

Social Calls Predict Foraging Success in Big Brown Bats

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Summary

Animals foraging in the dark are engaged simultaneously in prey pursuit, collision avoidance, and interactions with conspecifics, making efficient nonvisual communication essential. A variety of birds and mammals emit food-associated calls that inform, attract, or repel conspecifics (e.g., [1]). Big brown bats (*Eptesicus fuscus*) are insectivorous aerial hawkers that may forage near conspecifics and are known to emit social calls (e.g., [2–5]). Calls recorded in a foraging setting might attract (e.g., [6]) or repel [7] conspecifics and could denote territoriality or food claiming. Here, we provide evidence that the “frequency-modulated bout” (FMB), a social call emitted only by male bats (exclusively in a foraging context) [5], is used to claim food and is individually distinct. Bats were studied individually and in pairs in a flight room equipped with synchronized high-speed stereo video and audio recording equipment while sex and experience with a foraging task were experimentally manipulated. Male bats emitting the FMB showed greater success in capturing prey. Following FMB emission, interbat distance, diverging flight, and the other bat’s distance to the prey each increased. These findings highlight the importance and utility of vocal communication for a nocturnal animal mediating interactions with conspecifics in a fast-paced foraging setting.

Results and Discussion

We flew male and female big brown bats (*Eptesicus fuscus*) alone and in pairs in the presence of a tethered prey item and with one, both, or neither bat having experience with this novel foraging task. Synchronized high-speed video and audio recordings were acquired and digitally stored, allowing for careful analysis of call features and reconstruction of bat 3D flight paths and positions. We examined bats’ behavior surrounding the frequency-modulated bout (FMB): a sequence of three to four calls that are longer in duration and lower in frequency than typical big brown bat echolocation pulses ([5]; Figure 1). In total, we recorded 186 FMBs from at least six individuals. Several lines of evidence indicate that FMBs are individually distinct and serve a food-defense function in male bats.

FMBs Are Individually Distinct and Only Produced by Males

Of the 186 FMBs recorded, we successfully identified which bats emitted 90% of the calls. Six individuals flying in 17–57

paired trials each emitted at least two FMBs (range per bat: 2–65). Call parameters for each bat are listed in Table S1 (available online), and spectrograms are presented in Figure 1 and Figure S1. Results from a discriminant function analysis (DFA; quadratic, assuming unequal covariances) using start frequency, end frequency, midfrequency (frequency midway between start and end time), duration, and interpulse interval (IPI: time from the end of one pulse to the start of the next) revealed that 96.4% of FMBs were correctly assigned to the individual emitting the call (Figure 2), compared with a chance level of 25%. Correct classification for individual bats varied from 93.9% to 100%, and 98.2% of the variation was explained by the first two canonical dimensions. Much of the variation is accounted for by midfrequency and duration (Table S2). In addition to serving a food-defense function, these calls appear to provide information about the individual.

FMBs Are Produced Only When at Least One Skilled Forager Is Present

We never recorded FMBs when only two naive foragers were present ($n = 181$ trials), and FMBs were much more prevalent (80 of 152 trials) when two experienced bats were competing for the prey item than when only one skilled forager was present (11 of 170 trials). We considered trials with only naive bats to be a nonforaging context because neither bat was able to obtain the prey item, whereas trials with at least one skilled bat were considered to be a foraging context. Although communicative calls can serve to convey information about food and/or increase the foraging-related behavior of other individuals (e.g., rhesus macaques [*Macaca mulatta*] [8]; domestic chickens [*Gallus gallus domesticus*] [9]; chimpanzees [*Pan troglodytes*] [10]; bonobos [*Pan paniscus*] [11]; marmosets [*Callithrix geoffroyi*] [12]) or coordinate foraging among group members (e.g., *Phyllostomus hastatus* [6]), our results indicate the opposite function of FMBs. The bats from which we recorded FMBs were competing for a single prey item, thus making it much more likely that this social call serves to defend or claim food rather than to attract other bats to a feeding area.

FMB Emission Repels Conspecifics from Caller and Food

Following FMB emission, bats alter their flight configurations and increase their distance from one another, and the noncalling bat increases its distance from the prey item, as described below.

FMB Emissions Influence Flight Trajectories

Bats changed their flight configurations (see Experimental Procedures for details) following FMB emission significantly more often than expected by chance. Specifically, for two-thirds of the FMB emissions with corresponding 3D position data available, flight configurations changed between the 500 ms before and the 500 ms after FMB emission. When examining data for each bat emitting multiple FMBs over the course of all trials, flight configuration changed during more than half of the recordings containing an FMB (range: 54.5%–93.8%). For comparison, we examined changes in flight behavior in 12 time segments from non-FMB-emitting female-female pairs and found that flight behavior changed in 50% of segments. When the identities of the FMB emitter and the successful forager could be determined ($n = 69$

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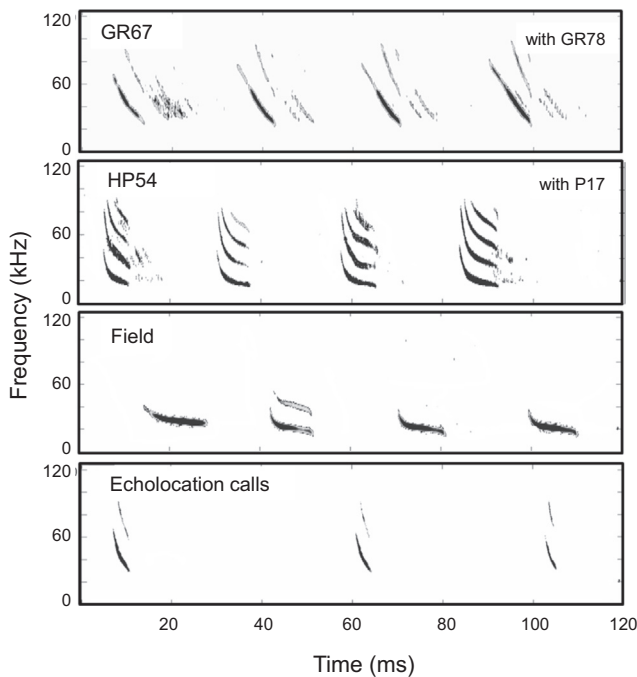


Figure 1. Spectrograms of FMBs and Echolocation Calls

Examples of FMBs recorded in a flight room from two male bats (top two panels) and in the field (third panel) from a third bat. Echolocation calls recorded in the flight room (bottom panel) are shown for comparison. Note that, compared with echolocation pulses, FMBs have longer duration, shorter PI, and lower end frequencies. The x axis indicates ms, and the y axis indicates kHz. Echoes are more prevalent in the laboratory recordings due to the enclosed flight room setting versus the field setting. Bat ID numbers correspond to those seen in Figure 2 and in Movies S1, S2, and S3. See Supplemental Information for additional examples of FMBs (Figure S1) and call parameters of each bat's FMBs and of echolocation pulses (Table S1).

FMBs), we also examined whether the calling bat was leading or trailing at the time the FMB was emitted. In only one instance out of 69, the calling bat was trailing prior to FMB emission: a juvenile male emitted the FMB, and the skilled adult male with whom he was flying caught the prey in this trial. During the 500 ms prior to FMB emission, the calling bat was either leading or converging with the other bat in 84% of cases (bats were diverging or the calling bat was trailing in remaining trials). In contrast, during the 500 ms after FMB emission, the calling bat was either trailing or diverging from the other bat in 65.2% of FMBs (Figure 3). A comparison of all four possible configurations revealed a significant difference in flight patterns before versus after FMB emissions ($X^2_3 = 46.12$, $p < 0.0001$, $n = 138$ values; Figure 3). If two bats were converging in flight (e.g., toward the prey item) or one bat was leading and the bats were flying close together, the leading bat (and/or the bat closest to the prey item) often emitted an FMB and then caught the prey item afterward. The second bat then often changed its flight path, such that it was diverging from or flying past the other bat and prey item, thus abandoning an attempt to catch the prey item during that trial.

FMB Emissions Increase Interbat Distances

We saw a pronounced change in interbat distance, with bats flying an average of almost 0.5 m farther apart immediately after FMB emission, indicating that emission of an FMB acts to repel the other individual (Movie S1). When considering

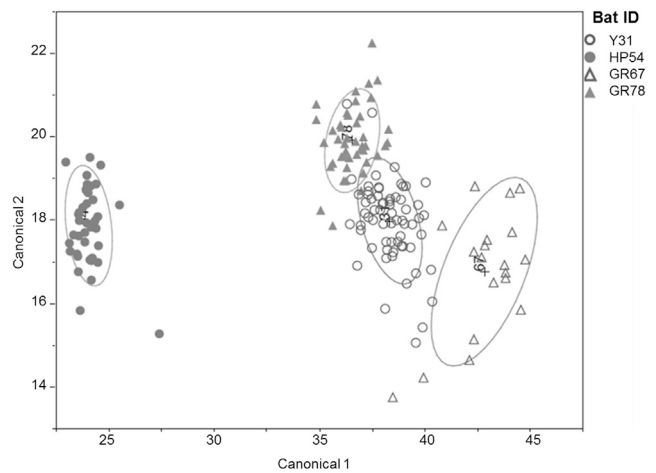


Figure 2. DFA Showing Individual Variations in FMBs

Plot of the first two canonical variables from a DFA, which correctly assigned 96.4% of calls to the correct bat. Each point represents an FMB, with ellipses marking 50% bivariate normal contours around individual centroids. See Table S2 for the relative importance of each parameter to each canonical variable.

the data from all pairs together, bats flew significantly farther apart during the time segment after FMB emission compared with the time segment before FMB emission ($F_{1,5} = 15.11$, $p = 0.012$; Figure 4). The interbat distance increased after FMB emission for 73.6% of the FMBs recorded, and the mean interbat distance was greater after FMB emission than before FMB emission for every pair except one female-male pair. In addition, free-flying, foraging big brown bats observed in the field appeared to be engaged in aggressive or territorial flight behavior during the same time period that FMBs were recorded (H. ter Hofstede, personal communication).

FMB Emissions Increase the Distance between the Competing Bat and Prey

We tested whether the non-FMB-emitting bat increased or decreased its distance to the tethered prey item following FMB emission. Comparison data from female-female trials (containing no FMBs; $n = 10$ time segments, with two bats for each) revealed that bats increased their distance to the mealworm 50% of the time, whether the initial distance was <1.5 m or >1.5 m when flying in our 6×7 m test room. Based on this observation, we compared the actual propensity of bats to increase their distance to the prey item following FMB emission to the prediction that they would do so 50% of the time. Although there was no significant difference in behavior when considering all bat-prey distances together (Fisher's exact test: $p > 0.05$), we found that bats positioned <1.5 m from the tethered prey item at the time of their competitor's FMB emission were significantly more likely than expected by chance to increase their distance to the mealworm following FMB emission (Fisher's exact test: $p < 0.007$; Movie S2). When a nonemitting bat's initial distance was <1.5 m from its prey, it increased its distance from the worm following 84.4% of FMBs ($n = 32$ FMBs), whereas there was an increase following only 36.4% of FMBs when the initial distance was >1.5 m ($n = 33$ FMBs). These findings indicate that when one bat was flying close to the prey item, FMB emission by its competitor resulted in the nonemitting bat increasing its distance to the mealworm, suggesting that it aborted a prey-capture attempt. This offers further evidence

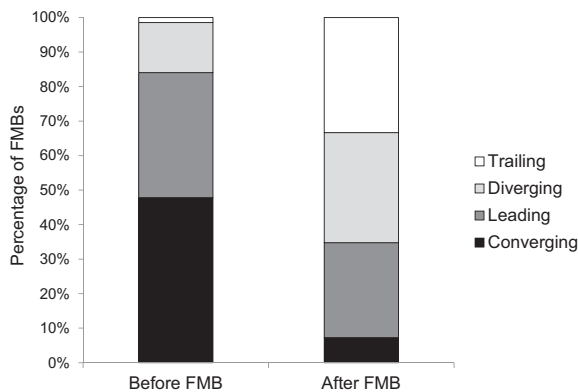


Figure 3. Bat Flight Configurations before and after FMB Emission
Average flight patterns of bats 500 ms before and 500 ms after FMBs were emitted (n = 69). “Trailing” and “leading” are in reference to the bat emitting a given FMB. Flight patterns differed significantly before versus after call emission.

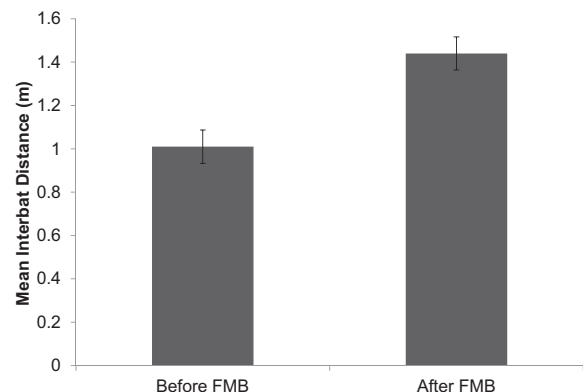


Figure 4. Interbat Distances before and after FMB Emission
Mean interbat distance during the 500 ms before versus the 500 ms after FMBs were emitted. Bats flew significantly farther apart after FMB emission (n = 72 sequences). Error bars indicate 1 SE. See also [Movie S1](#).

that FMBs serve to deter a competing bat, allow the calling bat to lay claim to the food item, and increase the calling bat’s chances of capturing the prey itself.

FMB Emission Is Associated with Successful Prey Capture

To determine whether FMB emission predicts prey capture attempts, we tested the relationship between FMB emission and subsequent feeding buzz emission. Compared with chance (each bat attacking the prey in 50% of trials), the bat emitting the most FMBs prior to feeding buzz emission in male-male trials was significantly more likely to attack the mealworm (70.6% of trials; n = 34 trials; $X^2_1 = 5.77$, $p = 0.016$; [Movie S3](#)).

Whereas food-related calls often attract conspecifics [1], use of vocalizations to deter others from food or promote spacing of foragers has been documented in some species. For example, white-faced capuchins (*Cebus capucinus*) emit calls to claim ownership of a food item, thus reducing chances of subsequent aggressive encounters over the food [13]. Similarly, ravens emit a specific call type when a food item is available in limited quantities [14], and green woodhoopoes and pied babblers use vocalizations to mediate spacing of conspecific competitors for food [15, 16]. Within the order Chiroptera, Barlow and Jones [7] found that *Pipistrellus pipistrellus* increased emission of social calls when foraging in areas with low insect densities and that playing back these calls resulted in decreased bat activity in the area. Additionally, Rydell [17] reported that female northern bats (*Eptesicus nilssonii*) defend foraging areas via vocalizations and aggressive chasing, and aerial “dogfights” among foraging *E. fuscus* have been reported in the field [18].

Territoriality related to food and mediated, in part, via vocalizations produced by males during flight has been observed in some bird species (see [19]), such as blue-throated (*Lampornis clemenciae*) and amethyst-throated (*Lampornis amethystinus*) hummingbirds [20, 21]. Despite FMBs being recorded exclusively from males, we have no evidence that these calls are used for mate attraction, given that they were produced outside of the mating season while foraging. However, it is possible that a similar call is used in a mating context. In the Barlow and Jones [7] study described above, the authors state that the social calls emitted during foraging are very similar to songflight calls given by males during the mating season [22]. Indeed, Monroy et al. (J. Monroy et al., 2005,

NASBR, conference) describe calls that resemble the first portion (initial three to four frequency-modulated [FM] sweeps) of FMBs, and they report that these signals are emitted by *E. fuscus* males in a mating context. Thus, it is possible that males use a variation of the same vocalization to assert territoriality in both mating and foraging contexts.

Calls used for territorial advertisement are expected to convey individual-specific information (e.g., [19]) to allow the listener to identify its competitor. Whereas some species (e.g., chimpanzees [23]) are known to emit individually distinct food-associated calls, few records of consistent individual variation in this type of call have been reported. However, individual variation in vocalizations is not uncommon in the contexts of group cohesion (e.g., pallid bats [24]), mate advertisement (e.g., frogs [25]; owls [26]), or territory defense (e.g., songbirds [19]). It seems likely that male big brown bats use FMBs to advertise dominance or a territory. Indeed, Fenton [27] describes a wild big brown bat “patrolling” a foraging area and chasing away some of the other bats that enter the area, along with chases sometimes including physical contact between pairs of bats. When multiple bats might be present at the same foraging site, individual identification could be especially useful in mediating subsequent interactions.

With regard to the FMB being recorded only from males, it is possible that males are more likely to vocally defend a feeding area or food source because they are less likely than females to be foraging near familiar individuals. Female big brown bats form nonrandom associations with their roostmates [28, 29], and colony members tend to leave the roost to forage within a close time period, suggesting that females may forage near familiar individuals. In contrast, males often roost alone or in much smaller bachelor colonies [30].

Here, we provide the first report of an ultrasonic social call produced exclusively by free-flying *E. fuscus* males in a foraging context. In addition to displaying individual variation, this call repels other individuals and is associated with higher foraging success by the caller. These findings highlight the importance of vocal communication in mediating interactions with conspecifics in a fast-paced, aerial-foraging environment, and they pave the way for other research investigating the potentially sophisticated nature and function of bat social calls, both in the laboratory and in the field. Considering the fact that most food-related calls appear to attract other

individuals and are not known to be individually distinct, these findings offer new insight into aerial foragers' use of vocalizations in social interactions.

Experimental Procedures

Subjects, Experimental Setup, and Identification of Social Calls

We flew individuals and pairs of big brown bats (*E. fuscus*) in the presence of a tethered prey item (mealworm: larval *Tenebrio molitor*) in a 7 × 6 × 2.5 m anechoic flight room between July and September of 2005–2007. We recorded paired-bat trials from 38 individuals (23 females, 15 males), including 14 young and 24 adult (at least 1-year-old) bats.

As bats flew, two high-frequency-sensitive microphones (Ultra Sound Advice), amplified and recorded at 250 kHz/channel (Wavebook, IOTech), captured 8 s segments that were synchronized with high-speed (240 frames/s in 2005 and 2006; 250 frames/s in 2007) stereo infrared-sensitive video data from two cameras (in 2005 and 2006, Kodak MotionCorder Analyzers, Model 1000, Eastman Kodak; in 2007, Photron PCI-R2, Photron) in a room with low-intensity and long-wavelength overhead lighting (>650 nm red filters, Reed Plastics; see [5, 31, 32] for detailed methods). This research was conducted with approval from the Institutional Animal Care and Use Committee at the University of Maryland (protocols R-05-15 and R-10-30) and under a Maryland Department of Natural Resources collecting permit. As a condition of the permit, bats were not released at the conclusion of the study and were subsequently used for other experiments.

Field recordings, which were provided courtesy of H. ter Hofstede (personal communication), were made in a clearing in front of a house surrounded by woods in New Hampshire. Calls were recorded using an Avisoft Bioacoustics Condenser microphone (CM16) and Avisoft UltraSoundGate 116 Hme with a USB connection to a tablet computer running Avisoft Recorder (sampling rate: 250 kHz, 16-bit format). A maximum of two bats were visually observed at the same time, and apparent aggressive interactions, including chasing and very small interbat distances, were visually observed during the same general time period that FMBs were recorded (H. ter Hofstede, personal communication). Bat species was determined from parameters of the echolocation calls recorded with the FMBs.

The FMB is a sequence of three to four FM sweeps often followed by several short, buzz-like calls, with relatively short pulse interval (PI; Figure 1). Using a combination of visual and auditory examination, confirmed with results from a DFA to distinguish this call type from others [5], we identified FMBs in 91 of the 322 two-bat recordings with at least one bat skilled at capturing the prey item, and in 0 of the 603 single-bat recordings in this study. Table S3 summarizes the number of trials in each context and the number of trials of each type containing one or more FMB.

Flight Behavior

Interbat Distance and Flight Configurations

Using data from reconstructed 3D flight paths, we calculated mean interbat distances for the 500 ms before the start and the 500 ms after the end of each FMB. Only video frames with both bats flying in the calibrated volume (in the area in view of both cameras) were included in the analyses. Therefore, position data were not available for every FMB, and we sometimes had fewer than 500 ms of video position data before or after a social call. For FMBs with position data available, we established the identity of the caller in all but three cases. We compared the mean interbat-distance values before and after each FMB, using a generalized linear mixed model (GLMM) that accounted for which bat emitted each FMB. Video position data were available for time segments both before and after FMB emission for 72 FMBs emitted by six individuals.

Using information about position, flight direction, and angle between the bats during the 500 ms segment before and the 500 ms segment after each FMB, we calculated mean flight configurations for each segment by averaging values from each video frame. We assigned each segment to following, converging, or diverging flight (see [31] for details). The "following" flight category was subdivided based upon which bat was leading and which was trailing. We compared mean flight configurations before and after FMB emission. We compared the number of FMBs with changes in flight behavior before versus after call emission, with a goodness-of-fit test and an expected change rate of 50%. We based this expected value both on chance and on the percentage of sample segments during which bats flying in female-female trials changed their flight configurations (as with trials containing FMBs, both bats were flying within the calibrated space of the video cameras during all female-only segments used).

To assess individual variation in calling behavior, we examined the number of FMBs during which flight configuration changed for each bat known to emit multiple FMBs ($n = 68$ FMBs from four bats; mean number of FMBs per bat \pm SD = 17 ± 7.35). In addition, we examined mean flight patterns before and after the FMBs were emitted. For pairs of bats with at least five FMBs emitted by a single individual (three pairs had three or fewer FMBs), we conducted a separate analysis of flight configurations before and after calls occurred. We conducted separate analyses (Fisher's exact tests, with a sequential Bonferroni correction to account for all six comparisons) for the same pair of bats if a different bat was emitting the FMB.

Bat Distances to Prey Item

To determine whether emission of an FMB by one individual influenced the behavior of the other bat toward the prey item (mealworm), we calculated the mean distance of each bat to the mealworm during the 500 ms before and the 500 ms after each FMB was emitted. For comparison, we used data from female-female trials (containing no FMBs) by matching the times that FMBs occurred in trials containing male bats and evaluating the distance of each female bat to the mealworm before and after this time segment. We then evaluated whether the distance of the non-FMB-emitting bat to the mealworm increased or decreased when the FMB was emitted across all trials and within trials wherein the nonemitting bat was initially closer (<1.5 m) to the prey item, using a Fisher's exact test to compare our findings to chance.

Call Emission and Prey Capture

We examined whether emission of FMBs was related to prey-capture success by either bat in male-male pairs (e.g., by attracting or repelling the noncalling bat). For this analysis, we considered only pairs of males because females never emitted FMBs in our study. We evaluated the relationship between the number of FMBs emitted before a feeding buzz and an attack on the prey item by the caller. Based on examination of >700 audio files, we considered the start of a feeding buzz (which is indicative of prey capture) to be the point at which the PI dropped below 9 ms and only used the last feeding buzz present in a given trial (bats sometimes emitted buzzes earlier in the trial without actually attacking or taking the prey). We then used a chi-square test to compare the percentage of trials in which the bat emitting the greatest number of FMBs prior to the buzz attacked the mealworm, with a chance rate of each bat in a given trial capturing the mealworm 50% of the time.

Individual Variation

We used a combination of video position and sound arrival time across multiple microphones to identify which bat had emitted each vocalization when possible (see [31]). We then conducted a DFA using start frequency (kHz), end frequency (kHz), midfrequency (kHz), duration (ms), and IPI (ms). We measured parameters of individual pulses but took the mean of all pulses within each FMB, and we used FMBs themselves as the unit in the DFA to look for differences in parameters of calls emitted by the four male bats known to emit ten or more FMBs (168 FMBs and 588 pulses total; 19–65 FMBs and 65–219 pulses per bat). For each of these four males, FMBs from multiple recording sessions (on 4, 8, 9, and 10 different days) were included in the DFA. Nested ANOVA using bat and test day (nested within bat) as random effects showed that test day never accounted for more than 6% of the variation for any of the three canonical variables generated by the DFA. In addition, for three bats, FMBs from trials with more than one partner were included, and for one bat (Y31), FMBs from 2 calendar years were included. Because a DFA using all of the data can overestimate correct classification, we ran cross-validation DFAs using four different subsets of data. Considering the fact that the cross-validation results were similar (88%–97% correct classification for independent calls after training on the other half) to those using all of the data at once (96.4% correct), we report the results from the entire data set.

Supplemental Information

Supplemental Information includes one figure, three tables, and three movies and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.02.058>.

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