



Vocal learning by greater spear-nosed bats

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Vocal learning is well known among passerine and psittacine birds, but most data on mammals are equivocal. Specific benefits of vocal learning are poorly understood for most species. One case where vocal learning should be favoured by selection is where calls indicate group membership and group mates are unrelated. Female greater spear-nosed bats, *Phyllostomus hastatus*, live in stable groups of unrelated bats and use loud, broadband calls to coordinate foraging movements of social group mates. Bats benefit from group foraging. Calls differ between female social groups and cave colonies, and playback experiments demonstrate that bats perceive these acoustic differences. Here I show that the group distinctive structure of calls arises through vocal learning. Females change call structure when group composition changes, resulting in increased similarity among new social group mates. Comparisons of transfers with age-matched half-sibs indicate that call changes are not simply due to maturation, the physical environment or heredity. These results suggest that studies testing vocal learning in mammals could profit by focusing on vocalizations that signify group membership.

Keywords: bat communication; *Phyllostomus hastatus*; group signatures; social learning

1. INTRODUCTION

Animals that live in stable social groups often produce vocal signals that indicate group membership (Schaller 1972; Feekes 1977; Harrington & Mech 1979; Mammen & Nowicki 1981; Raemaekers & Raemaekers 1984; Brown *et al.* 1988; Wright 1996). Frequently, social groups are composed of kin, as in many mammals, and some aspects of signals are heritable indicators of kinship (Scherrer & Wilkinson 1993). Less often, unrelated animals form groups and signals are acquired through association with the group, as in some passerine and psittacine birds (Nowicki 1989; Farabaugh *et al.* 1994). Few mammals form stable social groups of unrelated individuals. Selection should favour this type of social modification only for calls whose function is enhanced by the degree of similarity to social partners, whether these are territorial neighbours, mates, or members of a social group. Socially mediated vocal changes should be especially favoured when calls are badges of group membership (or passwords, Feekes 1977) and heritable variation cannot produce group differences, such as when group members are not relatives.

There is little evidence that taxa other than birds modify calls in response to their social environment. Most data on mammals are equivocal. Many studies have failed to find convincing evidence of vocal learning (Snowdon 1990; Owren *et al.* 1992; reviewed in Janik & Slater 1997). Other studies provide some evidence, but are equally consistent with low gene flow between populations (Winn *et al.* 1981; Ford & Fisher 1983; Thomas & Stirling 1983) or matching of call types in a partially shared repertoire (Tyack 1986; McCowan & Reiss 1995). A few captive bottlenose dolphins have mimicked arbitrary whistled sounds in the lab (Richards *et al.* 1984; Reiss & McCowan 1993) which demonstrates vocal plasticity.

Further study is required to establish that vocal learning occurs naturally and to address the functional significance of such plasticity (Tyack & Sayigh 1997). Descriptions of changes over years in humpback whale song (Payne & Payne 1985) and bat echolocation call frequencies (Jones & Ransome 1993) are consistent with vocal learning, but have not been experimentally tested.

Female greater spear-nosed bats, *Phyllostomus hastatus*, give broadband, audible frequency group contact calls, termed screech calls (figure 1), that differ among social groups, yet individuals within groups are statistically indistinguishable (Boughman 1997). This species gives what appears to be a single call type, and social groups differ in frequency and temporal characteristics of this basic call type. Female social groups are very stable, yet are composed of unrelated individuals (McCracken & Bradbury 1981; McCracken 1987). Consequently, the between-group differences and within-group convergence observed in these signals does not result from shared genes. Instead, call structure may be modified through association with the social group—a form of learning.

Observational and experimental evidence demonstrates that screech calls function as group signatures. Field observations suggest that screech calls facilitate recognition of social group mates who forage together on rich food resources (Goodwin & Greenhall 1961; Wilkinson & Boughman 1998a). Group foraging provides direct benefits (Wilkinson & Boughman 1998a,b) and group living appears to be obligate since we do not observe females roosting alone (G. S. Wilkinson & J. W. Boughman, unpublished data). Females that call when they exit their roost cave and at foraging sites are more likely to be accompanied by a roost mate, and bats in groups are more likely to give calls (Wilkinson & Boughman 1998a). Analyses of screech call acoustic structure reveal that calls

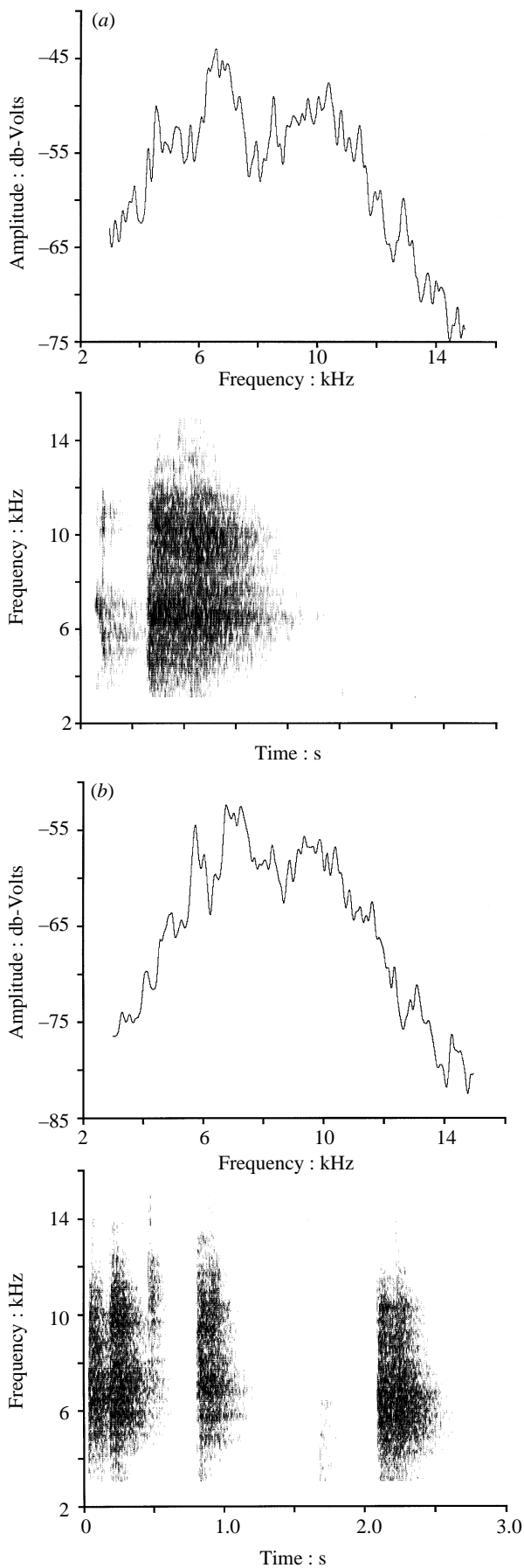


Figure 1. Sonograms and power spectra for representative screech calls from a bat in each group prior to transfer. (a) Bat 1021 from Group one. (b) Bat 1022 from Group two.

contain relevant information to function in group recognition (Boughman 1997). Habituation–discrimination experiments (Cheney & Seyfarth 1988) demonstrate that bats can discriminate between calls given by their group mates and other bats, but bats do not respond as though they discriminate among individuals in their group (Boughman & Wilkinson 1998). The difficulty of finding group mates during evening emergences of several hundred bats may favour group distinctive rather than individually distinctive calls in this species. Calls also differ among three caves in Trinidad (Boughman & Wilkinson 1998). Geographic variation is often cited as evidence of song learning in birds (Catchpole & Slater 1995) and may also reflect vocal learning of screech calls in *P. hastatus*.

2. METHODS

(a) *Social manipulation*

To test the hypothesis that group differences and within group convergence arise through social modification of screech calls, I mimicked naturally occurring dispersal. I transferred bats reciprocally between two social groups housed in separate rooms at the Department of Zoological Research, National Zoological Park. I moved bats at ages they would be expected to disperse in the wild. Offspring of both sexes disperse from the natal group during the first year to roost temporarily with other young bats. Females join an existing adult social group when reproductively mature, at about two years (McCracken & Bradbury 1981). Individual females remain with the same group for many years with a few individuals occasionally transferring to a new group (G. S. Wilkinson and J. W. Boughman, unpublished data).

The two captive groups are composed of wild-caught adults (11 and 12 respectively) and their descendant offspring (32 and 29 respectively). Prior to the social manipulation most offspring had partially segregated into a secondary roost of each group, in patterns similar to those observed for dispersal in the wild (McCracken & Bradbury 1981). Prior to this partial dispersal, acoustic analyses demonstrated that bats within a roost sounded similar, whereas social groups differed markedly in frequency and temporal characteristics of screech calls (Boughman 1997). Subsequent to this dispersal but before I transferred bats between groups, acoustic differences between roosts in the same group began to emerge (between roosts in group 1 Wilks' $\lambda=0.977$; $p=0.1832$; between roosts in group 2 Wilks' $\lambda=0.961$; $p=0.0071$), although overall group differences remained substantial (Wilks' $\lambda=0.941$; $p=0.0001$).

From the secondary roost in each group I moved two reproductively mature 2–3 year-old females and three one-year old juvenile females. Each transfer had at least one female age-matched paternal half-sib that remained resident in the natal group. These resident half-sibs serve as controls for the social manipulation, and allow me to test hypotheses that calls change due to maturation or the physical environment, or reflect heritable variation. After transfer, roosting affiliations coalesced quickly with most transfers joining the secondary roost of their new group, although adult transfers joined the primary roost in one group.

(b) *Call recording and measurement*

I recorded screech calls from ten transfers and 13 resident females (including six half-sibs) repeatedly prior to and after moving bats with a Marantz PMD 430 cassette recorder using a

Sennheiser ME 66 microphone onto metal tapes (the system has a flat response (± 2.5 dB) up to 18 kHz). All recordings were made in a single experimental room that was quite similar to the rooms that housed the bats, reducing the chance that physical acoustics would cause divergence in calls. The walls, floors, ceiling and roosts were constructed out of similar materials in both roost rooms and the experimental room, which were adjacent to one another. The rooms were approximately the same size (room one was $4.7 \times 4.3 \times 3.9$ m; room two was $5.4 \times 4.3 \times 3.9$ m; experimental room was $5.4 \times 4.3 \times 3.9$ m). Light cycle, temperature and humidity are controlled from the same source. These rooms are virtually identical and any physical changes that occur in one room are very likely to occur simultaneously in the other room. Consequently, acoustic accommodation should also occur simultaneously and should not cause acoustic divergence. I recorded bats flying freely around the experimental room in small groups. All bats were individually marked with unique combinations of coloured Scotchlite (3M) on metal wing bands and unique bleach-marked patterns on their backs and shoulders. I identified individuals in flight by their Scotchlite combinations and bleach marks, and only analysed calls I could unambiguously assign to an individual. I analysed 12 acoustic variables for 665 calls (see Boughman 1997 for variable description). I digitized calls using RTS: Real-Time Spectrogram (Engineering Design, Belmont MA), sampling at 46.5 kHz. I measured acoustic features of calls with SIGNAL: Digital Signal Analysis Language (Engineering Design, Belmont MA). When computing spectrograms I set the FFT window size to 512 points, used a Hanning window and obtained a frequency resolution of 91 Hz. I computed power spectra across an entire pulse with a maximum FFT of 32,000 points, and smoothed the resulting curves by computing a running average with window size of 50 Hz.

(c) Statistical analysis

Prior to analysis, I calculated average values for measured variables for each call. I analysed these data by two factor univariate and multivariate ANOVA, with group (four levels: group one residents, transfers to group one, group two residents, transfers to group two), period (three levels: pre-move, one month post-move, and five months post-move), and their interaction. I followed this analysis with univariate and multivariate contrasts among residents and transfers to test differences pre-move, one month post-move, and five months post-move and then compared transfers and half-sibs pre- and post-move. Change of frequency characteristics is likely to be more constrained than change of temporal characteristics (Janik & Slater 1997). I tested whether calls changed in frequency characteristics by conducting separate MANOVA contrasts including and then excluding temporal variables. I explored the influence of roosting affiliation and age on initial patterns in a separate MANOVA. I also performed a canonical linear discriminant analysis with the 12 measured variables (Johnson & Wichern 1991). I collapsed the 12 measured variables into two dimensions that represent composite scores of the original variables so that I could track how calls move in multivariate space. Data from residents pre-move were used to construct the discriminant function to separate groups, which was then used to classify calls from transfers pre-move and all post-move calls. From these analyses I obtained average canonical scores for individuals pre-move and post-move and calculated group averages for plotting. To determine how well groups could be separated post-move, I also conducted a separate discriminant analysis to compare all transfers and residents in group one with all bats in group two post-move.

Table 1. Variables that differ between residents and transfers before and after moving bats.

Probabilities from univariate contrasts averaged across two groups calculated for 665 calls from 23 bats.

variable	type	one month five months		
		pre-move	post-move	post-move
peak 1 (Hz)	F	0.3995	0.0134	0.6982
peak 2	F	0.0007	0.0313	0.0017
-12 dB below peak 1 (Hz)	F	0.0008	0.0788	0.5267
-12 dB above peak 2 (Hz)	F	0.0009	0.0129	0.2782
bandwidth (Hz)	F	0.0001	0.0032	0.454
frequency rise to peak 1 (dB/Hz)	F	0.0426	0.5112	0.325
frequency fall from peak 2 (dB/Hz)	F	0.3121	0.2661	0.735
amplitude difference pk1 & pk2 (dB)	F	0.1475	0.1488	0.3045
number of peaks	F	0.234	0.2028	0.313
number of pulses	T	0.0003	0.4146	0.1275
pulse repetition interval (ms)	T	0.0056	0.3359	0.5987
call duration (ms)	T	0.1279	0.1579	0.4959
total differences		7	4	1

3. RESULTS

Experimentally altering the social environment directly affects call structure. Both transfers and residents change characteristics of their calls in response to changing group membership. Before the move, bats who will transfer differ significantly from the residents in their eventual group for seven variables (table 1). These differences disappear over time. One month post-move, transfers and residents show fewer differences, and after five months of living together transfers and residents are indistinguishable for all but one variable. Both frequency and temporal variables show changes (figure 2). For some variables, residents show the largest changes (e.g. bandwidth in both groups, figure 2a), while for others, transfers change most (e.g., repetition interval in group two, figure 2b). These univariate results are corroborated by MANOVA contrasts that indicate significant differences between residents and transfers pre-move (group one Wilks's $\lambda=0.962$; $p<0.007$; group two Wilks's $\lambda=0.829$; $p<0.0001$). Five months later residents and transfers do not differ (group one Wilks's $\lambda=0.982$; $p=0.411$; group two Wilks's $\lambda=0.975$; $p=0.123$). These patterns of change are not altered when temporal variables are removed from the analysis (pre-move differences: group one Wilks's $\lambda=0.992$; $p<0.0063$; group two Wilks's $\lambda=0.831$; $p<0.0001$ and post-move differences: group one Wilks's $\lambda=0.987$; $p<0.4101$; group two Wilks's $\lambda=0.974$; $p<0.1175$) indicating that bats have changed frequency characteristics of their calls. Initially, power spectra of residents and transfers are relatively dissimilar in both groups, but overlap considerably five months post-move (figure 3). Frequency and temporal changes result in substantial acoustic convergence. After living together for

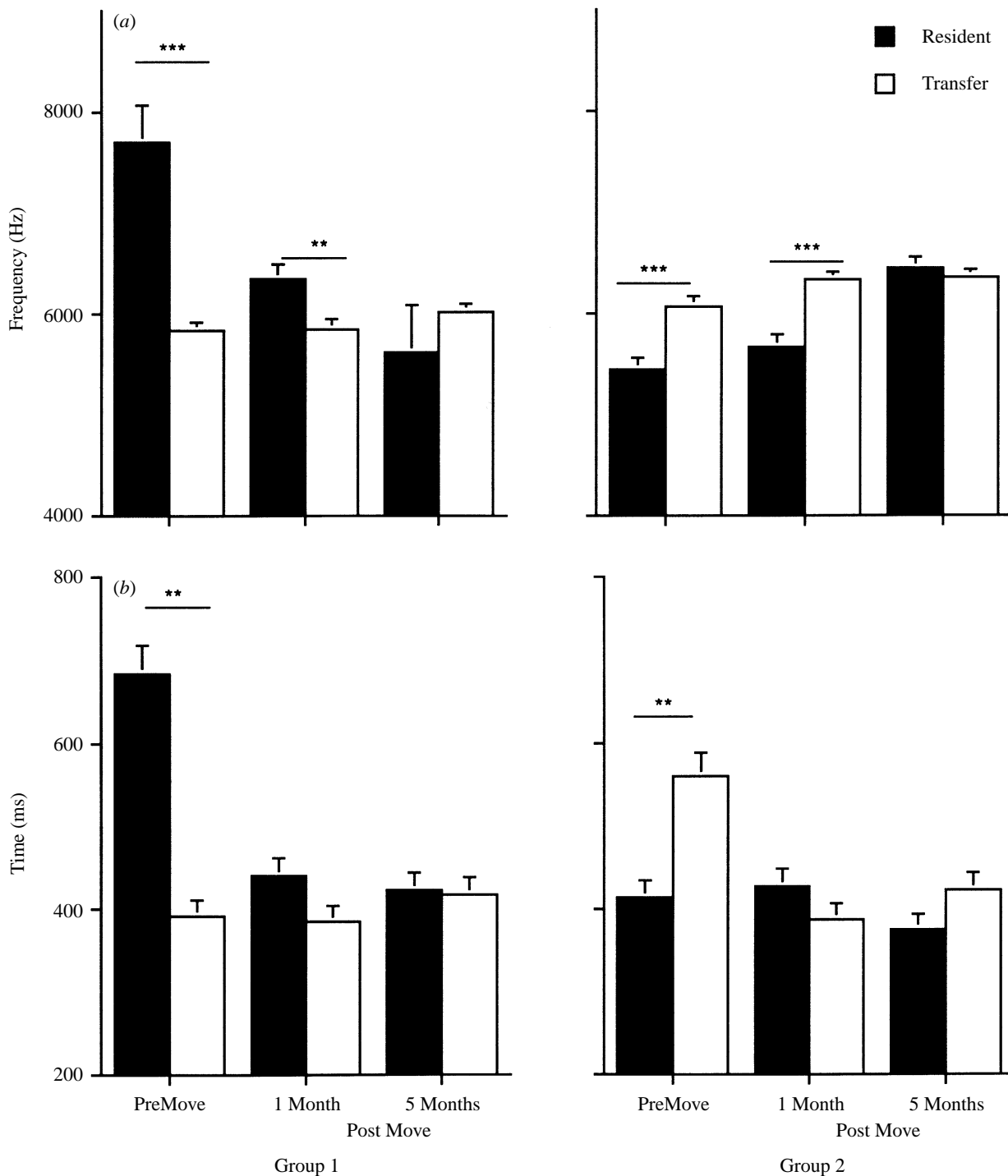


Figure 2. Bats in both social groups change call structure with changing social environment. Univariate means \pm s.e. for three periods: prior to moving bats (pre-move), one month, and five months after the move (post-move). Solid bars are residents and open bars are transfers. Comparisons for one representative frequency and one temporal measure previously shown to be important in differentiating groups. (a) Bandwidth. (b) Repetition interval. Contrasts are calculated for 23 bats and 665 calls. **, $p < 0.001$; ***, $p < 0.0001$.

five months, the calls of transfers and resident bats in both groups more closely resemble each other than those of their old group mates in multivariate space (figure 4, 5). It appears that all bats adjust their calls to resemble the bats they live with. Although groups are more similar at the end of the study, reciprocal convergence has not abolished group differences (Wilks's $\lambda = 0.928$; $p < 0.0033$).

If calls change passively because of maturational changes in vocal tract morphology or actively in response

to a changing physical environment, then transfers and their age-matched half-sibs should show similar patterns of change in call characteristics. Changes that occur should be in parallel in multivariate space. However, if the social environment plays an important role in structuring calls, transfers and half-sibs who differ in their social environment should show different patterns and non-parallel changes. I tested these hypotheses by comparing the difference between transfers and their

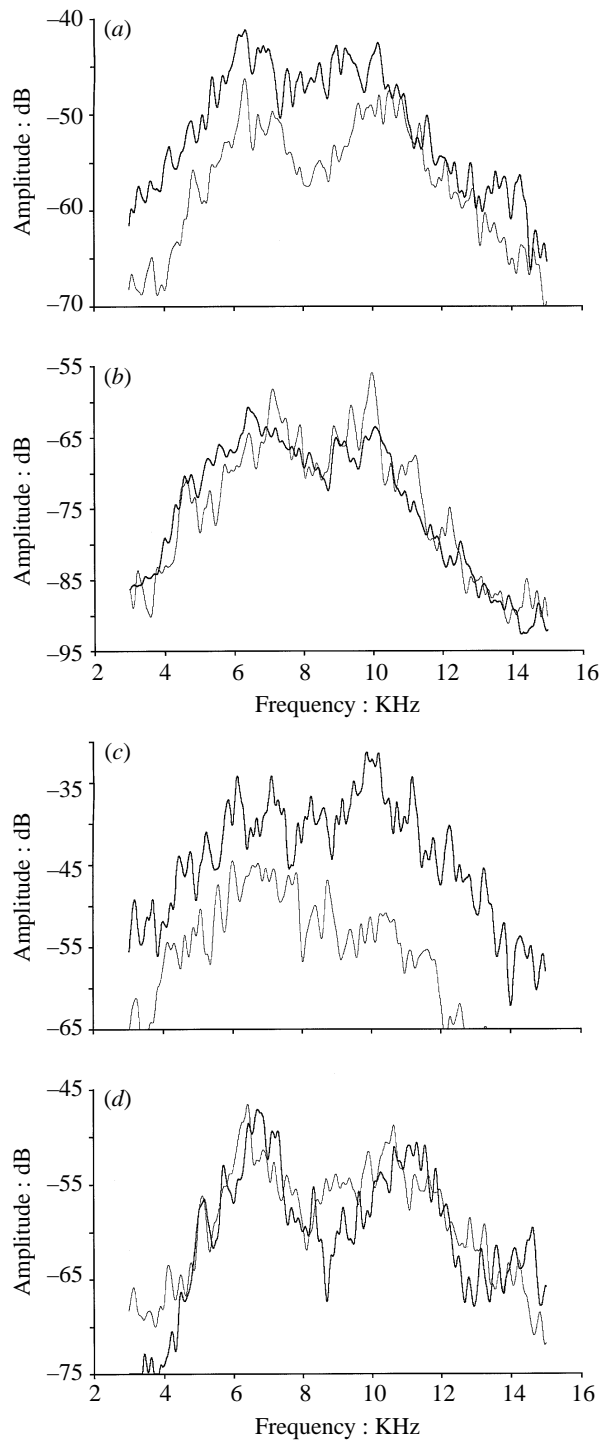


Figure 3. Residents (heavy line) and transfers (light line) converge in frequency characteristics, as illustrated by the increasing overlap in power spectra post-move as compared to pre-move. (a) Group one pre-move. (b) Group one post-move. (c) Group two pre-move. (d) Group two post-move.

age-matched half-sibs before and after the move (table 2). Both adult and juvenile transfers and their age-matched half-sibs have changed the degree of resemblance to one another (figure 4, 5). Resident bats who continue to live together change calls in parallel, while transfers who have new social partners diverge from resident half-sibs. Juvenile transfers joined the secondary

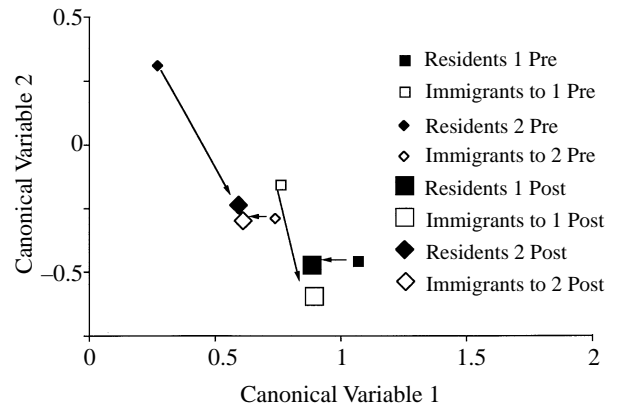


Figure 4. Calls from residents and transfers converge in multivariate space after living together for five months. Mean canonical scores for residents and transfers in both groups in two dimensions. Small symbols indicate mean values prior to moving bats; large symbols indicate means five months post-move. Closed symbols are residents and open symbols are bats transferring, or immigrating into a new group. Arrows indicate how each subset changed during the course of the experiment. Standard errors (x, y) for group one residents pre-move = 0.31, 0.12 and post-move = 0.035, 0.16; transfers to group one pre-move = 0.16, 0.10 and post-move = 0.073, 0.13; group two residents pre-move = 0.15, 0.36 and post-move = 0.12, 0.30; transfers to group two pre-move = 0.39, 0.074 and post move = 0.051, 0.094.

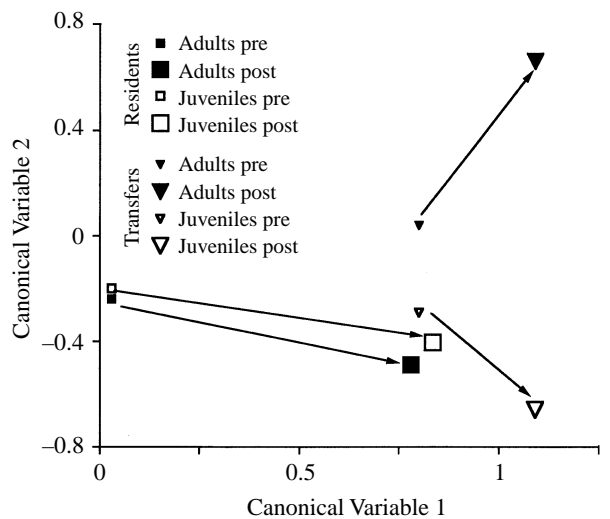


Figure 5. Transfers (triangles) and their age-matched half-sibs (squares) diverge in multivariate space once they no longer share roosts. I show canonical means for group two pre-move (small symbols) and five months post move (large symbols). Filled symbols are adults and open symbols are juveniles. Residents change calls in parallel and transfers diverge from residents, as predicted if the social environment influences call structure.

roost in their new group while adults joined the primary roost, resulting in additional divergence from each other. These comparisons indicate that observed changes cannot be explained by maturation or the physical environment alone. The social environment clearly influences acoustic structure of calls.

Table 2. Number of univariate contrasts of 12 total that indicate divergence of resident and transferred half-sibs

	2-3 year-old half-sibs	juvenile half-sibs	MANOVA Wilks's λ
group one	2	2	0.97***
group two	9	10	0.92***

4. DISCUSSION

Evidence presented here demonstrates that acoustic convergence within social groups and differences between groups arise through vocal learning. Greater spear-nosed bats achieve this convergence with group mates not by matching of call types in an existing repertoire, but by changing subtle frequency and temporal characteristics of their single call type. Changes are reciprocal, indicating that females respond acoustically to their group mates as group composition changes. These dynamic responses are not likely to lead to a static set of group identifying characters. Instead, calls are likely to move in acoustic space to maintain differences between social groups and similarity within. The degree of resemblance depends on the amount of social interaction. Each social group is partially segregated into two roosts in a single room that give calls sounding somewhat different. Individuals spend most of their time in their own roost, but bats from both roosts feed together and socialize outside the roost. Acoustic changes post-move reflect these affiliations. Call modification in *P. hastatus* is not limited to juveniles—essential since females join new groups as adults.

Social modification of screech calls is consistent with predictions for social learning (Laland *et al.* 1996) of calls that coordinate group movements (Wilkinson & Boughman 1998b). When an individual's social environment changes often, for instance when social groups are not stable, group membership is unlikely to be favoured. What matters is probably group size, not group composition, so we do not expect that the calls animals use to form groups (Elgar 1986; Brown *et al.* 1991) will convey caller identity. Individual variation in morphology may produce individual variation in call parameters and individual learning can occur, but calls are not likely to be susceptible to social modification. When the environment changes very slowly, for instance when individuals do not disperse but remain with their natal group, genetic transmission should be favoured and calls should be heritable indicators of kinship. When the social environment changes at an intermediate rate, for instance when individuals disperse from their natal group to form stable social groups, social learning should be favoured. Calls that coordinate group movements should indicate group membership and be modifiable by the social environment. Consistent with these predictions, female *P. hastatus* appear to copy only their group mates, ensuring that calls remain different between groups and can effectively indicate group membership. Continually high transfer rates could eventually wash out differences between groups, but adult females change group affiliation rarely (McCracken & Bradbury 1981; G. S. Wilkinson and J. W. Boughman

unpublished data) which should help maintain group differences. In this experiment, transferring several bats simultaneously may have contributed to the magnitude of changes exhibited by resident bats.

Group differences may also be maintained if group members actively differentiate themselves from other groups in the same cave. Not only should this improve the ability to discriminate groups, but may also be important to resist encroachment by conspecifics. When foraging groups control rich resources it may pay individuals from other groups to feign their identity to obtain access to food resources. Evolutionarily stable indicators of group membership should therefore be difficult or costly for outsiders to imitate (Grafen 1990). Large differences between groups may make copying relatively difficult. Controlling subtle frequency characteristics in these noisy calls may also be difficult, which could make changing calls physiologically costly. Possibly more important in *P. hastatus* are the costs of acquiring the group specific characteristics. Group convergence takes time. Potential cheaters must overcome initial aggression and invest considerable time in attempting to associate with the group, listening to the group's calls to determine the group's characteristics, and changing calls to match. This kind of time investment makes cheating unlikely to be cost effective.

Vocal learning is clearly not limited to birds and humans, and bats are a promising group for further study. Many bat species show remarkable vocal control during pursuit and capture of prey, changing the structure of echolocation pulses in precise ways to maximize prey detection and localization (Kalko & Schnitzler 1993). The work of Jones & Ransome (1993) on *Rhinolophus ferrumequinum* suggests that infants may fine-tune echolocation pulses through learning. Some social calls may also be learned. *Phyllostomus discolor* infants give isolation calls that facilitate reunion with mothers, and calls of infants raised in isolation differ from infants who hear maternal directive calls (Esser 1994) suggesting a role for auditory experience.

Calls that function to indicate social affiliation may have been selected to be modifiable by social experience. Consequently, study of group signatures is likely to change our view of the prevalence of vocal learning in mammals.

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