = 0.25$, $P = 0.80$; number of ties = 28; Figure 2a).

The second experiment, which tested if flying bats preferentially enter a furled leaf in reply to a response call from a group member, was conducted on 102 bats, but only 45 individuals belonging to 20 groups entered a furled leaf. We did not find a significant preference to enter leaves on either side of the flight cage (2-tailed exact binomial test of goodness-of-fit assuming an expected proportion of 1:1: $P = 1$), indicating that leaf position was not driving roost preference. However, we found that 69% of bats in successful trials entered the leaf with a response call from a group member. Based on the null assumption that bats would enter each leaf with equal proportions, we found a significant preference to enter leaves from which a call from a group member was being emitted (2-tailed exact binomial test of goodness-of-fit: $P = 0.01$, Figure 2b).

In the third experiment, where we addressed the question of whether flying bats preferentially approach inquiry calls emitted by group members, we used 45 individuals from 15 groups. Before broadcasting calls, bats spent approximately half of the time flying in each side of the flight cage (Figure 2c). In the second part of the experiment, when calls were being reproduced, bats significantly increased the time they spent near the speaker where an inquiry call from a group member was being broadcast (Wilcoxon signed ranks test: $Z = 2.25$, $P = 0.02$, Figure 2c). An increase in time spent near the speaker where an inquiry call from a group member was being broadcast occurred in 30 individuals, whereas a decrease was observed in 12 individuals.

Information capacity analyses resulted in an H_s value of 1.95 for inquiry calls and 3.65 for response calls. These findings can be extrapolated to estimate the number of unique signatures that can be encoded in each call type. Based on the estimated values, inquiry calls can encode approximately 4 unique signatures and response calls approximately 13 unique signatures.

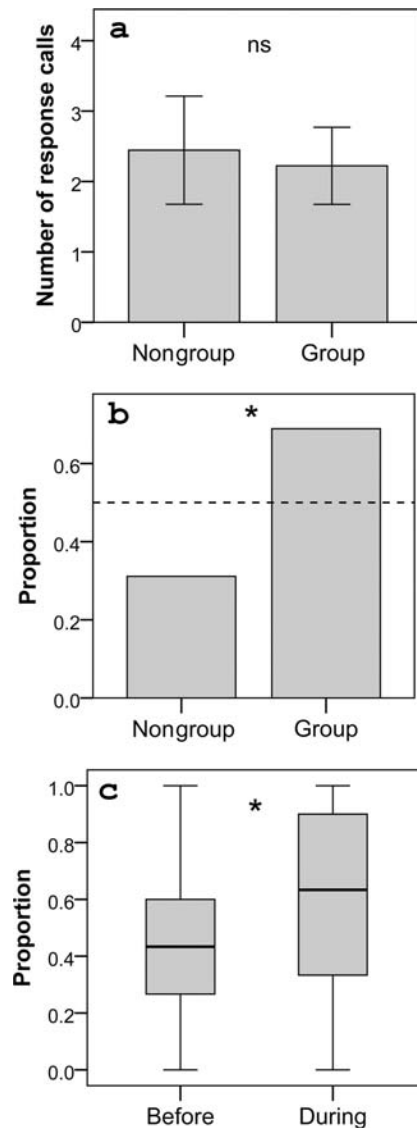


Figure 2

(a) Average number of response calls to inquiry calls from nongroup and group members. Data correspond to results of experiment 1, where we test the hypothesis that roosting bats will produce more response calls to inquiry calls of group members. The difference in mean response strength to nongroup and group members was not significant. (b) Proportion of times bats entered leaves where a response call from a nongroup and group member was being broadcast. Data correspond to results of experiment 2, where we test the hypothesis that flying bats will more frequently enter leaves from which response calls of group members are being emitted. Asterisk denotes a significant preference to enter leaves from which a call from a group member was being emitted, based on the null expectation that bats would enter either leaf with equal proportions. (c) Proportion of time bats spent in the side of the flight cage where an inquiry call of a group member was emitted during the experiment. Bars represent results before and during sound reproduction. Data correspond to results of experiment 3, where we test the hypothesis that flying bats will preferentially approach inquiry calls of group members. Asterisk denotes a significant increase in time spent near the speaker where an inquiry call from a group member was being broadcast during sound reproduction.

DISCUSSION

Our results show that acoustic signals with individual signatures facilitate the relocation of the same set of group

members that change roosting sites on a daily basis. Based on our results and previous studies, we argue that group cohesion is maintained in 2 ways. First, when flying within their small, relatively predictable roosting area (Vanhof et al. 2004; Chaverri and Kunz 2011b), bats regularly exchange inquiry calls, which allows them to recognize group from nongroup members and to preferentially associate with the former. Second, individuals that have located a suitable roost site produce response calls after detecting the inquiry call of a flying bat. These response calls allow flying individuals not only to recognize that other group members have occupied a suitable roost but also to identify its location. This calling system is similar to the one employed by meerkats and African elephants (Poole et al. 1988; Townsend et al. 2010; Bousquet et al. 2011) because it provides continuous information about the location of individuals while announcing a substantial change in activity.

Interestingly, flying bats appear to recognize group and nongroup members from both sets of calls, inquiry and response, whereas roosting individuals responded indiscriminately to the inquiry calls of flying individuals, exhibiting no preference for group members over nongroup members. This could be due to a variety of nonmutually exclusive explanations. First, if groups fly as a unit in a relatively small area, and home range overlap is minimal, it may not be necessary to assess the identity of the caller, as it is almost always a group member. This idea is supported by strong evidence suggesting that habitat patches are almost exclusively used by a single group and that *T. tricolor* is highly territorial (Chaverri and Kunz 2011b). Even if some home range overlap occurs, however, individuals can still avoid intergroup exchanges by emitting a response signal that carries a large amount of information and should thus be easily recognizable. In fact, our results show that response calls have a higher information capacity than inquiry calls and that based on information in response calls, flying bats can discriminate between leaves occupied by group or nongroup members.

Second, there may be insufficient information in the inquiry call to permit efficient assessment of group or individual identity. Information capacity analyses show that inquiry calls can encode only 4 unique signatures. Lacking information about the identity of the caller, it may be beneficial for roosting bats to always call rather than never call, especially species like *T. tricolor*, where there is high relatedness within groups (Chaverri and Kunz 2011a) and aiding group members may have indirect fitness benefits. Yet, our finding that bats in flight preferentially respond to the inquiry calls of group members does not support this hypothesis, as it appears that in a different context, individuals are able to extract information about group or caller identity from inquiry signals.

Third, accepting nongroup members at roost sites may not be costly to roosting bats and could even have positive effects. Attracting other individuals to their roost site, regardless of group identity, could provide thermoregulatory benefits through huddling (Krause and Ruxton 2002). Although tropical environments provide somewhat warm temperatures during the day, night temperatures may drop sufficiently to increase energetic demand in small vertebrates (Howell 1976; Roverud and Chappell 1991; Thomas et al. 1993). Additional benefits could be reduced individual costs of vigilance, earlier detection of predators (Quenette 1990; Krause and Ruxton 2002; Beauchamp 2008), and information exchange about foraging resources (Pacala et al. 1996; Mirabet et al. 2008).

The response of bats to our experimental treatments strongly suggest that individuals prefer to associate with group members, yet our data do not allow us to assess whether the ~30% of bats that joined nongroup mates (in experiments 2

and 3) is best explained by experimental errors, an inability to discriminate group from nongroup calls, or by dyadic preferences within groups. Studies on bats indicate that individuals often form nonrandom associations within colonies or groups (Wilkinson 1985; Willis and Brigham 2004; Campbell et al. 2006; Metheny et al. 2008; Kerth et al. 2011), and playback experiments suggest that individual signatures may facilitate recognition of close associates (Arnold and Wilkinson 2011; Carter et al. 2012). Because previous findings on the acoustic signaling system employed by *T. tricolor* suggest that inquiry and response calls have strong individual and weak group signatures (Gillam and Chaverri 2012), we propose that recognition of particular group members that have easily distinguishable signals may be easier than recognition of all group members based on a weak group-specific signal, thereby providing a plausible explanation for the noise in our results.

Characteristics of the *T. tricolor* signaling system align with evolutionary game theory predictions about signal dishonesty, specifically that the tendency to provide misleading information will be greater when the information payoffs to senders and receivers are very different (Bradbury and Vehrencamp 2011). Studies in bats suggest that flight is an energetically expensive activity (Thomas and Suthers 1972), particularly in species with short, broad wings well suited for maneuverable flight (Iriarte-Diaz et al. 2002), such as *T. tricolor* (Norberg and Rayner 1987). Also, several lines of evidence suggest that flying bats are more susceptible to predation (Fenton et al. 1994) and that roosts provide protection from extreme temperatures and rain (Kunz 1982). Hence, locating any suitable roost, whether occupied by group or nongroup members, should be highly beneficial to flying bats. Alternatively, roosting bats are in a much safer position, and the costs of a mistake (receiving a nongroup member) are likely low or nonexistent; in fact, bats could even benefit from having nongroup mates enter a roost (see above). As a result, we would anticipate that flying bats (senders) may purposefully provide ambiguous information to roosting bats (receivers) in an attempt to elicit a response that provides much needed information about the location of a suitable roost. Such a system can be evolutionary stable because signal receivers (roosting bats) do not suffer net fitness costs when advertising their location to nongroup mates.

The calls emitted by flying and roosting individuals have the potential to provide direct and immediate benefits to individuals, as explained previously, yet the ability to discriminate group from nongroup members and to preferentially associate with the former may provide additional long-term benefits. *T. tricolor*'s groups are composed of highly related individuals; offspring of both sexes are philopatric and remain within their natal group for extended periods of time, resulting in matrilineal societies (Chaverri and Kunz 2011a). Thus, any form of cooperative interaction among these individuals could result in increased kin-selected fitness benefits.

Unlike disc-winged bats, which use very ephemeral structures for roosting, most bats use more permanent structures that they should be able to relocate by memory (Ulanovsky and Moss 2008); these species possibly maintain contact with the same group members simply by returning to the same roost or set of roosts (Popa-Lisseanu et al. 2008; Fortuna et al. 2009). Yet, most species do not exhibit highly stable group membership, suggesting 1) few benefits to remaining with the same set of individuals, 2) potential high costs of roost fidelity, such as increased risk of predation or parasitism (Lewis 1996; Reckardt and Kerth 2006, 2007), and/or 3) less effective information communication systems. In this regard, communication among roost members in many species of bats may be less effective because individuals often have very large home ranges that overlap with hundreds of individuals

(Racey and Entwistle 2003). In this case, group cohesion may be difficult because contact signals are not audible to all group members due to signal attenuation, and signal recognition may be prohibitively demanding due to the large number of signals encountered daily (Bradbury and Vehrencamp 2011). Spix's disc-winged bats, unlike most species studied to date, appear to have characteristics that greatly facilitate the use of acoustic communication for relocating roost mates, such as the use of a small home range and roosting territories where few other individuals are encountered. Hence, it is not surprising that there has been selection for a signaling system comprised of contact calls that have individual signatures, which may allow discrimination of group from nongroup members. These characteristics appear highly effective in maintaining stable groups, as *T. tricolor* form one of the most cohesive aggregations known in bats despite using one of the most ephemeral roosting structures.

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