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ABSTRACT

Title of Dissertation: STRUCTURE, DETECTION, AND LEARNING OF GROUP MEMBERSHIP CALLS IN GREATER SPEAR-NOSED BATS

Janette Wenrick Boughman, Doctor of Philosophy, 1997

Dissertation directed by: Dr. Gerald S. Wilkinson, Associate Professor
Department of Zoology

Animals that live in stable social groups often cooperate to find and defend limiting resources, such as food or sites for reproduction. When social groups also control access to these limiting resources, membership in a social group can be an essential component of individual fitness. Indicating group membership and discriminating group mates from others should be favored under such circumstances. Signals that indicate group membership are shaped by the function they serve; they should vary among social groups either at the individual or group level, and individuals should be able to discriminate between signals given by group mates and others. To retain reliability, group membership signals should also be difficult or costly for outsiders to imitate.

Female greater spear-nosed bats, *Phyllostomus hastatus*, use audible frequency calls, termed screech calls, to coordinate foraging among long term associates. Field observations imply that females use screech calls to identify members of their social group. My dissertation work demonstrates that this communication system has the requisite features to function as a group signature system. I characterize the acoustic structure of screech calls recorded in the field and lab, and test which aspects of identity are encoded in calls. Results demonstrate that screech calls are structured to convey the group membership of the caller, but not individual identity. I also find that calls differ between cave colonies. I use field and lab playback experiments to test call detection and function, and find that bats can detect cave and group differences but do not differentiate among individuals based on screech calls. To determine the factors influencing screech call structure, I transferred bats reciprocally between social groups. This experiment provides good evidence that group differences arise through vocal learning. Social modification of calls allows females to adjust their calls when social group composition changes. Call modification is not immediate, and the time required for individuals to match a new group could provide protection against outsiders who might feign identity to obtain access to resources controlled by social groups. This work provides important and rare evidence of vocal learning in a non-human mammal.

STRUCTURE, DETECTION, AND LEARNING OF GROUP MEMBERSHIP CALLS IN GREATER SPEAR-NOSED BATS

by

Janette Wenrick Boughman

Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland at College Park in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
1997

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DEDICATION

To my mother, Peggy Wenrick, and grandmother, Pauline Mitchell, who by the strength of their character taught me to believe in myself.
To my father, Robert Wenrick, who gave me the desire to achieve.
And especially to my husband, John and children, Skye, Jihan and Ross who fill my life with goodness and make me whole.

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But my deepest gratitude goes to my family -- especially my husband John. Without his support and love I would not be doing the work I love most.

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INTRODUCTION

Animals that live in stable social groups often derive benefits from doing so, for example by controlling access to limiting resources such as food or nesting sites. Reduced competition within a social group can be favored if this improves ability to compete with other groups for these resources. But not all interactions within social groups are cooperative; group-living also entails competition and costs. For instance, theory predicts that group foraging will be advantageous when resources are distributed patchily in space and time (Clark & Mangel 1984; Caraco 1981). Animals may benefit directly from reduced predation, improved food finding or resource defense, but may also pay costs associated with sharing food resources. When benefits outweigh costs, selection will favor active foraging group formation, and behavior that facilitates this should evolve. In many species, vocalizations can readily serve this function (Elgar 1986; Brown et al 1991). In this dissertation, I 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.

Vocalizations that are used to coordinate foraging movements of social group mates should perform two related functions. Not only should calls attract others to foraging groups, they should also indicate the caller's group identity. Although we understand the economics of food calling in a few species (*toque macaques* -- Dittus 1984; *house sparrows* -- Elgar 1986; *ravens* -- Heinrich 1988; Heinrich & Marzluff 1991; *killer whales* -- Hoelzel 1991; *rhesus macaques* -- Hauser & Marler 1993; *pygmy marmosets* --

Caine et al 1995), in most species we have insufficient information to assess the call's second potential function of identifying group mates. If controlling limiting resources is an important benefit to group-living, then identifying group mates becomes essential and deserves further study.

GROUP FORAGING

Animals that forage in groups share resources, potentially resulting in less food available per capita (Barnard & Sibly 1981; Vickery et al 1991; Ranta et al 1993). When food is distributed in rich patches or groups are small, individuals in groups may still obtain ample food. Additionally, losses to sharing can be compensated if groups are better able to find or defend food resources. Considering these potential costs and benefits, theory predicts that group foraging will be likely to confer a net advantage when resources are distributed patchily in space and time (Clark & Mangel 1984; 1986) and patches are large. When food patches are ephemeral, food finding can be enhanced in a group (Cody 1971; Krebs et al 1972; Pitcher et al 1982; Pulliam & Caraco 1986; Wenzel & Pickering 1991). When patches persist over longer periods, resource defense becomes possible and may be more effective by a group (Heinrich & Marzluff 1991).

When group foraging is beneficial in either of these ways, selection should favor active group formation, which can promote the evolution of behavior that facilitates the formation of foraging groups. Vocalizations can readily facilitate group formation, and are used by several birds (Elgar 1986), primates (Dittus 1984; Chapman & Lefebvre 1990; Caine et al 1995) and even mole rates (Judd & Sherman 1996) to serve this function. Animals that live in stable social groups are likely to forage with group mates (Packer

1986; Hoelzel 1991; Hauser & Marler 1993). If groups are formed nonrandomly, vocalizations may also be used to indicate caller identity. The selection pressures that maintain group foraging behavior are likely to influence the composition of foraging groups and consequently the aspect of identity conveyed.

Bats are an intriguing taxon in which to study vocalizations associated with group foraging. Despite the paucity of studies on bat behavior, several studies have demonstrated that bats forage in groups (emballonurids -- Bradbury & Vehrencamp 1976; *Phyllostomus discolor* -- Sazima & Sazima 1977; *Leptonycteris curasoae* -- Howell 1979; *Nycticeius humeralis* -- Wilkinson 1992) and others have found evidence suggesting bats follow roost mates to foraging sites (reviewed in Wilkinson & Boughman in press a). Bats can travel fast and far at night; consequently any signal they use for foraging group formation must be detectable over long distance in the dark, and provide information about current location. Visual signals typically do not transmit long distances, especially in the dark and chemical signals are difficult to update rapidly, so neither is well suited to facilitate the formation of foraging groups in vertebrates. However, high amplitude, low frequency, broadband vocal signals fulfill the relevant criteria. Bats use of vocalizations in foraging for navigation and prey capture is well known and we have a fairly clear understanding of how calls are structured to serve these functions (Kalko & Schnitzler 1993; reviewed in Moss & Schnitzler 1995). This is in marked contrast to our limited knowledge of how bats use other vocalizations to mediate the social aspects of foraging. Individuals of several bat species appear to give audible calls while on foraging territories (Kingdon 1974; 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 in groups (Bradbury 1977). Functional hypotheses remain untested for almost all audible calls related to foraging (but see Barlow & Jones 1997; Wilkinson & Boughman in press b). Very few studies have described patterns of acoustic variation sufficiently well to determine whether calls could function to identify the members of foraging groups.

SIGNATURE SYSTEMS

Signals that convey caller identity are often termed signatures and have been the focus of active research for some time, in particular as mechanisms to mediate kin selection. Recognition of kin has been claimed for a number of taxa (reviewed in Fletcher & Michener 1987; Waldman 1987). Ants lay down pheromonal foraging trails that convey colony identity (Gordon 1989), but outside of this, signatures have rarely been carefully investigated in the context of group foraging. Fortunately, ideas developed to explain kin recognition (Beecher 1989; Reeve 1989; Grafen 1990) are broadly applicable to other kinds of signature systems. As with any communication system, we need to consider production of signals and their perception. For a signature system, animals must produce distinctive signatures. Usually these are individually specific, but the patterns of variation we find can reveal which aspects of identity are important to the animals that we study. Animals must also distinguish among signal variants that are produced. This is an important, but less well studied aspect of recognition systems.

The first requirement for any type of signature system is that signals must have the requisite kind of variation (Beecher 1982; Polakow & Telford in press). Signals that convey kinship should vary among kin groups but be shared among kin (Beecher 1982;

Brown & Eklund 1994). This results when some components of signals are heritable (Crozier 1987; Manning et al 1992; Scherrer & Wilkinson 1993), but can also occur if signals are acquired or modified by interaction with kin, e.g., in eusocial bees and ants (Greenberg 1979; Stuart 1987; 1988), the desert isopod, *Hemilepistus reaumuri* (Linsenmair 1985) and some tadpoles (Waldman 1985). Signals that convey group membership among unrelated individuals may vary among groups but converge within them -- analogous to the pattern expected when groups are composed of kin, except that group identifying information is based not on kinship, but on social bonds (Mammen & Nowicki 1981). This pattern almost certainly results from social modification of signals. Signals that convey individual identity vary among individuals but are highly repeatable within an individual (Beecher 1982). Of course, individually specific signals can function for both kin and group recognition if others learn to associate the signal with the individual and assess their relationship to that individual genetically or socially (Sherman & Holmes 1985). This seems to be the way vervet and rhesus monkeys recognize group mates and relatives (Cheney & Seyfarth 1982; Rendall et al 1996).

Production of distinctive signals is not sufficient, however. The species' perceptual system must be capable of discriminating among potentially subtle variants (Beecher 1982; 1989). Recognition systems could evolve, then, not by developing more signal variation but by developing an increasingly fine ability to discriminate among existing variants (Grafen 1990) and bats have demonstrated acute discrimination of vocal signals (Bartsch & Schmidt 1993; Esser & Keifer 1996). Production and perception probably evolve in concert much of the time. To fully explore signals that purport to indicate caller identity, one must describe the patterns of variation in signal structure and use, and determine whether conspecifics can discriminate among relevant structural variants.

An additional concern is the stability of the signature system. In some cases, it may pay individuals to feign their identity to obtain access to resources such as those acquired by foraging groups. Evolutionarily stable signature systems must be resistant to this kind of cheating. At least three mechanisms for cheater prevention may operate. Effective signals may be hard to mimic, perception may be sufficiently good to notice imitations, or multiple signals may be required for verification of identity.

In bats, the most thoroughly studied class of social signals are infant isolation and maternal directive calls (Gould 1977) which appear to function as individual signatures. These calls facilitate reunions between mothers and infants who may be separated while the mother forages. Several studies have shown that isolation calls are individually distinctive (Jones et al 1991; Scherrer & Wilkinson 1993). Fewer studies have demonstrated that individual variation is actually used in individual recognition (Balcombe 1990; Balcombe & McCracken 1992).

PRESENT STUDY

I investigated production, perception and development of a call that greater spear-nosed bats, *Phyllostomus hastatus*, use to coordinate foraging (Wilkinson & Boughman in press b). Female greater spear-nosed bats live in stable social groups and are not closely related to their group mates (McCracken & Bradbury 1981; McCracken 1987). In Trinidad, all adult females live in stable groups. This implies that group membership provides important benefits which do not depend on relatedness. One of these benefits appears to be improved access to rich food resources through group foraging. Females sometimes forage in groups and give loud broadband calls, termed screech calls, when departing from the roost, en route to and at foraging sites. Wilkinson and Boughman (in press b) determined that females forage preferentially with members of their social group, and describe observations that strongly suggest that screech calls are involved in active foraging group formation and in identifying members of the social group outside the roost. Although food finding might be enhanced for ephemerally patchy resources (Wilkinson & Boughman in press a), the primary benefit of group foraging appears to be improved defense of rich and relatively predictable resources (Wilkinson & Boughman in press b). Over 800 *P. hastatus* roost in Guanapo cave, a primary study site, and data indicates both that group mates forage together and that bats from several groups can be present in the same location (Wilkinson & Boughman in press b). Consequently, feeding competition has the potential to be rather intense, and defending rich food resources could be beneficial and more effective by a group.

To determine the specific function of screech calls, in this dissertation I describe the patterns of variation produced, test detection, and explore how the variation arises. In chapter one, I describe results of multivariate analyses of screech call structure. I recorded calls from 28 known individuals in three social groups from a single cave colony, and find that individuals in each group sound similar to group mates but distinct from other groups. These results verify that screech calls are structured appropriately to convey the callers' group membership; fulfilling the first criterion for calls that function as group membership signatures. Calls are not structured appropriately to convey individual identity. I also find evidence that calls differ among three cave colonies -- Caura, Guanapo, and Tamana caves -- and present these results in chapter two. The basic structure of screech calls is well suited to their apparent function, as loud, broadband signals can be localized more accurately than pure tones (Brown 1982;) and noisy 4 to 10 kHz calls may transmit through the forest environment with less attenuation (Morton 1975). Wilkinson (1995) estimates that screech calls transmit at least 50 m.

Chapter two describes results of playback experiments conducted in the field and lab to test whether bats detect the cave colony and group differences I find statistically. I also tested whether females could make this distinction even though I did not find evidence that individuals within groups differ. Results from field playbacks conducted at Guanapo cave indicate that response to Guanapo calls differs from response to Tamana calls, demonstrating that bats can make colony level distinctions. In the lab I used a habituation-discrimination design to test for group and individual discrimination. This experiment demonstrates that bats can use calls to discriminate among groups, but not among individuals. Not only do calls vary in ways that imply they are group membership signals, but the perceptual system can detect group and cave differences, indicating that screech calls can be used to identify group mates outside the roost. These results corroborate field observations that screech calls facilitate the active formation of foraging groups and help maintain contact with group mates while traveling to feeding sites (Wilkinson & Boughman in press b). Experimental verification that animals use vocalizations to discriminate group mates from others is rare. Chickadees use group specific calls (Nowicki 1983) and vervet and rhesus monkeys use apparently individually specific calls (Cheney & Seyfarth 1982; Rendall et al 1996).

Finding that calls differ among groups of unrelated individuals raises the question of how these group differences arise. Juveniles disperse from their natal group during their first year, and females join existing social groups when reproductively mature, at about two years of age. Although roosting groups are quite stable, adult females occasionally change groups (G.S. Wilkinson & J.W. Boughman unpublished data). Consequently, the implication is that females alter call characteristics after they join a new social group.

Chapter three describes an experiment that tests whether females change calls when their social environment changes. I transferred females reciprocally between two captive groups and monitored whether calls of transfers and residents changed following this manipulation. The results of this experiment reveal that calls come to differ among groups through a process of social modification, or vocal learning. Individuals appear to adjust call characteristics to resemble their group mates. This provides important and rare evidence that non-human mammals can modify calls. Motivated by a search for pre-linguistic ability, several studies have focused on the potential for vocal learning in primates, with disappointing results. Although some results initially seemed promising (Green 1975; Masataka & Fujita 1989; Elowson & Snowdon 1994), on closer inspection even this evidence fails to demonstrate convincingly that primates can alter the structure of the vocalizations they give based on social interactions (Snowdon 1990; Owren et al 1992). Several observational studies on marine mammal vocalizations have found geographic variation (Thomas & Stirling

1983; Winn et al 1981), use of similar call types (Tyack 1986), or changes over time (Payne & Payne 1985) suggesting vocal learning (Janik & Slater in press). Although some of these results are highly suggestive, experimental studies to rigorously test that the described patterns result from vocal learning are lacking. A few recent studies on bats also suggest vocal learning of infant isolation calls (Esser & Schmidt 1989) or echolocation calls (Jones & Ransome 1993), and one experimental study indicates that infant calls are influenced by the maternal calls they hear (Esser 1994). My results demonstrate that female greater spear-nosed bats alter screech calls in response to changing group composition at ages when dispersal is likely to occur.

Social modification of screech calls raises the question of whether outsiders can successfully imitate calls to gain access to defended feeding sites. Although social modification of calls does occur, changes are not immediate. Large acoustic differences between groups and the time required for females to modify calls may be important in preventing outsiders from imitating the group's call. Potential cheaters would have to invest considerable time in attempting to associate with the group, listening to their calls and changing calls to match. This kind of investment makes cheating unlikely to be cost effective in evolutionary terms.

Our understanding of screech call function is fairly clear, which enabled me to identify the social factors that should favor the evolution of vocal learning of these calls. Careful consideration of call function may help to identify vocalizations in other taxa where vocal learning should be advantageous. Part of the reason for past failures may be that people have studied calls whose function is not enhanced by vocal learning. Hopefully my results will help focus study on those vocalizations where vocal learning can reasonably be expected to evolve.

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CHAPTER ONE

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 (Wilkinson & Boughman in press). 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 implicate vocal learning in this species.

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 & Stoddard 1990; Lessells et al 1991), bottlenose dolphins (Sayigh et al 1990), and some bats (Esser & Schmidt 1989; Balcombe 1990) they enable parents to find young, reducing the likelihood of misdirected parental care; or allow young to find mothers (Balcombe & McCracken 1992), reducing mortality. Infant evening bats (*Nycticeus humeralis;* Scherrer & Wilkinson 1993) and greater spear-nosed bats (*P. hastatus;* D. Lill & G.S. Wilkinson unpublished data) 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 & 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 & Falls 1975; Shy & Morton 1986; Brindley 1991; Weary & Krebs 1992; Godard & 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-distinctive calls have been documented rarely. Black-capped chickadees (*Parus atricapillus*) give calls that converge acoustically on their flock mates' (Mammen & Nowicki 1981; Nowicki 1989). These calls may facilitate flock cohesion.

STUDY SPECIES

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

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 & 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 & Greenhall 1961; Wilkinson & 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 & 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.

In this paper, I describe 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 & 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 anothers' 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 groupnongroup distinction be made and may be a simpler cognitive task. I also describe differences among ages in calling behavior and call characteristics, and comment on potential ways individual bats' 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 underway 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, DC. There, groups were housed separately in 3 x 4 x 3 m rooms equipped with 0.75 m^3 roost boxes. Humidity was maintained above 40% and temperature was controlled to range within 23° to 35°C. A 12 h light cycle was reversed so that bats are active from 9:00am to 9:00pm. 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 two years as adults; those between one and two years as first year bats; and bats less than a 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 three years or less) to 5 (most worn and typically seen on bats more than 10 to 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 12-18 month old females (first year), and eight 3-5 month old female pups. Group 2 contained 12 adult females, one adult male, three 12-18 month old females (first year), and five 3-5 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 first year bats, and one pup. I held these 18 bats for nine nights in a 4 x 5 x 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 (scarabidae) beetles. I released this group at the point of capture after nine days. Although the location and time of recording differ for this group, all groups originate from the same cave 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 three nights in the Simla flight cage. In all cases, I recorded bats flying freely around the flight cage, within the first 2 hours of nightly activity when they were feeding. I recorded screech calls with a Marantz PMD 430 cassette recorder onto metal tape using either a B and K ½ inch 4130 microphone and amplifier, or a Sennheiser MKH-840 shotgun microphone. The B and K 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 12-18 month old females (five from group 1, three from group 2, and two from group 3), and seven 3-5 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 to 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 16-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 three temporal features from sound spectrographs and waveforms (see Figure 1 for variable description).

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 (3 social groups) and age (3 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 alpha = 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 & 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 (Figure 1; mean ± 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 11537 ± 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 interval).

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 percent, with an average of 14.3 percent. More than 30 percent 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 percent. Mean values for each of the three groups are presented in Figure 2.

The stepwise discriminant analysis finds that nine 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 percent of cases (86.6 percent by resubstitution). Expected correct classification is 33.3 percent by chance (Table 3). Group 1 and group 2 calls are rarely classified as group 3, suggesting this group's mean is farther from the others. Group 3 shows little overlap with either group 1 or 2 in multivariate space (Figure 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, 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 percent, none of these are significant when I use a sequential Bonferroni adjusted alpha. 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; $p < 0.0009$; adjusted 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, yet both are significantly younger than group 3 (Figure 4a).

Calling behavior depends on age. Callers are significantly younger across all groups than noncallers (Figure 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 kHz ($F_{1,731} > 7.6$; $p < 0.0001$ 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 hypothesis 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 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 & 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 & 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 & 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 & 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, broadband signals transmit through some environments more reliably than pure tones (Morton 1975; Romer & Lewald 1992). Noisy calls appear to attenuate less in the 4 to 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 to 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 to 9 kHz. When leaving the cave to forage, they typically call in flight from below the canopy, 3 to 20 m above ground. While traveling to foraging sites, they fly above the canopy and continue to call. 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 & 1975b; 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 SPL), 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 & 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 & 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 & 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 & Shuchmann 1990), and song learning has been studied intensively. An important consequence of learning is that it produces regional dialects (Baker & 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 & Payne 1993). Greater spear-nosed bat screech calls also differ among colonies (Chapter two), 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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Table 1. Variance components for thirteen 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 degrees of freedom. Within each effect, sequential Bonferroni adjusted alpha for first comparison = 0.0038; consequently, only probabilities < 0.0001 are significant by Bonferroni criteria.

Variable	Group$_{(3)}$	Age$_{(3)}$	Bat$_{(28)}$	Call$_{(161)}$	Pulse$_{(733)}$ Error
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 @ -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 Interval	7	0	1	0	92
Number of Pulses	0	0	20 *	78 ***	2
Total Call Duration	13*	3	13	18	62

* $p < 0.05$
** $p < 0.005$
*** $p < 0.0001$

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' lambda and the average squared canonical correlation are significant at the 0.0001 level for each step.

Variable	**R^2**
Pulse Duration	.305 ***
Frequency Fall from Peak 2	.223 ***
Pulse Repetition Interval	.170 ***
Number of Energy Peaks	.157 ***
-12 dB Below Peak 1	.122 ***
Amplitude Difference Pk1 & Pk2	.085 **
2nd Energy Peak	.058 *
-12 dB Above Peak 2	.032
Frequency Rise to Peak 1	.027
Wilks' λ	.270 ***

F ratio
* $p < 0.05$
** $p < 0.005$
*** $p < 0.0001$

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

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' λ=0.26; $F_{18,300} = 16.1$; $p < 0.0001$

FIGURE LEGENDS

Figure 1. Variables measured on screech calls. a) Average power spectrum (shown for last 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 interval (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.

Figure 2. Screech call means ± se for each social group. a) Five frequency variables (kHz), b) two change in amplitude with increasing frequency variables (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 alpha levels ($p = 0.0038$ for first comparison) indicate that only $p < 0.0001$ are significantly different among groups.

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

Figure 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 alpha 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 alpha of 0.0125 ($p < 0.0018$). Number of callers = 22; number of noncallers = 26.

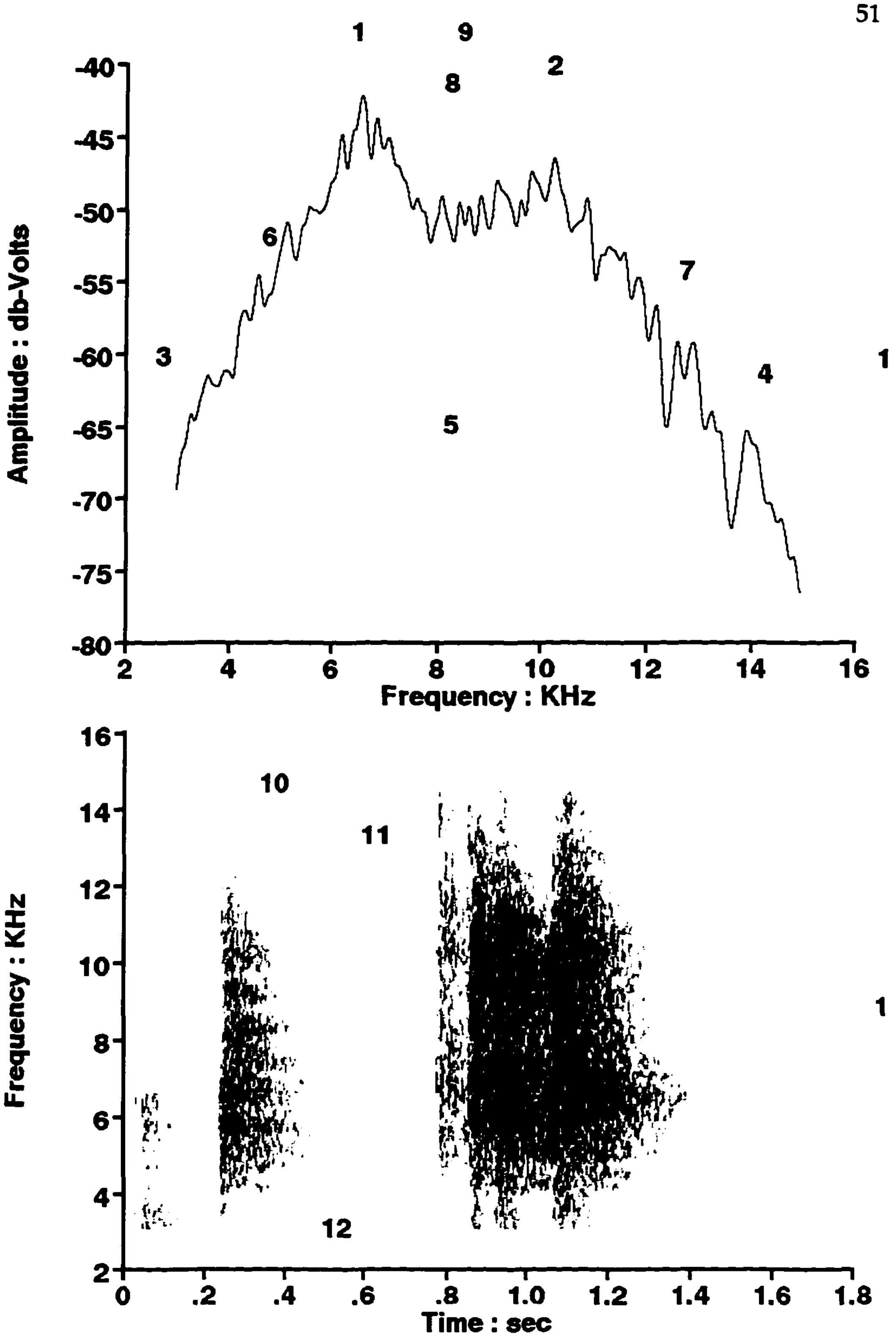

Figure 1. Variables measured on screech calls.

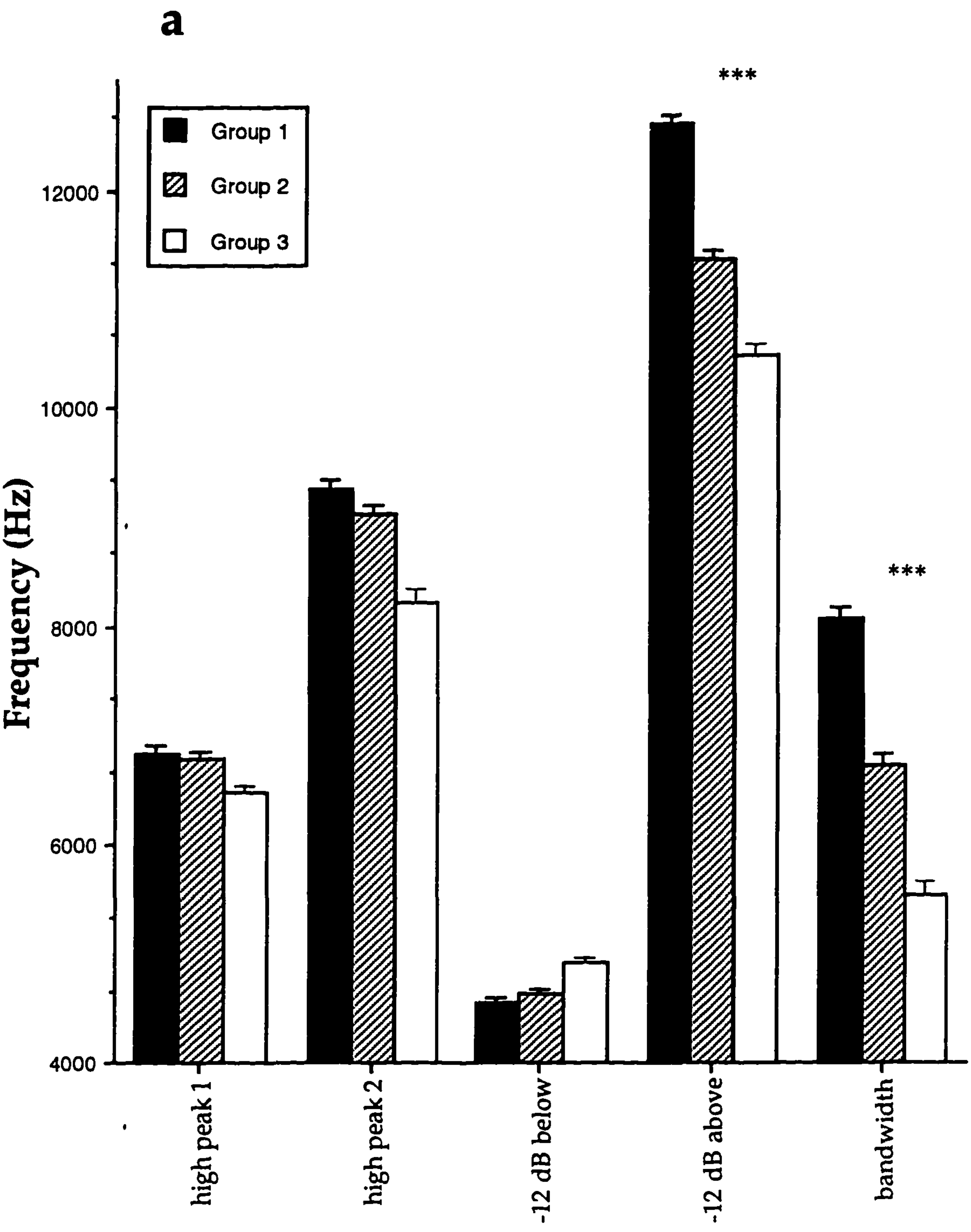

Figure 2a. Screech call means for each social group for frequency variables.

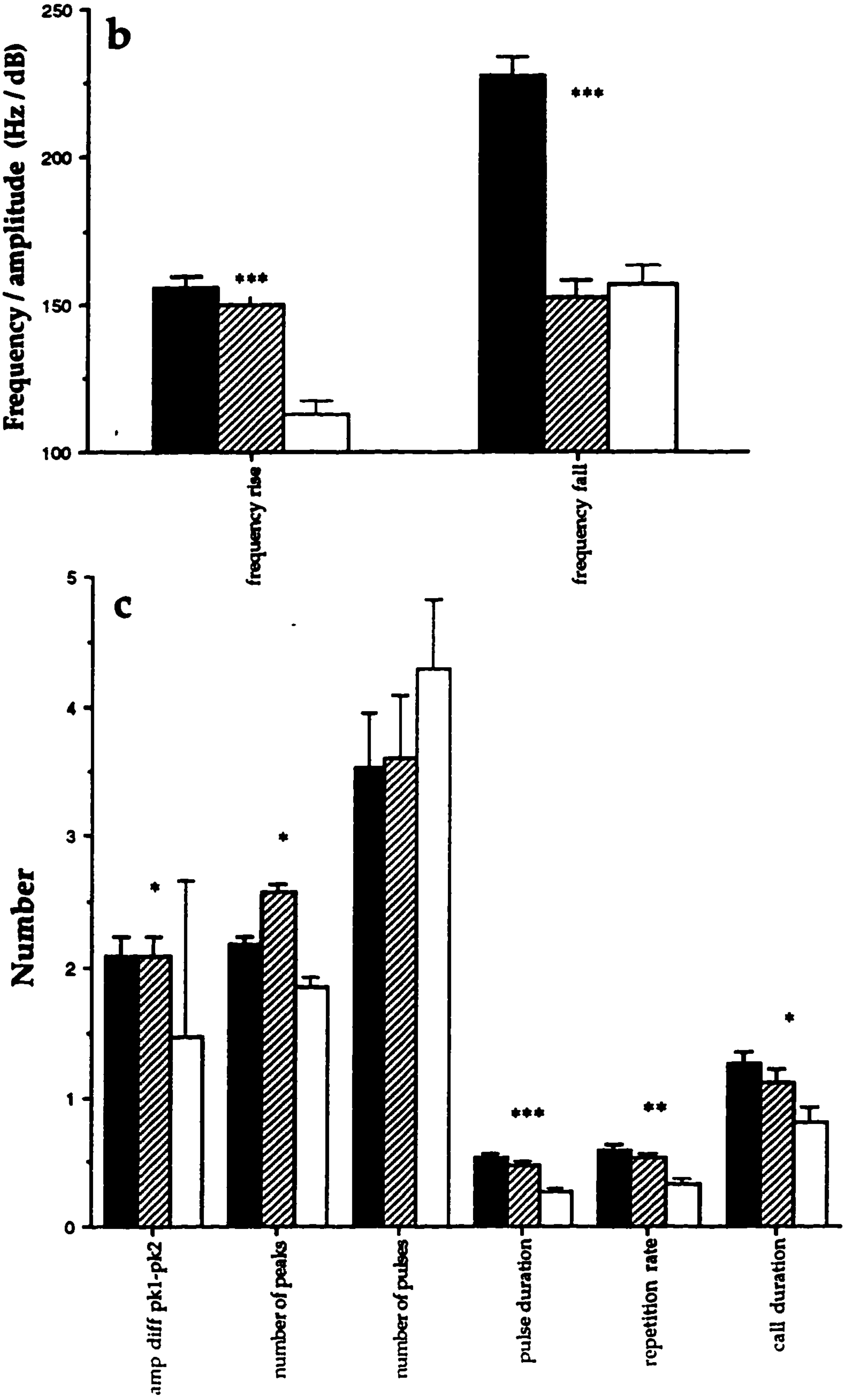

Figure 2 b, c. Screech call means for each social group for b) frequency by amplitude and c) count variables.

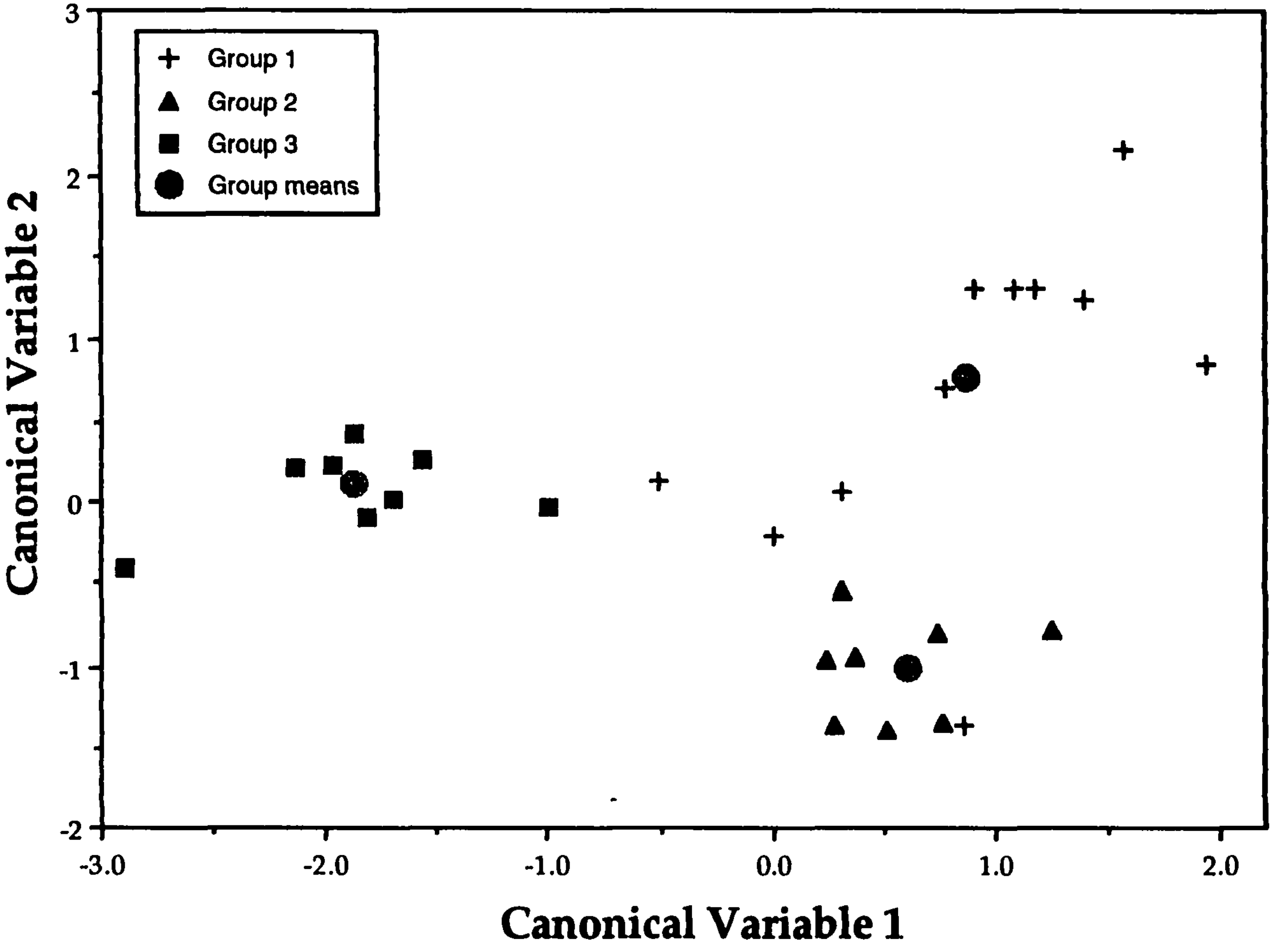

Figure 3. Acoustic canonical means for each of 28 bats in 3 social groups.

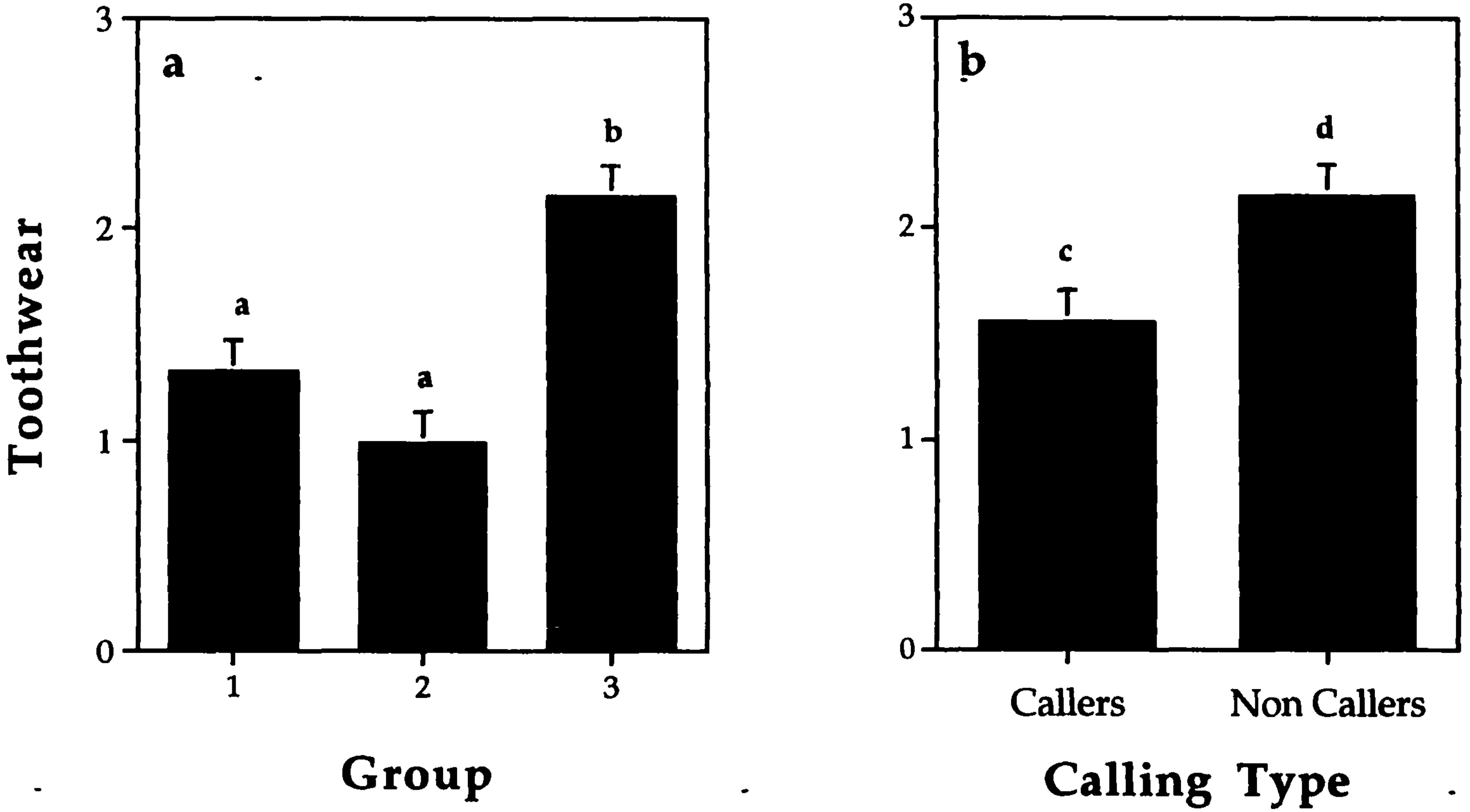

Figure 4 a,b. Toothwear means for a) calling bats in each group and b) callers and noncallers across all groups.

CHAPTER TWO

GREATER SPEAR-NOSED BATS DISCRIMINATE GROUP MATES BY VOCALIZATIONS

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 individually distinctive calls or signatures. Rarely have studies demonstrated that animals use vocalizations that differ between social groups to identify group mates. Female greater spear-nosed bats 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, I compare calls from three cave colonies using the same acoustic variables, and find that calls differ between caves. I 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, but provide no evidence that bats discriminate among individuals. I discuss the specific advantages of indicating group membership to female bats foraging with social group mates.

INTRODUCTION

Animals that live in stable social groups may benefit by improving their access to food resources, through either group foraging or group defense of resources. In this chapter, I 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 in a foraging group (Krebs et al 1972; Rabenold 1987; Brown 1988; Brown & Brown 1996; Wilkinson 1992). When food patches persist over time, resource defense becomes advantageous and may be more effective by a foraging group (Heinrich 1988). If group foraging is beneficial in either of these ways, 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 favor a mechanism to ensure association with particular individuals. Vocalizations are a potentially effective means of maintaining contact with group mates who 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 stable signature system. 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 behavior, 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 a). Bats are acoustically oriented and can travel fast and far; thus they are likely to communicate using vocalizations when outside the roost. Individuals of several species appear to give calls while on foraging territories that may function in territorial defense (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 who forage with conspecifics. At feeding sites, use of calls to attract group mates can carry costs since both potential cooperators and competitors may respond. Functional hypotheses remain untested for almost all audible calls related to foraging (but see Barlow & Jones 1997; Wilkinson & Boughman in press b). 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 Fenton 1995; Kalko & Schnitzler 1992; 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 (McCracken & Bradbury 1981) that sometimes forage together. Bats who forage with group mates apparently benefit from joint defense of rich food resources (Wilkinson & Boughman in press b) and may also find food more quickly (Wilkinson & Boughman in press a). 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 in press b). 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 appears to be important, as bats change call structure when social group composition changes (Chapter three). 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 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 nonetheless required.

Group distinctive calls resulting from socially mediated changes raises the possibility that colonies may also differ in call structure. Geographic 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). I compare calls from three cave colonies to determine whether caves differ. I then present results of playback experiments designed to test cave, group and individual discrimination. My objective for field playbacks was to determine whether bats can differentiate calls from different cave colonies. I 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 GEOGRAPHIC VARIATION

To determine if calls vary geographically I 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 (Figure 5).

METHODS

Call recording

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 setup provided nearly flat response (± 5 dB) up to 18 kHz. I analyzed 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, Trinidad, West Indies, using a different coloured LED for each group. We recorded calls from these marked bats as they departed from or circled in the vicinity of the cave. Thus, we know 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 (7 & 4 calls) respectively and an additional 17 calls from unmarked bats. I also recorded calls from three social groups from Tamana cave. One group I recorded over three nights in a flight cage at the Simla Research Station in June 1994 and obtained 16 good quality calls from this group. I released these bats at the point of capture after recording was complete. I used the same recording equipment to record calls from two captive groups during 1995 at the Department of Zoological Research, National Zoological Park and analyzed 31 calls from one group and 19 calls from the other. Screech calls consist of noisy broadband pulses repeated one to 12 times (Figure 6). I 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).

Statistical analysis

First, I determined how well calls could be classified to the correct cave using a linear discriminant function. For each of the 12 variables, I 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. I 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 then used to classify (Johnson & Wichern 1992). I also conducted a canonical discriminant analysis to estimate multivariate means for each cave colony and group. To verify that results were not unduly influenced by recording differences I conducted separate stepwise and canonical discriminant analyses including only calls recorded from free flying bats outside the cave (Caura and Guanapo calls).

To test the hypothesis that cave colonies differ from one another, I used calls from Guanapo and Tamana caves where I knew group identity and performed nested univariate and multivariate ANOVA on call averages, testing effects of cave and group nested within cave (Littell et al 1996). I obtained REML estimates of variance components and calculated the proportion of total variance attributable to group, which previous work had shown is substantial (Boughman 1997), and cave. No variables required transformation to meet the assumptions of ANOVA. I used SAS 6.11 for analyses.

RESULTS

Linear discriminant analysis classifies 71.3 percent of calls to the correct cave colony, significantly better than the chance rate of 33.3 percent (Table 4). Multivariate ANOVA indicates a significant difference between the caves (Wilks' ` = 0.38; $F_{2,103} = 8.5$; $p < 0.0001$). Multivariate means are distinct for each cave (Figure 7) and all caves differ significantly (Caura and Guanapo p_< 0.039; Tamana and Caura $p < 0.0001$; Tamana and Guanapo $p < 0.0001$). Groups within cave cluster around the cave means (Figure 7). To verify that differences in recording procedures are not the sole cause of cave differences, I restricted the data set to Caura and Guanapo calls recorded at the cave. This analysis still yields a significant ability to discriminate among cave (Wilks' ` = 0.64; $F_{1,38} = 6.8$; $p < 0.001$) and classifies 81.7 percent of calls correctly. Variable means (± se) for each cave are listed in Table 5. The proportion of total variance due to differences among cave colonies is 0.30 for two variables which also differ significantly by ANOVA (frequency of second power peak, and frequency -12 dB below the first power peak) and is above 0.10 for four other variables (Table 6). Variance attributable to cave differences is large for five variables but is negligible for six variables.

Groups within cave also differ significantly by nested MANOVA (Wilks' ` < 0.12; $F_{3,72} = 6.5$; $p < 0.0001$). For number of pulses, groups within cave accounts for half of total variance, and more than 0.10 for five other variables (Table 6). Nested univariate

ANOVA finds a significant difference among groups within cave for all variables ($p < 0.001$ for each comparison).

FIELD PLAYBACK: CAVE DISCRIMINATION

My objective for this playback experiment was to test whether geographic differences are detected by the bats. I conducted playbacks near Guanapo cave during June 1995. Although I cannot identify the individuals that responded, field playbacks provide important validation of whether bats can make discriminations in field conditions where the bats must perceive calls in an acoustically cluttered environment.

METHODS

Playback tape construction

I used the calls from Guanapo and Tamana caves that were analyzed for cave differences to create two separate 2 min playback tapes for each Guanapo group and the field recorded Tamana group, combining calls into bouts to mimic naturally occurring screech call behaviour. As estimated outside the entrance to Guanapo cave over five nights using log frequency bout analysis (Sibly et al 1990), bout length ranges from 8.5 to 32.9 s with a mean of 21.6 ± 3.9 s (Wilkinson & Boughman in press b). Using a Kay DSP 5500 Sonagraph, for each group I combined calls in varying order to construct 24 s bouts which I repeated four times with 6 s intervals to create 2 min playback stimuli. I balanced 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 that calls were broadcast, and average call duration. I also ensured that no amplitude differences existed between playback tapes.

Experimental design and analysis

I 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. I adjusted amplitude to about 79 dB (at 1 m), close to estimates of naturally occurring calls recorded in the field (75 dB at 2 to 3 m). The rated frequency response of my equipment is flat to about 18 kHz. A single trial consisted of a 2 min playback preceded by 2 min of silence. I focused a Javelin JE-7362 CCD video camera on the speaker illuminated with Kodak Wratten 87 gel filters over headlamps, and recorded this image with a Sony Hi-8 Handycam. I also recorded output from a Realistic 33-2050 sound level meter. From these tapes, I 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 respond to screech call playback by calling and approaching the sound source (Wilkinson & Boughman in press b). To adjust for baseline activity, I subtracted the number of passes or calls during the preceding silence period from the number scored during presentation of the playback. I conduct playbacks at Guanapo cave; therefore, Guanapo calls are potentially familiar while Tamana calls are unfamiliar to Guanapo bats.

I conducted four to eight trials per night over seven nights from 24 May to 1 June 1995. On two nights (16 trials) I conducted playbacks at a quarry about 200 m from the cave, on three nights (18 trials) outside the cave entrance, and on two nights (10 trials) at a foraging site about 1 km from the cave. I never conducted trials on successive nights at the same location. I analyzed 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. I used single degree of freedom contrasts to compare response to familiar calls (both Guanapo groups) to unfamiliar calls (the Tamana group). For repeated measures analyses I used the mixed procedure in SAS (version 6.11), and adjusted for correlations among time periods by modeling the error variance-covariance matrix as compound symmetric. I estimate 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 appear to discriminate among calls from Guanapo and Tamana caves (Table 7), and respond more vigorously to Guanapo calls (Figure 8). In fact, Tamana calls have no effect on the number of screeches and appear to deter approach. The multivariate test combines both variables to compare response to Guanapo and Tamana calls, and approaches significance (Table 7). A significant difference among locations results from differences between cave and foraging sites. Response at the foraging site is low because few bats are present during playbacks; evidenced by my hearing no screech calls and observing few passes (0.2 ± 0.13) during silent periods preceding playback. In contrast, baseline response at the roost cave is high (27.3 ± 5.99

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

LABORATORY PLAYBACK: GROUP AND INDIVIDUAL DISCRIMINATION

Laboratory experiments allow us to monitor responses of known individuals -- essential for assessing discrimination between groups and individuals. I 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 I used 28 female *P. hastatus* from two social groups housed at the Department of Zoological Research, National Zoological Park, Washington DC. These groups are composed of wild-caught adults (I used 4 from group 1 and 7 from group 2) and their descendent offspring (I used 7 and 5 respectively). Both groups originate from Tamana cave in Trinidad, West Indies. These two groups differ in call structure (Boughman 1997). The two social groups are housed separately in adjacent rooms and have no direct social contact, but they can hear each other, so they have acoustic interaction and are thus familiar with each others' calls.

Playback tape construction

I 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. I identified individuals in flight by their Scotchlite combinations and bleach marks, and used only calls I could unambiguously assign to individual in the construction of playback tapes. I also used calls recorded from one Tamana group in the field. In 1995 I digitized calls with a Kay 5500 Digital Sonagraph, sampling at 81.9 kHz. In 1996 I digitized calls with RTS: Real Time Spectrogram (Engineering Design, Belmont MA) sampling at 46.5 kHz. I constructed playback sequences digitally, in 1995 using a Kay Sonagraph and in 1996 using SIGNAL: Digital Signal Analysis Language (version 2.28, Engineering Design, Belmont MA). For each of 15 individuals I concatenated four or five calls with good signal to noise ratio to yield a 24 s playback sequence (Figure 9), and then played these sequences four times separated by 6 s silent intervals to produce 2 min playback stimuli. I then output stimuli to a Marantz PMD 430, recording onto metal cassette tapes. For seven bats I constructed two playback stimuli. I balanced playback stimuli for temporal and amplitude variables that could affect response, as above. I 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. I observed bats with a Javelin JE-7362 video camera under infrared illumination so that I could continually and remotely monitor response. A second observer recorded data during the experiment, and all trials were recorded onto VHS tapes for later scoring.

Experimental design and analysis

I used a habituation-discrimination design (Nelson & Marler 1989; Hauser 1996) to test for group and individual discrimination. Since prior feeding depresses activity levels and call production (Boughman 1997), I tested bats before peak feeding times. Each subject was introduced to the experimental room singly and allowed 2 to 10 min to acclimate. I waited until the bat was hanging quietly before beginning a playback trial. Field observations and playback experiments indicate that bats approach other bats who call (Wilkinson & Boughman in press b), and I monitored this aspect of response by counting the number of flights. How quickly bats respond may also be important to ensure effective defense of feeding sites or recruitment, so I measured latency to respond in seconds. Thus, the two response variables measure different aspects of response which may have different functions. During the experiment I monitored baseline activity level (number of passes) for 2 min of silence, followed by broadcast of playback stimuli for 2 min, when I also measured response latency. I measured latency as the number of seconds to the first flight after playback begins. I repeated this cycle until the animal habituated to the stimulus, as defined by a decreased response (number of passes) of at least 50 percent, although in many trials response dropped to near zero. At this time I broadcast a test stimulus. To serve as an internal control, I followed the test stimulus with rebroadcast of the habituation stimulus. I 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) *bat:* a different bat from the individual's own group. Each of 28 individuals experienced, at most, each type of test once in 1995 and once in 1996 for a total of 76 trials. If individuals failed to respond or failed to habituate I aborted that trial and did not include those data in the analysis. I did not retry that individual on the same test call type. A few individuals did not respond on the first exposure to the stimulus but did respond on the second, so I deleted the first stimulus exposure from the analysis. I separated trials with each group by at least one week, and avoided using the same individuals each week to avoid overall habituation to the experimental procedure.

To adjust for baseline activity I calculated response by subtracting the activity level (number of passes) in the preceding silence period from the number of passes in the playback period. I analyzed data with univariate repeated measures ANOVA using the mixed procedure in SAS (version 6.11). I included two fixed effects and their interaction in the model: test call type, and step in the habituation sequence. As above, I adjusted for correlations among steps in the habituation sequence by modeling the error variance-covariance matrix as compound symmetric. I assessed overall habituation by comparing mean response to the first and last habituation call. Trials showed successive average increase in response latency and decrease in number of passes, as expected with habituation (Figures 10, 11 and 12). Each individual habituated even though not all mean comparisons of the first and last habituation call were significant. To test for discrimination I 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. I also conducted multivariate ANOVA to test the combined response of calls and passes to playback stimuli.

RESULTS

Results from the lab playback experiment are summarized in Table 8. The *unfamiliar group* test indicates that bats can discriminate among calls given by their group mates and bats from an unfamiliar group. Bats show a significant change in response latency to the unfamiliar group calls (Figure 10), but not in passes. The multivariate test indicates a significant ability to make this discrimination when the two response variables are analyzed together. This discrimination may depend, in part, on the familiarity of the caller. However all bats originate from the same cave, indicating that group discrimination is not based simply on cave level differences.

In addition, the *familiar group* test indicates that group discrimination is not limited to a distinction between familiar and unfamiliar calls. Bats approach the speaker more in response to playback of the familiar group test calls (Figure 11) but latency does not rebound. The multivariate test results also demonstrate that bats can make the finer distinction between members of their own group and members of other groups. This is not just a novelty response; bats discriminate their group mates from other bats, even when acoustically familiar with members of the other group.

In contrast, bats do not appear to discriminate among the individuals in their social group. Test response to individual *bat* playback is not significantly different from habituated response for either measure alone or in combination (Table 8 & Figure 12).

DISCUSSION

CAVE LEVEL DIFFERENCES: EVIDENCE OF GEOGRAPHIC VARIATION

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

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 (Chapter three). In addition, genetic isolation could easily contribute to differences among caves. Although *P. hastatus* can fly these distances (Williams & Williams 1970), over five years of intensive banding (approximately 1000 bats banded) we have 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 geographic 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, *Nyctecieus humeralis*. However, this effect was weak compared to the high levels of individual and family variation. Geographic 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. Geographic variation has been described in Weddel seal vocal repertoires (Thomas & Stirling 1983), bearded seal trills (Cleator et al 1989), humpback whale song (Winn et al 1981), killer whale discrete calls (Ford & Fisher 1983), prairie dog alarm calls (Slobodchikoff & Coast 1980), and some tamarin long calls (Maeda & Masataka 1987), but is absent in vervet monkeys (Struhsaker 1970), and gibbon songs (Marshall & Marshall 1976).

The cause of geographic variation in mammalian vocalizations is unknown at present. Geographic 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). 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 that show individual differences 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.

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). Dialects have 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, song dialects reflect population differentiation.

EVIDENCE FOR CAVE AND GROUP DISCRIMINATION

Field playbacks indicate that bats can discriminate between calls given by their own and foreign colonies based solely on call structure. No visual or olfactory cues are 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 – since bats would not be expected to recruit to calls of unknown group identity unless they were attempting to compete with the caller. 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 a different 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. Foraging groups may defend food resources, which may also cause the reduced response to foreign calls.

Discrimination in the lab is not limited to differentiating familiar from unfamiliar bats, nor is group discrimination based on a colony level distinction, since all captive bats originate from the same cave. Bats 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 do not differ significantly among individuals within a group (Boughman 1997), and bats do 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 respond quickly to calls from an unfamiliar group but do not approach the source of sound. This is expected given that foraging groups appear to defend feeding sites (McCracken & Bradbury 1981; Wilkinson & Boughman in press b). In comparison, females investigate calls from a familiar group, but do not vary in the time taken to initiate response. This is consistent with the recruitment function that calls serve. Differences in recording procedures do not appear to confound results, since group discrimination occurs between calls recorded with similar methods. The results of the individual discrimination test indicate either that females do not perceive differences among group mates, or the calls of group mates are behaviourally equivalent. This experiment does not allow us to differentiate between these two explanations.

VOCAL RECOGNITION IN OTHER TAXA & CONTEXTS

Most taxa that use vocalizations for recognition base this recognition on individual signatures, whether the important task is to identify neighbors, 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, or to facilitate interactions among social partners.

Several territorial birds recognize unrelated neighbors by song (Brooks and Falls 1975; Shy and Morton 1986; Brindley 1991; Godard 1991; Weary and Krebs 1992; Godard and Wiley 1995; Stoddard 1996). Neighbors singing in the "wrong" location and unfamiliar individuals may both represent potential territory encroachment or cuckoldry risk, and territory owners respond equally vigorously to either type of song playback. Individual identity is key here, and birds appear to base recognition on individual variation in songs.

Recognition between parents and offspring often appears to be based on individual variation that represents kinship, and is favored in colonial and highly social animals. Mexican free tailed bats (*Tadarida brasiliensis)* roost in huge colonies. Mothers use individually distinctive isolation calls to find their pups (Balcombe 1990), and pups use the individual distinctiveness of maternal directive calls to identify their mothers (Balcombe & McCracken 1992). Colonial bank swallow (*Riparia riparia*) parents identify nestlings by call (Beecher & Stoddard 1990). However, production and detection of signatures is expected only where it provides a benefit. 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 noncolonial species (Beecher 1982).

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. Vervet monkeys and rhesus macaques form matrilineally-based social groups that establish and defend territories. Monkeys appear to use vocalizations to discriminate social group mates from individuals belonging to neighboring social groups (Cheney & Seyfarth 1982) and matrilineal kin from nonkin (Rendall et al. 1996). Social interactions within the group are complex and depend on dominance relationships, which may require individual recognition. Chickadee winter flocks defend group territories and birds respond differently to calls from their own and different flocks played at feeding sites within the territory (Nowicki 1983). Chickadees produce calls that differ among flocks and individuals within flocks (Mammen & Nowicki 1981) and both may provide the basis for recognition (Nowicki 1983). Dominance within flocks may be the factor favoring individual differences in this species also.

With the exception of chickadees, these examples rely on individual signatures. In contrast, greater spear-nosed bats do not 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 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 behavior 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 I 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. Female *T. brasiliensis* 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), and then combine olfactory and vocal cues to identify them (Gustin & McCracken 1987; Balcombe 1990).

ADVANTAGES OF INDICATING GROUP MEMBERSHIP AND RECOGNIZING GROUP MATES

What could be the selective advantage to identifying group status 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 in press b). 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 rather intense. Defending rich food sites, such as balsa trees, *Ochroma lagopus* with many open flowers (Wilkinson & Boughman in press b) could be beneficial and may be more effective 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 individuals own group (to elicit cooperative defense and deflect possible aggression) and potential intruders (to advertise site ownership and discourage feeding by non-group mates). Both are important for the cooperative defense that Wilkinson and Boughman (in press b) propose to occur.

As has been pointed out for kin recognition (Beecher 1982; 1989; Reeve 1989), a stable signature system requires both the production of distinctive signatures and their perception. This should be true for individual or group recognition even in the absence of relatedness. Female greater spear-nosed bats give screech calls that are group distinctive; thus calls contain relevant information to convey group membership (Boughman 1997). Females also perceive the group differences and can use calls to identify group mates.

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 relatedness levels in greater spear-nosed bat female 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 and Bradbury (1981) hypothesized that shared information about food or mutual defense of feeding sites might provide important advantages, and we have foraging data consistent with both explanations (Wilkinson & Boughman in press a, b). Additionally, group mates may cooperatively care for and defend pups (T.A. Porter unpublished data). We have observed non-offspring nursing and predation on pups in Guanapo cave (G.S. Wilkinson, J.W. Boughman & T.A Porter unpublished data). When pups are young, one or more females per group remain in the cave while the other adults are out foraging, presumably to defend pups. 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 do not observe females roosting alone. Identifying group mates by call is an important mechanism for maintaining these stable groups.

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Table 4. Discrimination into cave colonies using variables identified with stepwise discriminant analysis as contributing significantly to separating caves. Percent of 106 calls classified to each cave are indicated, as determined by cross validation

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

Table 5. Screech call means ± se for Caura, Guanapo and Tamana caves

Variable	Caura	Guanapo	Tamana
Peak 1 (Hz)	6069 ± 393.6	6524 ± 298.6	6630 ± 183.0
Peak 2 (Hz)	9122 ± 558.7	10297 ± 467.8	8639 ± 286.8
Hi 12 (Hz)	10864 ± 1134.6	11521 ± 637.5	11430 ± 390.8
Lo 12 (Hz)	4241 ± 249.4	5232 ± 171.7	4470 ± 105.3
Bandwidth (Hz)	6623 ± 1164.8	6288 ± 781.2	6960 ± 478.9
Rise (Hz/dB)	152.8 ± 21.14	107.6 ± 30.78	149.3 ± 18.87
Fall (Hz/dB)	146.1 ± 56.69	172.4 ± 24.98	147.1 ± 15.31
Number of Peaks	2.23 ± 0.416	2.07 ± 0.374	2.12 ± 0.229
Amplitude dif Pk1 & Pk 2 (dB)	1.96 ± 0.828	4.22 ± 0.851	2.09 ± 0.522
Repetition Interval (ms)	0.36 ± 0.119	0.13 ± 0.121	0.40 ± 0.074
Number of Pulses	9.98 ± 2.51	9.63 ± 3.245	4.42 ± 1.989
Call duration (ms)	1.39 ± 0.361	1.03 ± 0.370	0.92 ± 0.163

Table 6. Comparison of screech call variance for Guanapo and Tamana caves. Proportion of total variance is shown for cave, group within cave, and residual

Variable	**Cave**	**Group(Cave)**	**Residual**
Peak 1	0	0.09 **	0.91
Peak 2	0.3 *	0.05 **	0.65
Lo 12	0.3 *	0.05 **	0.65
Hi 12	0	0.17 **	0.83
Bandwidth	0	0.20 **	0.8
Rise	0.07	0.21 **	0.72
Fall	0.2	0.08 **	0.72
Number of Peaks	0.14	0.04 **	0.82
Amplitude dif Pk1 & Pk 2	0	0.13 **	0.87
Repetition Interval	0.19	0.08 **	0.74
Number of Pulses	0.14	0.55 **	0.3
Call Duration	0	0.17 **	0.83

* $p < 0.05$

Table 7. Field playback to test cave discrimination. Results are from univariate repeated measures ANOVA and MANOVA

Source of Variation	Bat Passes		Screech Calls		MANOVA	
	df	F	df	F	df	Wilks' λ
Location	2, 81	12.0 ***	2, 199	14.2 ***	4, 134	0.45 ***
Date (location)	6, 81	8.4 ***	6, 199	3.5 **	4, 134	0.42 ***
Period	2, 81	3.9 *	2, 199	2.4 ‡	4, 134	0.88 ‡
Playback v prior & post	1, 81	7.7 **	1, 199	4.5 *	2, 67	0.89 *
Call type ′	6, 81	1.7	6, 199	3.4 **	12, 134	0.67 **
Guanapo v Tamana	1, 81	4.5 *	1, 199	5.9 *	2, 67	0.93 ‡

‡ $p < 0.10$
* $p < 0.05$
** $p < 0.005$
*** $p < 0.0001$

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

Table 8. Habituation-discrimination response to test calls, analyzed with univariate repeated measures ANOVA and MANOVA and single degree of freedom constrasts. The contrasts give the results for a comparison of test call to mean habituated response just prior to and following test presentations for each test call type

Source of Variation	**No. Passes**		**Response Latency**		**MANOVA**	
	df	**F**	**df**	**F**	**df**	**Wilks' λ**
Test call type	2, 60	1.1	2, 60	0.6	4, 364	0.99
Habituation sequence	5, 218	3.7 **	5, 129	1.1	10, 364	0.95
Test call type * Habituation sequence	10, 218	1.5	10, 129	1.1	20, 364	0.86
Test vs pre & post habituation contrasts						
Unfamiliar group	1, 218	0.1	1, 129	5.5 *	2, 182	0.97 *
Familiar group	1, 218	11.3 ***	1, 129	0.1	2, 182	0.97 *
All group test calls	1, 150	7.4 **	1, 84	1.9	2, 120	0.97
Individual bat	1, 218	0.0	1, 129	0.4	2, 182	0.99

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

FIGURE LEGENDS

Figure 5. Map of Trinidad to show location of each cave.

Figure 6. Examples of screech calls from two groups. a) bat 1531 from Group 1, and b) bat 1022 from Group 2.

Figure 7. Acoustic canonical means for six groups (shown in open symbols) from three cave colonies (shown in filled symbols). n=168 calls.

Figure 8. Mean ± SE response to field playback conducted at Guanapo cave to test dialect discrimination. a) Number of screech calls given in response to playback ($n = 72$). b) Number of passes, or times bats approached within approximately 2 m of the speaker ($n = 35$). Values are adjusted for baseline activity by subtracting activity in preceding silence period from playback response levels. Significance (` =0.05) is obtained from comparisons of mean response to Guanapo calls and Tamana calls averaged across three playback locations (cave entrance, flyway, feeding site).

Figure 9. Example playback sequence used in laboratory playback experiments. a) Power spectrum for one pulse of call, b) waveform for entire sequence, and c) sonagram for entire sequence.

Figure 10. Response to the unfamiliar group test calls for the habituation-discrimination playback experiment. Test calls were recorded from a Tamana group which respondents could not have heard for at least three years, if ever. This experiment tests group discrimination that may rely on differences in familiarity. Mean ± SE ($n = 35$) are shown for a) the number of seconds after playback began before the bat responded and b) number of flights, corrected

for baseline activity. X-axis indicates stage of the habituation sequence. Habituation points are successive broadcasts of the habituation call preceding test playback and rehab is rebroadcast of this same call immediately following test call playback.

Figure 11. Response to the familiar group test calls for the habituation-discrimination playback experiment (n = 16). Test calls were from the other captive group, which respondents have heard but have not interacted with socially. This experiment tests group discrimination independent of familiarity. Details same as Figure 10.

Figure 12. Response to playback of individual bat test calls for the habituation-discrimination playback experiment (n = 27). Test calls were from different individuals in the respondents own social group. This experiment tests individual discrimination. Details same as Figure 10.

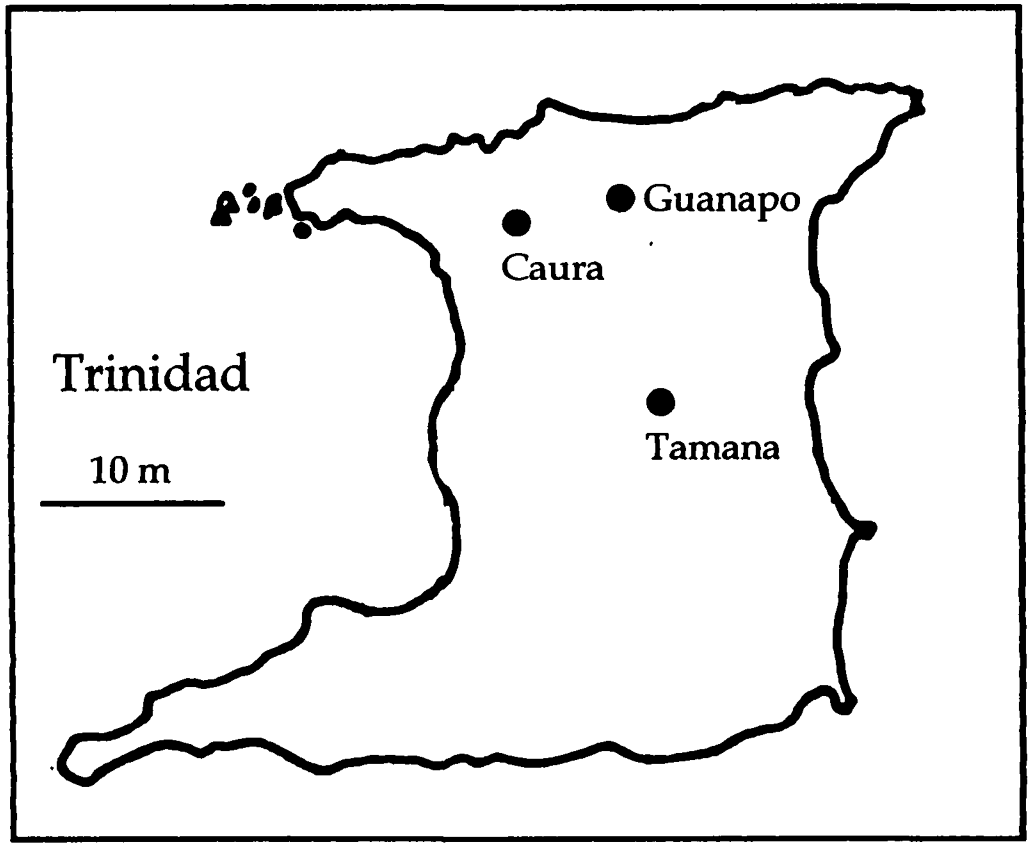

Figure 9. Map of Trinidad, WI indicating location of each cave.

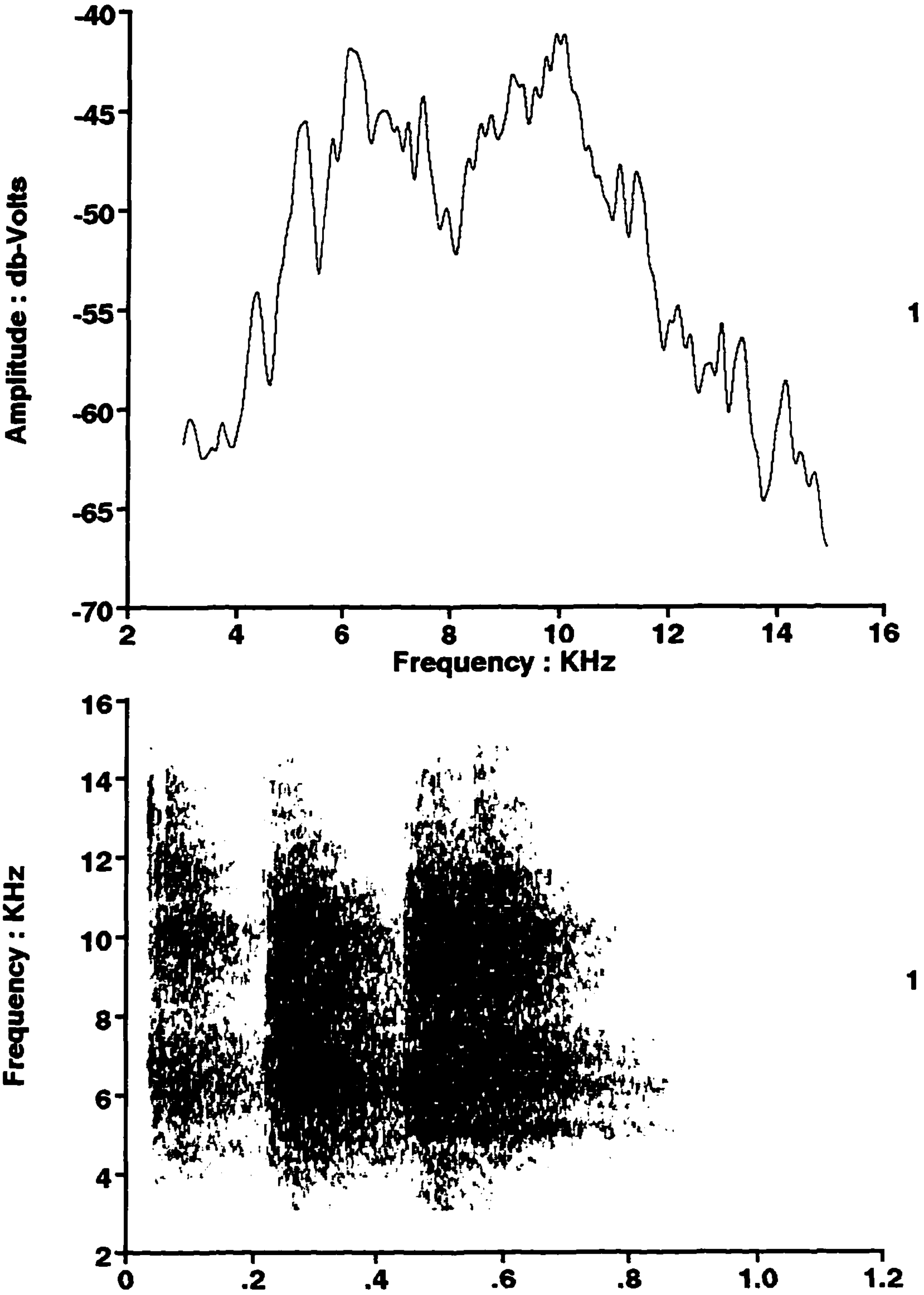

Figure 6a. Screech call from bat 1531 from Group 1.

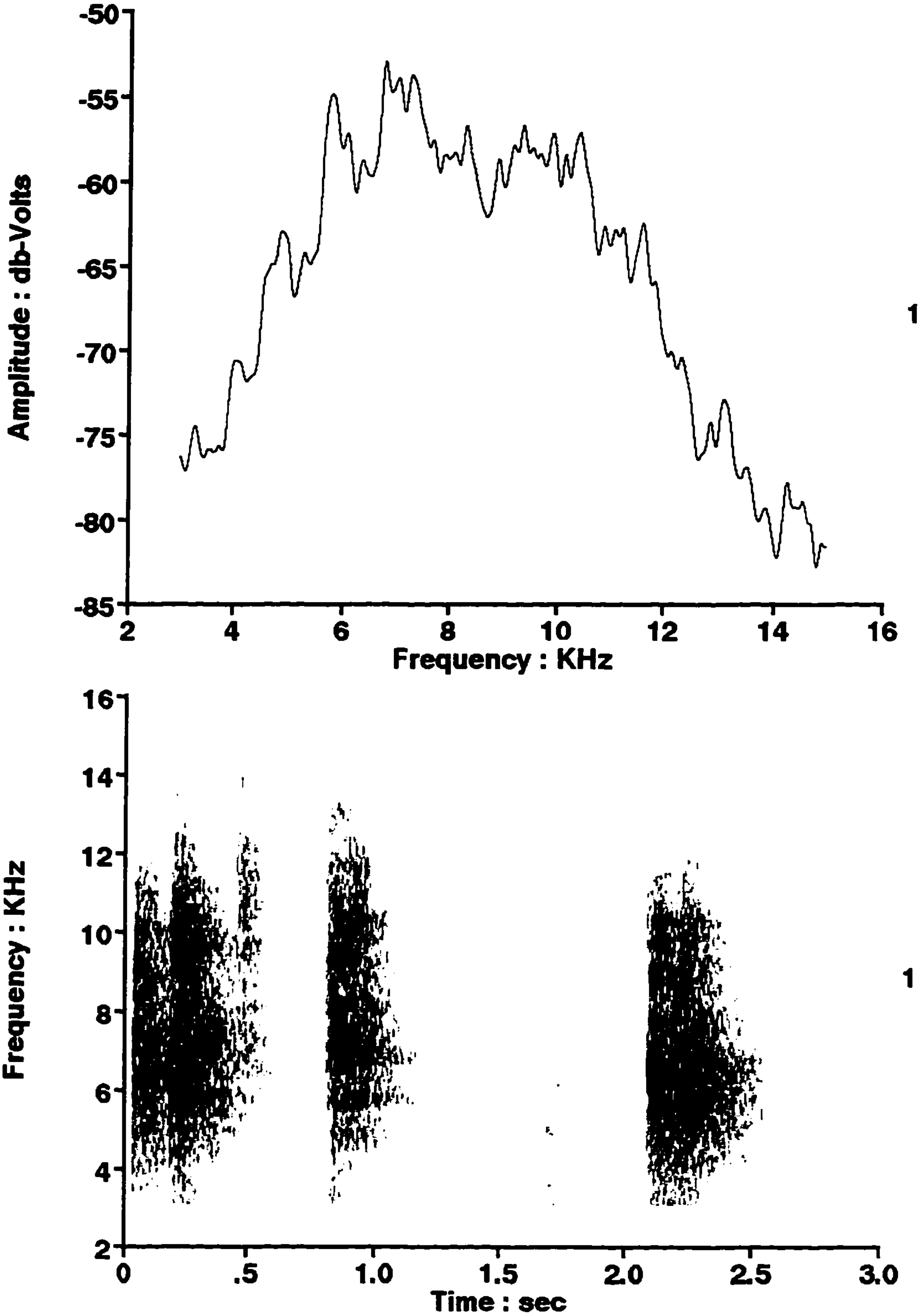

Figure 6b. Screech call from bat 1022 from Group 2.

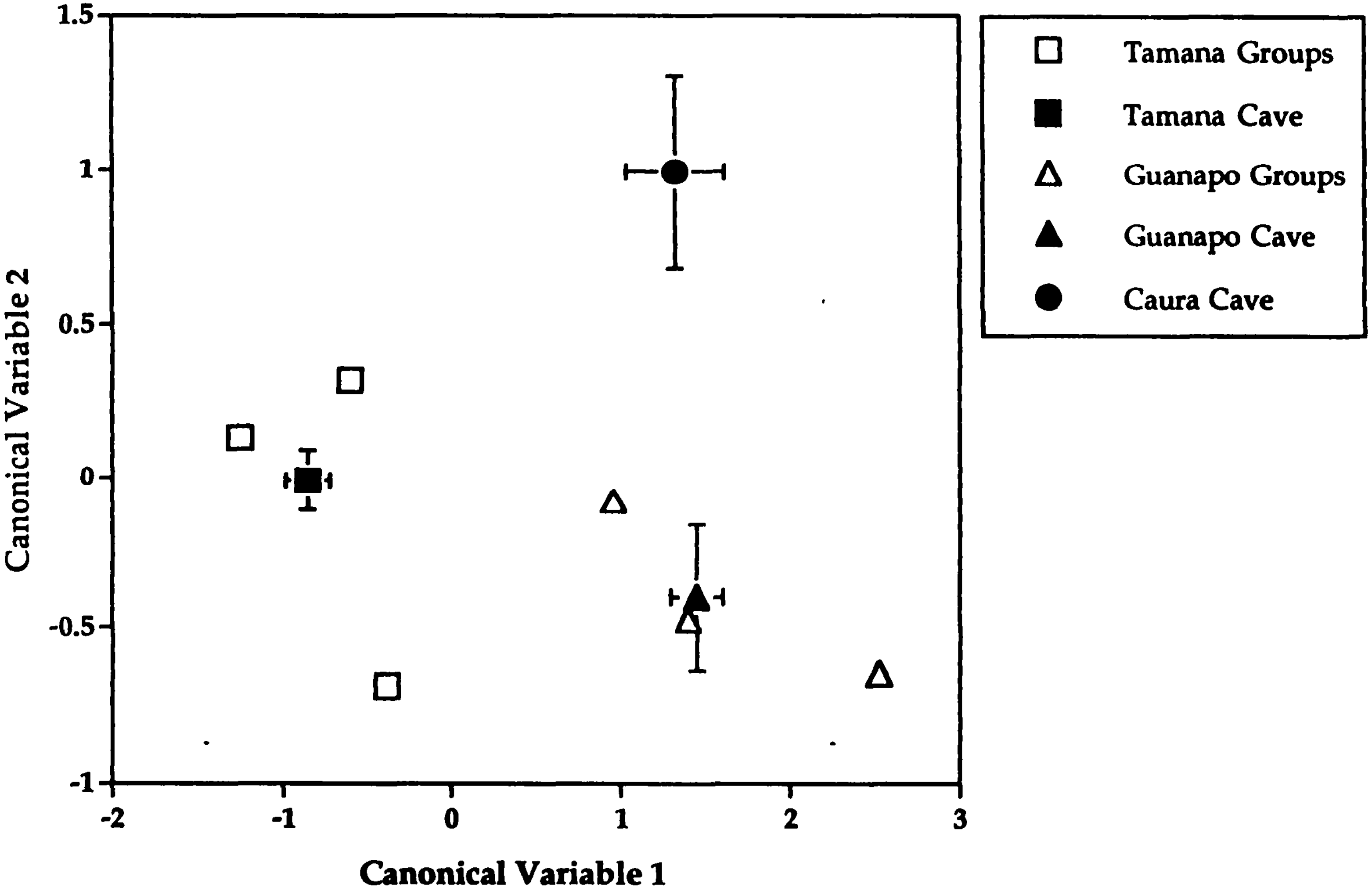

Figure 7. Acoustic canonical means for Tamana, Guanapo and Caura caves.

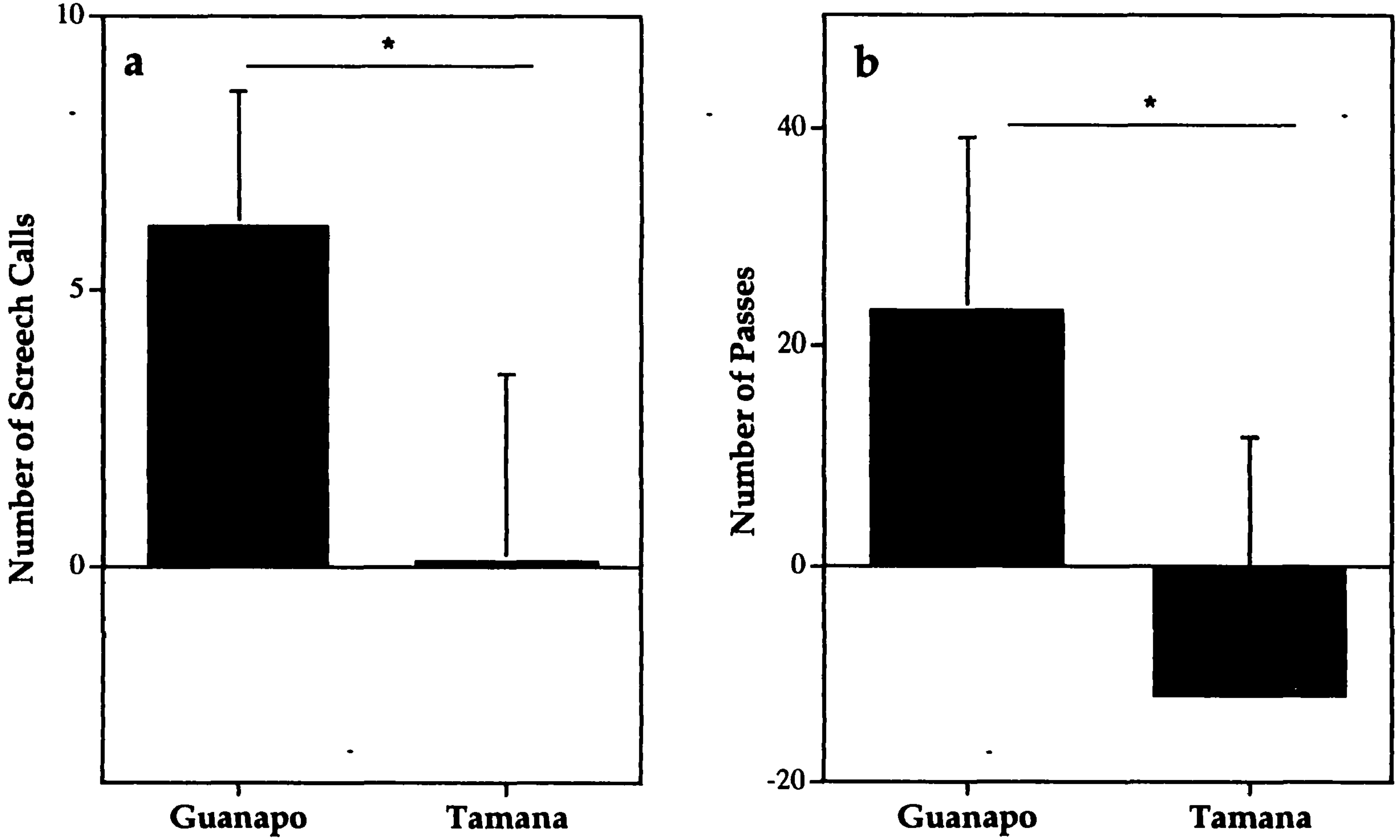

Figure 8. Response to field playback testing cave discrimination.

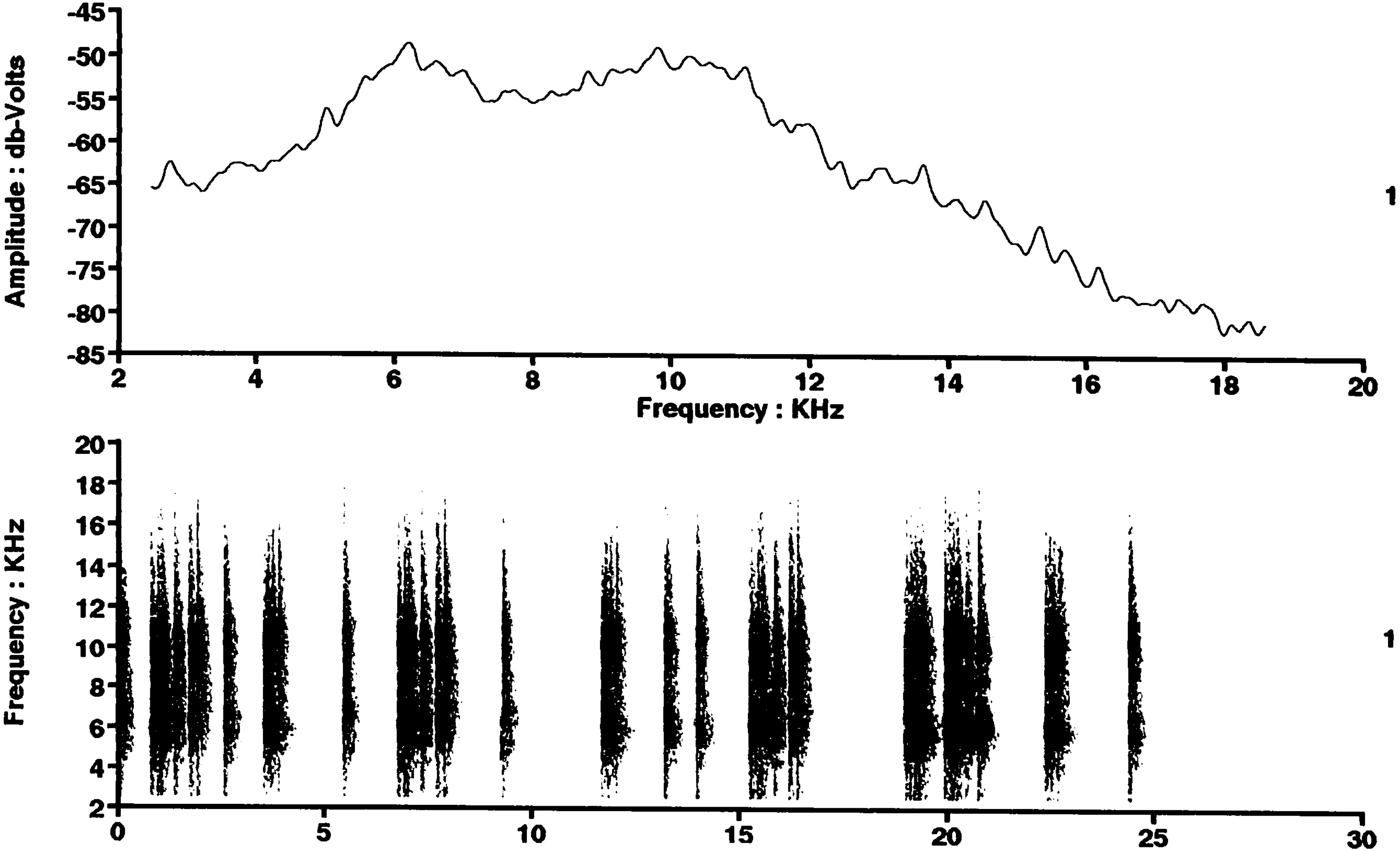

Figure 9. Example playback sequence used in lab playback experiment.

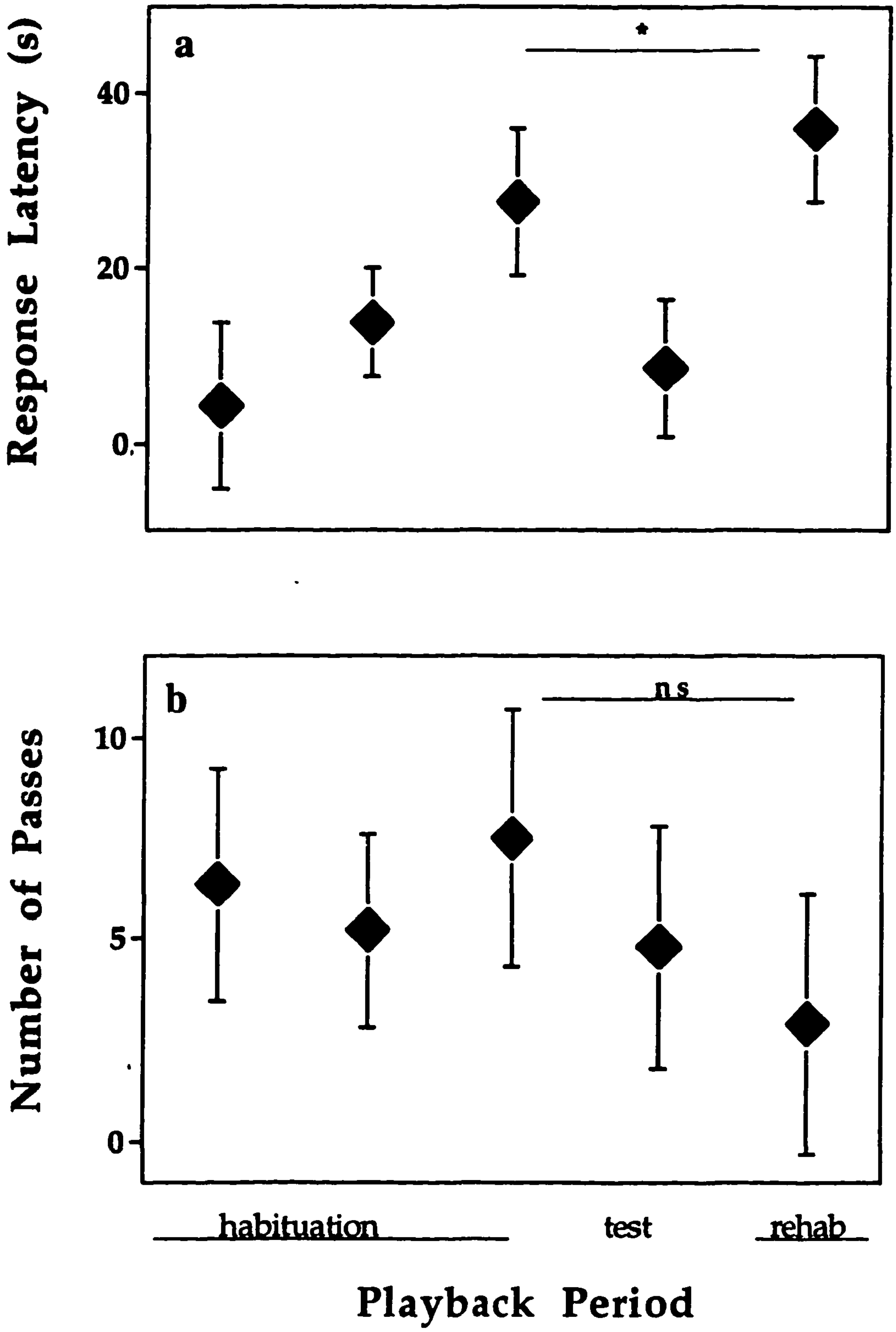

Figure 10. Response to unfamiliar group playback.

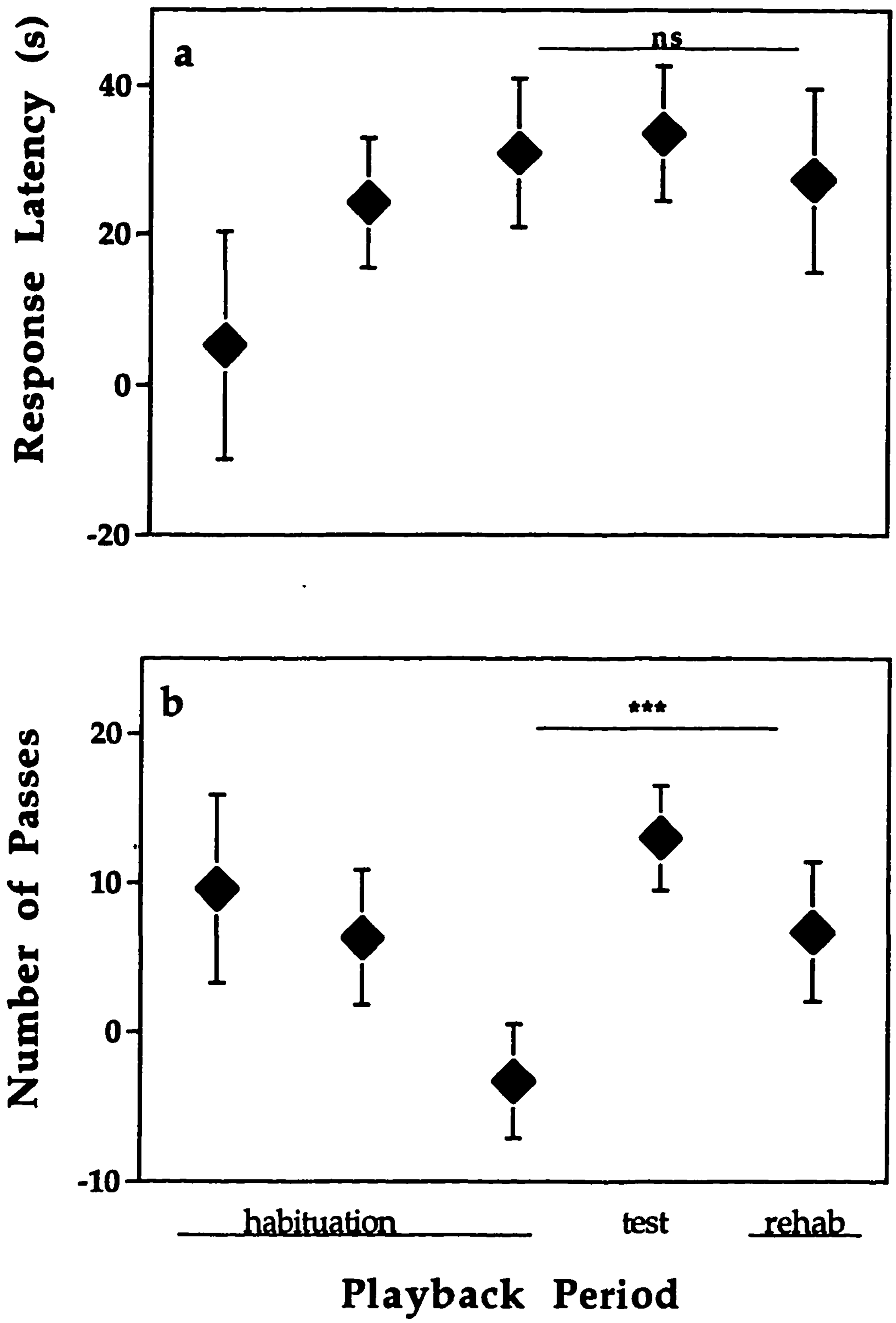

Figure 11. Response to familiar group playback.

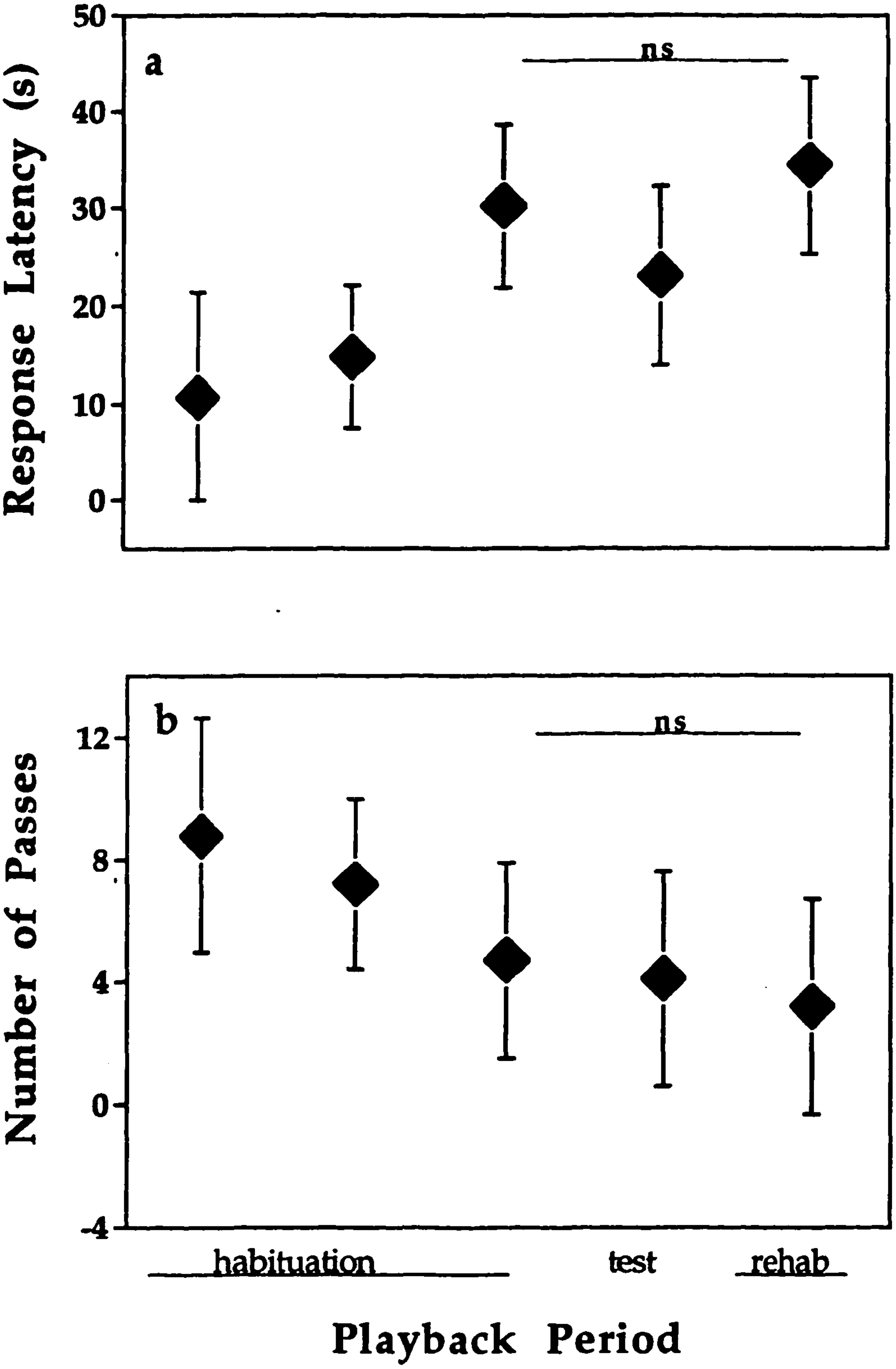

Figure 12. Response to individual bat playback.

CHAPTER THREE

VOCAL LEARNING BY GREATER SPEAR-NOSED BATS

ABSTRACT

Social modification of vocalizations should be favored by selection when calls indicate group membership and group mates are unrelated. Several birds change call structure when group composition changes (Nowicki 1989; Farabaugh et al 1994), but most data on mammals are equivocal (Owren et al 1992). Female greater spear-nosed bats, *Phyllostomus hastatus*, live in stable groups of unrelated bats and use loud, broadband calls to coordinate foraging movements (Wilkinson & Boughman in press a). Calls vary among female groups (Boughman 1997) and colonies, and playback experiments demonstrate that bats perceive these acoustic differences (Chapter two). 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.

INTRODUCTION

Animals that live in stable social groups often produce vocal signals that indicate group membership (Schaller 1972; 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). Selection should favor social modification only for calls whose function is enhanced by the degree of similarity to social partners, whether these be territorial neighbors, mates, or members of a social group. Socially mediated vocal changes should be favored when calls are badges of group membership and especially when group members are not relatives. Species that join or change groups as adults need to retain flexible signal production into adulthood.

There is little evidence that taxa other than birds modify calls in response to their social environment. Mammals are especially controversial vocal learners and are also unlikely to form groups of unrelated individuals. Many studies have failed to find convincing evidence of vocal learning (Snowdon 1990; Owren et al 1992; Janik & Slater 1997), and results of other studies 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). 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 13), that differ among social groups, yet individuals within groups are statistically indistinguishable (Boughman 1997). Female social groups are very stable, but 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.

Field observations suggest that screech calls facilitate recognition of social group mates who forage together on rich food resources (Goodwin & Greenhall 1961; Wilkinson & Boughman in press a). 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 in press a). Analyses of screech call acoustic structure reveal that calls 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 not among individuals in their group (Chapter two). Calls that sound similar among members of a social group and different between groups are probably more effective than individually distinctive calls at helping females to find their group mates during evening emergences of several hundred bats. Calls also differ among three caves in Trinidad (Chapter two). 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*.

METHODS

SOCIAL MANIPULATION

To test the hypothesis that group differences arise through social modification of screech calls, I mimicked naturally occurring dispersal by transfering bats reciprocally between two social groups housed 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 2 years. Individual females remain with the same group for many years with a few individuals occasionally transferring to a new group (G.S. Wilkinson & J.W. Boughman unpublished data).

The captive groups are composed of wild-caught adults (11 and 12 respectively) and their descendent offspring (32 and 29 respectively). Most offspring roost in a secondary roost separately from adults, in patterns similar to those observed in the wild (McCracken & Bradbury 1981). From each group I moved two reproductively mature 2-3 year old females and three 1 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. After transfer, roosting affiliations coalesced quickly with most transfers joining the secondary roost. I recorded 10 transfers and 13 resident females (including six half-sibs) before and after moving bats and analyzed 12 acoustic variables for 678 calls (see Figure 13 for variable description).

CALL RECORDING AND MEASUREMENT

I recorded screech calls from transfers and residents (including 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 (system's flat response (± 2.5 dB) up to 18 kHz). I recorded bats flying freely around the flight cage in small groups. All bats were individually marked with unique combinations of colored 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 analyzed calls I could unambiguously assign to an individual. I analyzed 678 calls from 23 individuals. I digitized calls using RTS: Real-Time Spectrogram (Engineering Design, Belmont MA), sampling at 46.5 kHz. I analyzed 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.

STATISTICAL ANALYSIS

Prior to analysis, I calculated average values for measured variables for each call. I analyzed these data by two factor univariate and multivariate ANOVA, with group (4 levels: group 1 residents, group 1 transfers, group 2 residents, group 2 transfers), period (3 levels: pre-move, 1 month post-move, and 5 months post-move), and their interaction. I followed this analysis with univariate and multivariate contrasts among residents and transfers to test differences pre-move, 1 month post-move, and 5 months post-move and then compared transfers and half-sibs pre- and post-move. 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 bats in group 1 with those in group 2 post-move (including transfers and residents).

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 most variables (Table 9). 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 almost all variables. Only frequency of second power peak and number of pulses remain different in group 1. For some variables, residents show the largest changes (e.g., bandwidth in both groups, Figure 14a), while for others, transfers change most (e.g., repetition interval in group 2, Figure 14b). These univariate results are corroborated by MANOVA contrasts which indicate significant differences between residents and transfers pre move (group 1 Wilks' ` = 0.962; $p < 0.007$; group 2 Wilks' ` = 0.829; $p < 0.0001$). Five months later residents and transfers do not differ (group 1 Wilks' ` = 0.982; $p = 0.411$; group 2 Wilks' ` = 0.975; $p = 0.123$). After living together for 5 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 15). 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' ` = 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. 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. I tested these hypotheses by comparing the difference between transfers and their age-matched half-sibs before and after the move (Table 10). Both adult and juvenile transfers and their age-matched half-sibs have changed the degree of resemblance to one another (Figure 16). These comparisons indicate that observed changes cannot be explained by maturation or the physical environment alone.

DISCUSSION

Social modification of calls differs from song learning in birds, especially in how closely it is tied to development. Juvenile oscine birds learn to produce adult-form songs during development, requiring exposure to species-typical song exemplars to produce normal song (Slater 1989; Nottebohm et al 1990; Kroodsma 1996). In contrast, juvenile *P. hastatus* produce screech calls spontaneously when they become volant (personal observation) and these calls are later modified by social interaction with group mates. Call modification in *P. hastatus* is not limited to juveniles -- essential since females join new groups as adults. Changes are reciprocal, suggesting that females respond acoustically to their group mates rather than an internal template.

Social modification of screech calls is consistent with predictions for social learning (Laland et al 1996) of calls that coordinate group movements (Wilkinson & Boughman in press b). When an individual's social environment changes often, for instance when social groups are not stable, indicating group membership is unlikely to be favored. 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 should not 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 favored and calls should be heritable indicators of kinship. When the environment changes at an intermediate rate, for instance when individuals disperse from their natal group to form stable social groups, social learning should be favored. Calls should indicate group membership and be modifiable by the social environment. 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 and Bradbury 1981; G.S. Wilkinson & 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 should make copying relatively difficult. Controlling subtle frequency characteristics in these noisy calls may also be difficult, which may make changing calls physiologically costly to produce. Possibly more important in *P. hastatus* are the costs of acquiring the group specific characteristics. Calls do not change immediately, which may indicate that time is required for females to modify screech calls after group composition changes. 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 investment makes cheating unlikely to be cost effective.

Greater spear-nosed bats demonstrate that vocal learning is not limited to birds and humans. There may be a phylogenetic component to this ability. *P. discolor* infants give isolation calls that facilitate reunion with mothers and can be modified by hearing particular maternal directive calls (Esser 1994). Perhaps the search for the ability to modify vocalizations in mammals should concentrate on calls whose function depends on flexibly indicating membership in a group.

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Table 9. Number of variables (of 12) that differ between resident bats and transfers before and after moving bats.

	PreMove	1 month Post-Move	5 months Post-Move
Group 1	7	5	2
Group 2	10	7	0

Table 10. Number of univariate contrasts (of 12) that indicate divergence of resident and transferred ½ sibs.

	2-3 year old ½ sibs	Juvenile ½ sibs	MANOVA Wilks' `
Group 1	2	2	0.97 ***
Group 2	9	10	0.92 ***

FIGURE LEGENDS

Figure 13. Representative screech calls from a bat in each group prior to transfer. a) bat 1021 from Group 1, and b) bat 1522 from Group 2.

Figure 14. Changes in call structure with changing social environment for both groups prior to moving bats (pre-move), 1 month, and five months after the move (post-move). Solid bars are residents and open bars are transfers. ** $p < 0.001$; *** $p < 0.0001$. I show a) a representative frequency measure -- mean bandwidth ± se; and b) a temporal measure shown previously to be important in differentiating groups -- mean repetition interval ± se.

Figure 15. Convergence among residents and transfers in multivariate space illustrated by 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. Prior to transfer, the calls of bats who roost separately differ in group 2 (Wilks' ` =0.961; p=0.007) but not in group 1 (Wilks' ` =0.977; p=0.183). After transfer, most transfers roost in the secondary roost.

Figure 16. Divergence of female transfers (▼) and female age-matched half-sibs (■). I show canonical means for group 2 pre-move (small symbols) and 5 months post move (large symbols). Filled symbols are adults and open symbols are juveniles.

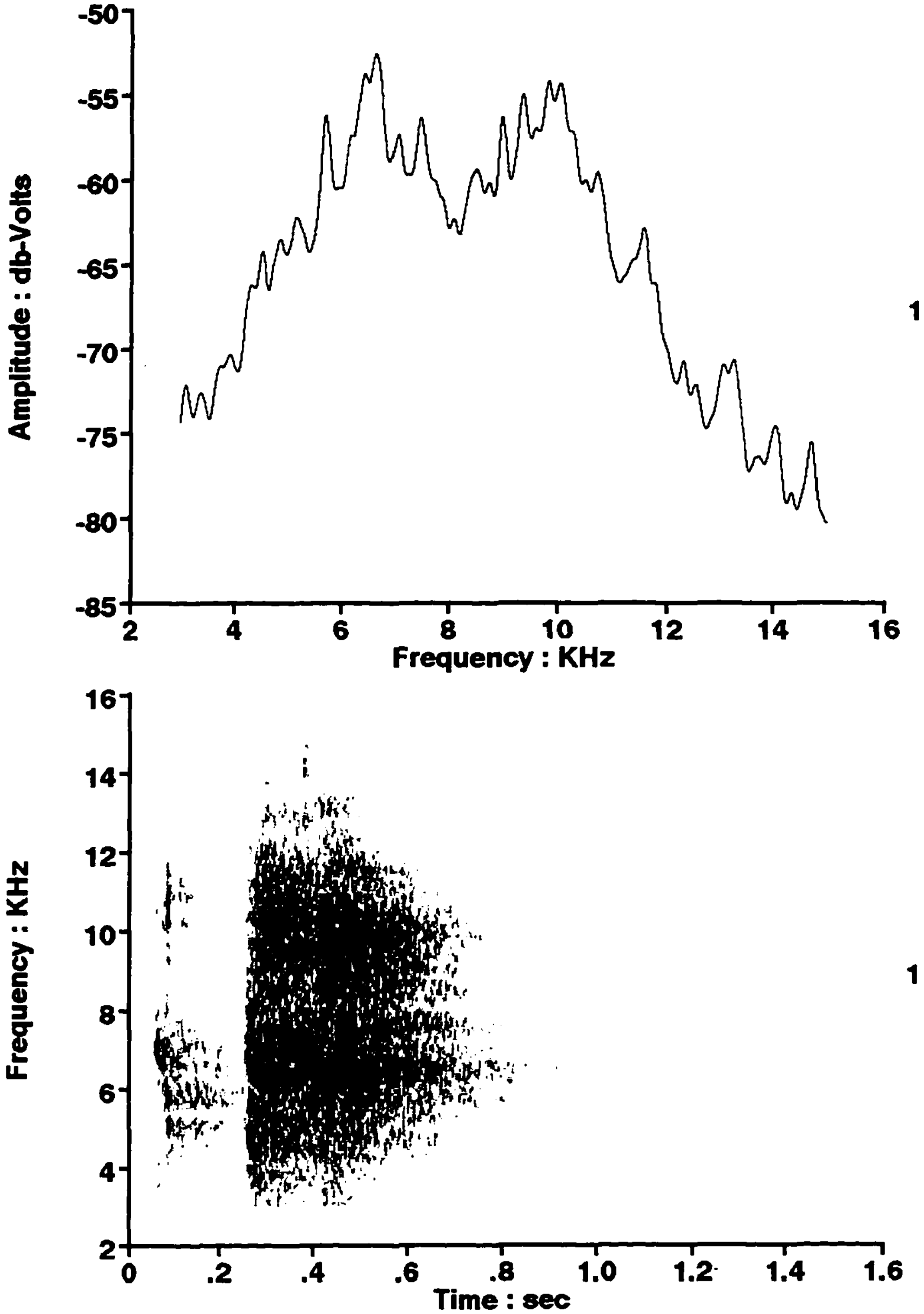

Figure 13a. Screech call from bat 1021 from Group 1.

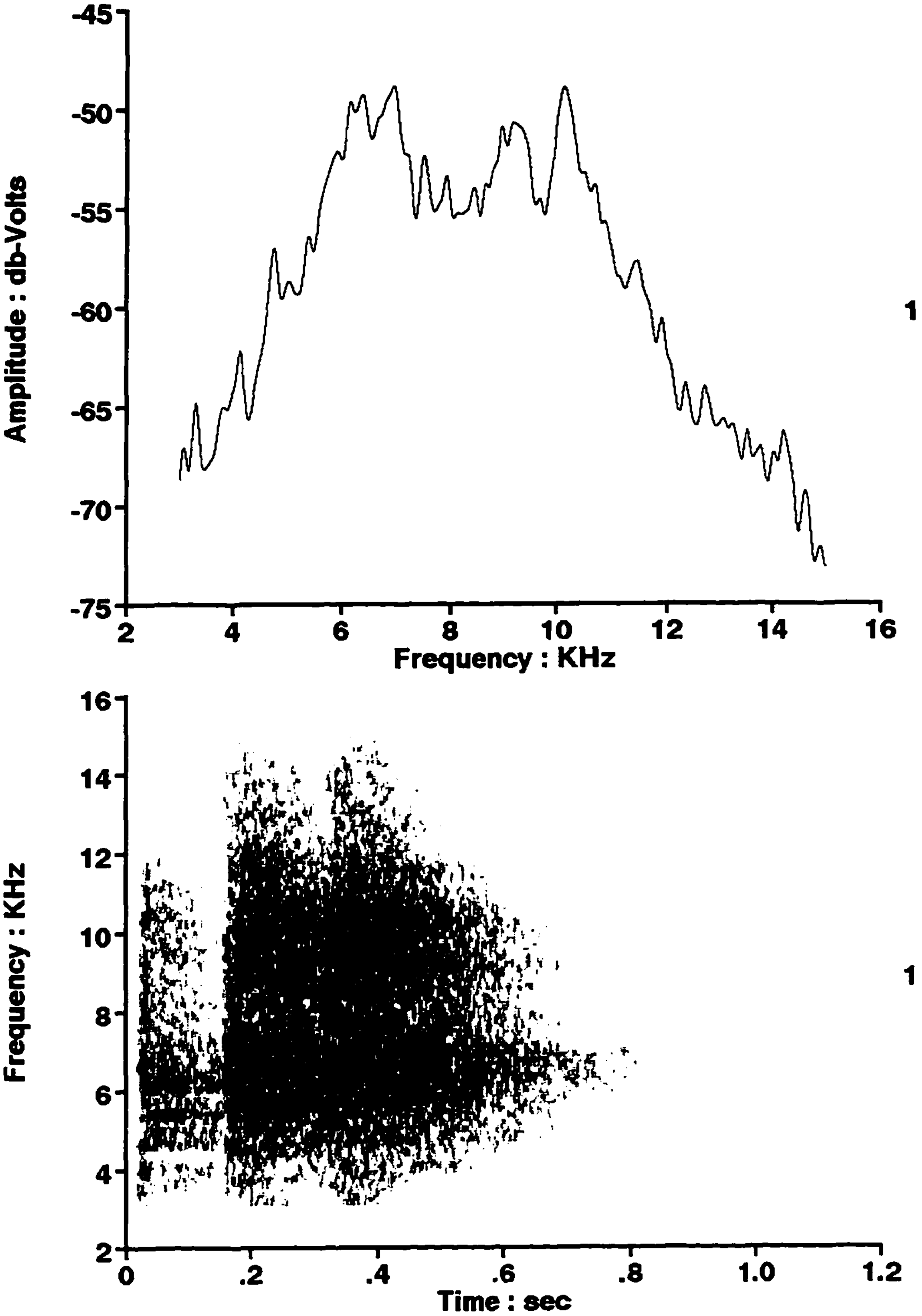

Figure 13b. Screech call from bat 1522 from Group 2.

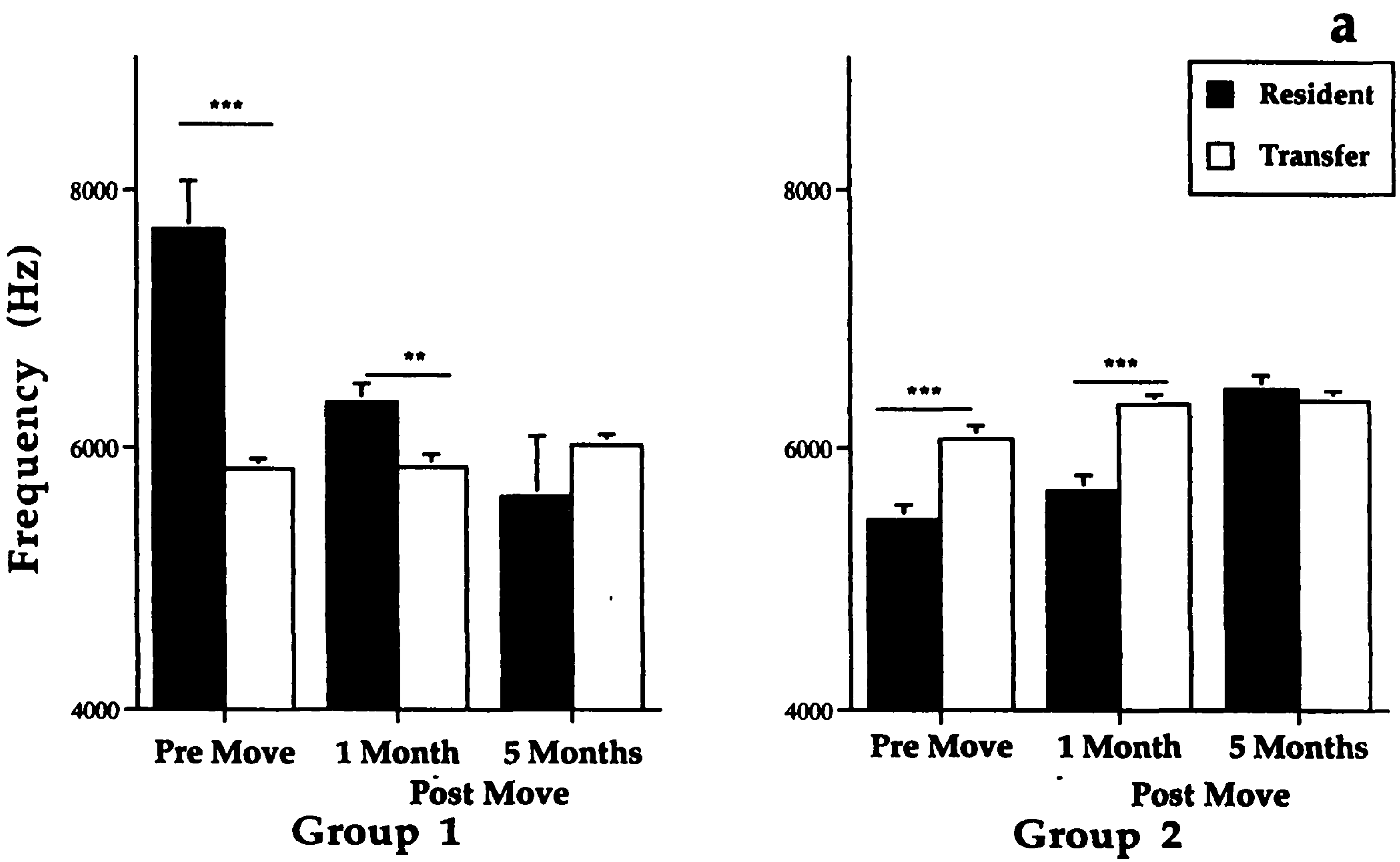

Figure 14a. Changes in call structure with changing group membership for bandwidth.

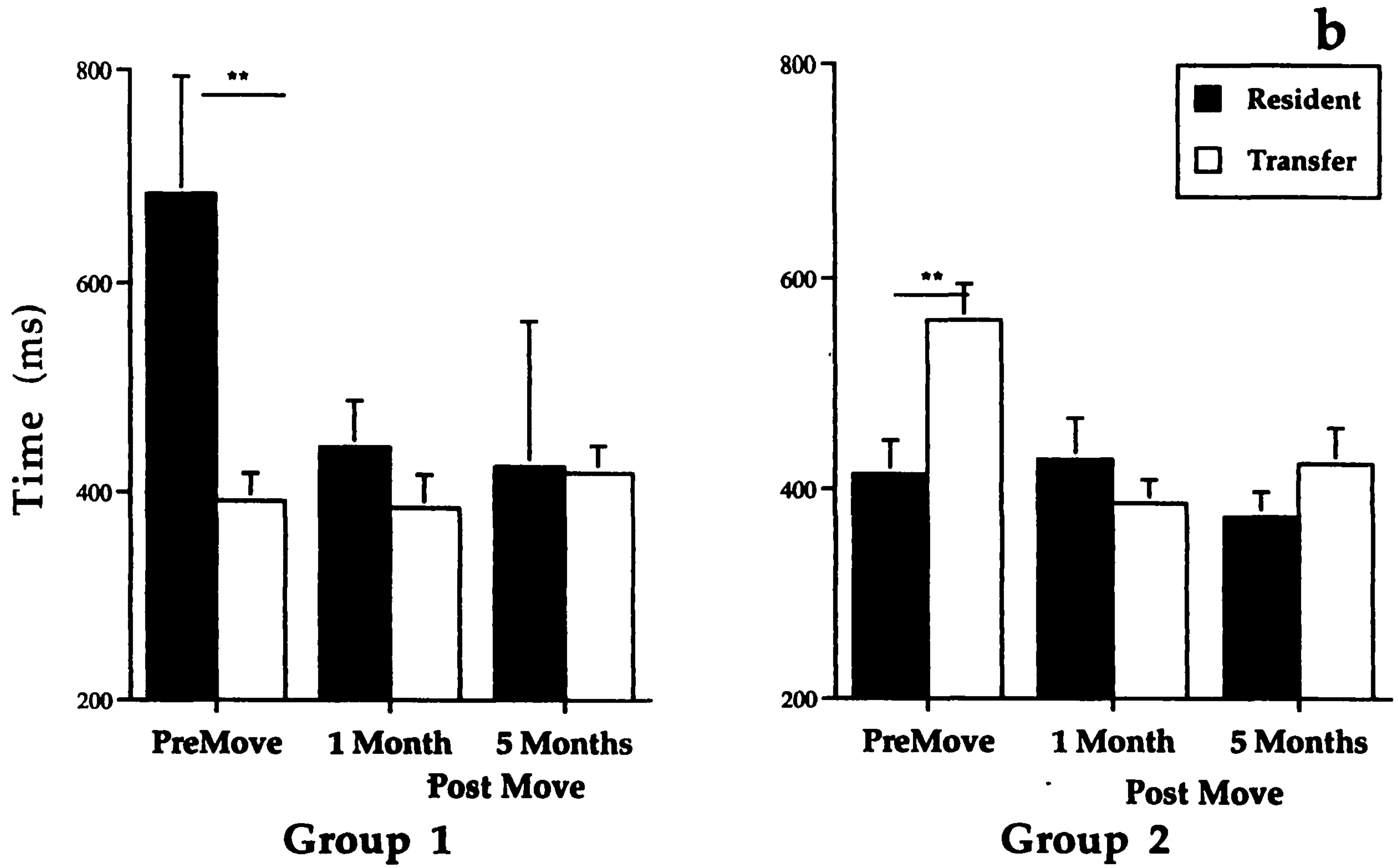

Figure 14b. Changes in call structure with changing group membership for repetition interval.

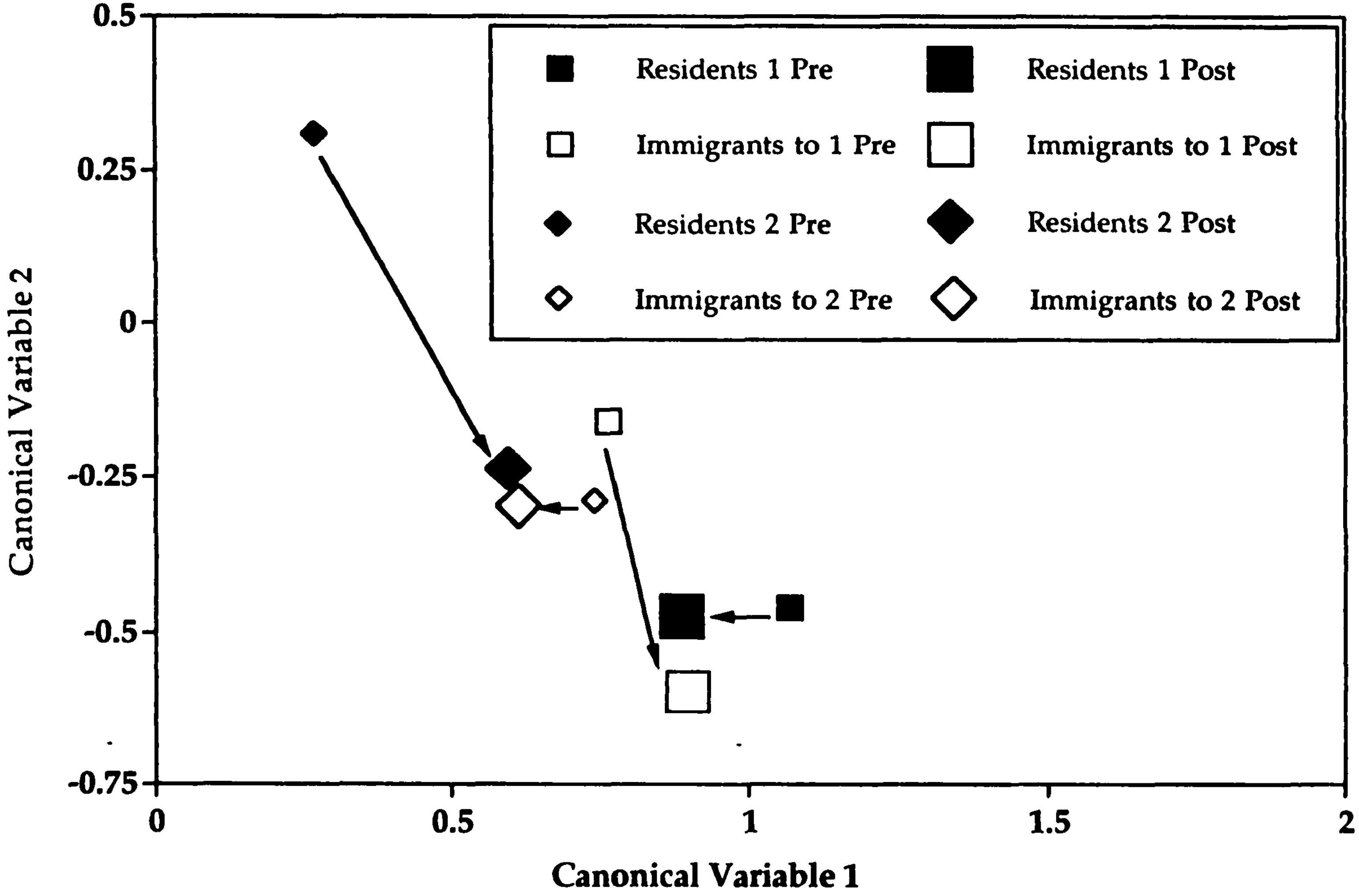

Figure 15. Convergence among residents and transfers in multivariate space.

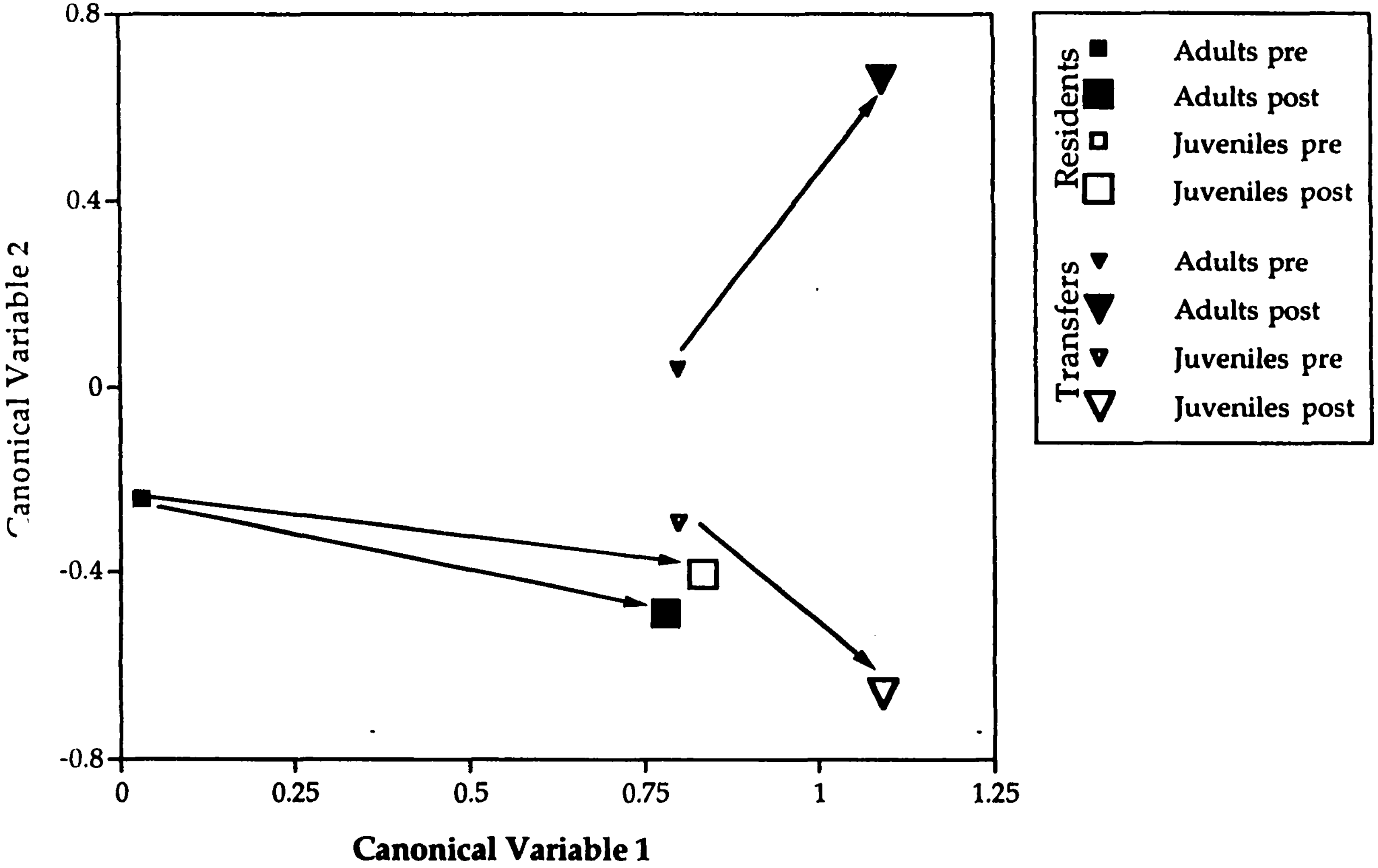

Figure 16. Divergence of female transfers and female age-matched half-sibs.