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Greater spear-nosed bats give group-distinctive calls

Abstract Individually distinctive vocalizations are ubiquitous; however, group distinctive calls have rarely been demonstrated. Under some conditions, selection should favor calls indicating social group membership in animals that forage in groups. Greater spear-nosed bats (*Phyllostomus hastatus*) give calls that appear to facilitate recognition of social group mates who are unrelated. Females give loud broadband (4–18 kHz) vocalizations termed screech calls when departing on foraging trips and at foraging sites. Screech calls help to establish foraging groups among social group members, and to maintain contact over the long distances they travel while foraging. I test two hypotheses about how screech calls may be structured to convey caller identity. Individual calls may be distinct and group members may learn to recognize each individual's calls and to associate the individual with the social group. Alternatively, groups may give distinct calls and individuals within groups may share call characteristics. To test these hypotheses I conducted multivariate acoustic analysis of multiple calls from 28 bats from three social groups. Although the ubiquity of individually distinctive calls in other taxa makes this result more likely, the results reveal that group calls are highly distinctive. Individual bats within groups are statistically indistinguishable. Calls appear to decrease slightly in frequency as bats age. Call convergence among unrelated group mates implies vocal learning in this species.

Key words Bat communication · Call convergence · Group foraging · Food associated calls

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Introduction

Individually distinctive calls have been demonstrated in many birds and mammals, and often reflect kinship. In colonial or group-living species, such as some swallows and bee-eaters (Beecher and Stoddard 1990; Lessells et al. 1991), bottlenose dolphins (Sayigh et al. 1990), and some bats (Esser and Schmidt 1989; Balcombe 1990) they enable parents to find young, reducing the likelihood of misdirected parental care; or allow young to find mothers (Balcombe and McCracken 1992), reducing mortality. Infant evening bats (*Nyceticeus humeralis*; Scherrer and Wilkinson 1993) and greater spear-nosed bats (*P. hastatus*; D. O'Reilly and G.S. Wilkinson, unpublished work) give individually distinctive and heritable isolation calls. If relatives form social groups, heritable variation might result in group differences. For instance, killer whale pods contain matrilines. Although heritabilities have not been measured, pod members give acoustically similar calls that may enable them to find each other when separated, and may help coordinate hunting (Ford 1989).

Unrelated animals may also use calls that are distinctive at either the individual or group level. Animals may learn to recognize the individually distinctive calls of group mates. Vervet monkeys appear to recognize their own group mates and individuals from neighboring groups (Cheney and Seyfarth 1982). In group-living lions, distinctive male roars enable mothers to detect unfamiliar and potentially infanticidal males, reducing cub mortality (McComb et al. 1993). In territorial birds, individual differences enable males to determine if a non-neighbor is present or intruding (e.g., Brooks and Falls 1975; Shy and Morton 1986; Brindley 1991; Weary and Krebs 1992; Godard and Wiley 1995), reducing territorial defense costs.

Alternatively, unrelated group mates may give calls that resemble one another. This resemblance arises not through shared genes, but through socially mediated changes or learning. Although this is plausible, group

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distinctive calls have been documented rarely. Black-capped chickadees (*Parus atricapillus*) give calls that converge acoustically on those of their flock mates (Mammen and Nowicki 1981; Nowicki 1989). These calls may facilitate flock cohesion.

Adult female greater spear-nosed bats (*Phyllostomus hastatus*) associate in stable social groups that are defended by single males (McCracken and Bradbury 1981). Females join a social group during their second year and remain with these same females for most of their lives (McCracken and Bradbury 1981; G.S. Wilkinson and J.W. Boughman, unpublished work). Estimated relatedness within social groups is near zero (McCracken and Bradbury 1977, 1981), although paternal half-sisters occasionally join social groups together (G.S. Wilkinson and J.W. Boughman, unpublished work).

Female greater spear-nosed bats sometimes forage in groups. Foraging groups are preferentially formed of social group mates who both travel and feed together (Wilkinson and Boughman in press). Females give loud broadband (4–18 kHz) vocalizations termed screech calls when departing on foraging trips and at foraging sites (Bloedel 1955; Goodwin and Greenhall 1961; Wilkinson and Boughman in press). Screech calls are involved in active group formation. They help to establish foraging groups among social group members, and to maintain contact over the long distances these bats travel while foraging (Wilkinson and Boughman in press). Screech calls preferentially recruit long term associates; therefore, they are likely to identify the group status of the caller. They may also identify individuals. Since most group mates are unrelated, calls are not likely to reflect kinship.

This paper describes the acoustic structure of screech calls that function to coordinate foraging in greater spear-nosed bats. Group member recognition must occur for group mates to find each other outside the cave roost, and field observations indicate that screech calls are likely to serve this function (Wilkinson and Boughman in press). I test two hypotheses about how screech calls might be structured to allow recognition of group mates. Individuals may give individually distinct calls that their group members learn to recognize (*the individual learning hypothesis*). Alternatively, individuals may share call characteristics with their group mates leading to group distinctive calls (*the group convergence hypothesis*). The individual learning hypothesis seems particularly plausible in *P. hastatus* given that the stability of social groups provides many opportunities for individuals to hear one another's calls. The group convergence hypothesis is also plausible, for the longevity of social groups should simplify the process of acquiring the group's characteristics. If screech calls are the primary basis for group member recognition, the individual learning hypothesis requires not only that calls are individually distinctive, but that bats associate the identified individual with the social group. The group convergence hypothesis requires only that a group-nongroup distinction be made and this may be a simpler

cognitive task. I also describe differences among ages in calling behavior and call characteristics, and comment on potential ways individual bat's calls may come to resemble their group mates. Results from testing group and individual differences implicate vocal learning. Clearly, describing call structure tells us only whether relevant information for identifying individuals or group mates is present. Playback experiments are under way to test the ability of bats to identify group mates based solely on calls.

Methods

Subjects

I captured about half of two groups of females, each with an attendant male, from Tamana Cave in Trinidad, West Indies during January 1993 and transported them to the Department of Zoological Research (DZR) at the National Zoological Park in Washington, D.C. There, groups were housed separately in $3 \times 4 \times 3$ m rooms equipped with 0.75-m^3 roost boxes. Humidity was maintained above 40% and temperature was controlled to range within 23–35° C. A 12-h light cycle was reversed so that bats were active from 9:00 a.m. to 9:00 p.m. We fed bats a diet consisting of watermelon, cantaloupe, honeydew melon, canned primate diet, commercial dog food and mice. I refer to bats older than 2 years as adults; those between 1 and 2 years as 1st-year bats, and bats less than 1 year old as pups. Some adults had been captured and marked as pups in previous years, so I knew precisely how old they were. For others I used toothwear and evidence of parity to estimate age. I scored toothwear on a scale of 1 (least worn and usually 3 years or less) to 5 (most worn and typically seen on bats of 10–12 years or more). Parity was assessed by nipple condition and the presence of a pup. Females who have never nursed have unused nipples and are two years old or less. During recording, group 1 contained 11 adult females, one adult male, four 12- to 18-month old females (1st year), and eight 3- to 5-month old female pups. Group 2 contained 12 adult females, one adult male, three 12- to 18-month old females (1st year), and five 3- to 5-month old female pups. All subadults were born in captivity.

During June 1994, I captured one additional female group (group 3) consisting of 18 females from Tamana Cave. This group contained 14 adults, three 1st-year bats, and one pup. I held these 18 bats for 9 nights in a $4 \times 5 \times 4$ m flight cage with adjacent 3-m^2 roost room at the Simla Research Station in Trinidad. I fed them papaya, mango, cucumber, and banana presented in hanging basket feeders, and large bodied insects such as katydids (Tettigoniidae), passalid (Passalidae) and scarab (Scarabaeidae) beetles. I released this group at the point of capture after 9 days. Although the location and time of recording differ for this group, all groups originate from the same colony and I used the same recording procedures and equipment.

All bats were banded on the left forearm with numbered metal bands. I individually marked all bats with unique color combinations of reflective tape (3M Scotchlite) on these forearm bands. I also bleach-marked unique patterns on the back and shoulders of bats housed at DZR to facilitate identification.

### Call recording and measurement

I recorded group 1 and group 2 adult females once a week from March to August 1994 and pups from July to September 1995 in their respective roost rooms at DZR. I recorded group 3 females over 3 nights in the Simla flight cage. In all cases, I recorded bats flying freely around the flight cage, within the first 2 h of nightly activity when they were feeding. I recorded screech calls with a

Marantz PMD 430 cassette recorder onto metal tape using either a Bruel and Kjaer half-inch 4130 microphone and amplifier, or a Sennheiser MKH-840 shotgun microphone. The Bruel and Kjaer provided nearly flat response (± 5 dB) up to 20 kHz and the Sennheiser up to 18 kHz. I identified individuals in flight by their Scotchlite and bleach marks, and analyzed only calls I could unambiguously assign to an individual. I recorded sufficient calls from 11 adults (three each from groups 1 and 2 and five from group 3) and 10 12- to 18-month old females (five from group 1, three from group 2, and two from group 3), and seven 3- to 5-month old pups (four from group 1, two from group 2 and one from group 3). Two bats were recorded as both pups and first year bats. I measured 4–9 calls with high signal-to-noise ratio from each of these 28 bats. Calls consisted of 1–12 pulses. The data set consists of 161 calls with 733 pulses. While recording I noted all bats present and those that gave screech calls. Some bats never gave screech calls during multiple recording sessions. I tested whether calling behavior and age were independent using contingency analysis and Fisher's exact test.

I digitized calls with a Kay Elemetrics DSP 5500, sampling at 81.9 kHz with 12-bit precision. When computing sound spectrograms and power spectra, I set the FFT size to 512 points and used a Hanning window to obtain a frequency resolution of 208 Hz. Each power spectrum was calculated over 6.3 ms of the call. I calculated an arithmetic mean of these power spectra to yield an average power spectrum across each pulse in the call. Overlap of calls with background noise in both environments was negligible. From each average power spectrum, I measured one relative amplitude and seven frequency variables, and counted the number of power peaks. I selected variables that revealed how energy is distributed across frequency in these noisy, broadband calls. I also measured four temporal features from sound spectrographs and waveforms (see Fig. 1 for variable description).

Fig. 1a, b Variables measured on screech calls. (**a**) Average power spectrum (shown for first pulse of call). Variables measured include: (1) *PK1* frequency at first power peak (kHz), (2) *PK2* frequency at second power peak (kHz), (3) *LO12* frequency –12 dB below peak 1 (kHz), (4) *HI12* frequency – 12 dB above peak 2 (kHz), (5) *BANDWIDTH* bandwidth at –12 dB (kHz), (6) *RISE* increase in amplitude with increasing frequency rising up to peak 1 (kHz/dB), (7) *FALL* decrease in amplitude with increasing frequency falling off from peak 2 (kHz/dB), (8) *ADIF* amplitude difference between peaks 1 and 2 (dB) , and (9) *NPK* number of energy peaks. (**b**) Sound spectrogram of one screech call. Variables measured include (10) *PDUR* pulse duration (ms), (11) *REP* pulse repetition rate (ms from the onset of one pulse to the onset of the next), (12) *CALLDUR* total call duration (ms) , and (13) *NPULSE* number of pulses
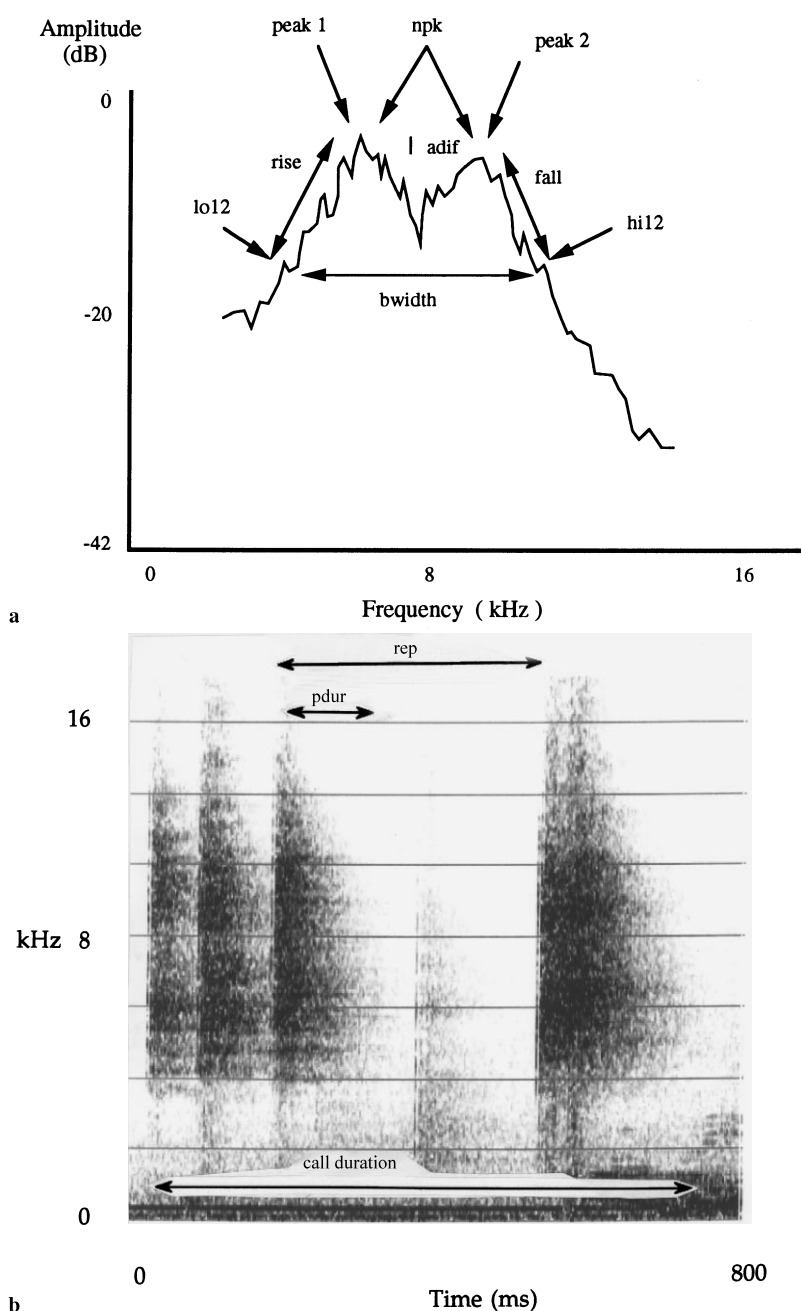
Statistical analysis

Comparing groups, ages, and individuals with analysis of variance

To test for group, age, and individual differences, I conducted two-factor mixed model nested univariate and multivariate analysis of variance (ANOVA) with group (three social groups) and age (three age classes) as the two factors. I included the group by age interaction, and had two nested random effects: bats within group and age (the individual component), and calls within bat. Bat within group and age is the error term for group, and for age. Call within bat is the error term for individual. The group by age interaction was nonsignificant for all but one variable (rise to peak 1), so I deleted it from subsequent analyses. The same model was used in all subsequent ANOVAs unless otherwise indicated. To determine significance of each variable in the univariate ANOVA I adjusted alpha levels using a sequential Bonferroni adjustment (Rice 1989). I controlled type I error within each effect, dividing 0.05 by the number of variables, giving an α of 0.0038 for the first comparison. For informational purposes, I indicate all probabilities less than 0.05, but only consider those that meet the Bonferroni criterion as significant.

To determine if differences in estimated age among recorded bats influenced group differences in calls, I conducted univariate ANCOVA using toothwear as the covariate. The ANCOVA indicates no significant effect of toothwear on 11 of the 12 measured variables (– 12 dB below peak 1 shows a significant effect of age), so I deleted the covariate from subsequent analyses.

No variables required transformation to meet ANOVA assumptions. I estimated variance components for each of the effects in the ANOVA model using restricted maximum likelihood. I then calculated the proportion of total variation within each variable due to group, age, individual bat within group and age, and call within bat.

Discrimination into groups

After determining whether multivariate group means differed, I conducted discriminant function analyses to determine how well calls could be assigned to social group. For each variable, I calculated average values across each call resulting in 161 calls from 28 bats. I used these averages in the discriminant procedure because it seemed more likely that, except for temporal patterning, bats would use the information from an entire call for classification rather than individual pulses. This is also a more conservative approach, since it reduces the degrees of freedom.

To select the model that maximally discriminates between groups, I conducted a stepwise discriminant analysis. I used a forward selection procedure which sequentially selects the variable with the highest partial R^2 while controlling for the other variables already in the model. The variables identified by this procedure as contributing significantly to discrimination were those used to construct the discriminant function. This procedure also reveals which variables might convey information on group membership.

To determine how well calls could be assigned to social group, I used a nonparametric approach, classifying each observation into group based on the group membership of its six nearest neighbors. The number of calls were approximately equal for the three groups, so I set prior probabilities equal. Consequently, each call had an equal chance of being assigned to any of the three groups. To assess the effectiveness of discrimination, I used a cross-validation procedure, in which a discriminant function is constructed withholding one observation at a time, and then that observation is classified. This procedure removes the bias inherent in using an observation to construct rules for classifying itself. It provides an unbiased estimate of the expected actual error rate, while the often reported resubstitution rates, on average, underestimate the proportion of erroneously classified observations (Johnson and Wichern 1992). I report resubstitution rates only for comparison to other studies. I also calculated the squared distance function (Mahalanobis distances) to estimate the magnitude of differences between groups in

multivariate space. I calculated multivariate means for each individual and group based on a canonical discriminant analysis and plot these values to show how individuals and groups are distributed in multivariate space. I used SAS 6.10 for all analyses.

Results

Screech call acoustic structure

Screech calls are broadband, noisy signals (Fig. 1; mean $\pm$ SE given below). Maximum energy in pulses is centered around 6725 ± 36.3 Hz with a second energy peak at 8822 ± 63.5 Hz. This second energy peak is 2 ± 0.1 dB less intense than the first. Some pulses have more than two energy peaks, as the average is 2.2 ± 0.03 peaks per pulse. Energy is broadly distributed across frequency. The bandwidth is 6838 ± 74.6 Hz, starting at 4700 ± 24.9 Hz and extending up to $11,537 \pm 68.9$ Hz. Amplitude increases in the rise up to the first peak (136 ± 2.3 Hz/dB) more rapidly than it decreases in the fall off from the second (185 ± 3.6 Hz/dB). Calls average 4.2 ± 0.2 pulses each and last 1065 ± 59 ms. Average pulse duration is 229 ± 7 ms. Pulses are given in rapid succession, and most have no interval between the end of one and the onset of another within a call (300 ± 13 ms pulse repetition rate).

Group comparisons

The nested multivariate ANOVA for group reveals that screech calls differ significantly between groups (Wilks' $\lambda_{22,28} = 0.07$; $P < 0.04$). In addition, the nested univariate ANOVA shows differences at the group level for four of nine frequency variables and one of four temporal variables (Table 1). Group variance component estimates range from 1 to 34% with an average of 14.3%. More than 30% of total variance is due to group for bandwidth, and –12 dB above peak 1. In addition, fall from peak 2 is close to 20%. Mean values for each of the three groups are presented in Fig. 2.

The stepwise discriminant analysis finds that 9 of the 12 measured variables contribute significantly to group discrimination (Table 2). Pulse duration contributes the most (partial $R^2 = 0.305$), and by itself results in significant discrimination (Wilks' $\lambda = 0.69$; $P < 0.0001$). Discriminant analysis using these nine variables correctly classifies calls to social group in 83.1% of cases (86.6% by resubstitution). Expected correct classification is 33.3% by chance (Table 3). Group 1 and group 2 calls are rarely classified as group 3, suggesting that this group's mean is farther from the others. Group 3 shows little overlap with either group 1 or 2 in multivariate space (Fig. 3). Pairwise squared distances confirm this. Mahalanobis distances between group 1 and 3 (7.9) and group 2 and 3 (7.4) are larger than the distance between groups 1 and 2 (3.1). Even though group 3 was recorded at a different time and place than the others,

Table 1 Variance components for 13 measured variables. Percent of variation in each variable for each source of variation is indicated. Probabilities on individual components are from univariate mixed model ANOVA comparing group, age, individual within group and age, and call within individual. *Bat within group and age* is the error term for group and for age; *call* is the error term for bat; and *pulse* is the error term for call. Values in parentheses are sample sizes. Call duration has 6 *df*. Within each effect, sequential Bonferroni adjusted α for the first comparison = 0.0038; consequently, only probabilities < 0.0001 are significant by Bonferroni criteria

Variable	Group$_{(3)}$	Age$_{(3)}$	Bat$_{(28)}$	Call$_{(161)}$	Pulse$_{(733)}$
1st Energy Peak	4	5	13 *	22 ***	57
2nd Energy Peak	6	1	33 **	14 ***	46
–12 dB Below Peak 1	1	6 *	23 *	13 ***	57
–12 dB Above Peak 2	30 ***	3	16 *	16 ***	34
Bandwidth at –12 dB	34 ***	0	14 *	13 ***	39
Frequency Rise to Peak 1	14 ***	2	6	20 ***	57
Frequency Fall from Peak 2	18 ***	8 **	5	1	69
Amplitude Difference Pk1 & Pk2	8 *	6 *	11	24 ***	51
Number of Energy Peaks	14 *	0	13 *	15 ***	57
Pulse Duration	7 ***	1	0	0	92
Pulse Repetition Rate	7	0	1	0	92
Number of Pulses	0	0	20 *	78 ***	2
Total Call Duration	13 *	3	13	18	62

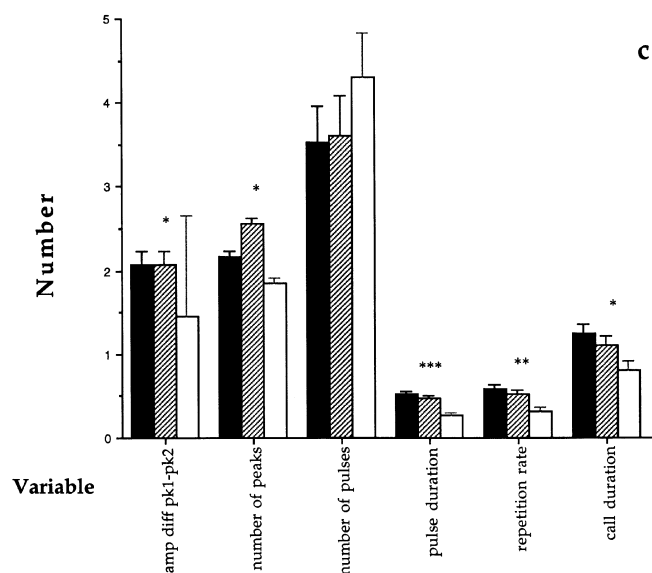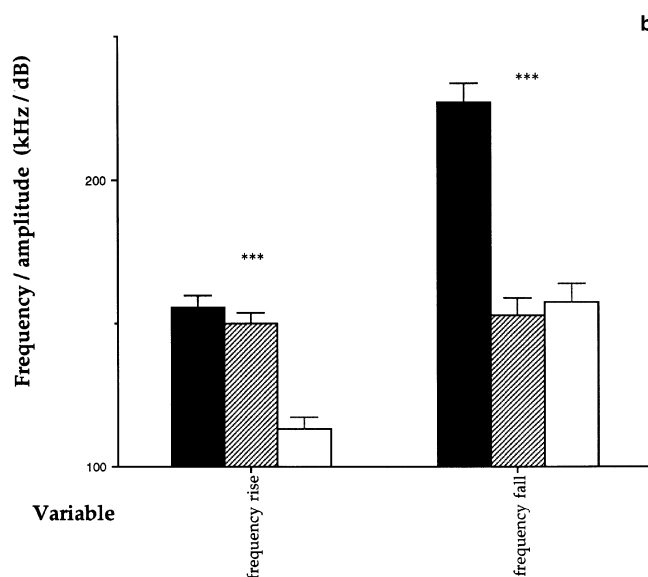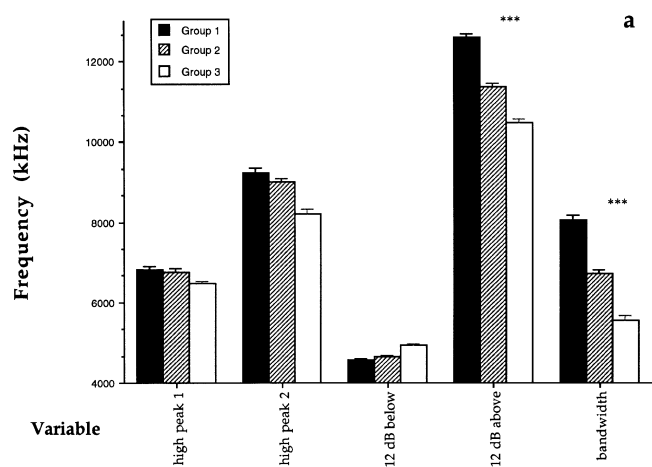$^{*}P < 0.05$, $^{**}P < 0.005$, $^{***}P < 0.0001$

Fig. 2a–c Screech call means ± SE for each social group. **a** Five frequency variables (kHz), **b** two variables expressing change in amplitude with increasing frequency (kHz/dB), and **c** temporal and counted variables. Probabilities from F-tests (*df* = 2,28) yield: *$P < 0.05$; **$P < 0.005$; ***$P < 0.0001$. Sequential Bonferroni adjusted α levels ($P = 0.0038$ for first comparison) indicate that only $P < 0.0001$ are significantly different among groups

Table 2 Variables that contribute to group discrimination. Variables were identified using a stepwise discriminant analysis with forward selection that selects the variable with the highest R^2, considering the other variables already in the model. Variables are listed in the order they entered the model. Wilks' λ and the average squared canonical correlation are significant at the 0.0001 level for each step

Variable	R^2	
Pulse Duration	0.305	***
Frequency Fall from Peak 2	0.223	***
Pulse Repetition Rate	0.170	***
Number of Energy Peaks	0.157	***
–12 dB Below Peak 1	0.122	***
Amplitude Difference Pk1 & Pk2	0.085	**
2nd Energy Peak	0.058	*
–12 dB Above Peak 2	0.032	
Frequency Rise to Peak 1	0.027	
Wilks' λ	0.270	***

F ratio: $^*P < 0.05$, $^{**}P < 0.005$, $^{***}P < 0.0001$

Table 3 Discriminant function analysis for group, showing the percent of calls given by 28 bats classified to group by cross-validation. Average correct by resubstitution is 86.6%

Actual group	Assigned group			Number of calls
	1	2	3	
1	72.6	24.2	3.2	62
2	9.4	81.1	9.4	53
3	0.0	4.4	95.7	46
				Average correct
% Correct	72.6	81.1	95.7	83.1

Wilks' $\lambda = 0.26$; $F_{18,300} = 16.1$; $P < 0.0001$

each group is significantly different from all others ($F_{12,147} > 7.7$; $P < 0.0001$ for each comparison).

Individual comparisons and within group convergence

Individuals' calls are not distinctive by nested MANOVA (Wilks' $\lambda_{209,279} = 0.0004$; $P < 0.28$). Univariate ANOVA provides no evidence that individuals within each group and age sound different either (Table 1). Although the variance component estimates for individual bat range from 0 to 33%, none of these are significant when I use a sequential Bonferroni adjusted α. Bats within groups sound similar.

Age comparisons

Upon initial capture, age estimates based on toothwear scores indicate significant differences between groups. A toothwear score of 1 corresponds roughly to an animal between 6 months and 3 years of age. Group 2 (toothwear = 1.12 ± 0.15) is significantly younger by t-test than either group 1 (toothwear = 1.83 ± 0.15; $P < 0.0001$; sequential Bonferroni adjusted $\alpha = 0.0125$) or group 3 (toothwear = 2.35 ± 0.15; $P < 0.0009$; ad-
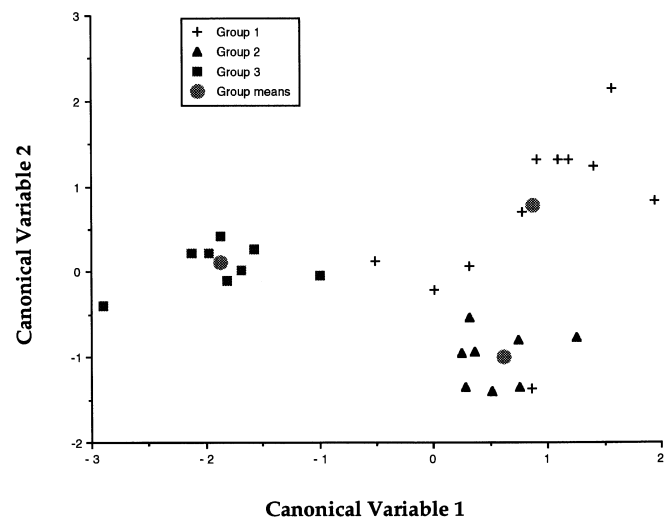

Fig. 3 Canonical means for each of the 28 bats and 3 social groups. One bat from group 1 falls squarely within group 2

justed $\alpha = 0.0167$). Groups 1 and 3 also differ in age by t-test ($P < 0.024$; adjusted $\alpha = 0.025$). However, some bats give screech calls (callers) while others do not (noncallers). When I restrict comparisons to callers, groups 1 and 2 do not differ by t-test, but both are significantly younger than group 3 (Fig. 4a).

Calling behavior depends on age. Callers are significantly younger across all groups than noncallers (Fig. 4b). Not only are pups and first year bats more likely to be callers, among all bats who called, they gave more calls than adults (Fisher's exact test $P < 0.038$; $n = 28$).

Although calling behavior depends on age, call characteristics show little age dependence. No significant differences between age classes are found by nested MANOVA (Wilks' $\lambda_{22,28} = 0.18$; $P = 0.43$) or ANOVA (Table 1). However, univariate regressions of measured variables on toothwear have significantly negative slopes for six of the seven frequency variables measured in kilohertz ($F_{1,731} > 7.6$; $P < 0.0001$ except for –12 dB below peak 1). This suggests that calls may decrease in frequency with age.

Discussion

Individual and group differences

The primary prediction distinguishing the group convergence from the individual learning hypothesis is the existence of group differences. The results presented here clearly show that screech calls are group distinctive, and individual bats within each group cluster around the group mean. Neither the nested univariate or multivariate ANOVA for individual are significant. The evidence of group distinctive calls and within group similarity allows us to reject the individual learning hy-
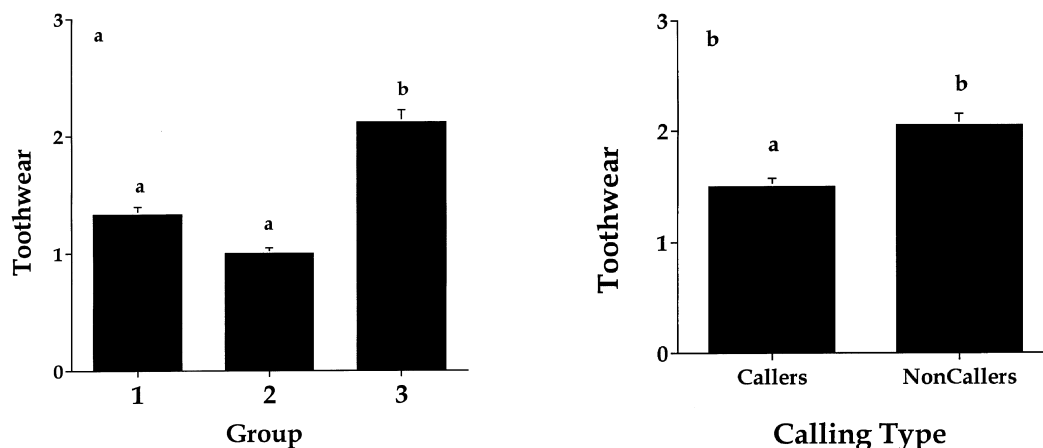
Fig. 4 a Toothwear means ± SE for calling bats in each group. Toothwear scores estimate age. Means marked with the same letter are not significantly different at a sequential Bonferroni adjusted α of 0.0125 for the first comparison. All probabilities were less than 0.001. Number of recorded bats in group 1 = 12, group 2 = 8, group 3 = 8.

b Toothwear means ± SE for callers and noncallers across all groups. Means marked with the same letter are not significantly different at a sequential Bonferroni adjusted α of 0.0125 ($P < 0.0018$). Number of callers = 22; number of noncallers = 26

pothesis as a sufficient basis for potential group discrimination in *P. hastatus*. The results follow closely the predictions of the group convergence hypothesis. Individuals may learn call characteristics to identify their group mates, but if bats can discriminate the group membership of calling bats, this discrimination is likely to rely on group differences, not individual ones.

Calling bats in group 3 are significantly older than in either group 1 or 2. This group's mean is also farther from group 1 and 2 than they are from each other. Does this suggest that group differences are due to age differences? Three lines of evidence argue against such an interpretation. First, no significant differences among age classes are found. Second, groups 1 and 2 do not differ significantly in age, but their calls do differ. Third, univariate ANCOVA indicates no significant effect of toothwear for 11 of the 12 measured variables. Only −12 dB below first peak shows a significant effect. Including the covariate does not change the patterns of significance.

Group distinctive calls may give females a means of identifying their social group mates outside of the cave. This is supported by field observations (Wilkinson and Boughman in press). The adaptive value of these calls is fairly clear; long term associates (potential group foraging partners or cooperators) can find one another outside the cave, and non-group members (potential competitors) can be excluded from rich resources (Wilkinson and Boughman in press). If bats are able to identify individuals in their foraging groups, it seems likely that they will use other cues. Perhaps they can tell the bat is a group mate by screech calls, but require close approach and either olfactory or other audible cues (such as echolocation pulses) to identify individuals.

Small differences in vocal tract morphology can easily give rise to individual differences in call structure in some taxa (e.g., Suthers and Hector 1988). This mechanism may contribute to the ubiquity of individually

distinctive vocalizations found across species. Many species appear to learn individually distinctive calls of offspring, kin, or group mates. Why do *P. hastatus* give group-specific screech calls rather than individually-specific ones? It could simply be that group differences make the discrimination task easier. In addition, perhaps indicating group membership is more important than indicating individual identity. Females may give screech calls as a badge of membership in a particular social group. Only group mates may be capable of giving the correct call. Acquiring a group-specific call probably requires close association with the group to learn the distinguishing features, and time to modify calls to match. The long term stability of female *P. hastatus* social groups (McCracken and Bradbury 1981) provides opportunities for close association, and time to learn characteristics and modify calls. Adult females are not likely to be related; consequently, similarity among adult group mates is not due to heritable variation.

Design of screech calls

Noisy, broadband, and highly variable calls are unlikely candidates for a group signature, and yet screech calls might be well suited to function in their particular context. Not only should screech calls identify the caller, to effectively facilitate group formation they should also indicate the caller's location. Broadband, noisy signals with sudden onset, such as screech calls, can be localized more accurately than pure tones (Brown 1982). Greater spear-nosed bats travel long distances while foraging, so the calls must carry far enough to be heard by group mates who may be some distance away. Although low frequency, pure tones are thought to be optimally designed for long distance propagation (Wiley and Richards 1982), broadband signals transmit through some environments more reliably than pure tones (Morton 1975; Romer and Lewald 1992). Noisy calls appear to

attenuate less in the 4–10 kHz range than pure tones, especially in the forest environment (Morton 1975). Low frequencies carry farther than high frequencies, and the frequency-dependent degradation may prove useful to determine the caller's range (Morton 1986). Although large for microchiropterans, *P. hastatus* weigh only 70–100 g. Their relatively small body size probably constrains *P. hastatus* to give fairly high frequency social calls. However, *P. hastatus* concentrate the energy in the lower frequencies of their broadband signals, between 6 and 9 kHz. When leaving the cave to forage, they typically call in flight from below the canopy, 3–20 m above ground. While traveling to foraging sites, they fly above the canopy and continue to call (personal observatory). Their height above ground should also aid long distance propagation. Thus, screech calls may be very effectively designed to propagate through the cluttered environment *P. hastatus* forage in, traveling more than 50 m (Wilkinson 1995). Several other species give broadband contact calls (Green 1975a, b; Ford 1989; Nowicki 1989). Unlike *P. hastatus*, the broadband nature of these species' calls is achieved through multiple harmonics rather than broadband noise.

Olfactory cues or variation in echolocation pulses are probably not effective over the large distances these bats travel while foraging. Low-amplitude (less than 70 dB), high-frequency (40–80 kHz) calls attenuate rapidly with distance, so that greater spear-nosed bat echolocation calls propagate only approximately 6–10 m (Griffin 1971; Mohl 1988; Wilkinson 1995). Yet, both types of cues are likely to be involved in group discrimination at close range.

As bats leave their roost cave in Trinidad, individuals often approach calling animals and fly close behind (less than 1 m; personal observation). This could give bats an opportunity to both smell the caller and listen to echolocation calls to confirm identification. On two occasions I held multiple social groups in the flight cage at the Simla field station. On both of these occasions, one group (the resident group) had been held for several days before I brought in the second (alien) group. I housed these groups separately during the day where they could not see each other. When I released bats from each group into the flight cage together at night, resident bats called and flew more when an individual from the alien group was in the flight cage than when alone, even though these alien bats almost never gave screech calls. Even resident bats in an adjacent room called. These observations suggest that resident bats distinguished the alien bats from group mates. Since alien bats almost never gave screech calls, the most likely means of group discrimination are echolocation pulses or olfactory cues. Echolocation pulses vary between sexes, families, or individuals in several bat species (Brigham et al. 1989; Masters and Jacobs 1989; Masters et al. 1995; Obrist 1995). Echolocation calls may also show group or individual differences in *P. hastatus*, and this deserves investigation. In addition, *P. hastatus* have a secretory gland on the throat and males rub these secretions over

the females in their group (McCracken and Bradbury 1981), which may give each group a characteristic odor. Other bats may use this olfactory cue to distinguish their group mates from others.

Acoustic differences among social groups in other species

Screech calls appear to be a kind of contact call, and also serve as a badge of social group membership. A few group-living birds also show acoustic differences between social groups. Adult chickadees (*Parus atricapillus*), Australian magpies (*Gymnorhina tibicen*) and budgerigars (*Melopsittacus undulatus*) form stable social flocks. Each of these species has a call that functions in flock cohesion and is also group-specific. Like *P. hastatus*, group members are typically not related. When new groups of unrelated birds are experimentally formed, calls begin to converge very rapidly (Nowicki 1989; Brown and Farabaugh 1991; Farabaugh et al. 1994). The group distinctive structure appears to facilitate the calls' function, and the social environment seems to strongly influence call structure. Birds sometimes change group membership; consequently selection appears to favor open-ended or age-independent call learning so that adults can modify calls to achieve convergence. Across taxa, vocal convergence among unrelated animals implies that calls are modified by social experience independently of (or in addition to) genetic influences. Thus, convergent calls are learned.

Passerine birds and even some hummingbirds learn to sing (Wiley 1971; Baptista and Shuchmann 1990), and song learning has been studied intensively. An important consequence of learning is that it produces regional dialects (Baker and Cunningham 1985). Although song dialects and group distinctive calls share a reliance on learning and result in similar-sounding neighbors, they differ in the scale at which they can be detected and in the details of how they are learned. Dialects are detected by comparing populations because they are a population-level phenomenon. Group-distinctive calls are detected by comparing social groups because they are a feature of these social groups, not populations. Even so, dialects and group-distinctive calls may represent points on a continuum. Some bird species share songs with only a few neighbors in song neighborhoods, and these neighbors interact socially (Wiley 1971; Payne et al. 1988; Payne and Payne 1993). Greater spear-nosed bat screech calls also differ among colonies (J.W. Boughman, unpublished work), suggesting that group level differences may lead to larger scale patterns.

Call learning is very different from most song learning. Songs typically do not develop normally without auditory feedback and an appropriate song tutor (Konishi 1965; Kroodsma 1982; Marler 1984). In contrast, calls may develop normally in isolation, but are able to change to match a call tutor or social partner. For instance, lesser spear-nosed bat infants, *P. discolor*,

spontaneously give isolation calls when separated from their mother. It appears that infants can modify isolation calls to match the maternal directive call they hear (Esser 1994). Both the function and structure of screech calls leads us to expect that the social environment affects screech call structure, and produces group differences. Call learning in *P. hastatus* needs to be explored.

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