

Social calls used by a leaf-roosting bat to signal location

Gloriana Chaverri^{1,*}, Erin H. Gillam^{2,*}† and Maarten J. Vonhof³

¹Biology Department, Boston University, Boston, MA 02215, USA

²Department of Biological Sciences, North Dakota State University, Fargo, ND 58108, USA

³Department of Biological Sciences, Western Michigan University, Kalamazoo, MI 49008, USA

*Authors for correspondence (gchaverri@upacificosur.org; erin.gillam@ndsu.edu).

†These authors contributed equally to this work.

Social calls in bats have many functions, including mate attraction and maintaining contact during flight. Research suggests that social calls may also be used to transfer information about roosts, but no studies have yet demonstrated that calls are used to actively attract conspecifics to roosting locations. We document the social calls used by Spix's disc-winged bat (*Thyroptera tricolor*) to actively recruit group members to roosts. In acoustic trials, we recorded two sets of calls; one from flying individuals termed 'inquiry calls', and another from roosting bats termed 'response calls'. Inquiry calls were emitted by flying bats immediately upon release, and quickly (i.e. 178 ms) elicited production of response calls from roosting individuals. Most flying bats entered the roost when roosting individuals responded, while few bats entered the roost in the absence of a response. We argue that information transfer concerning roost location may facilitate sociality in *T. tricolor*, given the ephemeral nature of roosting structures used by this species.

Keywords: information transfer; roost; social calls

1. INTRODUCTION

Social calls are important for conveying information to conspecifics in several species. In bats, most acoustic communication research has focused on echolocation, with little effort aimed at documenting the diversity and function of social calls. Compared with echolocation calls, social calls are longer, more broadband and highly complex, with extensive spectral variability and use of syllables and phrases (Ma *et al.* 2006). Further, bats often maintain a diverse repertoire of social calls that are used in a variety of social contexts (Bohn *et al.* 2008). Studies suggest that social calls in bats have many functions, such as announcing distress, aiding in mother–infant recognition and attracting mates (Pfalzer & Kusch 2003).

The role of social calls in actively maintaining associations among roost mates has received little attention. Wilkinson & Boughman (1998) described

how *Phyllostomus hastatus* departing from roosts emit screech calls that attract group members to foraging sites, and Carter *et al.* (2009) recorded calls that provide information about the location of conspecifics in *Diaemus youngi*. These authors suggest that maintaining contact while foraging may increase the defence of food sources. Social calls might also be used to attract conspecifics to roosts, as group living promotes social thermoregulation, predator avoidance and cooperation (Kerth 2008). Kerth & Reckardt (2003) provided *Myotis bechsteinii* with bat boxes, and found that bats located roosts through information transfer, as more naive females were recruited towards suitable boxes after an experienced individual had already discovered the roost. Unfortunately, since this study did not record sound, it was not possible to determine whether naive individuals were attracted to vocalizations and/or scent marks. Ruczyński *et al.* (2007, 2009) tested how various sensory cues were used by cavity-roosting species to locate roosts, and observed that conspecific echolocation calls significantly improved an individual's performance in locating cavities. Finally, Vaughan & O'Shea (1976) report 'directive calls' in *Antrozous pallidus* that apparently attract flying conspecifics to roost sites. While these studies document information transfer about roosts and the location of group mates, no research has yet examined if social calls are used to actively attract conspecifics to roosting locations.

Here, we provide evidence that social calls are used by a bat to advertise roosting locations to conspecifics. Our study describes the calls emitted by Spix's disc-winged bats, *Thyroptera tricolor*, when a flying individual is searching for group mates that are already roosting. *Thyroptera tricolor*, an insectivorous bat with highly stable social groups (Vonhof *et al.* 2004), roost in the developing tubular leaves of members of the order Zingiberales, which vary in density across sites and are suitable for roosting for 1 day (Vonhof & Fenton 2004). Thus, given the ephemeral and often sparse nature of tubular leaves, *T. tricolor* face the difficult daily task of locating suitable roosting sites while maintaining group cohesion. We propose that the social calls described in this study significantly improve *T. tricolor*'s performance in this task.

2. MATERIAL AND METHODS

Acoustic data collection was performed in March 2009, in La Gamba, southwestern Costa Rica. Bats were captured by searching suitable leaves; upon capture, bats were housed in cloth bags and fitted with numbered metal wing bands. A suitable tubular leaf was then located near the capture site to perform acoustic trials. If suitable leaves were not found, we cut an unoccupied tubular leaf from another site and planted it near the capture site. We conducted all trials in areas where bats would have enough space for manoeuvrability and access to the experimental leaf.

Three condenser microphones (CM16, Avisoft, Berlin, Germany) mounted on tripods were used to record calls produced in the release area; two microphones were located less than 5 cm from the tubular leaf at different heights, close to where bats would be roosting, and the other microphone was placed on the path between the release site and the tubular leaf. Release sites were usually located at approximately 5 m from the experimental leaf. Social calls were recorded onto a Dell Latitude laptop through Avisoft's ULTRASOUNDGATE 416 and Avisoft-RECORDER software (sampling rate 384 kHz, 16-bit resolution).

Trials began by placing one individual from the captured group inside the experimental leaf (i.e. roosting bat), and then placing a second bat from the same group in the researcher's hand at the release site (i.e. flying bat). The cloth bag with the remaining bats

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2009.0964> or via <http://rsbl.royalsocietypublishing.org>.

Received 20 November 2009
Accepted 14 December 2009



This journal is © 2010 The Royal Society

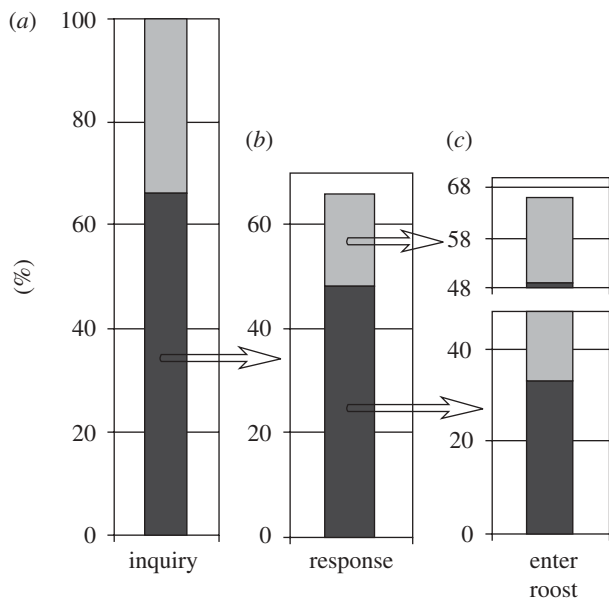


Figure 1. Percentage of times in which a specific behaviour was recorded (black) or not recorded (grey). (a) Occurrence of inquiry calls; (b) occurrence of response calls when an inquiry call was recorded (no response calls were recorded in the absence of inquiry calls); (c) bats entering the roost in the absence (upper) or presence (lower) of response calls.

was placed inside a waterproof bag to avoid acoustic interference. Recordings began when we released the flying bat, and ended when the bat entered the experimental leaf or after the flying individual left the area and was not visible for more than 1 min.

For every acoustic trial we noted the identity of the roosting and flying individuals, and whether the flying individual entered the leaf. Upon later analysis, we also noted if calls were emitted by the flying individuals ('inquiry calls'), and/or the roosting individuals ('response calls'). We ran two G -tests of independence to determine (i) if the presence of a response call was related to the presence of an inquiry call; and (ii) if entrance of the flying individual into the roost was related to the production of response calls by the roosting individual. Call characteristics were measured using Avisoft SASLAB PRO. For both call types, we measured call duration (Dur), frequency at call start (F_{start}), frequency at call end (F_{end}), peak frequency (F_{peak}) and bandwidth (BW). We also gauged how rapidly bats responded by measuring the time from the start of an inquiry call to the start of the corresponding response call. Since multiple response calls were emitted in quick succession (i.e. a bout), we also determined the average number of calls per bout and bout duration.

3. RESULTS

A total of 143 acoustic trials were conducted from 15 March to 22 March 2009. From these trials, we recorded inquiry calls from flying individuals on 95 occasions (66%; figure 1), and response calls from roosting individuals on 69 occasions (48%). We found that response calls were never emitted in the absence of an inquiry call, but often (48.3%) were produced after an inquiry call was emitted by the flying bat ($G = 24.09$, d.f. = 1, $p < 0.001$; figure 1). We also found that only 2.1 per cent of bats entered the leaf in the absence of response calls, while 33.6 per cent entered when response calls were produced by roosting bats ($G = 76.40$, d.f. = 1, $p < 0.001$). Only one individual entered the roost without producing an inquiry call.

Eighty inquiry calls were recorded and analysed from 37 individuals. Mean call characteristics (\pm s.d.), were: Dur = 35.82 ms (± 8.16), $F_{\text{start}} =$

39.12 kHz (± 7.08), $F_{\text{end}} = 16.53$ kHz (± 4.01), $F_{\text{peak}} = 25.84$ kHz (± 5.86) and BW = 22.59 kHz (± 5.57 ; figure 2a). Eighty-nine response calls were recorded from 20 individuals, with mean call characteristics of: Dur = 141.17 ms (± 42.88), $F_{\text{start}} = 45.56$ kHz (± 6.34), $F_{\text{end}} = 63.78$ kHz (± 5.92), $F_{\text{peak}} = 57.74$ kHz (± 7.17) and BW = 18.22 kHz (± 8.57 ; figure 2b; see table S1 in the electronic supplementary material for additional details). The average time between the start of an inquiry call and the start of response calls was 178 ms (± 50 ; figure 2c). We recorded an average of 6.22 response calls per bout (± 2.54), and an average bout duration of 1250 ms (± 530). Production of inquiry and response calls ceased immediately after the flying individual entered the roost.

4. DISCUSSION

Our study shows that while searching for roosts, *T. tricolor* emits calls that frequently elicit a response from individuals who have entered a tubular leaf. These response calls, in turn, appear to direct the flying individual into the roost. Inquiry calls were mainly used for locating roost mates, since these were recorded immediately upon release and ended when the bat located a suitable leaf. In turn, response calls appeared to be emitted by roosting individuals to announce their location. Response calls were presumably used to aid conspecifics in finding the roost, because they were emitted only after an audible inquiry call and ceased immediately after the flying individual entered the roost. Both calls differed notably from the echolocation calls previously described for *T. tricolor* (Fenton *et al.* 1999), and do not seem to be a byproduct of other activities being conducted while roosting. These results provide conclusive evidence of *T. tricolor* using social calls to actively transfer information about location of roost mates to social group members. While previous studies on bats also suggest the presence of information transfer about roost location, our study is the first to record and describe social calls specifically used for this purpose.

There are several mechanisms that can explain the evolution of calls used to signal location to conspecifics in *T. tricolor*. Kin selection may be an important mechanism, because the occurrence of offspring retention within groups results in a matrilineal social organization and high relatedness among group members (Vonhof 2001). Because cooperation may also evolve when it provides direct benefits to the donor (i.e. mutualism), it is possible that roosting bats signal their location to conspecifics because this increases group size, aiding in thermoregulation and for detecting predators more efficiently. Cooperation is also presumed to evolve in societies even if there are no immediate benefits to the donor (e.g. reciprocity). However, the evolution of reciprocity is difficult in large communities because it is hard to identify the reputation of each individual (Suzuki & Akiyama 2005), particularly when encounters among community members are rare (Ferriere & Michod 1996). Yet, the high cohesion and relatively small size of groups in *T. tricolor* (Vonhof *et al.* 2004) may make

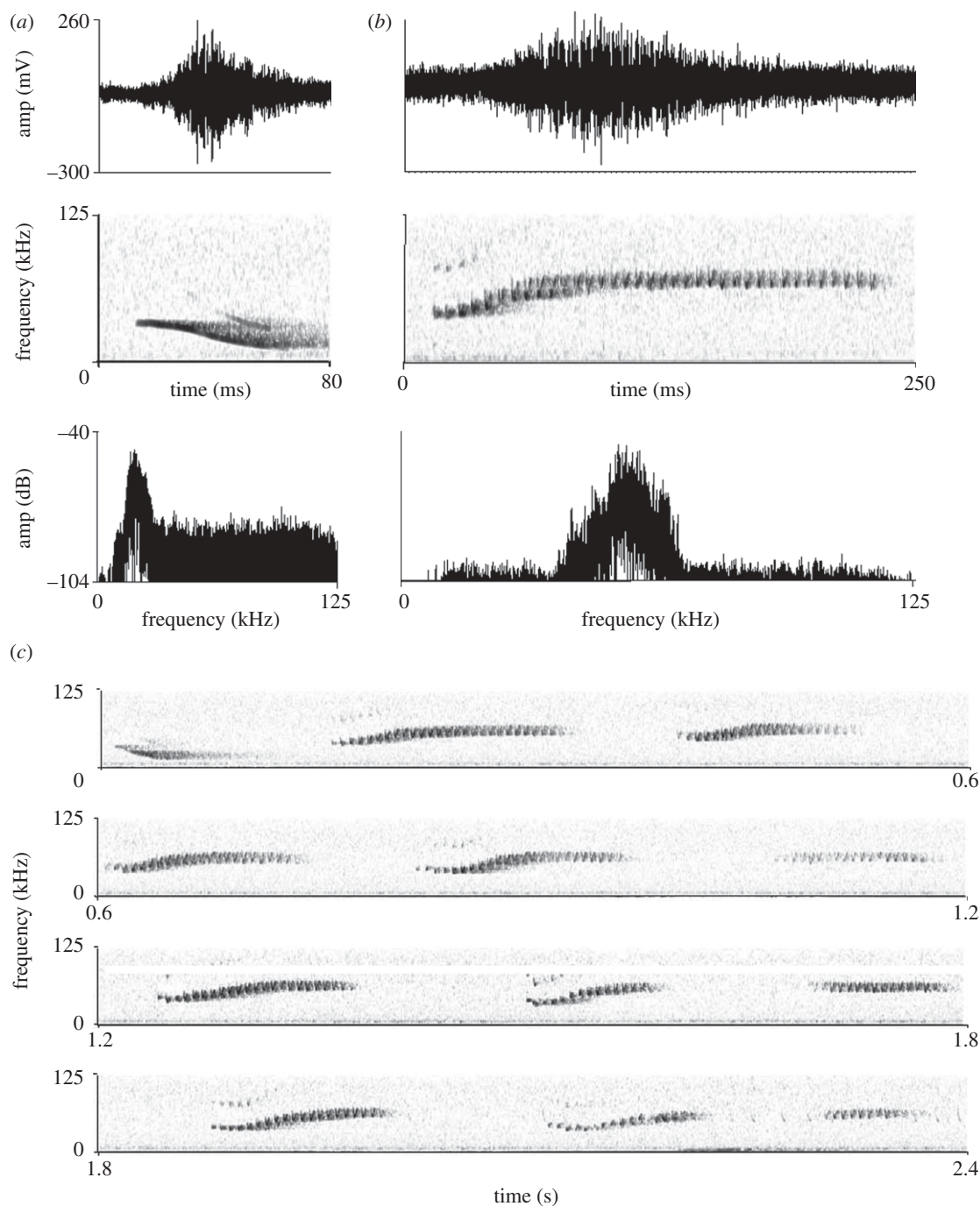


Figure 2. Waveform (top), sonogram (middle) and power spectrum (bottom) showing (a) an inquiry call and (b) a response call. (c) A bout spanning from the emission of the inquiry call at $t = 0.05$ until the last response call at $t = 2.4$.

reciprocity feasible, and favour the evolution of cooperation in this species.

Living in groups can enhance resource acquisition efficiency by providing opportunities for information transfer among group members, particularly in species that use clumped and unpredictable resources (Barta & Szep 1992). Tubular leaf-roosting bats, such as *T. tricolor*, face the unique challenge of having to locate suitable roosts on a daily basis. Depending on the habitat, this task may require long search times, as the plants used for roosting are often sparse. Because flying implies a large energetic cost, the ability to rapidly locate new roosts poses a great challenge for bats, one that may be offset by the help of individuals that have already located a suitable

roosting site. Thus, we suggest that active information transfer of roost location may be an important process shaping the evolution of sociality in bats such as *T. tricolor* because of the clumped and ephemeral nature of tubular leaves.

- Barta, Z. & Szep, T. 1992 The role of information-transfer under different food patterns: a simulation study. *Behav. Ecol.* **3**, 318–324. (doi:10.1093/beheco/3.4.318)
 Bohn, K. M., Schmidt-French, B., Ma, T. S. & Pollak, G. D. 2008 Syllable acoustics, temporal patterns and call composition vary with behavioral context in Mexican free-tailed bats. *J. Acoust. Soc. Am.* **124**, 1838–1848. (doi:10.1121/1.2953314)

- Carter, G. G., Fenton, M. B. & Faure, P. A. 2009 White-winged vampire bats (*Diademus youngi*) exchange contact calls. *Can. J. Zool.* **87**, 604–608. (doi:10.1139/Z09-051)
- Fenton, M. B., Rydell, J., Vonnhof, M. J., Eklof, J. & Lancaster, W. C. 1999 Constant-frequency and frequency-modulated components in the echolocation calls of three species of small bats (Emballonuridae, Thyropteridae, and Vespertilionidae). *Can. J. Zool.* **77**, 1891–1900. (doi:10.1139/cjz-77-12-1891)
- Ferriere, R. & Michod, R. E. 1996 The evolution of cooperation in spatially heterogeneous populations. *Am. Nat.* **147**, 692–717. (doi:10.1086/285875)
- Kerth, G. 2008 Causes and consequences of sociality in bats. *Bioscience* **58**, 737–746. (doi:10.1641/B580810)
- Kerth, G. & Reckardt, K. 2003 Information transfer about roosts in female Bechstein's bats: an experimental field study. *Proc. R. Soc. Lond. B* **270**, 511–515. (doi:10.1098/rspb.2002.2267)
- Ma, J., Kobayasi, K., Zhang, S. Y. & Metzner, W. 2006 Vocal communication in adult greater horseshoe bats, *Rhinolophus ferrumequinum*. *J. Comp. Physiol. A Sens. Neural. Behav. Physiol.* **192**, 535–550. (doi:10.1007/s00359-006-0094-9)
- Pfalzer, G. & Kusch, J. 2003 Structure and variability of bat social calls: implications for specificity and individual recognition. *J. Zool.* **261**, 21–33. (doi:10.1017/S0952836903003935)
- Ruczyński, I., Kalko, E. K. V. & Siemers, B. M. 2007 The sensory basis of roost finding in a forest bat *Nyctalus noctula*. *J. Exp. Biol.* **210**, 3607–3615. (doi:10.1242/jeb.009837)
- Ruczyński, I., Kalko, E. K. V. & Siemers, B. M. 2009 Calls in the forest: a comparative approach to how bats find tree cavities. *Ethology* **115**, 167–177. (doi:10.1111/j.1439-0310.2008.01599.x)
- Suzuki, S. & Akiyama, E. 2005 Reputation and the evolution of cooperation in sizable groups. *Proc. R. Soc. B* **272**, 1373–1377. (doi:10.1098/rspb.2005.3072)
- Vaughan, T. A. & O'Shea, T. J. 1976 Roosting ecology of the pallid bat, *Antrozous pallidus*. *J. Mammal.* **57**, 19–42. (doi:10.2307/1379510)
- Vonnhof, M. J. 2001 Habitat availability, population size, and the composition, stability, and genetic structure of social groups of Spix's disc-winged bat, *Thyroptera tricolor*. PhD thesis, York University, Toronto, Canada.
- Vonnhof, M. J. & Fenton, M. B. 2004 Roost availability and population size of *Thyroptera tricolor*, a leaf-roosting bat, in northeastern Costa Rica. *J. Trop. Ecol.* **20**, 291–305. (doi:10.1017/S0266467404001403)
- Vonnhof, M. J., Whitehead, H. & Fenton, M. B. 2004 Analysis of Spix's disc-winged bat association patterns and roosting home ranges reveal a novel social structure among bats. *Anim. Behav.* **68**, 507–521. (doi:10.1016/j.anbehav.2003.08.025)
- Wilkinson, G. S. & Boughman, J. W. 1998 Social calls coordinate foraging in greater spear-nosed bats. *Anim. Behav.* **55**, 337–350. (doi:10.1006/anbe.1997.0557)