Cannot see you but can hear you: vocal identity recognition in microbats

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ABSTRACT

Identity recognition is one of the most critical social behaviours in a variety of animal species. Microchiropteran bats present a special use case of acoustic communication in the dark. These bats use echolocation pulses for navigating, foraging, and communicating; however, increasing evidence suggests that echolocation pulses also serve as a means of social communication. Compared with echolocation signals, communication calls in bats have rather complex structures and differ substantially by social context. Bat acoustic signals vary broadly in spectrotemporal space among individuals, sexes, colonies and species. This type of information can be gathered from families of vocalizations based on voice characteristics. In this review we summarize the current studies regarding vocal identity recognition in microbats. We also provide recommendations and directions for further work.

Keywords: Individual recognition; Species recognition; Social call; Echolocation pulse; Microchiropteran bat

INTRODUCTION

Microchiropteran bats present a special case for vocal communication studies as they produce two different vocal signals: echolocation pulses and social calls. Social calls normally have low frequencies (<20 kHz) and are usually audible to humans (Fenton, 2003). In contrast, the ultrasonic echolocation pulses are transferred farther and can be heard by other bats (Fenton, 2003). The adaptive functions of the social calls include courtship displays (Behr & Von Helversen, 2004), group cohesion (Chaverri et al, 2010), and reunion of offspring and mother (Bohn et al, 2007). Echolocation pulses have traditionally been thought of as a tool to enable bats to navigate through their environments and to estimate the location and distance of targets, such as food (Schnitzler et al, 2003). However, as with social calls, echolocation pulses play a vital role in social communication. Social information, including that pertaining to individual (Yovel et al, 2009), species (Dorado-Correa et al, 2013) and sex (Kazial & Masters, 2004; Knörnschild et al, 2012b), is encoded in echolocation pulses.

Individual recognition, that is, distinguishing between mates, offspring, siblings, friends and rivals (Tibbetts & Dale, 2007), is a critical social behavior in many animals. It is most often achieved via visual, olfactory or acoustical cues (Tibbetts & Dale, 2007). Acoustical cues have been described as an important characteristic by which to identify individuals in some animals, i.e., frogs (Burmeister & Wilczynski, 2000), birds (Aubin & Jouventin, 2002), and mammals (Root-Gutteridge et al, 2014). To avoid costly hybridization, species recognition plays an important role in pre-mate isolation (Hopkins & Bass, 1981). In microchiropteran bats, the vast majority of research about individual recognition and species recognition by acoustical cues are associated with social contexts: maternal care, group cohesion and eavesdropping (Table 1, Figure 1). Isolation calls distinguish individuals, which helps mothers recognize their own pups. Contact calls, which are often individual-specific or group-specific, ensure adult bats can recognize individuals from a certain group. Echolocation pulses can be individual-specific or species-specific and are, therefore, most often used for individual or species recognition. The following section provides a short overview of the current knowledge on voice identity recognition in microbats, after which we propose that bats are well suited for vocal identity recognition and suggest areas for further study.

SOCIAL CALLS

Social calls in bats are used to maintain contact with conspecifics and to facilitate group cohesion. Statistical analysis has shown that various social calls are individual-specific and species-specific, each individual and species having unique acoustic parameters (Melendez & Feng, 2010; Pfalzer & Kusch,

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Table 1 Call variation and social context in different bats

Call types	Variation	Social context	Species	References
Isolation calls	Individual-specific	Mother-pup reunion	*Tadarida brasiliensis*	Balcombe, 1990
			Phyllostomus hastatus	Bohn et al, 2007
			Carollia perspicillata	Knörnschild et al, 2013
Contact calls	Individual-specific	Group cohesion	*Diaemus youngi*	Carter et al, 2008
			Thyroptera tricolor	Chaverri et al, 2012
			Megaderma lyra	Kastein et al, 2013
	Group-specific	Group cohesion	*Phyllostomus hastatus*	Boughman, 1998; Boughman & Wilkinson, 1998
			Saccopteryx bilineata	Knörnschild et al, 2012a
Echolocation pluses	Individual-specific	Unknown	*Myotis lucifugus*	Kazial et al, 2008a
	Group-specific	Unknown	*Noctilio albiventris*	Voigt-Heucke et al, 2010
	Species-specific	Species recognition	*Rhinolophus ferrumequinum, Rhinolophus mehelyi, Rhinolophus euryale, Rhinolophus hipposideros.*	Schuchmann & Siemers, 2010
			Nyctalus noctula, Myotis capaccinii, Pipistrellus nathusii, Myotis daubentonii.	Dorado-Correa, 2013
			Rhinolophus macrotis, *Rhinolophus lepidus, Rhinolophus sinicus.*	Li et al, 2014
	Sex-specific	Sex recognition	*Eptesicus fuscus*	Kazial & Masters, 2004
			Saccopteryx bilineata	Knörnschild et al, 2012b

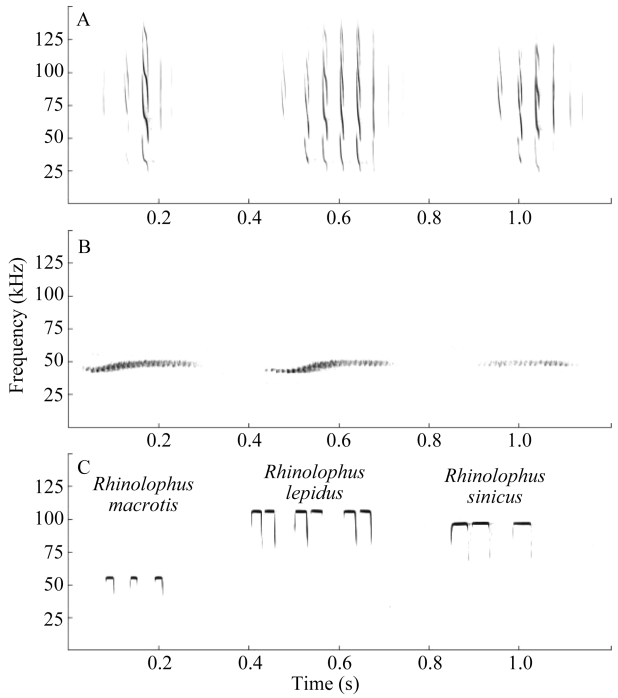

Figure 1 Different vocalization types from different bat species
A: Pup isolation calls of *Carollia perspicillata* (Knörnschild et al, 2013); B: Contact calls of *Thyroptera tricolor* (Chaverri et al, 2012); C: Echolocation calls of three bat species.

2003). Two of the social calls used by bats, isolation and contact calls, have been shown through behavioral studies to be used in individual and species recognition.

Isolation calls

Newborn bats are incapable of living independently and their survival depends entirely on maternal support and nourishment. Their mothers are critical for nutrition and thermoregulation (Lausen & Barclay, 2003). Pup vocalizations, known as isolation calls, are one of the mechanisms by which pups attract their mother's attention to provide them with maternal care and to facilitate their mother being able to discriminate between their own pup and individuals of other microchiropteran bat species, such as *Tadarida brasiliensis* (Balcombe, 1990), *Phyllostomus hastatus* (Bohn et al, 2007) and *Carollia perspicillata* (Knörnschild et al, 2013). Infant isolation calls are common precursors to adult echolocation pulses and communication vocalizations (Monroy et al, 2011).

Knörnschild et al (2013) measured the call parameters from different pups and extracted the principal components. Discriminant function analysis classified individuals to their class successfully above the level of chance, based on the principal components. This provides statistical evidence for the presence of individual signatures in isolation calls. Furthermore, behavioural research has demonstrated that mothers can recognize their own pups based on isolation calls. All of the mothers under study were presented with two isolation calls: one emitted by their own pup and one from a pup living in the same colony. The aim of the experiment was not to see if the

mothers could distinguish between familiar and unfamiliar calls but rather between the calls of two familiar individuals. They found that the mothers focused more attention on their own pups' isolation calls than on that of the other pups. Inter-individual variability of acoustic parameters is essential for successful individual recognition. Individual signatures encoded in calls can be tested for by discriminant analysis and habituation-rehabituation playback experiments.

Contact calls

Contact calls have been thought to encode a great deal of information about the caller to facilitate individual recognition or group member recognition in many animals (Bradbury & Vehrencamp, 2011). They can help adult bats relocate group members after periods of separation and to maintain group cohesion.

Individual signatures are often encoded in bats' contact calls, which enable them to recognize their group members. In analyses of the structure of contact calls, researchers have found that *Antrozous pallidus* (Arnold & Wilkinson, 2011) and adult vampire bats (*Diaemus youngi, Desmodus rotundus, Diphylla ecaudata*) (Carter et al, 2012) exhibit significant differences among individuals. Behavioural observations found that *Thyroptera tricolor* (Chaverri et al, 2012; Gillam & Chaverri, 2012), *D. youngi* (Carter et al, 2008), and *Megaderma lyra* (Kastein et al, 2013) use contact calls for individual recognition. In particular, *M. lyra* is able to distinguish between familiar individuals from the same group based on their contact calls. Furthermore, they recognize the individuals based on a novel contact call. It was argued that contact calls, which are composed of three different syllables, are much more complex than echolocation pluses, and could guarantee the detection of a novel stimulus (Kastein et al, 2013). Interestingly, *T. tricolor* (Chaverri et al, 2012) have antiphonal calling: "inquiry'' calls and "response" calls. "Inquiry'' calls are emitted by flying bats seeking a roost or roost mates; "response" calls are elicited from individuals who have already located a roost and "Response" calls are emitted by roosting bats after the flying bats have entered the roost. They provide information about the caller's identity and their location. Flying and roosting bats respond differently to calls from group members and non-members. Flying bats can discriminate between group members and non-members based on their "inquiry'' and "response" calls. However, roosting bats show no preference for "inquiry'' calls from group members over "inquiry'' calls from non-members. The benefits of accepting non-members (roosting bats involve deception) and the costs of flying may contribute to this behavior (Chaverri et al, 2012).

Like for many animals, call convergence results from vocal production learning. After finding group-specific calls in wild bats, Boughman (1998) studied vocal convergence by transferring female bats between two social groups reared in separate rooms. Two groups of wild-caught adult bats and their offspring were used in the experiment. Before being transferred, the offspring were separated from the adults and kept alone in their respective rooms. After the screech calls of some of the younger bats were recorded, they were then transferred from one room to another at the age at which the bats would normally disperse from their natal roosts to join new social groups. Before being transferred, the calls of the bats being transferred differed from those in the group they joined. Calls from the transfer and resident individuals converged a month after the transfer. After five months there was no statistical difference between the calls. Both resident and transferring bats adjusted the acoustic structure of their calls to reach a new shared group-specific call during the transfer. This demonstrates that call convergence in these bats occurs through vocal production learning.

Vocal learning may allow vocal signals to become more recognizable in individual bats when signal similarity is essential for choosing a group. *Phyllostomus hastatus* uses the group-specific calls resulting from vocal production learning to maintain social groups (Boughman & Wilkinson, 1998). Group signatures encoded in isolation calls are also the result of vocal production learning, as opposed to genetic factors as in the greater sac-winged bat, *Saccopteryx bilineata,* who lives in harem-based, resource defence polygyny with patrilineal kin groups and female-biased natal dispersal (Knörnschild et al, 2012a). Pups of both sexes, as well as adult males, use isolation calls with a constant individual signature and a group signature at the same time. They utter isolation calls for different purposes. Pups use the calls to attract maternal care. Adult males use the calls to appease dominant harem males and as courtship songs to court unfamiliar females. When courting nonresident females from a different natal colony, harem males produce complete isolation calls. By contrast, harem males never produce courtship songs with isolation call end syllables when courting resident females from the same natal colony. Based on these observations, Knörnschild et al (2012a) argued that the learned group-specific isolation calls may associate individuals with their natal colony, providing access to a colony and helping to ensure that inbreeding is avoided.

One of the hypotheses, the password hypothesis, has been proposed to explain vocal convergence among members of a group. Dahlin et al (2013) explained the password hypothesis by saying that "groups are exclusive and shared calls act as passwords that allow group members to distinguish between strangers and residents and to expel strangers". The findings in *P. hastatus* (see above) and *S. bilineata* may support the password hypothesis. Boughman & Wilkinson (1998) found that *P. hastatus* uses the group-specific calls to defend food resources and to discriminate between familiar group members and strangers. Females from the same colony forage closer to each other than females from different colonies. The authors suggested that the group-specific call is a password to access to food resources. However, there are numerous possible functions associated with vocal convergence, including: maintainance of group cohesion, an affiliate signal to ease the integration of new members into a group, and escalating threat in agonistic encounters (Tyack, 2008). Much more data are needed to fully understand the reason why bat calls converge.

ECHOLOCATION PULSES

Bat echolocation pulses, as with their social calls, have been shown to be individual-specific, colony-specific and species-specific, which facilitates the recognition of individuals and familiar group members. Kazial et al (2008b) examined individual signatures in echolocation pulses produced by crawling *Myotis lucifugus*. Call variables had a high level of repeatability indicating individual identity information within calls, and discriminant function analysis successfully classified calls down to the individual level, above the level of chance. Echolocation pulses emitted by flying bats show more additional variation compared with those produced by crawling bats (Kazial et al, 2008b). In a habituation-rehabituation experiment, bats successfully recognized individuals based on echolocation pulses produced by crawling bats (Kazial et al, 2008a). Echolocation pulses in *Noctilio albiventris* differ among colonies. The similarity of the call stimuli presented is critical for individual recognition by voice. Recognition by voice is a process based on an extraction of acoustic parameters and their comparison with memorised templates (Sidtis & Kreiman, 2012). If they are close to the limen of the receiver, then the adjacent stimulus is perceived as equal. In big brown bats, the frequency-time structure of echolocation pulses is simple and there is low intra-individual variability. Compared with the simple echolocation pulses of big brown bats, the contact calls of *M. lyra* consist of different syllable types with high intra-individual variability (Kastein et al, 2013). Therefore, big brown bats were not able to detect a novel echolocation pulse from the same individual (Kazial et al, 2008a) but the *M. lyra* has achieved this.

Not only do microbats identify individuals based on echolocation pulses, but they can also identify heterospecifics based on echolocation pulses. Lesser bulldog bats (*Noctilio albiventris*) use echolocation pulses to identify familiar conspecifics, roommates, and heterospecies (Voigt-Heucke et al, 2010). In captivity, some bat species are able to discriminate between the echolocation pulses of conspecifics from different sympatric species (Li et al, 2014; Schuchmann & Siemers, 2010). Likewise, wild bats find foraging or roosting locations based on the echolocation pulses of both conspecifics and the sympatric heterspecific species (Dorado-Correa et al, 2013; Schoner et al, 2010). They are more attracted to similar echolocation pulses of heterospecific than to less similar echolocation pulses. This may suggest that echolocation pulses provide information about food sites, which are used by conspecifics and the sympatric heterspecifics species to find food sites.

Each species has unique spectrotemporal structures in their echolocation pulses. Russo et al (2007) proposed that species recognition contributes to divergence in constant-frequency calls of sympatric species. Some species information is encoded in the constant-frequency of echolocation pulses. However, complete differentiation of the frequency bands is not essential for species recognition (Li et al, 2014; Schuchmann & Siemers, 2010). To some degree, these facts have refuted the hypothesis that recognition contributes to the divergence of calls. Therefore, attention should be focused on studying the significance of whole-structure echolocation pulses and other call features for species recognition.

DISCUSSION

Familiar voices play a major part in the biology of communication. It may be to signal reproductive fitness, foster mother / infant reunifications and bonding, determine friend and foe or to enable the formation of social groups (Sidtis & Kreiman, 2012). Vocal identity recognition is a process based on the extraction of acoustic parameters and their comparison with memorised templates (Sidtis & Kreiman, 2012). Many bat species are both very gregarious and long-lived (McCracken & Wilkinson, 2000), providing ample opportunity to evaluate their calls and create templates. Moreover, many microbat families have been found to be capable of vocal identity recognition (Table 1). Therefore, we think bats may be a promising taxon in which to study vocal identity recognition.

Bats build close relationships between stimulus structure and discrimination behavior. A combination of statistical and habituation-rehabituation playback methods can be used to demonstrate individual recognition by acoustical cues. Discriminant analysis is an important multivariate statistical method used to classify the call type. After the parameters from each call have been measured, a principal component analysis can be performed to extract the principal components that explain most of the total call variance. If discriminant function analysis successfully classifies calls to class above the level of chance, it suggests that the call can be used in recognition. However, the habituation-rehabituation playback experiment or spontaneous presentation experiment can test identity recognition on a behavioral level: by presenting different calls and observing receiver responses. Subjects are habituated to sounds from one speaker and then tested on whether they dishabituate the sounds of a different speaker. For example, a combination of statistics and a habituation-rehabituation playback method was used to demonstrate individual recognition by contact call in *M. lyra*. The habituated bats showed a significant rebound in response to the presentation of a familiar individual novel voice (Kastein et al, 2013).

Individuality in calls may evolve with colony size, when it is beneficial for the signaler to be recognized. As colony size increases, the number of individuals that must be recognized increases, making individual recognition tasks more difficult. Increased individuality is crucial for successful discrimination of all individuals in the group. Bat species breeding in large colonies have more individuality in pup isolation calls than species breeding in smaller colonies because of kin selection (Wilkinson, 2003). Additionally, the isolation calls of the chicks of two swallow species, the highly colonial cliff swallow and the less social barn swallow (*Hirundo rustica*), have been found to differ. Cliff swallow chicks produce calls containing 16 times as much variation as the corresponding calls of barn swallow chicks (Medvin et al, 1993). Cliff swallows are also superior to barn swallows in recognition of their young (Leonard et al, 1997). Coincidentally, ground-dwelling sciurids with individual-specific alarm calls are recognized by group mates based on these calls, and stand to gain fitness benefits from being

recognized (Pollard, 2011). So, species living in larger groups have more individual information in their calls (Pollard & Blumstein, 2011). Individual recognition is important for social behaviors and is harder in larger groups, however, increased individuality helps. Colony size, therefore, is a predictor of individuality.

In summary, microbats take up unique ecological niches in the night sky and mainly use calls to conduct social activities, providing an ideal model for vocal identity recognition research. Past experiments highlight that microbats use the spectrotemporal characteristics of sound to identify individual, sex, group member, and species. However, vocal identity recognition can be achieved in many other ways in other animals, such as by syllable rhythm (Gentner et al, 2000), call repertoire (Weary & Krebs, 1992), and call syntax (Briefer et al, 2013). Future research should focus on: (1) if microbats code identity information at the level of syllable rhythm, call repertoire and syntax; (2) whether bat receivers could extract complex information from the organisation of conspecific calls; (3) what drives the evolution of vocal recognition in microbats. Combined with other related work, these efforts could not only could improve our understanding of the nature of animal recognition behaviour, but also would provide insight into the balance of animal population and community.

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