

Greater spear-nosed bats discriminate group mates by vocalizations

JANETTE WENRICK BOUGHMAN*† & GERALD S. WILKINSON*

*Department of Zoology, University of Maryland, College Park

†Department of Zoological Research, National Zoological Park, Smithsonian Institution

(Received 20 May 1997; initial acceptance 18 August 1997;
final acceptance 23 October 1997; MS. number: A7930)

Abstract. Individuals often benefit from identifying their prospective social partners. Some species that live in stable social groups discriminate between their group mates and others, basing this distinction on calls that differ among individuals. Vocalizations that differ between social groups are much less common, and few studies have demonstrated that animals use group-distinctive calls to identify group mates. Female greater spear-nosed bats, *Phyllostomus hastatus*, live in stable groups of unrelated bats and give audible frequency, broadband calls termed screech calls when departing from the roost and at foraging sites. Previous field observations suggested that bats give screech calls to coordinate movements among group members. Prior acoustic analyses of 12 acoustic variables found group differences but not individual differences. Here, we use the same acoustic variables to compare calls from three cave colonies, and find that calls differ between caves. We also report results from field and laboratory playback experiments designed to test whether bats use acoustic differences to discriminate calls from different colonies, groups or individuals. Results from field playbacks indicate that response depends on the cave of origin, indicating that bats can discriminate among calls from different caves. This discrimination ability may be based, in part, on whether calls are familiar or unfamiliar to the listening bats. Laboratory playbacks demonstrate that bats discriminate calls given by their group mates from calls given by other bats from the same cave irrespective of familiarity. However, these experiments provide no evidence that bats discriminate among individuals. Previous field work indicates that females that forage with social group mates may benefit from shared information about food or mutual defence of feeding sites. Indicating group membership is essential, since these benefits appear to be restricted to group mates.

© 1998 The Association for the Study of Animal Behaviour

Animals that live in stable social groups may benefit by improving their access to food resources, through either group foraging or group defence of resources. We discuss two kinds of groups: long-term social groups that persist over much of an individual's lifetime, and short-term foraging groups that persist over a single foraging episode. When patchy resources are ephemerally available, food-finding can be enhanced by foraging in a group (Krebs et al. 1972; Rabenold 1987; Brown 1988; Wilkinson 1992; Brown & Brown 1996). When food patches persist over time, resource defence becomes advantageous and may be achieved more effectively by a foraging group (Heinrich 1988). If group foraging is beneficial in either case, animals should actively form foraging

groups. Foraging groups are likely to be composed of social group mates when animals live in stable social groups; therefore, selection may favour a mechanism to ensure association with particular individuals. Vocalizations are a potentially effective means of maintaining contact with group mates that travel long distances quickly, especially if they convey social group membership. Despite these potential benefits, few studies have demonstrated that animals use vocalizations to identify members of social groups when group mates are not relatives (Cheney & Seyfarth 1982).

If calls are the mechanism that promotes formation and maintenance of foraging groups among social group mates, then calls must identify social group mates in the foraging context. Both the production of distinctive signatures and their perception are essential components of a

Correspondence: J. W. Boughman, Department of Zoology, University of Maryland, College Park, MD 20742, U.S.A. (email: boughman@umail.umd.edu).

signature system (Beecher 1982, 1989; Reeve 1989). If calls function to identify members of a social group, then calls produced by members of one social group must differ from other groups. In addition, individuals must perceive differences among the calls given by individuals in their own and other social groups.

Bats are an intriguing taxon in which to study vocalizations associated with group foraging. Despite the paucity of studies on bat behaviour, several have demonstrated that bats forage with conspecifics (Bradbury & Vehrencamp 1976; Sazima & Sazima 1977; Howell 1979; Wilkinson 1992) and others have found evidence suggesting bats follow other individuals out of the roost (reviewed in Wilkinson & Boughman, *in press*). Bats are acoustically oriented and can travel fast and far; thus they are likely to communicate using vocalizations when outside the roost. While on foraging territories, individuals of several species appear to give calls that may function in territorial defence (Vaughan 1976; Tidemann *et al.* 1985; Vaughan & Vaughan 1986; Aldridge *et al.* 1990), but much less is known of the incidence of calling among bats that forage with conspecifics. Functional hypotheses remain untested for almost all audible calls related to foraging (but see Barlow & Jones 1997; Wilkinson & Boughman 1998). This lack of functional information is unfortunate because the use of calls to attract group mates can carry costs if both potential cooperators and competitors respond. Very few studies have described patterns of acoustic variation sufficiently well to determine whether calls could function to identify group mates (but see Boughman 1997). The paucity of information on audible calls serving a social function is in marked contrast to the wealth of knowledge on function and structure of echolocation calls used to navigate and locate prey (reviewed in Kalko & Schnitzler 1993; Fenton 1995; Moss & Schnitzler 1995).

Currently, enough is known about group foraging and call structure in greater spear-nosed bats, *Phyllostomus hastatus*, to ask whether vocalizations function to identify social group mates, and thus facilitate group foraging among long-term social partners. Female greater spear-nosed bats form stable social groups of unrelated individuals that roost together in specific ceiling depressions over several years (McCracken & Bradbury 1981). Group mates interact socially and forage in contiguous, partially overlapping areas (McCracken

& Bradbury 1981; G. S. Wilkinson, unpublished data), and sometimes even forage together (Wilkinson & Boughman 1998). Bats that forage with group mates apparently benefit from joint defence of rich food resources (Wilkinson & Boughman 1998) and may also find food more quickly (Wilkinson & Boughman, *in press*). Greater spear-nosed bats give audible frequency, broadband calls termed screech calls when departing from the roost, en route to, and at foraging sites (Greenhall 1965). These calls differ among social groups but not among individuals (Boughman 1997), so the first criterion of an effective group signature system is fulfilled. Field observations suggest that bats give screech calls to recruit social group mates to foraging groups (Wilkinson & Boughman 1998). These group contact calls may be similar in function to those given by many flock-living birds such as chickadees (Mammen & Nowicki 1981) and budgerigars (Brockway 1964). The group distinctive structure of screech calls is important, as bats change call structure when social group composition changes (Boughman 1998). These changes imply that bats detect the unique features of their social group mates' calls, and ensure that group mates sound similar to one another and distinct from members of other groups. Combined with field observations, these results strongly suggest that bats discriminate social group membership based on calls. A direct test of group discrimination is none the less required.

Group distinctive calls resulting from socially mediated changes raise the possibility that colonies may also differ in call structure. Geographical variation in vocalizations has been found in many birds (reviewed in Baker & Cunningham 1985; Catchpole & Slater 1995) and several mammals (reviewed in Janik & Slater 1997). We compare calls from three cave colonies to determine whether the calls from each cave differ. We then present results of playback experiments designed to test cave, group and individual discrimination. Our objective for field playbacks was to determine whether bats can differentiate calls from different cave colonies. We used the additional control possible in a laboratory setting to ask whether bats can discriminate their own social group mates from others. In addition, this habituation-discrimination experiment asked whether bats can discriminate among the individuals in their social group.

ACOUSTIC ANALYSIS OF CAVE-LEVEL VARIATION

To determine whether calls differ between caves, we compared 106 calls recorded from bats at three caves in Trinidad, West Indies: Caura, Guanapo and Tamana caves. Guanapo and Caura are about 6 km apart, separated by two intervening mountain valleys with relatively contiguous forest. Tamana is about 10 km from Guanapo, 16 km from Caura, and is in a different mountain range separated by towns and cultivated land.

Methods

Call recording

We sampled calls from these three caves, recording bats of known group membership where possible so we could account for group-level variation in our analyses. In May 1992 we recorded bats departing from Caura cave using a Sennheiser MKH804 directional microphone onto metal cassette tapes with a Marantz PMD 430 recorder. This set-up provided nearly flat response (± 5 dB) up to 18 kHz. We recorded frequencies up to 120 kHz with an UltraSound Advice S-25 bat detector and detected no energy in screech calls above 18 kHz that was higher than 40 dB below the peak amplitude of calls. We analysed data for 12 calls with good signal-to-noise ratio. We could not identify the group membership of the bats we recorded at Caura, although only four stable groups of females roosted in Caura cave at the time of recording (G. S. Wilkinson, unpublished data). In January 1993 we marked all females in two social groups inside Guanapo cave, using a different coloured LED (light-emitting diode) for each group. We recorded calls from these marked bats as they departed from or circled in the vicinity of the cave. Thus, we knew the group membership but not the individual identity of the calling bat. Using the same equipment as above, we obtained good recordings of 11 calls of known group membership for both marked groups (seven and four calls, respectively) and an additional 17 calls from unmarked bats. We also recorded calls from three social groups from Tamana cave. We recorded one group over 3 nights in a flight cage at the Simla Research Station in June 1994 and obtained 16 good-quality calls from this group. We released these bats at the point of capture after recording was

complete. We used the same recording equipment to record calls from two captive groups during 1995 at the Department of Zoological Research, National Zoological Park and analysed 31 calls from one group and 19 calls from the other. We analysed recordings made over several years. Groups persist over many years and few bats disperse between groups. Even though social modification of calls leads to dynamic changes in call structure, bats appear to copy only individuals with which they have frequent social interaction and acoustic changes take several months (Boughman 1998). The long time scale and small spatial scale of group level social and acoustic processes are unlikely to produce coordinated changes between caves on a yearly basis.

Screech calls consist of noisy broadband pulses repeated 1–12 times (Fig. 1). We characterized how energy was distributed across frequency and time by measuring 12 frequency, amplitude and temporal variables. For details of call measurement, see Boughman (1997). Measured acoustic variables include: Peak 1, frequency at first power peak; Peak 2, frequency at second power peak; Lo 12, frequency – 12 dB below Peak 1; Hi 12, frequency – 12 dB above Peak 2; bandwidth at – 12 dB; rise, increase in amplitude with increasing frequency rising up to Peak 1; fall, decrease in amplitude with increasing frequency falling off from Peak 2; amplitude difference between Peaks 1 and 2; number of energy peaks; pulse duration; repetition interval, ms from the onset of one pulse to the onset of the next; number of pulses; and total call duration.

Statistical analysis

First, we determined how well calls could be classified to the correct cave using a linear discriminant function. For each of the 12 variables, we calculated average values for each call and used these averages in the discriminant analysis, setting prior probabilities proportional to the number of calls per cave. We estimated error rates by cross validation, where the linear function is constructed withholding one observation at a time, and then that observation is classified. This controls for the classification bias inherent in generating a discriminant function with the same set of observations it is subsequently used to classify (Johnson & Wichern 1992). We also conducted a canonical-discriminant analysis to estimate multivariate means for each cave colony and group.

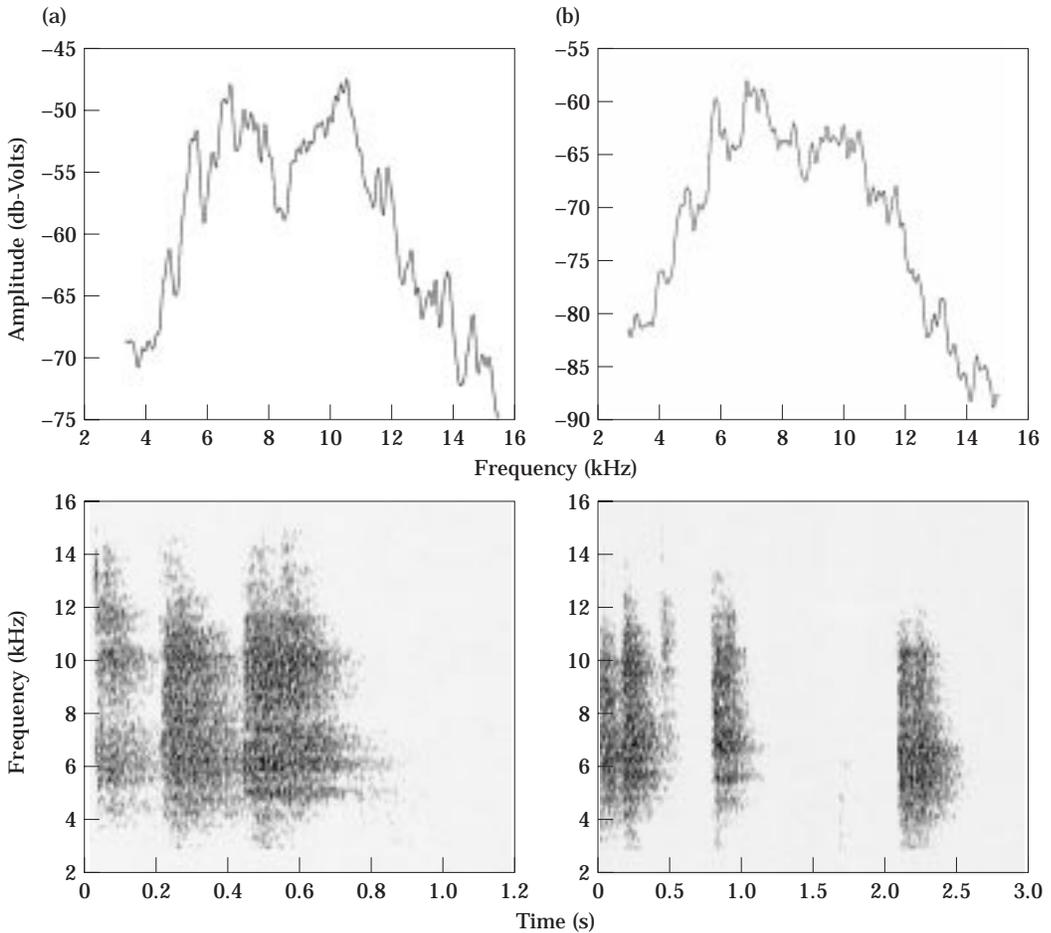


Figure 1. Examples of screech calls from two groups showing the power spectrum and sonagram for each. (a) Bat 1531 from group 1 and (b) bat 1022 from group 2.

To verify that results were not unduly influenced by recording differences between the field and laboratory, we conducted separate step-wise and canonical-discriminant analyses including only calls recorded from free-flying bats outside a cave (Caura and Guanapo calls).

To test directly the hypothesis that cave colonies differ from one another, we used calls from Guanapo and Tamana caves where we knew the identity of the social group. We performed nested univariate and multivariate ANOVA on call averages, testing effects of cave, and group nested within cave (Littell et al. 1996). No variables required transformation to meet the assumptions of ANOVA. We used SAS 6.11 for analyses.

Results

Screech calls clearly differed among caves. Linear discriminant analysis classified 71.3% of calls to the correct cave colony, significantly better than the chance rate of 33.3% (Table I). Multivariate ANOVA also indicated a significant difference in calls between the caves (Wilks' $\lambda=0.38$, $F_{2,103}=8.5$, $P<0.0001$). Multivariate acoustic means for all caves differed significantly (Caura and Guanapo $P<0.039$; Tamana and Caura $P<0.0001$; Tamana and Guanapo $P<0.0001$; Table II and Fig. 2). Acoustic canonical means of groups within a cave clustered around the cave means (Fig. 2). The restricted analysis of Caura and Guanapo calls still yielded a significant ability

Table I. Results of the linear discriminant analysis used to classify the screech calls of greater spear-nosed bats from three caves

Actual cave	Assigned cave			Number of calls
	Caura	Guanapo	Tamana	
Caura	50.0	25.0	25.0	12
Guanapo	14.3	71.4	14.3	28
Tamana	0.0	7.6	92.4	66
				Average correct
% Correct	50.0	71.4	92.4	71.3

We used step-wise discriminant analysis to identify variables that contributed significantly to separating caves, and constructed the discriminant function with these variables.

to discriminate among caves (Wilks' $\lambda=0.64$, $F_{1,23}=6.8$, $P<0.001$) and classified 81.7% of calls correctly. Variable means and standard errors for each cave are listed in Table II.

The screech calls of groups within a cave also differed significantly by nested MANOVA (Wilks' $\lambda<0.12$, $F_{3,72}=6.5$, $P<0.0001$). Nested univariate ANOVA showed a significant difference among groups within a cave for all variables ($P<0.001$ for each comparison).

FIELD PLAYBACK: CAVE DISCRIMINATION

Our objective for this playback experiment was to test whether differences in calls between caves are detected by the bats. We conducted

playbacks near Guanapo cave during June 1995. Although we could not identify the individuals that responded, field playbacks provided important validation of the ability of bats to make discriminations in an acoustically cluttered environment.

Methods

Playback tape construction

We used the calls from Guanapo and Tamana caves that were analysed for cave differences to create two separate 2-min playback tapes for each Guanapo group (four tapes) and the field-recorded Tamana group (two tapes), combining calls into bouts to mimic naturally occurring screech call behaviour. Bout length ranged from 8.5 to 32.9 s with a mean of 21.6 ± 3.9 s (Wilkinson & Boughman 1998), as estimated outside the entrance to Guanapo cave over 5 nights using log-frequency bout analysis (Sibly et al. 1990). Using a Kay DSP 5500 sonagraph, for each group we combined calls in varying order to construct 24-s bouts that we repeated four times with 6-s intervals to create 2-min playback stimuli. We balanced these six playback tapes for temporal and intensity variables that could affect response: average number of screech calls, average number of pulses, total duration of playback bout, number of calls per second, number of pulses per second, proportion of playback time during which calls were broadcast, and average call duration. We also ensured that no amplitude differences existed between playback tapes.

Table II. Means (\pm SE) for screech calls from Caura, Guanapo and Tamana caves

Variable	Units	Caura	Guanapo	Tamana
Peak 1	Hz	6069 \pm 393.6	6524 \pm 298.6	6630 \pm 183.0
Peak 2	Hz	9122 \pm 558.7	10 297 \pm 467.8	8639 \pm 286.8
Hi 12	Hz	10 864 \pm 1134.6	11 521 \pm 637.5	11 430 \pm 390.8
Lo 12	Hz	4241 \pm 249.4	5232 \pm 171.7	4470 \pm 105.3
Bandwidth	Hz	6623 \pm 1164.8	6288 \pm 781.2	6960 \pm 478.9
Rise	Hz/dB	152.8 \pm 21.14	107.6 \pm 30.78	149.3 \pm 18.87
Fall	Hz/dB	146.1 \pm 56.69	172.4 \pm 24.98	147.1 \pm 15.31
Number of peaks		2.23 \pm 0.416	2.07 \pm 0.374	2.12 \pm 0.229
Amplitude difference between Peak 1 and Peak 2	dB	1.96 \pm 0.828	4.22 \pm 0.851	2.09 \pm 0.522
Repetition interval	ms	0.36 \pm 0.119	0.13 \pm 0.121	0.40 \pm 0.074
Number of pulses		9.98 \pm 2.51	9.63 \pm 3.245	4.42 \pm 1.989
Call duration	ms	1.39 \pm 0.361	1.03 \pm 0.370	0.92 \pm 0.163

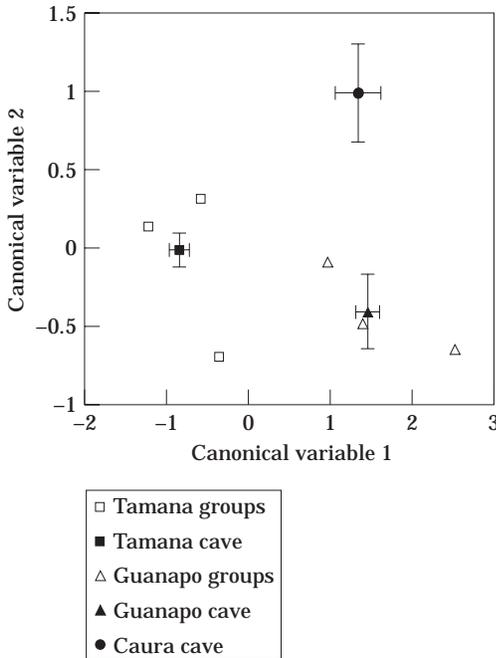


Figure 2. Acoustic canonical means for six groups of bats (open symbols) from Tamana, Guanapo and Caura caves (cave means shown in filled symbols). $N=106$ calls.

Experimental design and analysis

We broadcast calls with a Marantz PMD 430 cassette-recorder through Sony SRS-67 portable speakers hung 5 m above ground in front of the cave. We adjusted amplitude to about 79 dB (at 1 m), close to estimates of naturally occurring calls recorded in the field (75 dB at 2–3 m). The rated frequency response of playback equipment is flat to about 18 kHz. A single trial consisted of a 2-min playback preceded by 2 min of silence. We focused a Javelin JE-7362 CCD video camera on the speaker illuminated with infrared light by placing Kodak Wratten 87 gel filters over headlamps, and recorded this image with a Sony Hi-8 Handycam. We also recorded output from a Realistic 33-2050 sound-level meter. From these tapes, we scored the number of times a *P. hastatus* passed within approximately 2 m of the speaker and also counted the number of screech calls given during each playback period. Previous field playbacks indicated that bats would respond to screech-call playbacks by calling and approaching the sound source (Wilkinson & Boughman 1998). To adjust for baseline activity, we subtracted the

number of passes or calls during the preceding silence period from the number scored during presentation of the playback. Thus, negative values indicate that playback depressed response. We conducted playbacks at Guanapo cave; therefore, Guanapo calls were potentially familiar while Tamana calls were unfamiliar to Guanapo bats.

We conducted four to eight trials per night over 7 nights from 24 May to 1 June 1995. On 2 nights (16 trials) we conducted playbacks at a quarry about 200 m from the cave, on 3 nights (18 trials) outside the cave entrance, and on 2 nights (10 trials) at a foraging site about 1 km from the cave. We never conducted trials on successive nights at the same location. We analysed the number of passes and number of screech calls with univariate and multivariate repeated measures ANOVA with three fixed factors: location, trial period and call stimulus, and one nested factor: date within location. We used single degree of freedom contrasts to compare response to familiar calls (both Guanapo groups) with unfamiliar calls (the Tamana group). For repeated measures analyses we used the mixed procedure in SAS (version 6.11), and adjusted for correlations among time periods by modelling the error variance-covariance matrix as compound symmetric. This approach estimates the magnitude of covariance among time periods, rather than assuming that it equals zero (Littell et al. 1996). In both playback experiments reported here, no response variable required transformation to meet ANOVA assumptions.

Results

Bats at Guanapo appeared to discriminate among calls from Guanapo and Tamana caves (Table III), and responded more vigorously to Guanapo calls (Fig. 3). In fact, Tamana calls had no effect on the number of screeches and appeared to deter approach. The multivariate test combined both variables to compare response to Guanapo and Tamana calls, and approached significance ($P < 0.10$). A significant difference among locations resulted from differences between cave and foraging sites. Response at the foraging site was low because few bats were present during playbacks; that is, we heard no screech calls and observed few passes (0.2 ± 0.13) during silent periods preceding playback. In contrast, baseline response at the roost cave was high (27.3 ± 5.99 passes and

Table III. Field playback results testing the ability of bats to discriminate between calls from Guanapo and Tamana caves

Source of variation	Bat passes		Screech calls		MANOVA	
	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	Wilks' λ
Location	2, 25	12.0***	2, 25	14.2***	4, 134	0.45***
Date (location)	6, 25	8.4***	6, 25	3.5**	4, 134	0.42***
Period	2, 25	3.9*	2, 25	2.4	4, 134	0.88
Playback versus prior and post	1, 25	7.7*	1, 25	4.5*	2, 67	0.89*
Call type†	6, 25	1.7	6, 25	3.4**	12, 134	0.67**
Guanapo versus Tamana	1, 25	4.5*	1, 25	5.9*	2, 67	0.93

Data were analysed with repeated measures ANOVA and MANOVA.

* $P < 0.05$, ** $P < 0.005$, *** $P < 0.0001$.

†Call type includes two exemplars of each of two Guanapo groups and one Tamana group.

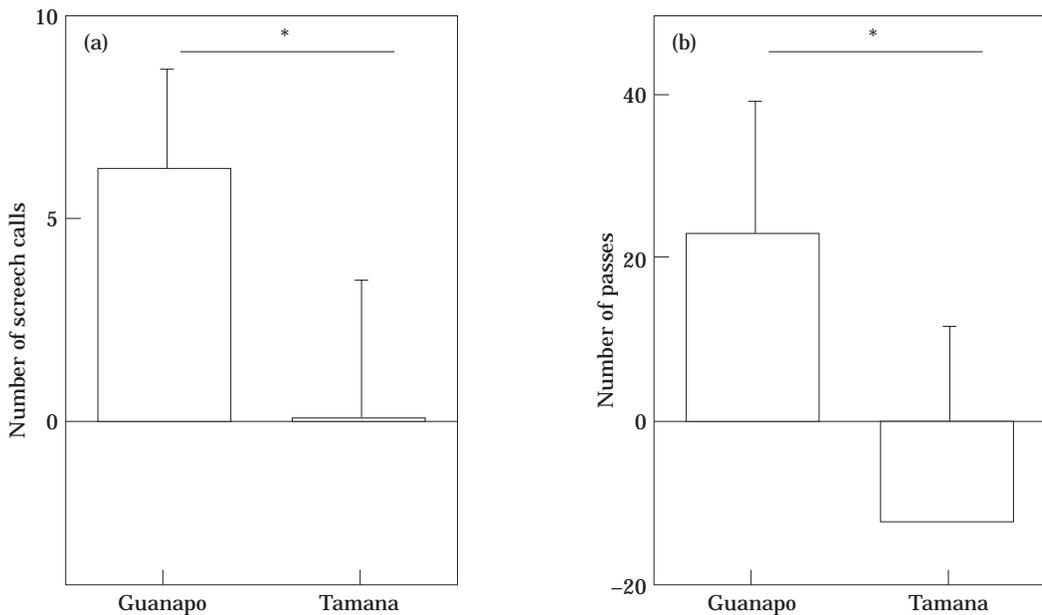


Figure 3. Mean (\pm SE) response for the number of (a) screech calls given in response to playback ($N=72$) and (b) passes, or times bats approached within approximately 2 m of the speaker ($N=35$). Values were adjusted for baseline activity by subtracting activity in the preceding silence period from playback response levels. Field playbacks showed that Guanapo bats differentiated between calls from their own cave and those from Tamana cave and responded more vigorously to Guanapo calls. Significance ($\alpha=0.05$) was obtained from comparisons of mean response to Guanapo calls and Tamana calls.

9.7 ± 1.5 screeches during silent periods). Nightly variation in playback response has been shown previously (Wilkinson & Boughman 1998) and may result from nightly variation in group foraging behaviour.

LABORATORY PLAYBACK: GROUP AND INDIVIDUAL DISCRIMINATION

Laboratory experiments allow us to monitor responses of known individuals, which is essential

for assessing discrimination between groups and individuals. We used a habituation–discrimination design in this experiment, as it provides a sensitive way to assess discrimination ability (Cheney & Seyfarth 1988) without the need to train animals in a psychoacoustic paradigm.

Methods

Subjects

As subjects we used 28 female *P. hastatus* from two social groups housed at the Department of Zoological Research, National Zoological Park, Washington, D.C. These groups are composed of wild-caught adults (we used four from group 1 and seven from group 2) and their descendent offspring (we used seven and five, respectively). Both groups originate from Tamana cave in Trinidad, West Indies and differ in call structure (Boughman 1997). The two social groups are housed separately in adjacent rooms and have no direct social contact. However, the bats can hear each other so they have acoustic interaction and are likely to be familiar with each other's calls.

Playback tape construction

We recorded calls from captive bats during 1995 and 1996 with a Marantz PMD 430 cassette-recorder using a Sennheiser ME 66 microphone onto metal tapes. The microphone and recorder provide a flat response (± 2.5 dB) up to 18 kHz. All bats were individually marked with unique combinations of coloured Scotchlite on metal wing bands and unique bleach-marked patterns on their backs and shoulders. We identified individuals in flight by their Scotchlite combinations and bleach marks, and used only calls we could unambiguously assign to individuals in the construction of playback tapes. We also used calls recorded from one Tamana group in the field. Calls recorded in the field were unfamiliar to the captive bats, allowing us to test whether discrimination relies entirely on familiarity. We used calls from Tamana cave to avoid confounding potential group discrimination with cave discrimination.

In 1995 we digitized calls with a Kay 5500 Digital sonograph, sampling at 81.9 kHz. In 1996 we digitized calls with RTS (real time spectrogram; Engineering Design, Belmont, Massachusetts)

sampling at 46.5 kHz. We constructed playback sequences digitally, in 1995 using a Kay sonograph and in 1996 using SIGNAL (Digital Signal Analysis Language, version 2.28; Engineering Design, Belmont, Massachusetts). For each of 15 individuals we concatenated four or five calls with good signal-to-noise ratio to yield a 24-s playback sequence (Fig. 4), and then played these sequences four times separated by 6-s silent intervals to produce 2-min playback stimuli. We then output stimuli to a Marantz PMD 430, recording onto metal cassette tapes. For seven bats we constructed two playback stimuli. We balanced the 22 playback stimuli for temporal and amplitude variables that could affect response, as above. We broadcast playback stimuli through Sony SRS-67 speakers, adjusting amplitude to approximately 80 dB at 1 m. Amplitude measurements of calls given in captivity are approximately 88 dB at 1 m. We observed bats with a Javelin JE-7362 video camera under infrared illumination so that we could continually and remotely monitor response. A second observer recorded data during the experiment, and all trials were video-recorded for later scoring.

Experimental design and analysis

We used a habituation–discrimination design (Nelson & Marler 1989; Hauser 1996) to test for group and individual discrimination. Prior feeding depresses activity levels and call production (Boughman 1997); therefore we tested bats before peak feeding times. Each subject was introduced to the experimental room singly and allowed 2–10 min to acclimatize. We waited until the bat was hanging quietly before beginning a playback trial. Field observations and playback experiments indicate that bats approach other bats that call (Wilkinson & Boughman 1998), and we monitored this aspect of response by counting the number of flights. How quickly bats respond may also be important to ensure effective recruitment and defence of feeding sites, so we measured latency to respond as the number of seconds to the first flight after playback began. The two response variables measure different aspects of response that may have different functions. During the experiment we monitored baseline activity level (number of passes) for 2 min of silence, followed by broadcast of playback stimuli for 2 min, when we also measured response latency. We repeated

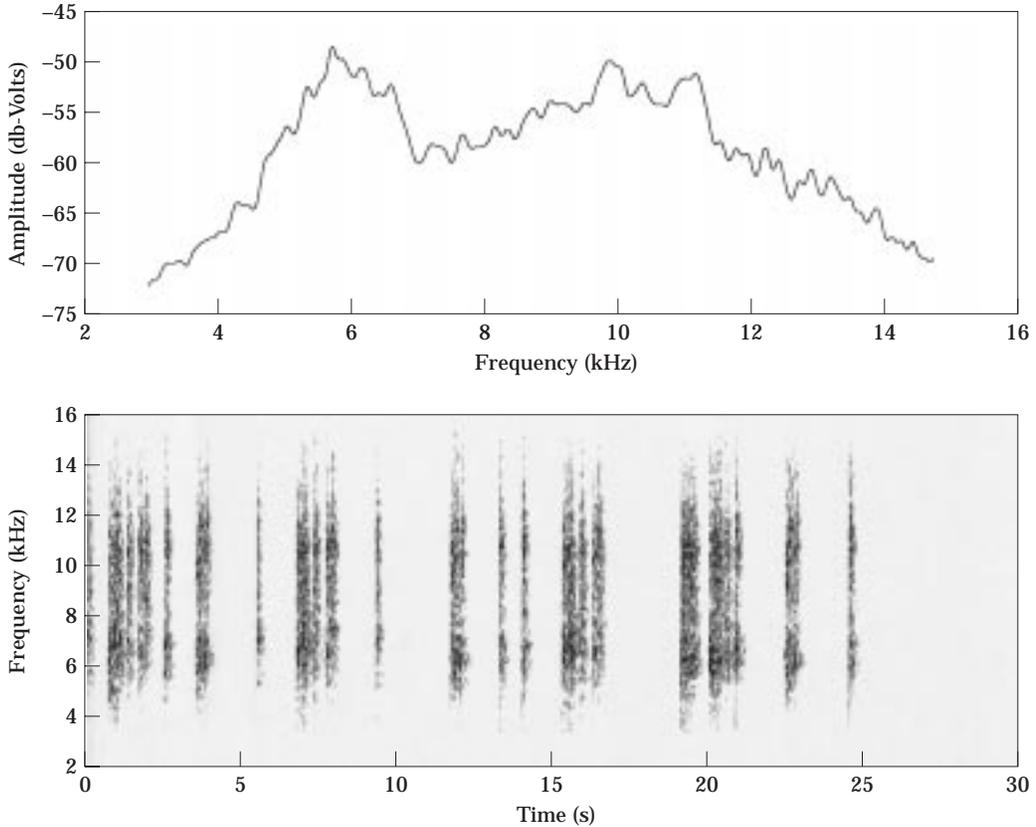


Figure 4. Example of playback sequence used in laboratory playback experiments. (a) Power spectrum for one pulse of call and (b) sonagram for entire sequence.

this cycle until the animal habituated to the stimulus, as defined by a decreased response (number of passes) of at least 50%, although in many trials response dropped to near zero. At this time we broadcast a test stimulus. To serve as an internal control, we followed the test stimulus with a re-broadcast of the habituation stimulus. We always habituated bats to calls from group mates. Test-call stimuli were one of three types: (1) unfamiliar group, a bat from a group recorded in the field, so responders could not have heard it for several years, if ever; (2) familiar group, a bat from the other captive group; and (3) group mate, a different bat from the individual's own group. To avoid overall habituation to the experimental procedure we used each of 28 individuals in each type of test no more than once in 1995 and once in 1996 for a total of 76 trials. If individuals failed to respond or failed to habituate we aborted that

trial and did not include those data in the analysis. We did not re-try that individual on the same test-call type. We separated trials with each group by at least 1 week, and avoided using the same individuals each week.

To obtain the change in response due to playback, we calculated response by subtracting the baseline activity level (number of passes in the preceding silence period) from the number of passes during playback. To adjust for variation among individuals in activity level, we included each individual's average baseline activity as a covariate. We analysed data with univariate ANCOVA using the mixed procedure in SAS (version 6.11). We also conducted multivariate ANCOVA to test the combined response of latency and number of passes to playback stimuli. We included the covariate, test call type, step in the habituation sequence and the interaction of

Table IV. Results from habituation–discrimination playbacks testing the ability of bats to discriminate between calls from their own group mates and others

Source of variation	No. passes		Response latency		MANCOVA	
	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	Wilks' λ
Test-call type	2, 57	0.8	2, 55	0.9	4, 342	0.99
Habituation sequence	5, 57	3.0*	5, 55	0.9	10, 342	0.95
Test-call type*habituation sequence	10, 57	1.8	10, 55	1.1	20, 342	0.86
Average baseline passes (covariate)	1, 57	0.2	1, 55	13.3***		
Test versus pre- and post-habituation contrasts						
Unfamiliar group	1, 57	0.03	1, 55	5.7*	2, 171	0.96*
Familiar group	1, 57	11.9***	1, 55	0.01	2, 171	0.97*
Individual bat	1, 57	0.1	1, 55	1	2, 171	0.99

Data were analysed with ANCOVA and MANCOVA. Contrasts compare test-call responses to mean habituated responses just prior to and following test presentations for each test-call type.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

the two fixed effects in the model. To test for discrimination we used single degree-of-freedom contrasts to compare mean response to test calls with mean habituated response just prior to and following test playback for each test-call type. We assessed the need for repeated measures analysis by testing for the presence of correlations among steps in the habituation sequence by modelling the error variance–covariance matrix, using compound symmetry, toeplitz and autoregressive structures. We found no evidence of correlations because no covariance structure that included such correlations provided an improved fit to the data over a variance–covariance matrix with zero correlation.

Results

Results from the laboratory playback experiment are summarized in Table IV. The unfamiliar group test indicated that bats discriminated among calls given by their group mates and bats from an unfamiliar group. Bats showed a significant change in response latency to the unfamiliar group calls (Fig. 5a, b), but not in passes. The multivariate test indicated a significant ability to make this discrimination when the two response variables were analysed together. This discrimination may depend, in part, on the familiarity of the caller. However, all bats originated from the same cave, indicating that group discrimination was not based simply on cave-level differences.

In addition, the familiar group test indicated that group discrimination was not limited to a distinction between familiar and unfamiliar calls. Bats approached the speaker more in response to playback of the familiar group test calls (Fig. 5c, d) but latency did not rebound. The multivariate test results also demonstrated that bats can make the finer distinction between members of their own group and members of other groups. This was not just a novelty response; bats discriminated their group mates from other bats, even when acoustically familiar with members of the other group.

In contrast, bats did not appear to discriminate among the individuals in their social group. Response to the test group mate was not significantly different from response to the habituated group mate for either measure alone or in combination (Table IV, Fig. 5e, f).

DISCUSSION

Evidence for Cave-level Variation

Screech calls differed between caves. Previous analyses demonstrated clear differences among groups within Tamana cave (Boughman 1997), and results presented here show that these groups clustered tightly around a multivariate acoustic mean for Tamana. Guanapo groups also clustered together in acoustic space. While groups within each cave clustered together, acoustic means for each cave differed substantially.

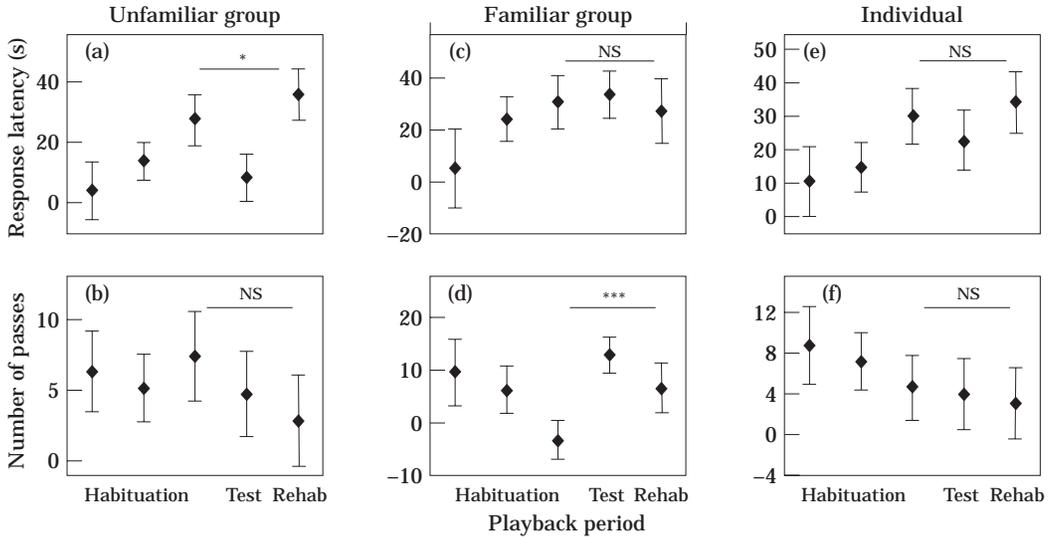


Figure 5. Results of the habituation–discrimination playback experiment testing group and individual discrimination. Graphs (a), (c) and (e) indicate the mean (\pm SE) response latency (the number of seconds after playback began before the bat responded) and graphs (b), (d) and (f) indicate the mean (\pm SE) number of passes (corrected for baseline activity). X-axis indicates stage of the habituation sequence. Habituation points are successive broadcasts of the group-mate habituation call preceding test-call playback and rehab is a re-broadcast of the same call immediately following test call playback. (a, b) Group discrimination: tests whether bats discriminate between calls from group mates and calls from an unfamiliar group; unfamiliar test calls ($N=35$) were recorded from a group that respondents could not have heard for at least 3 years, if ever. (c, d) Group mate discrimination: tests whether bats discriminate between groups based on familiarity; test calls ($N=16$) were from the other captive group, which respondents had heard but had not interacted with socially. (e, f) Individual discrimination: tests whether bats use screech calls to discriminate among individuals in their social group; test calls ($N=27$) were from different individuals in the respondent's own social group.

Social modification of calls may contribute to the pattern of divergence between caves and convergence within a cave, analogous to its effect on the development of group differences and within-group convergence (Boughman 1998). In addition, genetic isolation could easily contribute to differences among caves. Although *P. hastatus* can fly the distance between caves (Williams & Williams 1970), in over 5 years of intensive banding (ca 1000 bats banded) we have had no records of dispersal between any of the caves (G. S. Wilkinson & J. W. Boughman, unpublished data).

Almost no data are available for other bat species on geographical variation in vocalizations. In one study of social calls, Scherrer & Wilkinson (1993) found significant colony-level variation in the isolation calls of infant evening bats, *Nycticeius humeralis*. However, this effect was weak compared with the high levels of individual and family variation. Geographical variation in frequency has been reported for echolocation calls in

several bat species (Heller & von Helverson 1989; Rydell 1993). Information on other mammalian species is also sparse. Geographical variation has been described in Weddell seal, *Leptonychotes weddelli*, vocal repertoires (Thomas & Stirling 1983), bearded seal, *Erignathus barbatus*, trills (Cleator et al. 1989), humpback whale, *Megaptera novaeangliae*, song (Winn et al. 1981), killer whale, *Orcinus orca*, discrete calls (Ford & Fisher 1983), sperm whale, *Physeter macrocephalus*, codas (Weilgart & Whitehead 1997), prairie dog, *Cynomys gunnisoni zuniensis*, alarm calls (Slobodchikoff & Coast 1980), and some tamarin long calls (e.g. *Sanguinus labiatus*: Maeda & Masataka 1987), but is absent in vervet monkeys, *Cercopithecus aethiops* (Struhsaker 1970), and gibbon, *Hylobates* spp., songs (Marshall & Marshall 1976).

The cause of geographical variation in mammalian vocalizations is presently unknown. Geographical differences could be due to genetic differences between populations in vocal tract

morphology or body size, behavioural differences in foraging patterns, especially for bat echolocation calls (Rydell 1993), or even vocal learning (Payne & Payne 1985; Boughman 1998). Some data for bats suggests genetic variation is important, as some components of infant isolation calls are heritable (Scherrer & Wilkinson 1993; Masters et al. 1995; D. Lill & G.S. Wilkinson, unpublished data). Other data on bat vocalizations imply that social modification of calls may be involved. Esser (1994) provides evidence that infant lesser spear-nosed bats *P. discolor* modify their isolation calls based on auditory experience. Jones & Ransome (1993) suggest that the similarity of mother and pup echolocation calls may be due, in part, to social modification of calls. Other studies have suggested that maternal directive calls develop from infant isolation calls (Gould 1977; Esser & Schmidt 1989), implying developmental processes are important. Most importantly for this study, there is good experimental evidence that group differences and within-group convergence arise through vocal learning in *P. hastatus* (Boughman 1998).

We have more data on the occurrence of dialects and a better understanding of the factors that influence dialect development in birds (Payne 1981; Kroodsma et al. 1984; Baker & Cunningham 1985). In oscine passerines, dialects are common. Substantial evidence indicates that dialects are a consequence of vocal learning (Mundinger 1982; Kroodsma 1996; Payne 1996) with secondary contributions of limited dispersal and genetic differentiation (Slater 1989; Kroodsma 1996). Geographical variation has also been described in several non-song birds, including petrels (Bretagnolle 1996), and several quail and dove species (reviewed in Baptista 1996). These birds do not learn to sing and many species are strongly philopatric, implying that in some species geographical variation reflects population differentiation.

Evidence for Cave and Group Discrimination

Field playbacks indicated that bats discriminated between calls given by individuals in their own and foreign caves based solely on call structure. No visual or olfactory cues were required. This discrimination ability may rely, in part, on whether calls are familiar or unfamiliar to the

listening bats. The reduced response of Guanapo bats to Tamana calls is consistent with an important call function, recruitment to foraging groups, because bats would not be expected to recruit to calls of unknown group identity unless they were attempting to compete with the caller. Foraging groups may defend food resources which should also deter approach by unfamiliar bats. Decreased response to foreign calls may also reflect the difficulty of the discrimination task. Differences among groups may require confirmation through hearing multiple calls and approach, whereas calls from another cave may be sufficiently different that bats can immediately recognize that the caller is not a member of their group and thus, do not approach or call.

Discrimination in the laboratory was not limited to differentiating familiar from unfamiliar bats, nor was group discrimination based on a cave-level distinction, because all captive bats originated from the same cave. *Phyllostomus hastatus* can clearly discriminate calls given by their group mates from calls given by other bats, and can make this kind of discrimination irrespective of whether or not they have acoustic experience with these other bats. In contrast, calls did not differ significantly among individuals within a group (Boughman 1997), and bats did not respond differentially to calls from different individuals.

Both group-discrimination tests are consistent with field playback results, screech call function, and with groups defending food resources. Females responded quickly to calls from an unfamiliar group but did not approach the source of sound. This is expected given that foraging groups appear to defend feeding sites (McCracken & Bradbury 1981; Wilkinson & Boughman 1998). In comparison, females investigated calls from a familiar group, but did not vary in the time taken to initiate response. This is consistent with the recruitment function that calls serve. Differences in recording procedures did not appear to confound results, because group discrimination occurred between calls recorded with similar methods. The results of the individual discrimination test indicate either that females did not perceive differences among group mates, or that the calls of group mates were behaviourally equivalent. This experiment did not allow us to differentiate between these two explanations.

Vocal Recognition in Other Taxa and Contexts

Most taxa that use vocalizations for recognition base this recognition on individual signatures, whether the important task is to identify neighbours, kin or group mates. Both the production of individually distinctive calls and their discrimination appears to be tied closely to function. For example, vocal recognition can be used to differentiate between individuals that pose a competitive threat and those that do not, as in territorial song birds (Brooks & Falls 1975; Shy & Morton 1986; Brindley 1991; Godard 1991; Weary & Krebs 1992; Godard & Wiley 1995; Stoddard 1996) or to facilitate interactions among social partners. Recognition between parents and offspring often appears to be based on individual variation, and is favoured in colonial and highly social animals (e.g. Mexican free-tailed bats, *Tadarida brasiliensis*: Balcombe 1990; Balcombe & McCracken 1992; and bank swallows, *Riparia riparia*: Beecher & Stoddard 1990). In contrast, rough-winged swallows, *Stelgidopteryx serripennis*, do not produce individual signatures nor do parents recognize offspring by call, presumably because selection for parent-offspring recognition is lacking in this non-colonial species (Beecher 1982). Production and detection of signatures is expected only when it provides a benefit.

Production and recognition of calls that signify group membership should also reflect specific selection pressures. In many primates, group recognition appears to be based on individually distinctive calls (Cheney & Seyfarth 1982; Rendall et al. 1996). Social interactions within the group depend on dominance relationships, which may require individual recognition. Dominance within chickadee flocks may favour individual differences, although flock differences also exist (Mammen & Nowicki 1981). Chickadees may use both cues in their differential response to calls from their own and different winter flocks (Nowicki 1983).

With the exception of chickadees, these examples rely on individual signatures. In contrast, greater spear-nosed bats do not appear to use individual variation in screech calls to identify roost mates. Considering the widespread use of individual differences, finding that screech calls show only group-level differences and that bats do not appear to distinguish among group mates is

puzzling. We can understand this pattern more clearly by considering that it reflects selection to recognize social group mates in the context of group foraging in *P. hastatus*. In this species, basing group-member recognition on group-distinctive calls is probably more efficient than identifying individuals and then evaluating their association with the social group. Given that many hundreds of *P. hastatus* emerge from some cave roosts within a 45-min time span (personal observation), identifying individuals by voice and determining their social affiliation may simply be too demanding. The lack of individual signatures and individual discrimination implies that selection for individual identification is weak. This suggests that the evolutionary mechanism that maintains group foraging behaviour depends on group membership but is insensitive to individual identity.

The lack of individual discrimination based on screech calls does not mean that *P. hastatus* cannot discriminate among group mates, even though we have no evidence that they use screech calls to do so. Other cues are available, including many other social vocalizations given in the roost (Gould 1977; J. W. Boughman, unpublished data), echolocation calls and olfactory cues (Boughman 1997). Using multiple cues is not unexpected when the discrimination task is difficult. For example, female Mexican free-tailed bats face an extremely difficult task of finding their pup in dense creches. Mothers use locational information to focus the search for their pups (McCracken 1993), produce individually distinctive directive calls that elicit calling by pups (Balcombe & McCracken 1992), and then combine olfactory and individually distinctive vocal cues to identify their pup (Gustin & McCracken 1987; Balcombe 1990).

Advantages of Indicating Group Membership and Recognizing Group Mates

What could be the selective advantage to identifying group membership in these contexts? Over 800 *P. hastatus* roost in Guanapo cave. Netting at flyways and feeding sites indicates both that group mates forage together and that bats from several groups can be present at the same location (Wilkinson & Boughman 1998). Radio-tracking data support this finding (McCracken & Bradbury

1981; G. S. Wilkinson & J. W. Bradbury, unpublished data). Consequently, feeding competition has the potential to be intense. Defending rich food sites, such as balsa trees, *Ochroma lagopus*, with many open flowers (Wilkinson & Boughman 1998) could be beneficial and may be achieved more effectively by a group. Thus discrimination of group mates becomes important to determine which bats in the vicinity are group mates and which are not. Calls may advertise an individual's presence and social-group membership both to members of the individual's own group (to elicit cooperative defence and deflect possible aggression) and potential intruders (to advertise site ownership and discourage feeding by non-group mates). Both are important if the cooperative defence that we propose does occur (Wilkinson & Boughman 1998).

The occurrence of group member signatures implies that there is an advantage to living in these stable groups. Stable matrilineal groups are common in mammals (Rasa 1972; Wrangham 1980), but the low levels of relatedness in female greater spear-nosed bat groups is unusual (McCracken 1987). Young females may disperse from their natal group to avoid breeding with their father. Yet, what advantages keep unrelated females together? McCracken & Bradbury (1981) hypothesized that shared information about food or mutual defence of feeding sites might provide important advantages, and we have foraging data consistent with both explanations (Wilkinson & Boughman 1998, in press). Some benefits may be derived from social interactions inside the cave. For instance, we have observed non-offspring nursing (G. S. Wilkinson & T. A. Porter, unpublished data), indicating that group mates may cooperatively care for and defend pups. When pups are young, one or more females per group remain at the roost while the other adults are out foraging, presumably to defend pups against the several predators we have observed in caves (G. S. Wilkinson & J. W. Boughman, unpublished data). Pups also huddle together which reduces heat loss and energy consumption (T. A. Porter & M. Power, unpublished data). Living in a group appears to be obligate for females, as we have not observed females roosting alone. Data presented here demonstrate that identifying group mates by call is an important mechanism for maintaining these stable groups, emphasizing that foraging benefits are important.

ACKNOWLEDGMENTS

Heather Alcorn, Skye Boughman and Jason Wolf provided able assistance conducting playbacks, Sue Perkins assisted with field recordings and Ronnie Hernandez at Simla Research Station helped with field logistics. Peter Miller and the animal care staff at the Department of Zoological Research at the National Zoological Park cared expertly for the captive animals. The comments of Gene Morton, Daven Presgraves, and Dave Yager improved the manuscript. Our thanks to all these people. This research was supported by an NSF dissertation improvement grant, and University of Maryland and Smithsonian Institution fellowships to J.W.B., and an NSF grant to G.S.W.

REFERENCES

- Aldridge, H. D. J. N., Obrist, M., Merriam, H. G. & Fenton, M. B. 1990. Roosting, vocalizations, and foraging by the African bat, *Nycteris thebaica*. *J. Mammal.*, **71**, 242–246.
- Baker, M. C. & Cunningham, M. A. 1985. The biology of bird-song dialects. *Behav. Brain Sci.*, **8**, 85–133.
- Balcombe, J. P. 1990. Vocal recognition of pups by mother Mexican free-tailed bats, *Tadarida brasiliensis mexicana*. *Anim. Behav.*, **39**, 960–966.
- Balcombe, J. P. & McCracken, G. F. 1992. Vocal recognition in Mexican free-tailed bats: do pups recognize mothers? *Anim. Behav.*, **43**, 79–88.
- Baptista, L. F. 1996. Nature and its nurturing in avian vocal development. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 39–60. Ithaca, New York: Cornell University Press.
- Barlow, K. E. & Jones, G. 1997. Function of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) social calls: field data and a playback experiment. *Anim. Behav.*, **53**, 991–999.
- Beecher, M. D. 1982. Signature systems and kin recognition. *Am. Zool.*, **22**, 477–490.
- Beecher, M. D. 1989. Signalling systems for individual recognition: an information theory approach. *Anim. Behav.*, **38**, 247–261.
- Beecher, M. D. & Stoddard, P. K. 1990. The role of individuality in bird song: contrasting field and laboratory perspectives. In: *Comparative Perception II: Complex Signals* (Ed. by M. Berkley & W.C. Stebbins), pp. 385–408. New York: John Wiley.
- Boughman, J. W. 1997. Greater spear-nosed bats give group distinctive calls. *Behav. Ecol. Sociobiol.*, **40**, 61–70.
- Boughman, J. W. 1998. Vocal learning by greater spear-nosed bats. *Proc. R. Soc. Lond. Ser. B*, **265**, 227–233.

- Bradbury, J. & Vehrencamp, S. 1976. Social organization and foraging in emballonurid bats. I. Field studies. *Behav. Ecol. Sociobiol.*, **1**, 337–381.
- Bretagnolle, V. 1996. Acoustic communication in a group of nonpasserine birds, the petrels. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 160–178. Ithaca, New York: Cornell University Press.
- Brindley, E. L. 1991. Response of European robins to playback of song: neighbour recognition and overlapping. *Anim. Behav.*, **41**, 503–512.
- Brockway, B. F. 1964. Ethological studies of the budgerigar (*Melopsittacus undulatus*): non-reproductive behaviour. *Behaviour*, **22**, 193–222.
- Brooks, R. J. & Falls, J. B. 1975. Individual recognition by song in white-throated sparrows III. Song features used in individual recognition. *Can. J. Zool.*, **53**, 1749–1761.
- Brown, C. R. 1988. Social foraging in cliff swallows: local enhancement, risk sensitivity, competition and the avoidance of predators. *Anim. Behav.*, **36**, 780–792.
- Brown, C. R. & Brown, M. B. 1996. *Coloniality in the Cliff Swallow*. Chicago: The University of Chicago Press.
- Catchpole, C. K. & Slater, P. J. B. 1995. *Bird Song: Biological Themes and Variations*. Cambridge: Cambridge University Press.
- Cheney, D. L. & Seyfarth, R. M. 1982. Recognition of individuals within and between groups of free-ranging vervet monkeys. *Am. Zool.*, **22**, 519–529.
- Cheney, D. L. & Seyfarth, R. M. 1988. Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Anim. Behav.*, **36**, 477–486.
- Cleator, H. J., Stirling, I. & Smith, T. G. 1989. Underwater vocalizations of the bearded seal (*Erignathus barbatus*). *Can. J. Zool.*, **67**, 1900–1910.
- Esser, K. H. 1994. Audio-vocal learning in a non-human mammal: the lesser spear-nosed bat, *Phyllostomus discolor*. *Neuro. Report*, **5**, 1718–1720.
- Esser, K. H. & Schmidt, U. 1989. Mother–infant communication in the lesser spear-nosed bat *Phyllostomus discolor* (Chiroptera, Phyllostomidae): evidence for acoustic learning. *Ethology*, **82**, 156–168.
- Fenton, M. B. 1995. Natural history and biosonar signals. In: *Hearing by Bats* (Ed. by A. N. Popper & R. R. Fay), pp. 37–86. New York: Springer-Verlag.
- Ford, J. K. B. & Fisher, H. D. 1983. Group-specific dialects of killer whales (*Orcinus orca*) in British Columbia. In: *Communication and Behavior of Whales* (Ed. by R. Payne), pp. 129–161. Boulder, Colorado: Westview Press.
- Godard, R. 1991. Long-term memory of individual neighbours in a migratory songbird. *Nature, Lond.*, **350**, 228–229.
- Godard, R. & Wiley, R. H. 1995. Individual recognition of song repertoires in two wood warblers. *Behav. Ecol. Sociobiol.*, **37**, 119–123.
- Gould, E. 1977. Echolocation and communication. In: *Biology of Bats of the New World Phyllostomatidae* (Ed. by R. J. Baker, J. K. Jones & D. C. Carter), pp. 247–279. Texas: Texas Tech University.
- Greenhall, A. M. 1965. Sapucaia nut dispersal by greater spear-nosed bats in Trinidad. *Carib. J. Sci.*, **5**, 167–171.
- Gustin, M. K. & McCracken, G. F. 1987. Scent recognition in the Mexican free-tailed bat *Tadarida brasiliensis mexicana*. *Anim. Behav.*, **35**, 13–19.
- Hauser, M. 1996. *Evolution of Animal Communication*. Boston: MIT Press.
- Heinrich, B. 1988. Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven, *Corvus corax*. *Behav. Ecol. Sociobiol.*, **23**, 141–156.
- Heller, K.-G. & von Helverson, O. 1989. Resource partitioning of sonar frequency bands by rhinolophid bats. *Oecologia (Berl.)*, **80**, 178–186.
- Howell, D. J. 1979. Flock foraging in nectar-feeding bats: advantages to the bats and to the host plants. *Am. Nat.*, **114**, 23–49.
- Janik, V. M. & Slater, P. J. B. 1997. Vocal learning in mammals. *Adv. Study Behav.*, **26**, 59–99.
- Johnson, R. A. & Wichern, D. W. 1992. *Applied Multivariate Statistical Analysis*. Englewood Cliffs, New Jersey: Prentice-Hall.
- Jones, G. & Ransome, R. D. 1993. Echolocation calls of bats are influenced by maternal effects and change over a lifetime. *Proc. R. Soc. Lond. Ser. B*, **252**, 125–128.
- Kalko, E. K. V. & Schnitzler, H.-U. 1993. Plasticity in echolocation signals of European pipistrelle bats in search flight: implications for habitat use and prey detection. *Behav. Ecol. Sociobiol.*, **33**, 415–428.
- Krebs, J. R., MacRoberts, M. H. & Cullen, J. M. 1972. Flocking and feeding in the great tit *Parus major*: an experimental study. *Ibis*, **114**, 507–530.
- Kroodsma, D. E. 1996. Ecology of passerine song development. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 3–19. Ithaca, New York: Cornell University Press.
- Kroodsma, D. E., Baker, M. C., Baptista, L. F. & Petrinovich, L. 1984. Vocal 'dialects' in Nuttall's white-crowned sparrow. *Curr. Ornithol.*, **2**, 103–133.
- Littell, R. C., Milliken, G. A., Stroup, W. W. & Wolfinger, R. D. 1996. *SAS System for Mixed Models*. Cary, North Carolina: SAS Institute.
- McCracken, G. F. 1987. Genetic structure of bat social groups. In: *Recent Advances in the Study of Bats* (Ed. by M. B. Fenton, P. Racey & J. M. V. Rayner), pp. 281–298. Cambridge: Cambridge University Press.
- McCracken, G. F. 1993. Locational memory and female-pup reunions in Mexican free-tailed bat maternity colonies. *Anim. Behav.*, **45**, 811–813.
- McCracken, G. F. & Bradbury, J. W. 1981. Social organization and kinship in the polygynous bat *Phyllostomus hastatus*. *Behav. Ecol. Sociobiol.*, **8**, 11–34.
- Maeda, T. & Masataka, N. 1987. Locale-specific vocal behavior of the tamarin (*Sanguinus labiatus*). *Ethology*, **75**, 25–30.
- Mammen, D. L. & Nowicki, S. 1981. Individual differences and within-flock convergence in chickadee calls. *Behav. Ecol. Sociobiol.*, **9**, 179–186.

- Marshall, J. T. & Marshall, E. R. 1976. Gibbons and their territorial songs. *Science*, **193**, 235–237.
- Masters, W. M., Raver, K. A. S. & Kazial, K. A. 1995. Sonar signals of big brown bats, *Eptesicus fuscus*, contain information about individual identity, age and family affiliation. *Anim. Behav.*, **50**, 1243–1260.
- Moss, C. E. & Schnitzler, H.-U. 1995. Behavioral studies of auditory information processing. In: *Hearing by Bats* (Ed. by A. N. Popper & R. R. Fay), pp. 87–145. New York: Springer-Verlag.
- Mundinger, P. C. 1982. Microgeographic and macrogeographic variation in the acquired vocalizations of birds. In: *Acoustic Communication in Birds. Vol. 2* (Ed. by D. E. Kroodsma, F. H. Miller & D. Ouellet), pp. 147–208. New York: Academic Press.
- Nelson, D. A. & Marler, P. 1989. Categorical perception of a natural stimulus continuum: birdsong. *Science*, **244**, 976–978.
- Nowicki, S. 1983. Flock-specific recognition of chickadee calls. *Behav. Ecol. Sociobiol.*, **12**, 317–320.
- Payne, K. & Payne, R. 1985. Large scale changes over 19 years in songs of humpback whales in Bermuda. *Z. Tierpsychol.*, **68**, 89–114.
- Payne, R. B. 1981. Population structure and social behavior: models for testing the ecological significance of song dialects in birds. In: *Natural Selection and Social Behavior* (Ed. by R. D. Alexander & D. W. Tinkle), pp. 108–120. New York: Chiron Press.
- Payne, R. B. 1996. Song traditions in indigo buntings: origin, improvisation, dispersal, and extinction in cultural evolution. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 198–220. Ithaca, New York: Cornell University Press.
- Rabenold, P. P. 1987. Recruitment to food in black vultures: evidence for following from communal roosts. *Anim. Behav.*, **35**, 1775–1785.
- Rasa, O. A. E. 1972. Aspects of social organization in captive dwarf mongooses. *J. Mammal.*, **53**, 181–185.
- Reeve, H. K. 1989. The evolution of conspecific acceptance thresholds. *Am. Nat.*, **133**, 407–435.
- Rendall, D., Rodman, P. S. & Emond, R. E. 1996. Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Anim. Behav.*, **51**, 1007–1015.
- Rydell, J. 1993. Variation in the sonar of an aerial-hawking bat (*Eptesicus nilssonii*). *Ethology*, **93**, 275–284.
- Sazima, I. & Sazima, M. 1977. Solitary and group foraging: two flower-visiting patterns of the lesser spear-nosed bat *Phyllostomus discolor*. *Biotropica*, **9**, 213–215.
- Scherrer, J. A. & Wilkinson, G. S. 1993. Evening bat isolation calls provide evidence for genetic signatures. *Anim. Behav.*, **46**, 847–860.
- Shy, E. & Morton, E. S. 1986. The role of distance, familiarity, and time of day in Carolina wrens responses to conspecific songs. *Behav. Ecol. Sociobiol.*, **19**, 393–400.
- Sibly, R. H., Nott, H. M. R. & Fletcher, D. J. 1990. Splitting behaviour into bouts. *Anim. Behav.*, **39**, 63–69.
- Slater, P. J. B. 1989. Bird song learning: causes and consequences. *Ethol. Ecol. Evol.*, **1**, 19–46.
- Slobodchikoff, C. N. & Coast, R. 1980. Dialects in the alarm calls of prairie dogs. *Behav. Ecol. Sociobiol.*, **7**, 48–53.
- Stoddard, P. K. 1996. Vocal recognition of neighbors by territorial passerines. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 356–374. Ithaca, New York: Cornell University Press.
- Struhsaker, T. T. 1970. Phylogenetic implications of some vocalizations of *Cercopithecus* monkeys. In: *Old World Monkeys: Evolution, Systematics, and Behavior* (Ed. by J. R. Napier & P. H. Napier), pp. 365–444. New York: Academic Press.
- Thomas, J. A. & Stirling, I. 1983. Geographic variation in the underwater vocalizations of Weddell seals (*Leptonychotes weddelli*) from Palmer Peninsula and McMurdo Sound, Antarctica. *Can. J. Zool.*, **61**, 2203–2212.
- Tidemann, C. R., Priddel, D. M., Nelson, J. E. & Pettigrew, J. D. 1985. Foraging behaviour of the Australian ghost bat, *Macroderma gigas* (Microchiroptera: Megadermatidae). *Austral. J. Zool.*, **33**, 705–713.
- Vaughan, T. A. 1976. Nocturnal behavior of the African false vampire bat (*Cardioderma cor*). *J. Mammal.*, **57**, 227–249.
- Vaughan, T. A. & Vaughan, R. P. 1986. Seasonality and the behavior of the African yellow-winged bat. *J. Mammal.*, **67**, 91–102.
- Weary, D. M. & Krebs, J. R. 1992. Great tits classify songs by individual voice characteristics. *Anim. Behav.*, **43**, 283–288.
- Weilgart, L. & Whitehead, H. 1997. Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behav. Ecol. Sociobiol.*, **40**, 277–285.
- Wilkinson, G. S. 1992. Information transfer at evening bat colonies. *Anim. Behav.*, **44**, 501–518.
- Wilkinson, G. S. & Boughman, J. W. In press. Social influences on foraging in bats. In: *Social Learning among Mammals* (Ed. by H. O. Box & K. A. Gibson). Cambridge: Cambridge University Press.
- Wilkinson, G. S. & Boughman, J. W. 1998. Social calls coordinate foraging in greater spear-nosed bats. *Anim. Behav.*, **55**, 337–350.
- Williams, R. & Williams, J. M. 1970. Radio tracking of homing and feeding flights of a neotropical bat, *Phyllostomus hastatus*. *Anim. Behav.*, **18**, 302–309.
- Winn, H. E., Thompson, T. J., Cummings, W. D., Hain, J., Hudnall, J., Hays, H. & Steiner, W. W. 1981. Song of the humpback whale – population comparisons. *Behav. Ecol. Sociobiol.*, **8**, 41–46.
- Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour*, **75**, 262–300.