biology letters

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Biol. Lett. 2006 **2**, 561-564
doi: 10.1098/rsbl.2006.0501

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Correlated evolution between hearing sensitivity and social calls in bats

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Echolocating bats are auditory specialists, with exquisite hearing that spans several octaves. In the ultrasonic range, bat audiograms typically show highest sensitivity in the spectral region of their species-specific echolocation calls. Well-developed hearing in the audible range has been commonly attributed to a need to detect sounds produced by prey. However, bat pups often emit isolation calls with low-frequency components that facilitate mother–young reunions. In this study, we examine whether low-frequency hearing in bats exhibits correlated evolution with (i) body size; (ii) high-frequency hearing sensitivity or (iii) pup isolation call frequency. Using published audiograms, we found that low-frequency hearing sensitivity is not dependent on body size but is related to high-frequency hearing. After controlling for high-frequency hearing, we found that low-frequency hearing exhibits correlated evolution with isolation call frequency. We infer that detection and discrimination of isolation calls have favoured enhanced low-frequency hearing because accurate parental investment is critical: bats have low reproductive rates, non-volant altricial young and must often identify their pups within large crèches.

Keywords: bats; communication; evolution; hearing

1. INTRODUCTION

Auditory systems are expected to be under selection to increase detection of signals that affect survival or reproduction. In the absence of physical or physiological constraints, such selection may result in correlated evolution between vocalizations and auditory tuning (Endler 1992). Indeed, correlations between audiograms and vocalization frequencies within species have been reported (e.g. Brown & Waser 1984). However, only one study on frogs has attempted to incorporate evolutionary history, and in this case correlated evolution between call frequency and hearing sensitivity was not detected (Wilczynski *et al.* 2001).

Echolocating bats provide an interesting system for evolutionary analysis because they have two regions of heightened hearing sensitivity. They exhibit enhanced sensitivity to ultrasonic echolocation frequencies (Grinnell 1970) and to frequencies below 30 kHz (Moss & Schnitzler 1995). Low-frequency hearing sensitivity may be attributed to a need for eavesdropping on prey-generated noises (Neuweiler 1990). However, infant isolation calls have fundamental frequencies between 13 and 30 kHz (Gould *et al.* 1973), and in one species, a correlation between the spectral energy of isolation calls and hearing sensitivity has been found (Bohn *et al.* 2004). Isolation calls are frequency-modulated, multi-harmonic vocalizations that are emitted by pups when separated from their mothers (Gould *et al.* 1973).

Here, we test whether low-frequency hearing exhibits correlated evolution with isolation call frequency. We also consider two alternative explanations for variation in low-frequency hearing: body size and echolocation frequency. In many species, body size is inversely related to both hearing (Koay *et al.* 1997) and call frequency (Ryan & Brenowitz 1985; Jones 1999) due to constraints on signal reception and sound production. In addition, if low-frequency hearing depends on high-frequency hearing (Koay *et al.* 1997), then differences in low-frequency hearing may simply be due to selection on the echolocation system.

2. MATERIAL AND METHODS

We used published data from species for which echolocation calls, isolation calls and audiograms were available (see appendix in the electronic supplementary material). We used median forearm length to estimate body size. For some species, only spectrograms were available for estimating echolocation or isolation call frequencies, making it impossible to determine peak frequencies. Thus, for consistency we used the median frequency of the fundamental for isolation calls and the median frequency of the entire call for echolocation calls. The fundamental frequency was used for isolation calls because it often contains the most energy (e.g. Habersetzer & Marimuthu 1986; Sterbing 2002). Isolation calls typically increase in frequency during development and older pups' calls may be intermixed with developing echolocation calls (reviewed in Altringham & Fenton 2003). We minimized inclusion of echolocation call precursors by only using calls from pups less than two weeks of age. For measures of hearing sensitivity, we did not use neural audiograms recorded from anaesthetized bats because they show reduced sensitivity to low frequencies (Neuweiler 1990). Most bat audiograms have two regions of enhanced sensitivity separated by a relatively insensitive region (figure 1*a*; appendix, electronic supplementary material). We used the frequency of greatest sensitivity in these regions. If two adjacent frequencies within a region showed the same hearing threshold, we used the midpoint between those two values. Many bat species that produce constant frequency echolocation calls show three frequency regions of increased auditory sensitivity. For these species, we used the lowest and highest frequency regions (figure 1*b*; appendix, electronic supplementary material).

When testing evolutionary hypotheses, comparing traits across taxa can be misleading because species may be similar as a result of common descent, rather than independent evolution (Felsenstein 1985). Consequently, we used the comparative analysis by independent contrasts program (CAIC v. 2.0.0; Purvis & Rambaut 1995) to determine if evolutionary change in one variable correlates with evolutionary change in a second variable. Relationships between contrasts were tested using least-square regressions on log-transformed values forced through the origin (Harvey & Pagel 1991). We tested for correlated evolution between (i) call and hearing frequencies and body size; (ii) high-frequency hearing and echolocation call frequency; (iii) low-frequency hearing and high-frequency hearing; and (iv) low-frequency hearing and isolation call frequency. We treated call frequencies as independent variables under the supposition that the requirements of a task affect call design (Simmons & Stein 1980), and that hearing sensitivity should then be under selection to maximize call detection.

To determine if the results depended on the phylogenetic hypothesis used, we estimated three sets of independent contrasts. First, we calculated contrasts using a bat super-tree (Jones *et al.* 2002) with branch lengths (Jones *et al.* 2005). Second, we incorporated the relationships between the four vespertilionid

The electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2006.0501 or via http://www.journals.royalsoc.ac.uk.

Received 12 April 2006
Accepted 4 May 2006

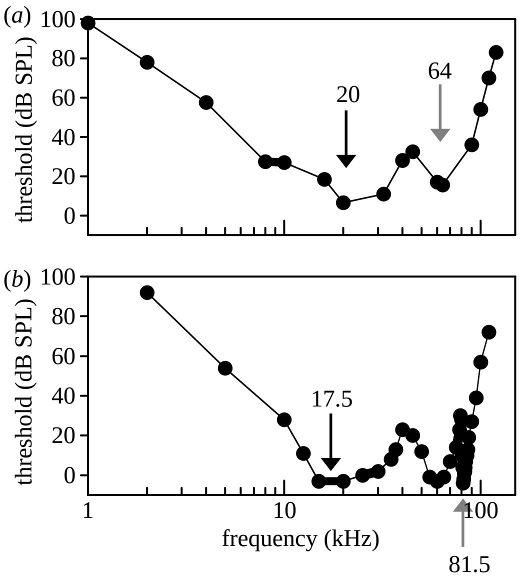

Figure 1. Behavioural audiograms for two species of bat show the minimum sound pressure (SPL) in decibels that an animal responds to across frequencies. (*a*) *Eptesicus fuscus* (Koay *et al.* 1997) and (*b*) *Rhinolophus ferrumequinum* (Long & Schnitzler 1975). Black arrows show low-frequency hearing sensitivity and grey arrows show high-frequency hearing sensitivity. For *R. ferrumequinum*, there are three peaks in hearing sensitivity and low-frequency sensitivity was calculated as the midpoint between two adjacent values with equal thresholds.

species in the study using Hoofer & Van den Bussche (2003), as these relationships were unresolved in Jones *et al.* (2002). However, we could not estimate these branch lengths, so they were set equal. For the third analysis, we used a recent molecular phylogeny (Teeling *et al.* 2005) with branch lengths from Jones *et al.* (2005). We present the results from the phylogeny of Jones *et al.* (2002) because branch length data permit a more realistic model of evolutionary change (Felsenstein 1985). However, all three analyses gave similar results, and we include the range of *r*-values for each analysis.

3. RESULTS

Phylogenetic analyses resulted in 10 independent contrasts for each comparison (figure 2*a*). We did not find evidence of correlated evolution between forearm length and echolocation call frequency ($F_{1,9}=1.31$, $p=0.28$, $r=0.36$, range 0.36–0.48), high-frequency hearing ($F_{1,9}=0.005$, $p=0.94$, $r=0.02$, range 0.02–0.09), isolation call frequency ($F_{1,9}=0.18$, $p=0.74$, $r=0.1$, range 0.08–0.14), or low-frequency hearing ($F_{1,9}=0.002$, $p=0.96$, $r=0.04$, range 0.04–0.10). In contrast, high-frequency hearing showed evidence of correlated evolution with echolocation call frequency ($F_{1,9}=27.41$, $p=0.0005$, $r=0.87$, range 0.71–0.87; figure 2*b*) and low-frequency hearing exhibited correlated evolution with high-frequency hearing ($F_{1,9}=8.05$, $p=0.02$, $r=0.69$, range 0.64–0.69; figure 2*c*). To control for high-frequency hearing, we compared residuals from a high- versus low-frequency hearing regression to contrasts in isolation call frequency. We found a significant positive relationship between change in isolation call frequency and change in residual low-frequency hearing ($F_{1,9}=24.75$, $p=0.0008$, $r=0.85$, range 0.79–0.85; figure 2*d*), and infer that low-frequency hearing exhibits correlated evolution with pup call frequency.

4. DISCUSSION

This study presents evidence of correlated evolution between vocalizations and auditory sensitivity for frequency regions that correspond to echolocation and pup isolation calls. These results did not depend on the topology or branch lengths of the phylogeny. In apparent contrast to another study (Jones 1999), we did not find evidence of correlated evolution between body size and either vocalization or hearing frequency. However, Jones (1999) examined correlations on species data within families without any phylogenetic correction. Examination of his data reveals that vocalization and hearing frequencies are not correlated between families. Thus, these apparently disparate results can be reconciled if echolocation evolution has been decoupled from body size evolution among families.

Given that echolocation functions in autocommunication (Neuweiler 1990), one would expect aural sensitivity to match echolocation call frequency. However, finding evidence of correlated evolution between low-frequency hearing and isolation call frequency, after removing correlated effects of echolocation, is more surprising. An alternative function for low-frequency hearing is that it facilitates prey detection. This explanation is plausible for two gleaning species that use prey-generated sounds, *Plecotus auritus* (Anderson & Racey 1991) and *Nyctophilus gouldi* (Grant 1991), as these bats respond to frequencies below their pup isolation calls (see appendix in the electronic supplementary material). However, prey detection cannot explain low-frequency hearing sensitivity in frugivorous species, such as *Carollia perspicillata* and *Artibeus jamaicensis*, which supports our interpretation of an auditory specialization for parent–offspring communication.

Auditory tuning is unlikely to match isolation call frequency as a consequence of signal production. Only infants emit isolation calls and hearing sensitivity changes during the course of development. Thus, adult hearing does not match that of young bats (Rubsamen *et al.* 1989). In some species, pups begin vocalizing before they can hear (Brown *et al.* 1978) and isolation calls are heritable (Scherrer & Wilkinson 1993). Thus, auditory feedback may not be as crucial to the production of isolation calls in bats as in other vocal communication systems.

Female bats give birth to non-volant altricial young that are left in roosts while their mothers forage. As a result, females must frequently locate, and for group-living species, recognize their offspring among others. Because most bats have low reproductive rates, infant survival should have a large impact on adult fitness. Correlated evolution between hearing and isolation calls may, therefore, reflect selection for detection of young. Although here we have focused on echolocating bats, the young of many other mammalian species emit vocalizations (Symmes & Biben 1985; Branchi *et al.* 2001), and adult hearing sensitivity can be similar to the frequency of infant vocalizations (Ehret 1989; Aitkin *et al.* 1994). Thus, detection of young may have been a significant selective factor in the evolution of auditory function in a variety of mammals.

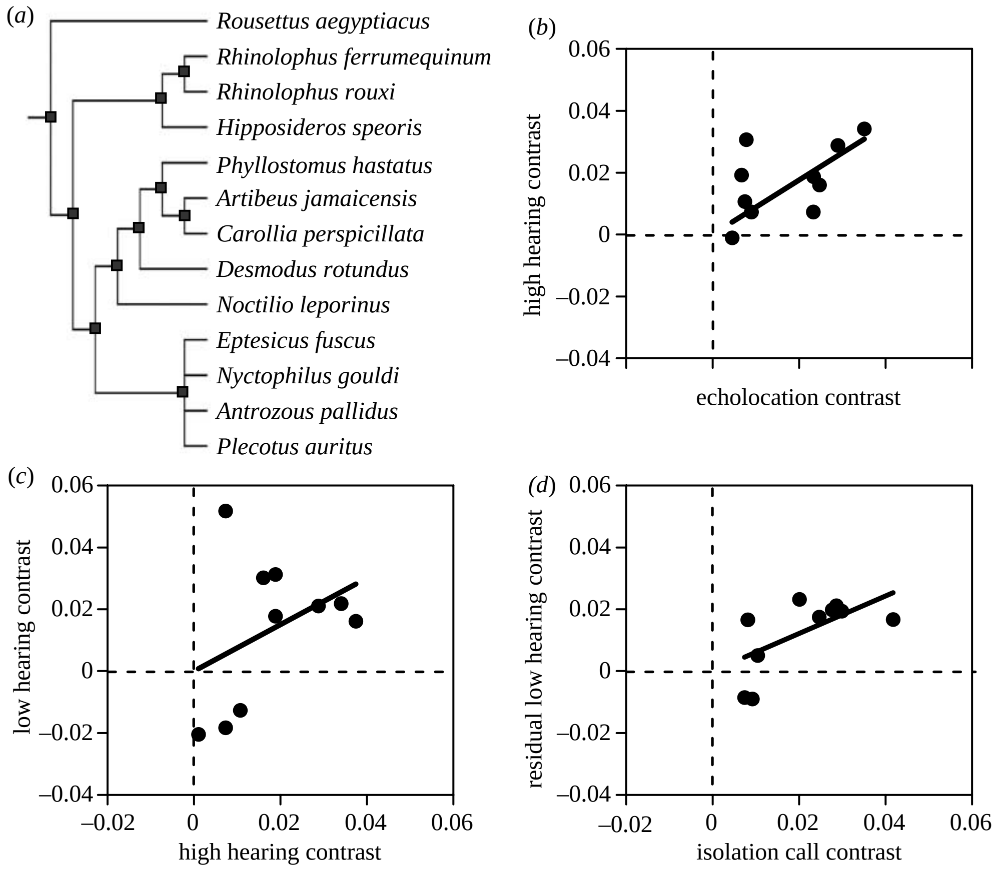

Figure 2. (*a*) Phylogenetic relationships of species used in the analysis based on Jones *et al.* (2002). Independent contrasts were calculated for nodes designated by black squares. Branch lengths are not drawn to scale. Relationships between (*b*) high-frequency hearing and echolocation call contrasts, (*c*) low-frequency hearing and high-frequency hearing contrasts and (*d*) residual low-frequency hearing and isolation call contrasts.

We wish to thank U. Schmidt for *Desmodus rotundus* vocalizations, J. J. Wenstrup for *Nocitilio leporinus* vocalizations and audiograms, G. Schuller for *Rhinolophus rouxi* and *Hipposideros speoris* audiograms and G. Koay for *Carollia perspicillata* and *Eptesicus fuscus* data. We also thank K. E. Jones for providing the branch lengths used in the phylogenetic analyses.

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