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Social calls coordinate foraging in greater spear-nosed bats

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Abstract. The function of social calls emitted by foraging bats has received little study. Here we use observations of free-ranging greater spear-nosed bats, *Phyllostomus hastatus*, and field playbacks to determine whether audible, broad-band 'screech' calls attract mates, warn conspecifics or influence access to food. Five lines of evidence suggest that screech calls enable adult females from the same roosting group to fly together from the day roost to feeding sites. (1) Seasonal differences in diet influenced the rate of screech calling recorded outside the cave roost, as well as how often bats departed together. Bats called more often and flew in larger groups when feeding on a concentrated resource, balsa, *Ochroma lagopus*, flowers, in winter than on more dispersed *Cecropia peltata* fruit in spring. (2) Observations of bats flying outside the cave, in flyways and at feeding sites indicated that screech calls occurred more often when bats flew in groups than alone. (3) Females from the same roosting group were netted at the same feeding site, sometimes simultaneously, several kilometres from the cave. (4) Calling colour-marked adult females outside the cave were joined by a female group member, both on initial departures and on second foraging trips, more often than non-calling bats. (5) Playbacks attracted conspecifics at roost and feeding sites. Screech calls appear to function as contact calls that recruit and coordinate foraging among group members. We postulate that females benefit from foraging with unrelated roost-mates because they can defend feeding sites more effectively.

Although extensive vocal repertoires have been reported for several bat species (Gould 1977; Fenton 1985; Kanwal et al. 1994), most work on bat communication has focused on a few vocalizations used either during courtship and mating or during maternal reunion with offspring (reviewed in Fenton 1985; Wilkinson 1995). Studies of communication between foraging bats have focused on testing the hypothesis that insectivorous bats searching for feeding sites eavesdrop on echolocation pulses emitted by other foraging bats as they attack prey (Barclay 1982; Balcombe & Fenton 1988). Although echolocation calls can serve other communication roles, such as defending a feeding area (Leonard & Fenton 1984), in most microchiropteran species they are ill-suited for long-range communication because their high frequency and low amplitude results in rapid atmospheric attenuation (Griffin 1971; Wilkinson 1995). In contrast, loud social calls emitted by some foraging bats, such as *Taphozous peli* (Kingdon 1974), *Phyllostomus hastatus* (Greenhall 1965; Wilkinson 1995), *Macroderma gigas* (Tidemann et al. 1985), *Cardioderma cor* (Vaughan 1976) and *Nycteris thebaica* (Aldridge et al. 1990), are sufficiently low in frequency to carry considerable distances and could serve several possible functions.

Social calls given by a foraging bat might be used in the context of attracting mates, avoiding predators or either defending or advertising food. Each of these possibilities yields testable predictions. Calls that attract mates should be produced during the mating season by the sex with higher variance in mating success. Alarm calls, on the other hand, should occur in the presence of predators, particularly when vulnerable individuals, such as young, are at risk. Food calls might either repel or recruit other animals. If calls function to defend feeding areas, then calling rate should increase as prey density declines and calls should repel conspecifics, such as in *Pipistrellus pipistrellus* (Barlow & Jones 1997). In contrast,

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calls may advertise food discovery (reviewed in Hauser 1996) or indicate food quality or divisibility (Caine 1995; Elgar 1986). Calling rate should increase when food is found in concentrated patches and calls should recruit conspecifics into foraging groups.

We used these predictions to determine the function of loud, broad-band ‘screech’ calls given by foraging *P. hastatus*. This large (70–100 g) Neotropical bat eats a variety of insect, vertebrate and plant material including the fruit, pollen or nectar of more than 30 different species of trees (Gardner 1977; Gorchov et al. 1995). Screech calls have been reported when several bats were observed at a food source, such as a fruiting sapacaia nut tree (Greenhall 1965) or termite swarm (Bloedel 1955). Group foraging has also been reported when *P. hastatus* depart from a roost (Goodwin & Greenhall 1961) or feed on *Hymenaea coubaril* pollen and nectar (McCracken & Bradbury 1981). Although foraging group composition has not been previously determined, radio-tracking indicates that females that roost in the same social group hunt in contiguous areas (McCracken & Bradbury 1981).

Phyllostomus hastatus that forage in groups are not likely to be related. Females form stable groups in cave day roosts containing an average of 17 individuals (McCracken & Bradbury 1981). Offspring of both sexes disperse from their natal group by the end of their first year. Females then join new or pre-existing groups where they can remain together for 16 years or more (G. F. McCracken, G. S. Wilkinson & J. W. Boughman, unpublished data). Most females in a group are, therefore, unrelated (average $r=0.037$; McCracken 1987). Most males roost in large, temporary assemblages. One male defends and mates with most or all of the females in a group (McCracken & Bradbury 1977, 1981).

To evaluate alternative functions for *P. hastatus* screech calls, we present data on the diet, group foraging and calling activity of bats observed at two times of the year in Trinidad, West Indies. Because reproduction in this bat is seasonal, with mating occurring between October and December (James 1977) and parturition in April and May (Goodwin & Greenhall 1961; McCracken & Bradbury 1981), comparison of group foraging and calling rates between seasons can reveal whether screech calls are related to mating, defence of young, or access to resources. The mate attraction hypothesis predicts that males should call more than females and calling rates should be higher in December and January rather than April–June. If calls function to defend young, then adults with dependent young should call more, and calling rates should be higher in April–June rather than December–January. If another function is to either advertise or defend feeding sites, calling rates should vary by season according to resource distribution and availability. A correlation between group foraging and calling activity is expected with either advertisement or group defence. Finally, to determine whether bats are recruited or repelled by screech calls, we present results from playback experiments in which calls were broadcast at day roost and feeding sites.

METHODS

Faecal Collections

To determine how diet changes over seasons, we placed faecal traps on bamboo tripods beneath three or four groups of females in Guanapo cave, Trinidad, West Indies (McCracken & Bradbury 1981). We identified 24 different groups of *P. hastatus*, as well as two other bat species, *Natalus tumidirostris* and *Carollia perspicillata*, which used this cave as a day roost. To avoid contamination from other bats, we placed traps only beneath *P. hastatus* female groups that occupied isolated ceiling cavities. Each faecal trap consisted of white cloth stretched over a frame, 60 × 60 cm. We replaced traps every 24 h and estimated the proportion of different types of faecal material by counting the number of faecal pellets containing recognizable items, such as seeds, pollen or diced insect exoskeleton. Since bats sometimes dropped fruits or insects, we were able to identify most of the plants and some of the insects the bats were eating. We scored traps during five periods: 22 April–6 May 1992 (15 days), 17–23 December 1992 (7 days), 31 December 1992–12 January 1993 (10 days), 17–31 May 1994 (12 days), 1–31 June 1994 (30 days). We refer to these five periods as April, December, January, May and June, respectively. To test whether diet changed each month, we conducted an analysis of variance on the arcsine square-root proportion of faecal trap material comprising each food source, averaged across groups each day.

Observations of Calling and Foraging by Unmarked Bats

To test for an effect of season on calling behaviour, we counted, from videotapes, the number of screech calls and the number of bats entering and departing the cave. We recorded these tapes during 4 h after sunset on three nights during the dry season (21 December 1992, 3 and 10 January 1993) and three nights at the beginning of the wet season (30 April and 4 May 1992, 20 June 1993) when females were pregnant or lactating.

The video-image came from a Javelin model JE-7362 CCD camera with a 12-mm lens and was recorded using a Sony TR-81 stereo Hi-8 camcorder. We used Kodak Wratten 87 gel filters over headlamps to provide i.r.-illumination. We recorded both audible vocalizations and a heterodyne representation of echolocation pulses on the videotape using an Ultra-Sound Advice S-25 bat detector tuned to 37 kHz, the dominant frequency of *P. hastatus* echolocation calls (Griffin & Novick 1955). We identified *P. hastatus* unambiguously on videotapes because this bat is much larger than the other two bat species in the cave and because the bat detector produced distinctive sounds from *P. hastatus* echolocation calls.

To determine whether bats at the cave departed, entered or vocalized in groups, we computed the interval in seconds between consecutive departures, arrivals or screech calls from the videotapes. We then used two- and four-parameter non-linear regressions of log frequency by interval duration to determine the probability associated with any clustered activity occurring by chance (Sibly et al. 1990). If bat activity or calling occurs at random with respect to time, then the frequency of each interval class should decay as a negative exponential. Hence, the log of this relationship is expected to be linear and fit a two-parameter regression. If, on the other hand, a four-parameter regression provides a significantly improved fit, then activity is significantly clustered. Fitting a four-parameter non-linear regression requires large samples. In a 4-h sample, the number of calls varied from 278 to 1062, and the number of bats leaving and entering the cave ranged from 1717 to 4314. Alternative methods for detecting clustered departures (e.g. Speakman et al. 1992; Wilkinson 1992) gave qualitatively similar results to these analyses.

In addition to scoring bat activity at the cave, we also observed bats flying en route to and at feeding sites in the upper Guanapo valley. This valley contains lowland, wet tropical forest on ridges, steep slopes and drainages interspersed with small farms on shallow slopes (Beard 1946). From a quarry about 100 m from the cave, we counted how often bats flying towards or away from the cave were in a group and whether they were calling. We observed bats for at least 2 h on each of four nights (7, 11 January 1993, 9 January and 7 June 1995) when the moon was nearly full and flying bat silhouettes could be seen. Here and elsewhere we assumed that bats travelled in a group when they were flying in the same direction no further than a few metres from each other.

On 19 nights when we either conducted playbacks or counted screech calls (see below) at feeding sites, we noted the number of bats flying around a food tree and whether screech calls were heard. We also counted screech calls at six flowering balsa trees on five nights in January 1993 and five nights in January 1995 for a total of 17 h. In 1993, we recorded screech calls onto videotapes with an i.r.-illuminated video-camera focused on one or more open flowers. In 1995, an observer sat beneath a flowering tree and recorded the number of screech calls heard every minute. To sample peak foraging activity at feeding sites, we restricted screech call comparisons to 80 ± 34 min ($\bar{X} \pm \text{SD}$) beginning at 1900 hours each night. Radio telemetry (G. S. Wilkinson, unpublished data) during January 1995 indicated that most bats foraged between 1830 and 2030 hours at this time of year.

Foraging Bat Captures

To determine whether bats foraged independently of their roosting group members, we netted bats at feeding trees. To enhance capture success, we periodically broadcast *P. hastatus* screech calls from behind the nets. We netted for nine nights at three flyway sites, between 50 and 300 m from Guanapo cave, and for 19 nights at 10 feeding sites between 1 and 3 km from the cave. Nine nights of netting occurred at female *Cecropia peltata* with fruit in June, nine nights at flowering balsa, *Ochroma lagopus*, in January, and one night near a fruiting sapacaia, *Lecythis zabucajo*, in

December. We determined roost group affiliations for unmarked bats by gluing coloured reflective Scotchlite tape to head fur or bands and these bats were subsequently located in the cave.

To test for seasonal differences in foraging patterns, we compared the number and sex of bats netted at each site in each season. We also tested for an association between roost group identity and netting site location using a randomization method for estimating the significance associated with chi-square values calculated from contingency tables with small samples (Roff & Bentzen 1989).

Observations of Calling by Marked Bats

To determine whether bats from the same roosting group departed from the cave independently of each other, we captured (McCracken & Bradbury 1981) and marked all of the bats in each of six roosting groups with a group-specific coloured light-emitting diode (LED). We attached LEDs to each bat's back with colostomy adhesive. Because we soldered LEDs to 3 V batteries directly, these 2.5-g lights were bright but short-lived: flying bats carrying LEDs could be observed up to 50 m away but rarely for more than two nights. Consequently, we limited these observations to two nights after marking. We watched two groups containing 16 and 22 LED-tagged females on 10–11 January 1993, two groups with 10 and 22 females on 18–19 May 1994, and one group with 16 females and another with 22 males on 28–29 May 1994. On these nights, we also monitored either the cave entrance or the group roosting site inside the cave with i.r.-illuminated video from dusk until 2200 hours to determine departure and arrival times for LED-tagged bats.

We tested whether screech calls were given by LED-tagged bats independently of the presence of another bat from the same roosting group, the sex of the group, and the direction of flight (either into, out of, or circling around the cave entrance) using multi-way contingency table analysis (Fienberg 1981). In this analysis, the difference between the goodness-of-fit likelihood ratio obtained from log-linear models with and without an interaction term is used to test the significance of the association defined by the interaction.

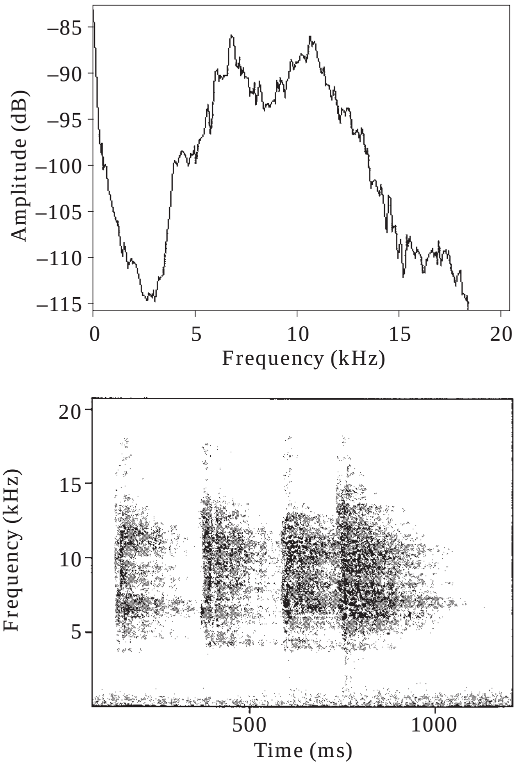

Figure 1. Spectrogram and power spectrum for a four-note screech call digitized at 44 kHz and computed with a 512-point FFT and a Hamming window. Frequency resolution is 176 Hz. The power spectrum was computed for a single note of the call.

Playbacks

To determine whether screech calls repel or attract bats, we conducted playbacks outside the day roost and at food trees. At each site, we conducted a series of 15-min trials in which a 5-min playback was preceded and followed by 5 min of silence. Natural bouts of screech calling sometimes lasted more than 5 min. We used a Marantz PMD-430 cassette-recorder, Radio Shack 40 W stereo amplifier, and Sony SRS-67 portable loudspeakers to broadcast the calls. We adjusted playback amplitude to match free-flying bats. The average peak amplitude of bats calling 1–2 m from a B & K 4134 microphone was 88 dB. Screech calls vary in frequency from 2 to 18 kHz (Fig. 1), which is within the rated dynamic range of our recording and playback equipment. During each 5-min response period, two observers counted screech calls while an i.r.-illuminated video camera with a bat detector sound track recorded bat activity at the speaker. We used screech call counts averaged between the two observers and the number of *P. hastatus* that flew past the speaker as response variables.

For playback stimuli, we combined bouts of screech calls recorded over seven nights from unmarked bats outside the cave with a Sennheiser MKH-804 shotgun microphone and the Marantz recorder. Each 5-min playback typically contained 80 calls, most of which probably did not come from the same individual because the cave contained over 700 *P. hastatus*. As a control stimulus we used screech owl, *Otus choliba*, calls. A pair of owls commonly perched and called near the Guanapo cave entrance. We used owl rather than bat calls as a control because we never heard *P. hastatus* emit any audible vocalizations other than screech calls while flying.

To determine the effect of screech calls on conspecifics near the roost, we conducted 10 screech call and 10 owl call trials outside the cave between 28 April and 7 May 1992. We broadcast calls from one of two speakers hung 5 m above ground, 20 m apart and 20 m from the cave entrance. We began trials after 1900 hours to avoid the initial exodus from the cave at dusk. To minimize habituation, we (1) conducted no more than two screech call trials per night, (2) alternated between owl call and screech call presentations, (3) separated each trial by at least 30 min, and (4) alternated playbacks between the two speakers.

We also conducted 17 trials near four feeding sites (three flowering balsa trees and a fruiting sapacaia nut tree) on seven nights between 16 December 1992 and 3 January 1993. As we failed to detect responses to owl call playbacks at the cave, we used only screech call playbacks at trees. We positioned the speaker close to open flowers or fruit by hoisting it into the tree. Feeding site playbacks occurred between 1830 and 2100 hours. Because the speaker and the bats were up to 50 m from the observer, we sometimes had difficulty distinguishing playbacks from calls of responding bats. Consequently, we analysed only the number of bat passes transcribed from videotapes of each trial.

We used repeated measures ANOVA to analyse bat responses to both playback experiments. Neither response variable required transformation to meet ANOVA assumptions. Unless otherwise noted, we report $\bar{X} \pm \text{SE}$ throughout.

RESULTS

Diet

We found significant differences between months in the amount of material comprising insects ($F_{4,50}=8.9$, $P<0.0001$), *Rollinia multiflora* fruit ($F_{4,50}=52.5$, $P<0.0001$), *C. peltata* fruit ($F_{4,50}=228.9$, $P<0.0001$), wild cucumber fruit ($F_{4,50}=12.6$, $P<0.0001$) and balsa pollen ($F_{4,50}=126.3$, $P<0.0001$; Fig. 2). During December and January, most faecal pellets contained balsa pollen. We often netted *P. hastatus* at balsa trees and observed bats within the cave after their first feeding flights covered in balsa pollen. The second most common food source during this period was *R. multiflora*, an annonaceous fruit about 2 cm in diameter. From April to June, the most common faecal pellet constituent was *C. peltata* seeds and pulp, although by June less fruit and more insect material was present in the traps. Cucumber seeds (*Gurania spinulosa* and *Anguria angustifolia*) decreased in the traps from December to June and never made up more than 10% of the material. The amount of insect material in the traps reflected the rainfall pattern in the valley. More insect material was present in the wettest month sampled, June, rather than in the dry months, December–May. Common recognizable parts of insects, such as elytra and wings, came from large-bodied passalid and scarab beetles, as well as large tettigoniids and alate leaf-cutter ants, *Atta cephalotes*. Faecal material observed on the cave floor in other years indicated that these food sources are used every year by *P. hastatus*.

Group Foraging

Three results provided evidence that seasonal variation in diet influenced the tendency for females to forage together. First, bout analyses revealed that *P. hastatus* departed and entered the cave in groups more often in the dry than in the wet season. Clustered departures occurred on all three nights sampled in December and January, but only one of three nights in April and June (Fig. 3). The number of bats entering the cave showed significant clustering for two nights in the dry season, but none in the wet season (Fig. 3). Second, observations at dusk of bats flying around feeding trees revealed that the foraging

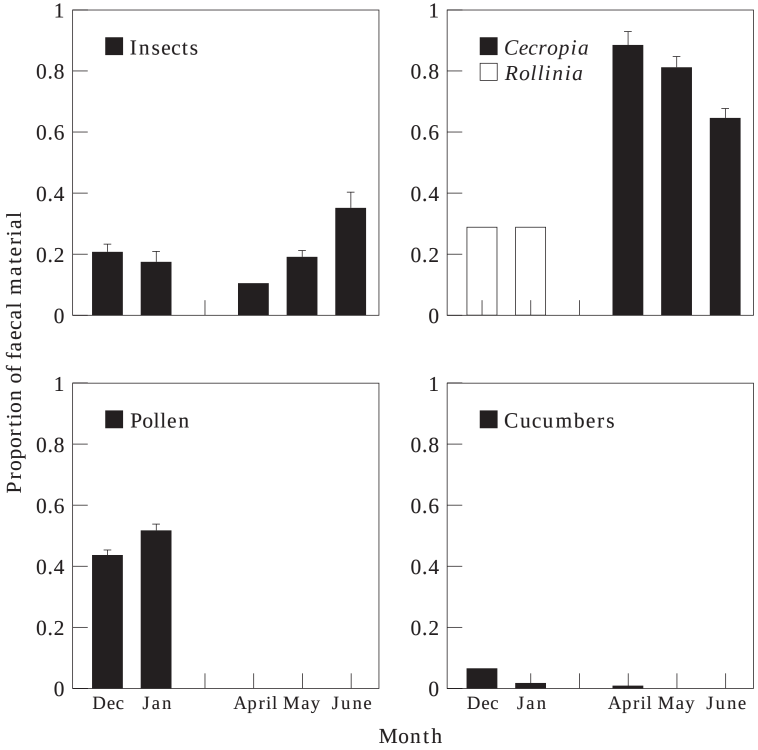

Figure 2. Mean proportion of faecal pellets containing insect material, pollen (*Ochroma lagopus*), or fruit (*Cecropia peltata*, *Rollinia multiflora*, *Anguria angustifolia* and *Gurania spinulosa*). Samples are averaged over groups and days.

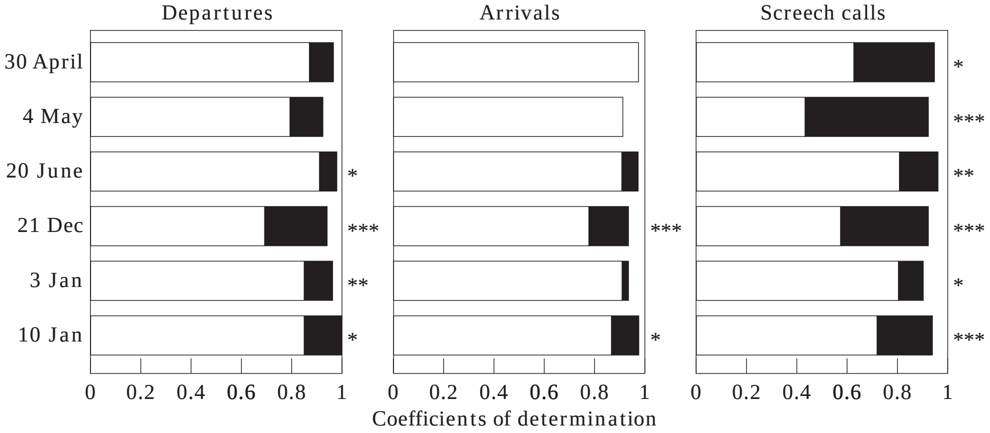

Figure 3. Coefficients of determination (r^2) for two-parameter (☐) and four-parameter (☐ plus ■) regressions of log frequency by interval duration for departures, arrivals and screech calls outside the cave. Significant four-parameter regressions indicate that intervals were clustered into bouts. *$P<0.05$, **$P<0.01$, ***$P<0.001$.

group size was larger at balsa trees during December and January (2.65 ± 0.33 bats/group, $N=20$ groups) than at *Cecropia* trees in June (1.73 ± 0.13 bats/group, $N=59$ groups, $t=3.19$, $P=0.002$). Finally, we netted males less often at balsa than at *Cecropia* trees (Mann–Whitney

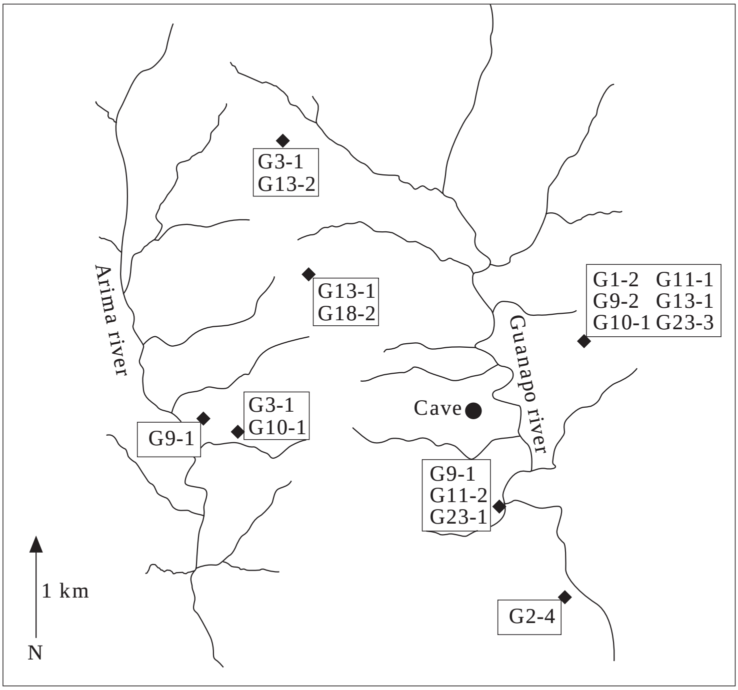

Figure 4. Location and number of adult females from different roosting groups in Guanapo cave netted at feeding sites in the Guanapo and Arima valleys, Trinidad.

U-test; $z = 2.34$, $P = 0.019$, $N = 19$), but we captured females equally often at these two feeding sites ($z = 0.46$, $P = 0.64$). Of the 54 bats we captured at feeding sites, 74% were females.

We captured more females from the same roosting group at each feeding site than expected if captures at each site occurred at random with respect to group membership (Fig. 4). In other words, the number of females captured from each group depended on the location of the feeding tree (small sample $\chi^2_{24} = 83.5$, $P < 0.01$, 1000 randomizations). This result was not due to any bias in how often females from a particular roosting group were captured. The frequency with which bats were captured from each group at feeding sites did not differ from that expected if captures occurred in proportion to the number of bats from each group either banded ($\chi^2_{15} = 19.7$, $P = 0.15$, 1000 randomizations, 963 bats banded) or captured in flyways ($\chi^2_{15} = 15.5$, $P = 0.41$, 1000 randomizations, 51 bats netted). In addition to capturing more female group-mates at the same site than expected, we also captured females from more than one group at most sites (Fig. 4).

Several captures are worth noting because they suggest that adult females from the same social group sometimes fly together from the cave to feeding sites. On two occasions, we simultaneously netted two females from the same group 100 m from the cave entrance. On another night, within 2 min we netted three females from the same group beneath a feeding tree 2 km from the cave. On this occasion, we failed to capture two other bats that were among the five that we observed calling and circling this tree for several minutes.

Screech Calling and Group Foraging

Although *P. hastatus* produced clustered bouts of screech calls outside the cave on every night sampled (Fig. 3), the number of calls given per bat entering or leaving the cave depended on the season and the time since sunset (Fig. 5). The number of calls per bat was higher during the dry months at the end of the mating season than during the wet months when volant young were present ($F_{1,4} = 16.6$, $P = 0.015$). Furthermore, calls per bat differed between hours after dark

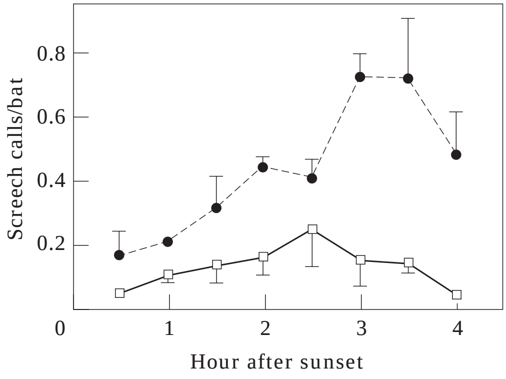

Figure 5. Number of screech calls recorded on videotape outside Guanapo cave divided by the sum of the number of bats either entering or leaving the cave each 30 min. —□—, May–June; – – –●– – –, December–January.

($F_{6,24}=5.6$, $P=0.0009$) and showed an interaction between hours after dark and season ($F_{6,24}=4.8$, $P=0.0024$). These differences were caused by more bats leaving and entering the cave and producing fewer calls during May and June (3807 ± 254 bats and 483 ± 111 screech calls recorded per night) than during December and January (1207 ± 257 bats and 823 ± 120 screech calls recorded per night). Videotapes made inside the cave revealed that the difference in activity between the seasons reflected an increase in the number of foraging trips per adult female during the lactation period in May and June, and the presence of volant pups in June.

Observations of bats calling while flying en route to and at feeding sites revealed that screech calls occurred more often from bats in groups than from solitary bats. Flight direction ($F_{1,113}=21.1$, $P<0.0001$), call production ($F_{1,113}=71.9$, $P<0.0001$) and the interaction between these two factors ($F_{1,113}=19.9$, $P<0.0001$) all influenced foraging group size. The number of bats flying together towards feeding sites observed from the quarry was greater when bats gave screech calls (2.08 ± 0.19, $N=12$), than when they were silent (1.07 ± 0.03, $N=56$) or when they were returning to the cave, either calling (1.38 ± 0.13, $N=16$) or not calling (1.06 ± 0.04, $N=33$). Similarly, at feeding trees we observed more bats flying together when giving screech calls (2.60 ± 0.20, $N=40$) than when silent (1.31 ± 0.10, $N=39$, $t=5.78$, $P<0.0001$).

Observations at balsa trees indicated that bouts of screech calling coincided with the arrival of two or more bats, which then flew around the tree visiting flowers for several minutes before disappearing. Comparison of the average variance to mean ratio (V/M) of the number of calls per minute between 1900 and 2000 hours each night (6.5 ± 1.1) confirmed that screech calls were clustered in time (one-sample $t_9=4.8$, $P=0.009$) under the assumption that random ordering results in V/M = 1. Video-recordings of bats visiting balsa flowers revealed that the number of screech calls recorded during 10-min periods over five nights correlated with the number of *P. hastatus* visits to an open balsa flower ($r_s=0.33$, $P=0.031$, $N=44$) and with the number of times a bat flew by a flower ($r_s=0.55$, $P=0.0003$, $N=44$). The number of screech calls did not correlate with the number of visits to open flowers by other bat species ($r_s=0.22$, $P=0.16$, $N=44$).

Observations of LED-tagged bats outside the cave provided direct evidence that some of the bats we observed flying together and calling were females from the same roosting group. Multi-way contingency table analysis showed that females from the same group flew together significantly more often while departing and circling than entering the cave (Tables I and II). On first foraging flights, we observed same-group females departing together on 24% of 115 observations (Table I). Females returning from their first foraging trip often circled the cave prior to departing on a second trip. Circling females were joined by an LED-tagged female from the same group on 40% of 51 observations. In contrast, only 9% of 84 LED-tagged females entering the cave were accompanied by a bat from the same group (Table I).

Screech calls were given significantly more often when two or more females from the same roosting group were either departing or circling together than when flying alone (Table II). Fifty per cent of the LED-tagged female bats observed departing with a group-mate gave screech calls, compared to only 5% of females that departed alone (Table I). We also observed 60% of females calling while circling outside the cave with one or more bats from the same group compared to only 13% of females calling when circling without a marked group member (Table I). On several occasions, we observed LED-tagged females fly out of the cave and join a circling female group member that was

Table I. Number of LED-tagged bats observed calling and flying with another LED-tagged individual from the same roosting group while either departing, entering or circling outside the cave roost

		Females		Males	
Action	Proximity	Silent	Calling	Silent	Calling
Depart	Solitary	83	4	15	0
	Same group pair	14	14	4	1
Circle	Solitary	27	4	9	0
	Same group pair	8	12	0	0
Enter	Solitary	76	1	18	0
	Same group pair	8	0	0	0

Female totals contain observations on five roosting groups of adult females; male totals represent observations on one roosting group of bachelor males. Each light-tagged group was observed on two successive nights.

Table II. Multi-way contingency analysis on the number of LED-tagged bats from the same group observed calling and flying together as given in Table I

Log-linear model or comparison†	χ^2	*df*	*P*
1. Sex + action + proximity + calling	112.9	18	<0.001
2. Model 1 + action $*$ proximity	93.6	16	<0.001
3. Model 2 + proximity $*$ calling	34.2	15	<0.001
4. Model 3 + action $*$ calling	19.1	13	0.12
5. Model 4 + sex $*$ calling	11.9	12	0.46
$\Delta\chi^2$ between models 2 and 1, H_0: action independent of proximity	19.3	2	<0.001
$\Delta\chi^2$ between models 3 and 2, H_0: calling independent of proximity	59.4	1	<0.001
$\Delta\chi^2$ between models 4 and 3, H_0: calling independent of action	15.2	2	<0.001
$\Delta\chi^2$ between models 5 and 4, H_0: calling independent of sex	7.2	1	0.007

†Only model comparisons producing significant difference likelihood-ratio values are shown. Sex: male or female; action: departing, circling or entering the cave roost; proximity: flying alone or flying 1–2 m from a LED-tagged bat from the same roosting group; calling: either calling or silent.

calling prior to the two bats departing together. In contrast, we never heard screech calls when two females from the same group entered the cave together (Table I). Females also called significantly more often than males. Only one of five bachelor males gave screech calls when departing with a male from the same group.

Response to Playbacks at Roosting and Feeding Sites

Playbacks outside of the cave demonstrated that screech calls attracted rather than repelled conspecifics and elicited calling (Fig. 6). Repeated measures ANOVA on both bat passes and screech-call counts revealed significant differences between silent and playback periods within a trial and between the type of call used (Table III). Only screech calls elicited responses (Fig. 6). The two response variables differed in that the number of passes returned to pre-playback levels immediately after a playback, while screech-call counts persisted at an elevated rate after the playback ended (Fig. 6).

Broadcasting screech calls near feeding sites also attracted *P. hastatus* (Fig. 7). Repeated measures ANOVA confirmed a difference between playback and silent periods ($F_{2,28}=22.8$, $P<0.001$)

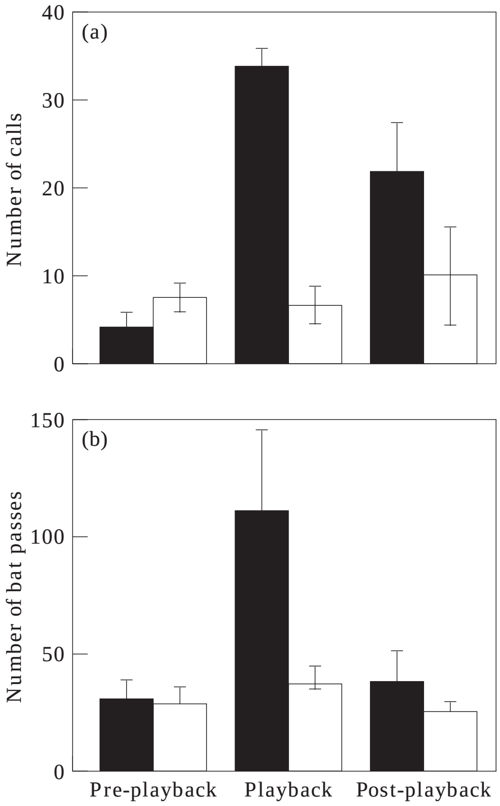

Figure 6. Mean response to screech call playbacks outside Guanapo cave. (a) Number of screech calls counted; (b) number of bats passing by the playback speaker scored from i.r.-illuminated videotape during 5-min trials. ■, Responses to *P. hastatus* screech calls; □, responses to owl calls.

but no difference between playback trials ($F_{14,28}=1.0$, $P=0.48$). Relative to control periods, the number of bat passes increased five-fold at both cave and feeding sites.

DISCUSSION

Function of Screech Calls

Four lines of evidence indicate that screech calls function primarily as contact calls enabling bats from the same roosting group to fly together from the cave to feeding sites.

(1) Seasonal differences in diet coincided with differences in screech calling outside the cave, as well as how often bats departed in groups. Bats showed more clustered departures and flew in larger groups when feeding predominantly on balsa flowers in winter than on *Cecropia* fruit in spring. Balsa trees provide more predictable and concentrated resources than *Cecropia* trees. A large balsa tree can have 50 open flowers in a night, with each flower producing 3 ml of nectar (Opler 1983). In contrast, relatively few *Cecropia* fruits ripen on a tree each night (Fleming & Williams 1990). Censuses indicated that the number of new balsa flowers each day is less variable between trees than the number of ripe *Cecropia* fruit (G. S. Wilkinson & J. W. Boughman, unpublished data).

(2) Observations of bats outside the cave roost, in flyways and at feeding sites indicated that screech calls occurred more often when bats flew in groups than alone.

(3) Females from the same roosting group were captured at the same feeding site, sometimes simultaneously, several kilometres from the cave.

(4) Calling colour-marked adult females outside the cave were joined by a female group member, both on initial departures and on second foraging trips, much more frequently than non-calling bats.

Thus, screech calls appear not only to coordinate foraging, but also to recruit roost mates into foraging groups.

If screech calls also attracted mates, we would expect males to call more than females during the mating period. In contrast, adult females produced more screech calls than males, and calls occurred in and out of the mating season. If screech calls also functioned as alarm calls, we would expect higher calling rates when predation is most likely. Although adult *P. hastatus* have no documented predators, several large owls and hawks take prey of similar size. Since aerial predation by raptors on bats typically happens at dusk (Fenton et al. 1994), most alarm calls should occur then. In contrast, during the winter months the number of screech calls per bat increased, rather than decreased, for 3 h after dusk. Furthermore, screech calls occurred less, rather than more, often when newly volant young were present. Finally, flying adult bats gave screech calls outside the cave, in flyways and at feeding sites in the absence of any predator. Thus, screech calls are not given in appropriate contexts to either attract mates or warn conspecifics.

Playbacks at the cave and feeding sites confirmed that screech calls attract, rather than

Table III. Repeated measures ANOVA results from playbacks conducted outside the cave

Response variable	Source of variation	*df*	*F*	*P*
Bat passes	Call type	1, 18	2.75	0.115
	Periods within trials	2, 36	7.26	0.002
	Call type by period	2, 36	4.32	0.021
Screech calls	Call type	1, 18	8.58	0.009
	Periods within trials	2, 36	4.00	0.027
	Call type by period	2, 36	4.28	0.022

Call type refers to whether bat or owl calls were used as stimuli; period indicates the three consecutive 5-min periods (silent, presentation and silent) during which responses were scored. Means are illustrated in Figure 6.

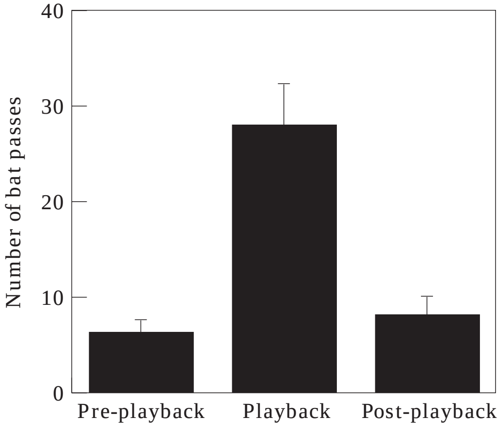

Figure 7. Mean number of bats passing by the playback speaker during 5-min trials at a flowering or fruiting-tree feeding site.

repel, bats. Both males and females from more than one group were captured in nets set in front of loudspeakers at some feeding sites. Such responses suggest that screech calls attract bats independent of their group identity. Observations of light-tagged bats joining group members that called can be reconciled with these results in at least two ways. Group discrimination could require mutual comparison of multiple calls. The increase in call production that we observed in response to playbacks is consistent with this interpretation. Alternatively, females may selectively give screech calls only when group members are likely to be nearby. Our playbacks lacked such specificity, because we continuously broadcast calls recorded from multiple individuals for 5 min.

Spectrographic analysis of screech calls from individually identifiable bats recorded in captivity and in the field reveals that these calls do contain sufficient acoustic information for reliable group discrimination (Boughman 1997). Audiograms based on evoked potentials recorded from both the auditory nerve and the inferior colliculus indicate that *P. hastatus* is sensitive to frequencies below 20 kHz (Grinnell 1970). Recent playbacks of screech calls from known individuals in a habituation–dishabituation design indicate that in captivity bats can discriminate calls from different groups (Boughman & Wilkinson, in press). Thus, available evidence indicates that *P. hastatus* can probably identify roosting-group affiliation from conspecific screech calls. If this conclusion is correct, then why should bats preferentially forage with group members? Without some compensatory benefit, joining any foraging group should decrease the fitness of all group members (Clark & Mangel 1984; Vickery et al. 1991).

Possible Advantages of Coordinated Foraging

Several possible advantages for recruiting conspecifics to foraging sites have been proposed. These include (1) reducing predation through improved vigilance (Elgar 1986), (2) avoiding aggression from dominants (Hauser & Marler 1993), (3) improving prey capture success (Brown et al. 1991), (4) enhancing food finding (Wilkinson 1992), (5) increasing inclusive fitness by sharing with relatives (Judd & Sherman 1996), and (6) improving resource defence (Heinrich 1988). The first three advantages seem unlikely for *P. hastatus* because bats fly in darkness and captive females from the same social group routinely feed simultaneously from the same piece of fruit without aggression (J. W. Boughman & G. S. Wilkinson, unpublished data).

Furthermore, it is difficult to imagine how bats in a group could obtain balsa nectar and pollen more effectively than *Cecropia* fruits.

Group foraging bats might, however, locate open balsa flowers more readily than solitary bats. New balsa flowers, however, are conspicuous, with large white blossoms that stand erect 12 cm above planar foliage. Furthermore, such a local enhancement hypothesis predicts that bats should join groups irrespective of their roosting-group affiliation. If this were the only advantage to group foraging, group-specific calls would be unnecessary.

Group foraging might increase inclusive fitness if bats preferentially foraged with relatives. Although the low average level of relatedness among females in a group (McCracken 1987) casts doubt on any inclusive fitness advantage to group foraging, over the past 3 years we have documented five cases of two to five probable paternal half-sibling sisters emigrating from their natal group and subsequently roosting in the same social group. Such half-sibling subgroups would not have been detected by past allozyme studies. Although these observations suggest that the role of kinship in foraging-partner choice deserves further study, kinship alone is insufficient to account for seasonal differences in calling behaviour or group distinctive calls (Boughman, 1997).

The hypothesis that we find most plausible is that females recruit roost-mates into foraging groups using screech calls to improve the defence of predictable feeding sites. The most compelling evidence for group defence comes from radiotelemetry data. Females from the same social group repeatedly foraged in adjacent or overlapping areas throughout the year, while females from different groups typically foraged in distinct areas (McCracken & Bradbury 1981; G. S. Wilkinson & J. W. Bradbury, unpublished data). Our captures of more than one female from the same group at the same feeding site confirm that group-mates can feed from and potentially defend a flowering tree. Competition between females from different social groups is possible, assuming that food is occasionally limited, since we also captured females from more than one group at feeding sites. Higher rates of screech calling and group foraging in winter than summer are consistent with group defence because balsa trees represent more concentrated resources than *Cecropia* trees.

A group should be more effective than an individual bat at defending a flowering or fruiting tree because several bats should be able to monitor a larger area and thereby detect intruders sooner from their relatively weak 75-dB echolocation calls (Griffin 1971; Wilkinson 1995) or by sight. For group defence to be evolutionarily stable, individuals that feed without providing defence must be recognized and excluded. Group distinctive screech calls could, hypothetically, provide a mechanism for detecting cheaters if they are used as passwords to gain access to a defended feeding site. Because screech calls are loud enough to hear at least 50 m from a calling bat (Wilkinson 1995), these calls could also be used to advertise that a bat has been detected while foraging. If this individual failed to respond with an acoustically similar call, it could be identified as an intruder. For screech calls to remain honest indicators of group membership, they must be difficult to copy (Grafen 1990). Further study is needed to test these ideas and confirm that female *P. hastatus* use screech calls to coordinate cooperative group defence.

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