Animal Behaviour 142 (2018) 157–164

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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.

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.

https://doi.org/10.1016/j.anbehav.2018.06.018
0003-3472/

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 × 3 × 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 × 4 × 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