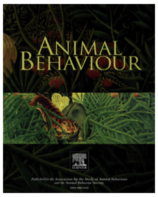
Animal Behaviour 127 (2017) 101–108

Contents lists available at ScienceDirect

Animal Behaviour

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



Social calls honestly signal female competitive ability in Asian particoloured bats

Bo Luo [a, b], Guanjun Lu [c], Kelly Chen [d], Dongge Guo [a], Xiaobin Huang [a], Ying Liu [a, *], Jiang Feng [a, b, *]

[a] *Jilin Provincial Key Laboratory of Animal Resource Conservation and Utilization, Northeast Normal University, Changchun, China*
[b] *College of Animal Science and Technology, Jilin Agricultural University, Changchun, China*
[c] *College of Urban and Environment Sciences, Changchun Normal University, Changchun, China*
[d] *College of Veterinary Medicine, University of Illinois Champaign Urbana, Urbana, IL, U.S.A.*

ARTICLE INFO

Article history:
Received 6 September 2016
Initial acceptance 26 October 2016
Final acceptance 27 February 2017

MS. number: 16-00788R

Keywords:
aggressive interaction
bat
competitive ability echolocation
foraging
social call

Why a variety of social animals vocalize during agonistic foraging interactions remains obscure. One possibility is that these signals advertise the signaller's competitive ability, playing a role in the defence of food resources, yet there is limited evidence in support of this idea. Here, we used adult female Asian particoloured bats, *Vespertilio sinensis*, to test whether individual variation in competitive ability when foraging can be explained by social calls. Using synchronized infrared video and audio recording, we monitored bat social vocalizations, dominance rank and weight gain in triads under controlled food conditions. Additionally, subsequent playbacks, consisting of experimental stimuli, echolocation pulses and silence, were presented to feeding bats in a laboratory. Analyses showed that females uttered low-frequency social calls composed of one to five syllable types during feeding competition. The rates of social vocalizations increased with reduced food availability. Interestingly, dominance score and weight gain correlated weakly with body size, but positively with call rate and associated parameters. Playback of social calls inhibited the visits of bats to the focal food dish compared to playback of silence and echolocation pulses. The amount of food consumed was greatly reduced in the presence of experimental stimuli versus controls. Collectively, these results highlight that acoustic signals serve as an honest indicator of bat competitive ability.

Competitive ability is the capacity of organisms to obtain resources, which has consequences for individual survival, reproductive success and population dynamics (Aarssen, 1984; Packer, Collins, Sindimwo, & Goodall, 1995; Pusey & Schroepfer-Walker, 2013). Exaggerated characters may correspond to competitive ability in foraging animals. In particular, the contribution of body size to intragroup dominance status has been observed in fish cohorts (Gill & Hartf, 1996), songbirds (Piper, 1997) and nonhuman primates (Pusey & Schroepfer-Walker, 2013). In great tits, *Parus major*, personality traits and problem-solving performance account for individual variation in food intake (Cole & Quinn, 2012). How acoustic signals might be linked to competitive ability while foraging has rarely been investigated, however, especially in females.

Many social animals produce repetitive vocalizations while competing for food within and between groups (Amorim & Hawkins, 2000; Marzlufi & Heinrich, 1991; Sazima & D'Angelo, 2012). These calls may indicate the signaller's competitive ability due to energy constraints (Vehrencamp, 2000). Producing sounds at greater rates requires more energy, and only superior individuals are thought to be capable of sustaining costly sound output (Vehrencamp, 2000). Consequently, call rate may provide information about the signaller's body quality, which helps intimidate potential rivals away from food sources. In streaked gurnards, *Trigloporus lastoviza*, for example, dominant foragers repeatedly growl to claim ownership of food (Amorim & Hawkins, 2000). In ring-tailed lemurs, *Lemur catta*, high-ranking males frequently produce squeals while engaging in agonistic interactions and consequently gain preferred access to food (Bolt, 2013). In these circumstances, call rate and associated acoustic parameters are predicted to be positively associated with dominance rank and food intake.

In addition to honest information on body quality, calls produced in feeding competition may reflect the signaller's body size

---

* Correspondence: J. Feng and Y. Liu, Jilin Provincial Key Laboratory of Animal Resource Conservation and Utilization, Northeast Normal University, 2555 Jingyue Street, Changchun 130117, China.

E-mail addresses: liuy252@nenu.edu.cn (Y. Liu), fengj@nenu.edu.cn (J. Feng).

http://dx.doi.org/10.1016/j.anbehav.2017.03.012
0003-3472/

and therefore competitive ability. Larger individuals tend to have longer vocal tracts and thicker vocal chords, allowing them to produce comparatively low-frequency sounds (Fitch & Hauser, 2003). Since larger individuals are more likely to win fights (Morton, 1977), low-frequency calls may signal higher fighting ability, and further enhance resource-holding potential. Davies and Halliday (1978) documented a prominent allometric relationship between body size and fundamental frequency of advertisement calls in male toads, *Bufo bufo*. Playback of the low-pitched calls elicited fewer attacks from male toads than playback of high-frequency calls. In male fallow deer, *Dama dama*, low-frequency groans are linked to larger body size and higher dominance rank (Vannoni & McElligott, 2008). If this holds for calls involved in feeding competition, individual body size and competitive ability should be predicted by frequency parameters of the calls.

Echolocating bats primarily use acoustic signals for social communication (Fenton, 2003). In addition to the use of echolocation pulses for spatial orientation and prey pursuit, echolocating bats utter social calls to defend feeding territory (Barlow & Jones, 1997; Racey & Swift, 1985; Rydell, 1986). Social calls in some foraging bats are emitted at greater rates when insect abundance is lower, along with an increase in aggressive chases and physical contact (Rydell, 1986). Previous work on common pipistrelle bats, *Pipistrellus pipistrellus*, has shown that social calls can impair intraspecific activity in foraging areas (Barlow & Jones, 1997). Recently, a controlled experiment demonstrated that male big brown bats, *Eptesicus fuscus*, utilized frequency-modulated bouts to announce food ownership, resulting in greater foraging success for the callers (Wright, Chiu, Xian, Wilkinson, & Moss, 2014). Nevertheless, the relationship between bat social calls and competitive ability (i.e. dominance and food intake) when foraging remains uncertain.

The aim of this study was to establish the relationship between social calls and competitive ability in the Asian particoloured bat, *Vespertilio sinensis*, which is an aerial forager that requires open habitats. These bats are widely distributed in central and eastern China, Russia, Mongolia, Korea and Japan (IUCN, 2016). Adult females form maternal colonies between May and August, which may consist of several tens to thousands of individuals (Fukui & Agetsuma, 2010). At that time, food competition within maternal colonies appears to be intense because of high energy demands for reproductive output, as indicated by frequent chases and loud screams in foraging sites (Luo & Lu, 2014). We hypothesized that social calls given by female bats honestly signal their competitive ability, and play a role in the defence of food resources. To test this hypothesis, we first monitored female social vocalizations, dominance rank and weight change in groups of three under controlled food conditions. We then explored the function of social calls by performing playbacks in a laboratory. We made the following predictions: (1) bat social vocalizations increase with reduced food availability; (2) rates of social vocalizations and frequency parameters correlate with individual dominance score and weight gain; (3) playback of social calls reduces foraging activity in comparison with neutral playback.

METHODS

Ethical Note

Experimental procedures complied with the relevant laws for studies involving vertebrates of the People's Republic of China and ASAB/ABS Guidelines for the Use of Animals in Research. This work was approved by the Committee on the Use and Care of Animals at the Northeast Normal University (approval number: NENU-W-2014-101). In the wild, *V. sinensis* roosts in artificial structures near residential areas. They are not sensitive to marking, recapture and weighing when exposed to the light. They have poor flight manoeuvrability, allowing us to easily recapture them with a hand net in the feeding room. To minimize potential adverse effects, bats were fed mealworms and given water after each recording trial. We did not cause physical harm to bats and no bats died. All captured bats were released into the wild after this study.

Study Subjects

In August 2014, we caught 15 adult female *V. sinensis* with mist nests from a maternal colony in Hacheng, Heilongjiang, P. R. China. This colony roosted in an abandoned highway bridge, and contained more than 500 members. During this period young bats were weaned and were capable of flight and foraging. All captured adults were maintained in a feeding room (3 × 3 m and 2.5 m high) with regulated temperature (20–25 °C), humidity (50–70%) and light-dark cycles (natural photoperiod in Changchun). During the first week, we trained bats to capture mealworms and drink water in 12 plastic dishes (six food dishes, six water dishes) positioned on the walls. During the second week, we quantified individual food intake under excess food conditions when all bats were housed together. We weighed the mealworms before and after each feeding using an electronic balance (ProScale LC-50), which indicated that each bat consumed 10.98 ± 0.41 g of mealworms per day. We measured bat forearm length as an indicator of body size using a vernier calliper (TESA-CAL IP67, TESA Tech., Renens, Switzerland).

Call and Video Collection

After a 2-week acclimation period, 15 experimental bats were randomly divided into five groups, each containing three members (referred to as triads). The use of triads allowed us to conveniently monitor individual vocalizations and aggressive interactions. To recognize individual identity within each triad, we marked bats with numbered aluminium alloy bands (0.05 g, which is less than 0.25% of the bat's body mass; Porzana Ltd, Icklesham, U.K.) on their left forearm, right forearm or both. We ensured that the bands could move loosely on the bat's forearm but could not fall off. Based on our recent study (Jin et al., 2015), the bands had no negative impact on flying behaviour of bats. To record social vocalizations, we transferred each triad from the feeding room into a recording room (3 × 3 m and 2.5 m high) in soft cloth bags. We then housed each triad in an experimental cage (1 × 0.6 m and 0.8 m high) in the recording room, where environmental conditions were similar to those in the feeding room. After allowing bats 1 day to familiarize themselves with the cage, we used two conditions of food availability to encourage agonistic interactions. The excess food condition was 60 g of mealworms and the limited food condition was 20 g of mealworms. Combined with synchronized video via an infrared camera (Sony HDR-CX760PJ760), we recorded social vocalizations from 2000 to 0700 hours the next day, using an UltrasoundGate 116 (Avisoft Bioacoustics, Berlin, Germany) connected to a laptop computer. The sampling frequency of sounds was set as 375 kHz at 16 bits/sample. The condenser microphone (CM16/CMPA; frequency range: 10–200 kHz) was mounted on a small tripod about 1 m from focal bats. The gain was adjusted to avoid signal overload. Acoustic recordings were repeated on five separate occasions for each triad under separate food conditions, in a 1- or 2-day interval. After each recording, we released experimental bats into the feeding room.