



The importance of group vocal behaviour in roost finding

Maria Sagot^{a,*}, Caroline R. Schöner^b, Abigail J. Jago^{a,c,1}, Imran Razik^{a,1},
Gloriana Chaverri^d

^a Department of Biological Sciences, State University of New York at Oswego, NY, U.S.A.

^b Zoological Institute and Museum, University of Greifswald, Germany

^c Department of Environmental and Forestry Biology, State University of New York, College of Environmental Science and Forestry, Syracuse, NY, U.S.A.

^d Recinto Golfito, Universidad de Costa Rica, Golfito, Costa Rica

ARTICLE INFO

Article history:

Received 3 December 2017

Initial acceptance 8 January 2018

Final acceptance 18 May 2018

MS. number: A17-00952R3

Keywords:

animal personality
bat
behavioural syndrome
contact call
Thyroptera tricolor

Individuals benefit from socially acquired information to avoid predation risks and enhance foraging efficiency. Spix's disc-winged bats, *Thyroptera tricolor*, form very stable social groups despite their need to find a new roosting site daily. *Thyroptera tricolor* produce two contact calls: inquiry calls, emitted during flight, and response calls, produced by bats after finding a suitable roost (in a furled leaf). Bats within social groups exhibit consistent individual differences in vocal behaviour and thus, groups are composed by a mix of less vocal and more vocal individuals. To date, it is not known whether consistent individual differences in contact calling behaviour decrease the time required for roost finding and whether vocal behaviour is correlated with an individual's ability to quickly locate roosts, thus constituting a behavioural syndrome. Here, we compared the time spent by social groups in finding roosts when a bat called from inside the roost, either frequently or infrequently. Moreover, we estimated how well calling rates inside a roost predicted a bat's ability to later find a new roost. Results of behavioural experiments and field observations show that social groups enter roosts faster when the bat inside the roost called more. This suggests that more frequent calling decreases search time, which may allow groupmates to save energy and decrease exposure to predators. Moreover, vocal activity also predicted discovery of more roosts (furled leaves) in their natural habitat, which emphasizes the relevance of more vocal individuals for the group. Our work represents a step in understanding the importance of communication and individual vocal behaviour in group formation and stability in gregarious animals.

© 2018 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Animals living in social groups have access to socially acquired information that may help individuals reduce predation risk (Elgar, 1986; Newman & Caraco, 1989), increase mating opportunities (Evans & Marler, 1994), recruit assistance in resource defence (Heinrich & Marzluff, 1991; Wilkinson & Boughman, 1998) and increase individuals' ability to find food or other resources (e.g. Brown, Brown, & Shaffer, 1991). In fact, sharing information about resources is thought to drive the evolution of sociality in species that utilize patchy and ephemeral resources (Barta & Szép, 1992; Beauchamp, Belisle, & Giraldeau, 1997; Buckley, 1997; Safi & Kerth, 2007). In bats, for example, individuals use acoustic cues from group members to increase their efficiency in food acquisition (Dechmann et al., 2009) and reduce search time of roost sites

(Ruczynski, Kalko, & Siemers, 2007). Thus, by picking up on social cues, bats may be able to reduce the energetic cost associated with finding and selecting resources.

A species that commonly uses social calls to locate a critical resource is the Spix's disc-winged bat, *Thyroptera tricolor*. These bats roost in furled leaves that are only available from 5 to 31 h (Findley & Wilson, 1974; Vonhof & Fenton, 2004), and must therefore locate a new leaf on an almost daily basis. To facilitate this task, *T. tricolor* uses two social calls: 'inquiry' and 'response'. The so-called 'inquiry calls' are used to maintain contact with group members during flight. When an individual finds and enters a roost, it produces a complex signal called a 'response call' in reply to inquiry calls from flying group and nongroup members (Chaverri, Gillam, & Kunz, 2013). This call system facilitates roost location by group members (Chaverri, Gillam, & Vonhof, 2010). Moreover, individuals within social groups exhibit consistent differences in their vocal behaviour (i.e. in the number of response calls emitted) for periods of up to 3 years, and social groups are composed of individuals with different calling rates (Chaverri & Gillam, 2015).

* Correspondence: M. Sagot, Department of Biological Sciences, State University of New York at Oswego, 230 Shineman Center, Oswego, NY 13126, U.S.A.

E-mail address: maria.sagot@oswego.edu (M. Sagot).

¹ Equal contributions.

For example, groups are often composed of four to six individuals and typically there is one that is consistently very vocal, one that consistently emits some response calls, and the rest are consistently nonvocal (Appendix, Fig. A1). Prior studies support the hypothesis that response calls advertise the location of suitable roosts; thus, two questions arise. (1) Can groups find roosts faster if they have individuals that produce more response calls? (2) Do individuals that produce more response calls locate roosts more quickly than less vocal individuals?

Social groups are often composed of individuals showing a range of different personalities (e.g. (Beauchamp, 2000; Hollander, Van Overveld, Tokka, & Matthysen, 2008)). In the context of exploration behaviour, animals that have a bold or exploratory personality can produce by-product benefits for groupmates, but can also suffer higher risks and can be exploited (Beauchamp, 2006, 2000). On the other hand, if the costs of being exploratory are very high (e.g. predation risk or high costs of foraging), it could be beneficial for some individuals to rely on bolder individuals capable of taking the risks (e.g. Dyer, Croft, Morrell, & Krause, 2008; Kurvers et al., 2009). Moreover, different personality traits can be correlated, a term commonly referred to as personality syndromes (e.g. Sih, Bell, & Ziemba, 2004). For instance, in foraging groups, bolder, more exploratory individuals are usually at the leading edge of the moving group (Beauchamp, 2000; Harcourt, Sweetman, Johnstone, & Manica, 2009; Kurvers et al., 2009; Schuett & Dall, 2009), and are also more likely to produce information about resource location because they are the first to encounter resources (Barta, Flynn, & Giraldeau, 1997; Kurvers et al., 2009; Mónus & Barta, 2008). Furthermore, individuals that are more active in exploring the environment are also more efficient in finding resources when foraging (e.g. Beauchamp, 2006; Kurvers et al., 2009).

To date, experimental work on animal personalities and personality syndromes have focused primarily on understanding why individuals exhibit behavioural consistency (e.g. Hollander et al., 2008). However, only a few studies have focused on personalities in the context of vocal behaviour and its consequences for group cohesion and resource finding. Here, our aim was to determine whether calling rates influence group roost finding, by comparing the time that social groups took to enter a roost when a less vocal versus a more vocal group member was in the roost. We expected social groups to locate roosts faster when there were more response calls emitted from the roosts (i.e. there was a more vocal individual inside the roost), as social information is known to be critical for resource finding in a diversity of organisms (e.g. Couzin, Krause, Franks, & Levin, 2005; Kurvers et al., 2009). Moreover, multiple studies have found that more vocal individuals tend to be more exploratory (e.g. Friel, Kunc, Griffin, Asher, & Collins, 2016; Guillette & Sturdy, 2011). Thus, we aimed to determine whether more vocal individuals are more successful in discovering potential roost sites compared to less vocal group members.

METHODS

We collected data on response calling production for 24 different social groups (100 individuals) in the Barú Biological Station in southwestern Costa Rica, in July 2016. We further examined the response calling and exploration behaviour of 11 social groups (46 individuals) from January to March 2017. Every day we searched for social groups (i.e. individuals found roosting together) by locating *Heliconia* spp., *Calathea* spp. and *Musa* spp. furled leaves, commonly used by *T. tricolor* as roosting sites (Vonhof & Fenton, 2004). Once a roost was located, we captured all the bats inside the tubular leaf and placed them inside a cloth holding bag. We sexed, aged and determined the reproductive condition for all bats captured. Moreover, we weighed them and measured their

forearm length (as a measure of body length). We conducted our experiments during the morning, as *T. tricolor* performs calling behaviours during the day, not at night (Chaverri et al., 2010). First, we measured vocal rates (experiment 1). Then, we conducted another experiment (experiment 2) to examine whether groups entered a roost faster if there was a more vocal bat within it. Finally, we conducted field observations to answer the question of whether more vocal bats are more successful in discovering potential roost sites than less vocal individuals.

Experiments

Experiment 1

In experiment 1, we gauged individual calling behaviour based on response calling rates. To do this, we removed a furled leaf and placed it into a small portable flight cage ($3 \times 3 \times 2$ m). We placed one bat inside the leaf and we placed a circular piece of mesh at the entrance to prevent escape. Because bats only produce response calls after an inquiry call has been emitted (Chaverri et al., 2010), we prerecorded inquiry calls and broadcast them for 1 min through an UltrasoundGate Player to a broadband loudspeaker (Ultrasonic Omnidirectional Dynamic Speaker Vifa, Avisoft Bioacoustics, Berlin, Germany) placed near the leaf. This recording had a total of 67 inquiry calls from a single group that we previously captured near our study site. *Thyroptera tricolor* respond indiscriminately to group and nongroup inquiry calls (Chaverri et al., 2013), and our playback was effective at prompting response calling from roosting bats. We categorized 'nonvocal individuals' as individuals that did not produce response calls, while vocal bats were individuals that emitted at least one response call. We recorded response calls with an Avisoft condenser microphone (CM16, Avisoft Bioacoustics) through Avisoft's UltraSoundGate 116Hm onto a laptop computer running Avisoft-Recorder software (sampling rate 384 kHz, 16-bit resolution), placed near the entrance of the furled leaf. We repeated this process for all individuals captured. For each trial, we measured the total number of response calls produced per bat per min. We analysed recordings in SASLab Pro (Avisoft Bioacoustics). We used a chi-square test of independence ('chisq.test' function in MASS) and a negative binomial regression model ('glm.nb' function in MASS) to determine whether vocal behaviour varies with sex (male and female), age (adult and juvenile), or their interaction. We selected the negative binomial model after testing for goodness of fit on the residual deviance and degrees of freedom. We performed both tests in R 3.2.2 (R Foundation for Statistical Computing, Vienna, Austria).

Experiment 2

In experiment 2, we aimed to establish whether social groups locate roosts more quickly when a more vocal bat is inside the furled leaf. Prior studies have demonstrated that *T. tricolor* individuals exhibit strong consistency over time in their response call behaviour (Chaverri & Gillam, 2015). Thus, we selected as the vocal bat the individual that produced the most response calls based on experiment 1, and we placed it inside a furled leaf in a larger flight cage ($3 \times 4 \times 9$ m). Then, we released the rest of the group and recorded the time that each individual took to enter the leaf. We tested each group twice, once with a vocal and once with a nonvocal group member inside the tubular leaf. For the nonvocal bat, we selected the individual that produced the fewest response calls, which was always 0. Whenever there was more than one individual with no response calls recorded, we randomly selected one for experiment 2. We also randomly assigned the order of the test, and we performed each test with the leaf randomly positioned in different sections of the flight cage. We considered a trial unsuccessful if a bat was not able to find the leaf after 5 min. We repeated this experiment for all the social groups captured. To

analyse the data from this experiment, we log transformed the time taken to enter the roost and we used a paired t test to compare the average entering time per group, the time when the first individual entered and the time difference between the first and last individuals that entered the roost, when a more vocal versus a less vocal group member was placed in the leaf. To ensure that the vocal behaviour exhibited in experiment 1 was consistent with the results found in this experiment, and thus, reinforcing previous knowledge on consistent vocal behaviour (Chaverri & Gillam, 2015), we looked for an association between the number of response calls produced per inquiry call in experiment 1 and experiment 2, using correlation analyses.

Field Observations

We marked all adult bats monitored in the wild with transponders (ISO 11784/11785; Peddymark Ltd, Essex, U.K.) for individual identification. To investigate individual exploratory behaviour and roost visiting, we monitored 15 furred leaves in the bats' home range per night with automatic transponder readers (LID 665-Multi; Euro I.D., Frechen, Germany). We only used leaves with an opening of 4–20 cm in diameter, which is the preferred size by *T. tricolor* (Vonhof & Fenton, 2004). In total, we monitored 40 furred leaves in the home range of each of the 11 *T. tricolor* groups (i.e. all monitored leaves were located within a radius <20 m to one of the former day roosts) over a mean (\pm SD) time period of 16.72 ± 2.30 days. We moved the transponder readers to new furred leaves almost every day and left them until the shape of the leaves changed or after the leaf had been inspected by one or several bats during the previous night (maximum time period = 3 nights). We did not remove the reader when we found *T. tricolor* roosting inside a monitored leaf, to avoid disturbing the bats. As a proxy for explorative behaviour, we counted how many of the 40 monitored leaves for each bat group were entered first by a focal bat (an event that we define as 'discovery'). This means that we only counted the very first entering of a bat when no bat of the same group had entered the leaf before. Moreover, bats from other colonies must have left the leaf for at least 30 min as they might have attracted the bat via social calls otherwise. For bats entering the roost later, it is not clear whether they found the leaf on their own or whether an experienced bat led them or attracted them to the potential roost site, as has been observed in other bat species (Kerth & Reckardt, 2003; Safi & Kerth, 2007).

We investigated whether more explorative bats also produced more social calls to attract group members. For this, we separately released the monitored adult bats in the flight cage with artificial furred leaves. After the bat had chosen a roost, we played back inquiry calls and analysed the produced response calls following the procedure described in experiment 1. After tracking multiple bats over time, we have determined that some individuals never produce response calls after inquiry call playback, while others vary their calling rates (Chaverri & Gillam, 2015; Appendix, Fig. A2). Thus, to analyse the relationship between exploratory activity (= number of discovered furred leaves) and the acoustic behaviour of the bats, we computed zero-inflated models with negative binomial error distributions. We performed the analysis and the model selection (e.g. by testing for goodness of fit on the residual deviance and degrees of freedom) using the package 'pscl' and 'MuMIn' in R 3.4.2. Because relative body condition of individuals determines whether they are vocal or not (Humfeld, 2013; Leary, Jessop, Garcia, & Knapp, 2004), we used bat body condition (assessed via the scaled mass index (SMI); Peig & Green, 2009) in the logit model, as a probable factor explaining why some individuals never produce response calls, while others vary their vocal rates over time. We expected individuals in worse body condition to be nonvocal. For females, we used the body mass either

before pregnancy became obvious or after birth. To calculate the index, we used bat mass and the forearm length (as a measure of body length) (see equations (1) and (2), L = mean forearm length of the bats, L_i = individual forearm length and M_i = body mass of each individual). Both forearm length and body mass were ln transformed and used to calculate b_{SMA} (scaling exponent, equation (2)).

$$\text{Scaled mass index (SMI)} = M_i \left[\frac{\text{Median}(L)}{L_i} \right]^{b_{SMA}} \quad (1)$$

$$b_{SMA} = \frac{\text{Slope}_{\text{linear regression}}}{\text{Coefficient}_{\text{Pearson correlation}}} \quad (2)$$

Moreover, we analysed whether the number of response calls produced per bat was correlated (Kendall rank correlation test) with the time that it took an individual to attract a group member to a day roost. In cases where the same individual was measured during several time periods attracting groupmates to different roosts, we calculated the average time per individual.

Ethical Note

All sampling protocols followed guidelines approved by the American Society of Mammalogists for capture, handling and care of mammals (Sikes et al., 2016) and the ASAB/ABS Guidelines for the use of animals in research. This study was conducted in accordance with the ethical standards for animal welfare of the Costa Rican Ministry of Environment and Energy, Sistema Nacional de Áreas de Conservación, permit no. ACOPAC-INV-021-16.

Flight cage experiments

We captured 100 *T. tricolor* bats (8 juvenile females, 41 adult females, 13 juvenile males, 38 adult males) in the wild by searching *Heliconia* spp., *Calathea* spp. and *Musa* spp. furred leaves. To avoid disturbing bats while in their roosts, we approached the leaf very quietly. If the leaf was occupied, we placed a transparent plastic bag in the opening of the leaf and carefully pinched the leaf at the bottom, so that the bats could crawl to the opening and into the plastic bag. Once the bats were in the plastic bag, they were transferred into cloth bags for transportation to flight cages (experiment 1, 2); capture sites were no more than 15 min away (by foot) from the flight cage where experiments were conducted.

While performing flight cage experiments, we kept each social group together in the same bag to avoid any social disturbance; this does not result in conflicts and mimics natural social conditions that may decrease stress. Moreover, we kept bags in a ventilated area with no direct exposure to sunlight. If bats were participating in individual trials, after the trial we returned them to the same bags. We performed the flight cage experiments with minimal manipulation of bats. For this, we liberated the bats inside the flight cage directly from the cloth bag. If the bats entered the furred leaf placed inside the cage, we retrieved them following the procedure explained above. If bats failed to enter the leaf after 5 min, we captured them using a hand-net. At the end of the flight cage experiments, we provided mealworms (*Tenebrio molitor*) and water to all individuals. We released the entire social group by placing all the individuals inside the same or a nearby leaf where they were found roosting earlier in the day. The procedures explained above, including manipulation, might cause some distress to some individuals. Thus, we decided not to perform individual trials on bats that were visually in distress and/or showing uncommon behaviours. However, these measures were not necessary during our experiments.

Experiments in the wild

To examine exploration behaviour in natural conditions, we captured 46 adult bats (29 females and 17 males) following the procedure explained above. For all the bats captured, an experienced person injected transponders (Mini ISO-Transponder PM-100) subcutaneously using the pre-loaded injector, in the mid-dorsal area to 46 adult bats (29 females and 17 males). These transponders were 1.4×8.5 mm and weighed 0.09 g. Thus, they represented an average of 1.87% (range 1.52–2.45%) of the bat's body mass. No anaesthesia was necessary for this procedure. The transponders were not removed after the experiments as this is an ongoing project.

RESULTS

Experiments

We performed experiments on 24 social groups, for a total of 100 bats (49 females and 51 males). Groups were composed of an average of four individuals (range 2–7).

Experiment 1

After playing back inquiry calls, males were more likely to produce response calls than females (chi-square test: $\chi^2_1 = 8.351$, $P = 0.004$; Fig. 1a), and juveniles were more likely to produce response calls than adults ($\chi^2_1 = 3.905$, $P \leq 0.001$; Fig. 1b). However, when they called, both males and females produced a similar number of response calls (mean \pm SD: males: 42.33 ± 42.12 ; females: 51.35 ± 42.02 ; $P = 0.559$). Juveniles and adults also produced a similar number of response calls (juveniles: 44.11 ± 44.04 ; adults: 46.12 ± 41.34 ; $P = 0.270$). The interaction between sex and age was also not significant ($P = 0.675$).

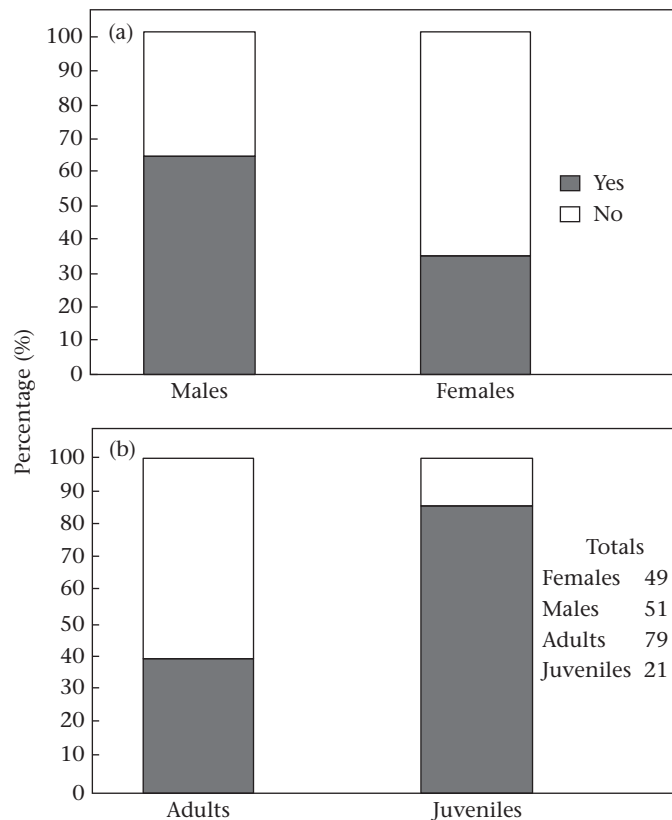


Figure 1. Percentage of (a) males and females, (b) adults and juveniles that produced (grey) and did not produce (white) response calls.

Experiment 2

There was a strong positive correlation (Pearson correlation coefficient: $r_p = 0.64$, $P < 0.0001$) between the number of response calls produced per inquiry call in experiment 1 and experiment 2, suggesting that vocal behaviour was consistent between experiments.

The average time groups spent finding the roost (i.e. from release to entrance) was significantly less when a vocal individual was placed in the furled leaf, compared to trials where a nonvocal bat was inside (paired t test: $t_{57} = 1.779$, $P = 0.040$; Fig. 2a). Moreover, the first individual entering the leaf did so faster when a vocal group member was in the roost ($t_{57} = 1.953$, $P = 0.027$; Fig. 2b). However, the time difference between the first and the last bat entering the roost did not differ significantly in trials when a vocal versus a nonvocal member was inside the roost ($t_{36} = 1.147$, $P = 0.129$; Fig. 2c).

Field Observations

The 46 adult bats monitored in natural conditions (29 females and 17 males) found a median of 2.5 (range 0–17) of the 40 furled leaves monitored per group. In the flight cage, 20 of these bats produced a median of 67.5 (range 4–251) response calls when inquiry calls were played back; 26 bats did not respond at all. The body condition/body mass of the bats influenced their general responsiveness, as bats that had poor body condition/low body mass were more likely to be nonvocal than bats that had good body condition/high body mass. Additionally, bats that were more explorative and that found more leaves in natural conditions were also more responsive to inquiry calls (for statistical details see Table 1, Fig. 3, Appendix, Table A1).

Overall, the median time that a bat ($N = 16$) took to attract a group member to a day roost was 573.5 s (range 2–16 420 s) in natural conditions. In cases where the first bat was a vocal individual ($N = 8$), the median time period for a second bat to enter was 7 s (range 2–1960 s). In contrast, if the first bat had not responded to inquiry calls ($N = 8$), the time for a group member to enter the roost was significantly longer (median: 1064 s, range 545–16 420 s; exact Wilcoxon rank-sum test: $W = 5$, $P = 0.003$). The more response calls that a bat produced, the shorter was the time for a second bat to find and enter the roost (Kendall rank correlation test: $\tau = -0.63$, $P = 0.002$).

DISCUSSION

Our results indicate that groups require significantly less time to locate a roost when the bat announcing its position is more vocal, which supports the findings of previous studies showing that production of social calls promote location of critical resources, such as roosts and food (Galef & Giraldeau, 2001; Kondo & Watanabe, 2009). In our experiments and field observations, whenever a vocal bat was inside a roost, the group invested significantly less time finding and entering the tubular leaf. On average, bats spent 1.6 min locating a roost (i.e. flying) when a quiet bat was inside the roost, whereas flying individuals spent less than 1 min locating and entering a roost with the aid of a vocal bat within it. In natural conditions, the time difference was even more extreme: bats found roosts after 4.5 min on average, with a more vocal bat; however, it took them 52.9 min to find the roost when a nonvocal bat entered first. Further studies should reveal why nonvocal bats do not support their groupmates in finding potential roosts – a behaviour that could be a risk for group cohesion. If nonvocal bats are in suboptimal body condition, then energetic constraints might prevent them from indicating their position to others. Alternatively, nonvocal bats may be concealing their position to minimize predation risk. Our results suggest that body condition influences vocal behaviour due to the energy costs associated with call production (Dechmann et al., 2009; Ophir, Schrader,

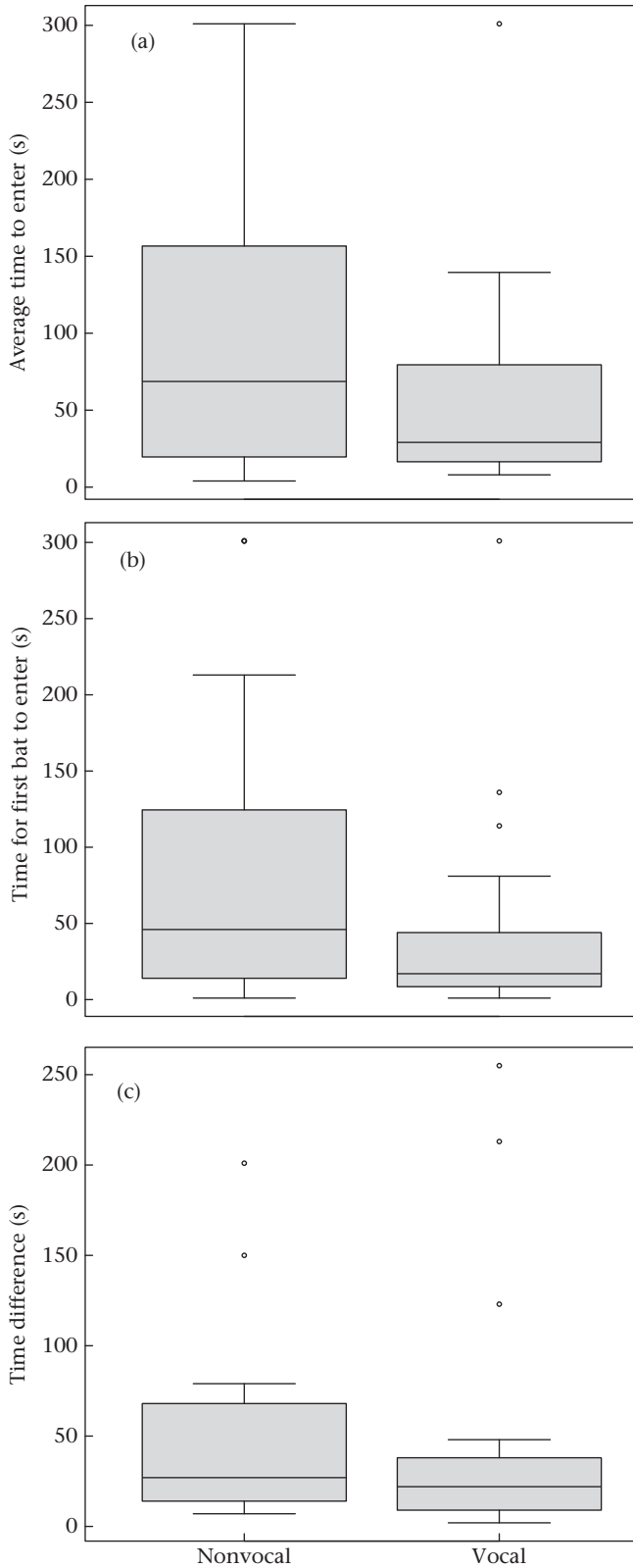


Figure 2. Time spent by social groups entering roosts when a vocal or a nonvocal bat was inside the roost. (a) Average group time. (b) Time of the first group member. (c) Time difference between the first and last group members. Vocal bats are defined as individuals that produced the largest number of response calls based on experiment 1, while nonvocals bats were individuals that produced the least number of response calls, which was always 0. Box plots show 25% and 75% quartiles (boxes), medians (lines in the boxes), outermost values within the range of 1.5 times the respective quartiles (whiskers) and outliers (circles).

Table 1

Results of the zero-inflated models with negative binomial error distributions

	Estimate	SE	Z	P
Females				
Count component: Exploration activity	0.13	0.06	2.34	0.02
Zero component: SMI	−66.65	26.55	−2.51	0.01
Males				
Count component: Exploration activity	0.23	0.08	2.68	0.007
Zero component: SMI	−55.76	24.72	−2.26	0.02

There was a positive relationship between exploration activity and response call production of the tested bats. Moreover, the body condition of the bats (SMI) explained the excess zeros in the data set.

& Gillooly, 2010; Peig & Green, 2009; Speakman, Anderson, & Racey, 1989). However, it is highly debated whether body condition indices purely reflect the energy reserves of focal animals and more detailed studies will be necessary to justify this observation (Peig & Green, 2009).

The use of social signals in the context of roost finding clearly decreases search time in *T. tricolor*, which can reduce the amount of energy required for powering flight, which is a very expensive mode of locomotion (for estimates of the energetic impact, see Appendix). Predation is another potential risk associated with a delay in roost finding. Many diurnal birds of prey consume bats (e.g. Boinski & Timm, 1985; Fenton et al., 1994; Robinson, 1994; Speakman, 1991). *Thyroptera tricolor* is known to change roosts during the day (G. Chaverri, personal observation), making them vulnerable to visually guided predators such as diurnal raptors. Thus, social signalling during roost searching may significantly reduce the risk of predation.

Our results also show that bats that were more vocal were also more efficient at finding potential roosts in the wild. In many studies of animal personalities and behavioural syndromes, individuals that are more exploratory (i.e. active in novel environments) also tend to be more vocal (Friel et al., 2016; Guillette & Sturdy, 2011; Hollander et al., 2008; Naguib, Kazek, Schaper, van

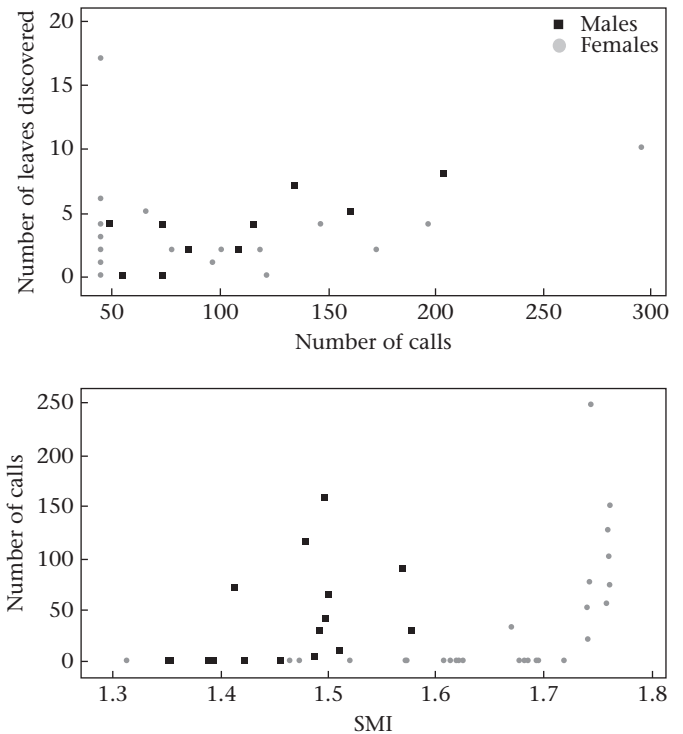


Figure 3. Relationship between the number of response calls produced by the bats and their exploration activity in the field (number of leaves discovered) as well as their body condition (SMI).

Oers, & Visser, 2010). This seems to be true in *T. tricolor*. However, bats that did not produce any response calls in our playback experiments strongly varied in their exploratory behaviour. Thus, it is possible that other factors influence the acoustic activity of these bats as well. Moreover, other studies in *T. tricolor* have shown that many group members seem to find roosts at night without social signals (Montero & Gillam, 2015), so it seems that all bats, not just the most vocal ones, are capable of locating roosting resources on a regular basis. *Thyroptera tricolor* is known to emit other acoustic signals (Montero & Gillam, 2015), and further studies are needed to address whether exploratory behaviour also correlates with production of other types of acoustic signals, including inquiry calls.

Overall, our results highlight the importance of vocal behaviour during location of critical resources; by producing acoustic signals that help group members quickly find roost sites, more vocal individuals may decrease the energetic costs of roost finding and predation risk of conspecifics while allowing groups to remain cohesive. So far, we do not understand how group composition, particularly the number of more vocal and less vocal bats, affects the process of roost finding and maintenance of cohesion. It is tempting to postulate that having fewer vocal bats may decrease fitness and group cohesion, yet other studies suggest that only a small proportion of informed individuals within a group is necessary for effective decision making (Couzin et al., 2005). Another topic that requires further scrutiny is whether bats within groups have vocal roles (equivalent to social roles sensu Bergmüller & Taborsky, 2010); that is, whether some group members are consistently vocal while others are consistently nonvocal. If groups are formed based on distinct vocal roles, we would expect that when the most vocal individual is removed from a group, that either another individual would increase its calling rate or a new individual would be recruited into the group to serve in that necessary 'vocal role'. Alternatively, vocal behaviour may be determined by physiological condition; if so, then we would expect that altering the body condition of group members would change their vocal behaviour. Regardless of the process promoting distinct calling rates, we now know that having individuals that call frequently is important during the process of roost finding, yet still we do not know whether their loss may have significant implications for the fitness of group members; this topic also clearly requires further research. An answer to these questions will provide a deeper understanding of how communication and sociality may affect social interactions in bats and other gregarious animals.

Acknowledgments

We thank Ronald Villalobos for logistics support during fieldwork, Julio Bustamante for his help during research permit application and Gerald Kerth for facilitating field equipment. We also thank Cristian Castillo, Michael Schöner, Jose Pablo Barrantes, Paula Iturralde-Pólit and Staminira Deleva for their help in the field and Joshua McKeown and the Office of International Education and Programs at SUNY Oswego for support during international travel. Finally, we thank Dr Michael Ferkin, Dr Brok Fenton and Dr Gerald Carter for their constructive comments and suggestions during the review process.

References

- Barta, Z., Flynn, R., & Giraldeau, L.-A. (1997). Geometry for a selfish foraging group: A genetic algorithm approach. *Proceedings of the Royal Society B: Biological Sciences*, 264(1385), 1233–1238.
- Barta, Z., & Szép, T. (1992). The role of information transfer under different food patterns: A simulation study. *Behavioral Ecology*, 3(4), 318–324.
- Beauchamp, G. (2000). Individual differences in activity and exploration influence leadership in pairs of foraging zebra finches. *Behaviour*, 137(3), 301–314.
- Beauchamp, G. (2006). Phenotypic correlates of scrounging behavior in zebra finches: Role of foraging efficiency and dominance. *Ethology*, 112(9), 873–878.
- Beauchamp, G., Belisle, M., & Giraldeau, L.-A. (1997). Influence of conspecific attraction on the spatial distribution of learning foragers in a patchy habitat. *Journal of Animal Ecology*, 66(5), 671–682.
- Bergmüller, R., & Taborsky, M. (2010). Animal personality due to social niche specialisation. *Trends in Ecology & Evolution*, 25(9), 504–511. <http://doi.org/10.1016/j.tree.2010.06.012>.
- Boinski, S., & Timm, R. M. (1985). Predation by squirrel monkeys and double-toothed kites on tent-making bats. *American Journal of Primatology*, 9, 121–127.
- Brown, C. R., Brown, M. B., & Shaffer, M. L. (1991). Food-sharing signals among socially foraging cliff swallows. *Animal Behaviour*, 42, 551–564.
- Buckley, N. J. (1997). Spatial-concentration effects and the importance of local enhancement in the evolution of colonial breeding in seabirds. *American Naturalist*, 149(6), 1091–1112.
- von Busse, R., Waldman, R. M., Swartz, S. M., Voigt, C. C., & Breuer, K. S. (2014). The aerodynamic cost of flight in the short-tailed fruit bat (*Carollia perspicillata*): Comparing theory with measurement. *Journal of the Royal Society Interface*, 11, 20140147. <http://doi.org/10.1098/rsif.2014.0147>.
- Chaverri, G., & Gillam, E. H. (2015). Repeatability in the contact calling system of Spix's disc-winged bat (*Thyroptera tricolor*). *Royal Society Open Science*, 2(1), 140197. <http://doi.org/10.1098/rsos.140197>.
- Chaverri, G., Gillam, E. H., & Kunz, T. H. (2013). A call-and-response system facilitates group cohesion among disc-winged bats. *Behavioral Ecology*, 24(2), 481–487. <http://doi.org/10.1093/beheco/ars188>.
- Chaverri, G., Gillam, E. H., & Vonhof, M. J. (2010). Social calls used by a leaf-roosting bat to signal location. *Biology Letters*, 6(4), 441–444. <http://doi.org/10.1098/rsbl.2009.0964>.
- Chaverri, G., & Kunz, T. H. (2011). Response of a bat specialist to the loss of a critical resource. *PLoS One*, 6, e28821.
- Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature*, 433, 513–516.
- Dechmann, D. K. N., Heucke, S. L., Giuggioli, L., Safi, K., Voigt, C. C., & Wikelski, M. (2009). Experimental evidence for group hunting via eavesdropping in echo-locating bats. *Proceedings of the Royal Society B: Biological Sciences*, 276(1668), 2721–2728. <http://doi.org/10.1098/rspb.2009.0473>.
- Dyer, J. R. G., Croft, D. P., Morrell, L. J., & Krause, J. (2008). Shoal composition determines foraging success in the guppy. *Behavioral Ecology*, 20(1), 165–171.
- Elgar, M. A. (1986). The establishment of foraging flocks in house sparrows: Risk of predation and daily temperature. *Behavioral Ecology and Sociobiology*, 19(6), 433–438.
- Encarnação, J. A., & Dietz, M. (2006). Estimation of food intake and ingested energy in Daubenton's bats (*Myotis daubentonii*) during pregnancy and spermatogenesis. *European Journal of Wildlife Research*, 52(4), 221–227. <http://doi.org/10.1007/s10344-006-0046-2>.
- Evans, C. S., & Marler, P. (1994). Food calling and audience effects in male chickens, *Gallus gallus*: Their relationships to food availability, courtship and social facilitation. *Animal Behaviour*, 47, 1159–1170.
- Fenton, M. B., Rautenbach, I. L., Smith, S. E., Swanepoel, C. M., Grosell, J., & van Jaarsveld, J. (1994). Raptors and bats: Threats and opportunities. *Animal Behaviour*, 48, 9–18.
- Findley, J. S., & Wilson, D. E. (1974). Observations on the Neotropical disk-winged bat, *Thyroptera tricolor* Spix. *Journal of Mammalogy*, 55(3), 562–571. <http://doi.org/10.1126/science.95.2469.427-b>.
- Friel, M., Kunc, H. P., Griffin, K., Asher, L., & Collins, L. M. (2016). Acoustic signalling reflects personality in a social mammal. *Royal Society Open Science*, 3(6), 160178. <http://doi.org/10.1098/rsos.160178>.
- Galef, B. G., & Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. *Animal Behaviour*, 61, 3–15. <http://doi.org/10.1006/anbe.2000.1557>.
- Guillette, L. M., & Sturdy, C. B. (2011). Individual differences and repeatability in vocal production: Stress-induced calling exposes a songbird's personality. *Naturwissenschaften*, 98(11), 977–981. <http://doi.org/10.1007/s00114-011-0842-8>.
- Harcourt, J. L., Sweetman, G., Johnstone, R. A., & Manica, A. (2009). Personality counts: The effect of boldness on shoal choice in three-spined sticklebacks. *Animal Behaviour*, 77, 1501–1505.
- Heinrich, B., & Marzluff, J. M. (1991). Do common ravens yell because they want to attract others? *Behavioral Ecology and Sociobiology*, 28(1), 13–21.
- Hollander, F. A., Van Overveld, T., Tokka, I., & Matthysen, E. (2008). Personality and nest defence in the great tit (*Parus major*). *Ethology*, 114(4), 405–412. <http://doi.org/10.1111/j.1439-0310.2008.01488.x>.
- Humfeld, S. C. (2013). Condition-dependent signaling and adoption of mating tactics in an amphibian with energetic displays. *Behavioral Ecology*, 24(4), 859–870. <http://doi.org/10.1093/beheco/art024>.
- Kerth, G., & Reckardt, K. (2003). Information transfer about roosts in female Bechstein's bats: An experimental field study. *Proceedings of the Royal Society B: Biological Sciences*, 270(1514), 511–515. <http://doi.org/10.1098/rspb.2002.2267>.
- Kondo, N., & Watanabe, S. (2009). Contact calls: Information and social function. *Japanese Psychological Research*, 51(3), 197–208. <http://doi.org/10.1111/j.1468-5884.2009.00399.x>.
- Kurvers, R. H. J. M., Prins, H. H. T., van Wieren, S. E., van Oers, K., Nolet, B. A., & Ydenberg, R. C. (2009). The effect of personality on social foraging: Shy barnacle geese scrounge more. *Proceedings of the Royal Society B: Biological Sciences*, 277(1681), 601–608. <https://doi.org/10.1098/rspb.2009.1474>.
- Leary, C. J., Jessop, T. S., Garcia, A. M., & Knapp, R. (2004). Steroid hormone profiles and relative body condition of calling and satellite toads: Implications for

proximate regulation of behavior in anurans. *Behavioral Ecology*, 15(2), 313–320. <http://doi.org/10.1093/beheco/arih015>.

McLean, J. A., & Speakman, J. R. (1999). Energy budgets of lactating and non-reproductive brown long-eared bats (*Plecotus auritus*) suggest females use compensation for lactation. *Functional Ecology*, 13, 360–372.

Montero, B. K., & Gillam, E. H. (2015). Behavioural strategies associated with using an ephemeral roosting resource in Spix's disc-winged bat. *Animal Behaviour*, 108, 81–89. <http://doi.org/10.1016/j.anbehav.2015.07.014>.

Mónus, F., & Barta, Z. (2008). The Effect of within-flock spatial position on the use of social foraging tactics in free-living tree sparrows. *Ethology*, 114(3), 215–222.

Naguib, M., Kazek, A., Schaper, S. V., van Oers, K., & Visser, M. E. (2010). Singing activity reveals personality traits in great tits. *Ethology*, 116(8), 763–769. <http://doi.org/10.1111/j.1439-0310.2010.01791.x>.

Newman, J. A., & Caraco, T. (1989). Co-operative and non-co-operative bases of food-calling. *Journal of Theoretical Biology*, 141(2), 197–209.

Norberg, U. M., Kunz, T. H., Steffensen, J. F., Winter, Y., & Vonhelversen, O. (1993). The cost of hovering and forward flight in a nectar-feeding bat, *Glossophaga soricina*, estimated from aerodynamic theory. *Journal of Experimental Biology*, 182, 207–227.

Ophir, A. G., Schrader, S. B., & Gillooly, J. F. (2010). Energetic cost of calling: General constraints and species-specific differences. *Journal of Evolutionary Biology*, 23, 1564–1569.

Peig, J., & Green, A. J. (2009). New perspectives for estimating body condition from mass/length data: The scaled mass index as an alternative method. *Oikos*, 118(12), 1883–1891. <http://doi.org/10.1111/j.1600-0706.2009.17643.x>.

Robinson, S. K. (1994). Habitat selection and foraging ecology of raptors in Amazonian Peru. *Biotropica*, 26(4), 443–458.

Ruczynski, I., Kalko, E. K. V., & Siemers, B. M. (2007). The sensory basis of roost finding in a forest bat, *Nyctalus noctula*. *Journal of Experimental Biology*, 210(20), 3607–3615. <http://doi.org/10.1242/jeb.009837>.

Safi, K., & Kerth, G. (2007). Comparative analyses suggest that information transfer promoted sociality in male bats in the temperate zone. *American Naturalist*, 170(3), 465–472.

Schuett, W., & Dall, S. R. X. (2009). Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, 77, 1041–1050.

Sih, A., Bell, A. M., & Ziemba, R. E. (2004). Behavioral syndromes: An integrative overview. *Quarterly Review of Biology*, 79(3), 241–277.

Sikes, R. S. (2016). Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy*, 97(3), 663–688. <http://doi.org/10.1093/jmammal/gyw078>.

Speakman, J. R. (1991). The impact of predation by birds on bat populations in the British Isles. *Mammal Review*, 21(3), 123–142. <http://doi.org/10.1111/j.1365-2907.1991.tb00114.x>.

Speakman, J. R., Anderson, M. E., & Racey, P. A. (1989). The energy cost of echolocation in pipistrelle bats (*Pipistrellus pipistrellus*). *Journal of Comparative Physiology A-Sensory Neural and Behavioral Physiology*, 165(5), 679–685.

Vonhof, M. J., & Fenton, M. B. (2004). Roost availability and population size of *Thyroptera tricolor*, a leaf-roosting bat, in northeastern Costa Rica. *Journal of Tropical Ecology*, 20, 291–305.

Vonhof, 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. *Animal Behaviour*, 68, 507–521.

Wilkinson, G. S., & Boughman, J. W. (1998). Social calls coordinate foraging in greater spear-nosed bats. *Animal Behaviour*, 55, 337–350.

Appendix

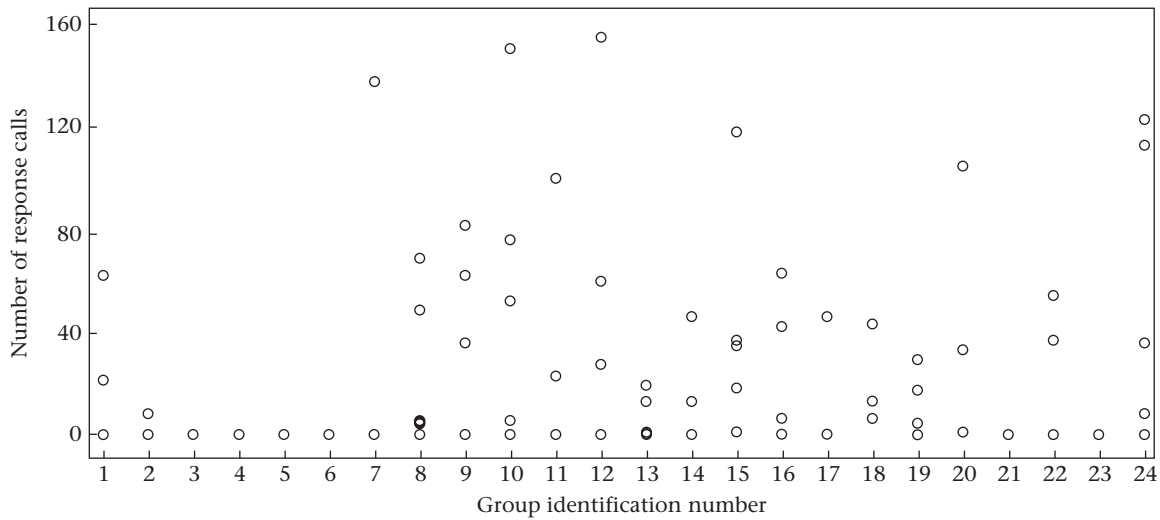


Figure A1. Distribution of vocal rates (i.e. number of response calls) within the 24 groups sampled in the Barú Field Station. Each circle represents an individual in a specific group. Data are based on results of experiment 1.

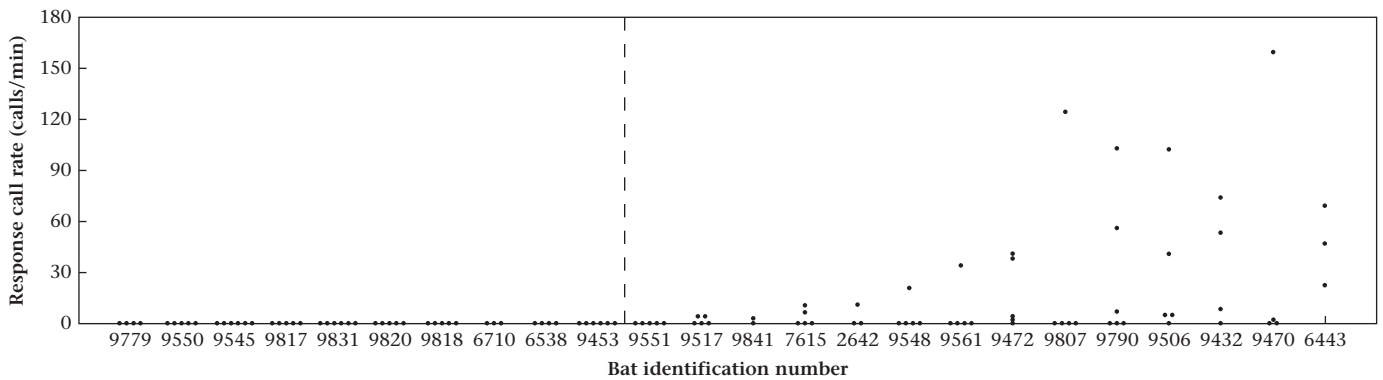


Table A1
Results of the zero-inflated models with negative binomial error distributions

	Estimate	SE	Z	P
Females				
Count component: Exploration activity	0.13	0.06	2.16	0.03
Zero component: Body mass	-11.46	4.55	-2.52	0.01
Males				
Count component: Exploration activity	0.23	0.08	2.68	0.007
Zero component: Body mass	-12.99	5.71	-2.28	0.02

There was a positive relationship between exploration activity and response call production of the tested bats. Moreover, the body mass of the bats explained the excess zeros in the data set.

Estimates of the Energetic Impact of Roost Searching in Thyroptera tricolor

In the flight cage (area = 36 m²), bats invested 54 s to locate tubular leaves in the presence of response calls and 1.6 min in their absence. This bat species is known to use roosting home ranges of 0.14–0.19 ha (Chaverri & Kunz, 2011; Vonhof, Whitehead, & Fenton, 2004), which would require an average investment of 62–85 min to sample for tubular leaves in the absence of social signals or

previous knowledge of the location of suitable roost sites, and 35–47 min with them. The mechanical power needed to sustain horizontal forward flight near the minimum flight speed in small bats is approximately 9 J/min (von Busse, Waldman, Swartz, Voigt, & Breuer, 2014; Norberg, Kunz, Steffensen, Winter, & Vonhelversen, 1993). Therefore, without social signals, the energy invested in finding roosts could be extrapolated to represent 0.55–0.76 kJ (depending of the size of the home range), whereas 0.31–0.43 kJ would be needed to power the search of roosts with the help of response calls. The energy invested in finding roosts without social signals thus represents up to 5–6.95% of the total daily energy intake of some insectivorous bats (Encarnaç o & Dietz, 2006; McLean & Speakman, 1999), whereas the use of social signals reduces the percentage of daily energy intake invested for roost finding to 2–3%. Of course, these numbers are a gross estimate of the energetics involved during roost finding with and without social signals in *T. tricolor*, and the relationship between search time and area of a patch may not be linear. We still need data on the mechanical power needed to sustain flight in this species, coupled with field experiments to determine whether the absence of vocal individuals increases search time of roosts and consequently individuals' daily energetic investment.