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The effect of body size and habitat on the evolution of alarm vocalizations in rodents

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When confronted with a predator, many mammalian species emit vocalizations known as alarm calls. Vocal structure variation results from the interactive effects of different selective pressures and constraints affecting their production, transmission, and detection. Body size is an important morphological constraint influencing the lowest frequencies that an organism can produce. The acoustic environment influences signal degradation; low frequencies should be favoured in dense forests compared to more open habitats (i.e. the 'acoustic adaptation hypothesis'). Such hypotheses have been mainly examined in birds, whereas the proximate and ultimate factors affecting vocalizations in nonprimate mammals have received less attention. In the present study, we investigated the relationships between the frequency of alarm calls, body mass, and habitat in 65 species of rodents. Although we found the expected negative relationship between call frequency and body mass, we found no significant differences in acoustic characteristics between closed and open-habitat species. The results of the present study show that the acoustic frequencies of alarm calls can provide reliable information about the size of a sender in this taxonomic group, although they generally do not support the acoustic adaptation hypothesis. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **00**, 000–000.

KEYWORDS: acoustic adaptation hypothesis – bioacoustics – evolutionary constraints – phylogenetic comparative method – Rodentia.

INTRODUCTION

In birds and frogs, the finding that larger species produce lower frequency vocalizations is widely reported (Podos, 2001; Bertelli & Tubaro, 2002; Seddon, 2005; Mason & Burns, 2015). In birds, the cause of the body size–frequency relationship has been attributed to the existence of an allometric relationship between body size and syrinx size, which in turn determines the range of fundamental frequencies that an organism can produce. Specifically, long folds tend to vibrate more slowly and are able to emit lower frequencies (Ryan & Brenowitz, 1985). In mammals, the fundamental frequency of vocalizations is set by the vibration of vocal folds and depends primarily on the vibrating portion of vocal folds, which is related to the length of the vocal tract (Fitch & Hauser, 2002). Thus, all else being equal, a species with a larger larynx has larger vibration structures, and should produce a lower fundamental frequency. However, the size of the larynx is not always as tightly constrained by body size; some mammalian species possess an exceptionally large larynx, which, in response to selection, may have evolved to produce low-pitched sounds (Fitch, 2006). Thus, although vocal displays typically scale with the mass of the signaller, this rule is not universal. For example, previous studies in humans and primates failed to find a correlation between body size and call fundamental frequency within same-sex and same-age classes (Collins, 2000; Tanaka, Sugiura & Masataka, 2006; Peters & Peters, 2010).

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The effectiveness of sound propagation is influenced not only by intrinsic characteristics of the signaller (e.g. body size), but also by attributes of the habitat in which it is emitted. The 'acoustic adaptation hypothesis' (AAH) (Morton, 1975) explains how the acoustic signal structure is shaped by habitat-driven selection that enhances the propagation of relatively undegraded vocalizations. A relatively common trend is that species found in closed habitats produce songs with lower frequencies than open-habitat species (Wiley, 1991; Slabbekoorn, 2004). However, most of evidence in support of the AAH comes from intraspecific studies (i.e. geographical variation in acoustic signals) or comparisons between a few closely related species (Ey & Fischer, 2009).

Alarm calls are striking vocalizations whose main function is to warn conspecifics about the presence of a predator. The structure and function of mammalian alarm vocalizations have been investigated extensively in some taxonomic groups (e.g. sciurids; Sherman, 1977). For example, in several rodent species, differences in the frequency parameters of their calls have been reported to be closely related to the type of habitat that they occupy (Emmons, 1978; Viljoen, 1983). In this regard, le Roux, Jackson & Cherry (2002) found that *Parotomys littledalei*, a whistling rat inhabiting dense shrubs and bushes, emits calls with a lower frequency than *Parotomys brantsii*, a sister species preferring areas with minimal vegetation. Similarly, Perla & Slobodchikoff (2002) reported that frequency components of calls in prairie dogs (*Cynomys gunnisoni*) were clearly influenced by habitat structure. Although the evolution and function of alarm calling in rodents has aroused considerable interest during the last decade (Shelley & Blumstein, 2004; Blumstein, 2007a, b), the relative contributions of physical and environmental constraints to explanations of interspecific acoustic variation in rodents remain largely unexplored.

In the present study, we report a comparative analysis of alarm vocalizations in relation to body size and habitat across 65 rodent species. Species in the Order Rodentia span an impressive array of body sizes (from 8 g to 60 kg), vocal displays, and habitat preferences (from high-altitude grasslands to dense tropical rainforests) (Wolff & Sherman, 2007). Thus, rodents provide an excellent opportunity for exploring the effects of morphology and the acoustic environment on the evolution of mammalian vocalizations.

MATERIAL AND METHODS

We collected information on acoustic properties of alarm calling in 65 rodent species from a variety of sources published up to July 2015 (see Supplementary References). Most information originates from studies published in specialized journals (*Bioacoustics*, *Journal of the Acoustical Society of America*) and species reviews (http://www.science.smith.edu/departments/Biology/VHAYSSEN/msi). Specifically, we collected information on mean maximum and minimum frequencies (MAX and MIN) (kHz) and bandwidth (BW = MAX – MIN). Only audible (non-ultrasonic) calls of adult individuals were included. 'Fear screams' (e.g. sharp squeals) and tooth chattering or other defensive noises were not considered as alarm calls. When male and female calls were reported, we focused on male calls (the same criteria was adopted for body mass). However, previous studies have reported very little or a total absence of sex-related variation in the structure of alarm call notes (Miller & Engstrom, 2007; Matrosova *et al.*, 2011; Schneiderová & Policht, 2012). This is not entirely unexpected given that many rodents are typically monomorphic or exhibit slight sexual size dimorphism (Schulte-Hostedde, 2007; Lu, Zhou & Liao, 2014).

As in previous studies (Fitch, 2000; Fletcher, 2004), we used body mass as a proxy for body size. Body mass is strongly correlated with skull length and vocal tract length and, accordingly, has been highlighted as a crucial size parameter for sound production apparatus in mammals (Fitch, 2000). Body mass information was obtained from Hayssen (2008) and the PANTHERIA database (Jones *et al.*, 2009). In those cases in which body masses were broken down by age and/or season, we consistently chose body mass estimates reported for adult individuals during the reproductive period. Data on habitat type are based on the information provided by the species accounts in The IUCN Red List of Threatened Species 2015 (http://www.iucnredlist.org). We differentiated between two broad categories in respect of conditions for sound propagation: open habitats and closed habitats. The raw data (MAX, MIN, body mass, and habitat designation) listed for each species included in the present study are summarized in Table 1.

We used a recent maximum likelihood rodent phylogeny based on 11 mitochondrial and nuclear genes (Fabre *et al.*, 2012) to account for the shared evolutionary history between the species. First, we tested for the need to fit phylogenetic models by estimating the strength of phylogenetic signal (measured in form of Pagel's λ and Blomberg's K) in our focal variables [and the residuals of simple ordinary least square (OLS) regression models] using a randomization test implemented in the *phytools* package (Revell, 2012). In addition, we evaluated whether an early-burst, an Ornstein–Uhlenbeck or a Brownian motion (BM) model (or any of its vari-

Table 1. Information on body mass (g), minimum and maximum frequencies (MIN, MAX) (kHz) of alarm calls, and habitat type for the 65 rodent species included in the present study

Species	Mass	MIN	MAX	Habitat
Baiomys taylori	8.0	21.3	39.6	Open
Baiomys musculus	9.0	27.5	47.8	Closed
Reithrodontomys fulvescens	11.5	11.2	13.5	Closed
Scotinomys teguina	11.6	12.6	36.1	Closed
Peromyscus polionotus	13.0	22.1	29.8	Open
Scotinomys xerampelinus	15.1	11.7	29.6	Closed
Reithrodontomys mexicanus	15.7	9.2	11.2	Closed
Peromyscus leucopus	18.1	20.0	22.7	Closed
Peromyscus eremicus	22.7	19.6	34.2	Open
Onychomys arenicola	26.0	11.9	13.4	Open
Onychomys leucogaster	27.9	10.3	12.0	Open
Peromyscus melanophrys	40.0	5.8	22.7	Open
Peromyscus californicus	42.7	11.5	21.0	Closed
Microtus guentheri	43.8	11.9	17.1	Open
Lasiopodomys brandtii	55.0	2.7	20.0	Open
Neotamias umbrinus	56.0	4.5	15.0	Closed
Meriones unguiculatus	60.0	–	23.3	Open
Tamias ochrogenys	72.7	5.5	12.0	Closed
Tamias siskiyou	75.0	3.0	16.0	Closed
Tamias obscurus	69.0	1.0	16.0	Closed
Spalacopus cyanus	81.0	0.3	10.2	Open
Tamias senex	86.0	4.0	13.0	Closed
Ammospermophilus interpres	95.8	0.6	–	Open
Tamias striatus	101.0	3.0	5.1	Closed
Ammospermophilus insularis	102.0	0.2	–	Open
Paraxerus poensis	114.0	–	5.5	Closed
Ammospermophilus harrisii	116.4	1.5	–	Open
Parotomys littledalei	126.9	6.0	13.0	Open
Parotomys brantsii	129.5	4.0	11.5	Open
Ctenodactylus vali	173.6	2.0	4.3	Closed
Callospermophilus lateralis	178.0	–	7.1	Closed
Octodon degus	182.0	1.3	6.0	Closed
Ammospermophilus nelsoni	186.3	0.1	–	Open
Tamiasciurus hudsonicus	194.0	2.0	11.0	Closed
Massoutiera mzabi	194.0	1.5	5.7	Closed
Spermophilus taurensis	200.7	4.7	8.2	Open
Felovia vae	205.0	1.5	5.0	Closed
Tamiasciurus douglasii	206.9	–	6.2	Closed
Spermophilus suslicus	212.3	9.3	9.8	Open
Urocitellus beldingi	228.6	2.0	9.3	Open
Spermophilus pygmaeus	235.2	–	5.3	Open
Callospermophilus saturatus	237.1	–	10.3	Closed
Spermophilus citellus	255.7	8.7	11.3	Open
Rhombomys opimus	285.0	1.6	2.4	Open
Pectinator spekei	288.0	1.2	3.4	Closed
Ctenodactylus gundi	288.4	1.2	6.0	Closed
Spermophilus fulvus	290.3	–	3.8	Open
Spermophilus xanthoprymnus	311.0	3.9	10.7	Open
Fukomys mechowii	570.0	0.4	5.8	Open
Kerodon rupestris	612.0	1.0	5.0	Closed
Otospermophilus beecheyi	621.3	3.0	13.0	Open
Cavia aperea	637.0	0.9	13.4	Open

Table 1. *Continued*

Species	Mass	MIN	MAX	Habitat
Cynomys gunnisoni	816.0	–	7.8	Open
Marmota caligata	2250.0	0.8	6.0	Open
Marmota monax	2854.5	1.9	5.7	Open
Marmota camtschatica	3824.0	–	3.0	Open
Marmota flaviventris	3909.0	2.5	3.8	Open
Marmota caudata	3978.0	2.1	3.4	Open
Marmota bobak	4033.0	–	5.0	Open
Marmota marmota	4303.3	2.0	3.2	Open
Marmota himalayana	6000.0	0.2	3.9	Open
Marmota baibacina	7850.0	0.1	3.4	Open
Marmota sibirica	8000.0	1.0	3.8	Open
Marmota olympus	5500.0	0.7	5.2	Open
Hydrochoerus hydrochaeris	60000.0	0.5	2.0	Open

ants) best explained the evolution of our acoustic variables (for more details, see Supporting Information). Because two out of our three acoustic variables showed an historical component (MAX and MIN), we used phylogenetic generalized least square (PGLS) regression models (Felsenstein, 1985; Pagel, 1999) implemented in the R package *caper* (Orme *et al.*, 2013) to test for the relationship between such variables and body mass. PGLS is a flexible phylogenetic comparative method that incorporates the phylogenetic correlation of the data in the structure of errors (Revell, 2010). BW did not have a significant phylogenetic signal (i.e. residuals from closely related species were not more similar on average than residuals from distantly related species) and, thus, the results of the PGLS model will be the same as the OLS model. To assess the influence of environment on acoustic traits, we performed phylogenetic analyses of variance (PhylANOVAs) (10 000 iterations) using the *geiger* package (Harmon *et al.*, 2008) (for the case of MAX and MIN) and a one-way ANOVA (when testing of the influence of habitat type on BW). To avoid confounding effects of body size differences in habitat comparisons, we computed the residuals of variation (size-free residuals) in acoustic frequencies and controlled again for phylogeny (if necessary). In some cases, we gathered information on MAX but not on MIN ($N = 10$) and vice versa ($N = 4$); thus, sample sizes differ among analyses (61, 55, and 51 species for MAX, MIN, and BW, respectively). Body mass did not vary significantly with habitat type [mean body mass (g); open habitat: 2957.5 ± 1506.1, closed habitat: 138.3 ± 26.6; $F_{1,63} = 2.17$, $P = 0.14$]; thus, we only included habitat type as a predictor in these models when testing for its influence on acoustic frequencies. All continuous variables were log transformed prior to analysis and all analyses were conducted in the R statistical environment (R Foundation for Statistical Computing).

RESULTS

Body mass, as well as maximum (MAX) and minimum (MIN) frequency, were significantly influenced by phylogeny (body mass: $\lambda = 0.99$, $P < 0.001$; $K = 0.79$, $P = 0.001$; MAX: $\lambda = 0.93$, $P < 0.001$; $K = 0.28$, $P = 0.001$; MIN: $\lambda = 0.82$, $P < 0.001$; $K = 0.18$, $P = 0.01$), whereas BW showed a weak phylogenetic signal (BW: $\lambda = 0.24$, $P = 0.018$; $K = 0.06$, $P = 0.84$). The comparison of the continuous models using maximum likelihood showed that the BM + λ was the best-supported model for the evolution of acoustic frequencies (Table 2). There was a significant correlation between body mass and acoustic properties of alarm calls. Both maximum (PGLS: $r^2 = 0.44$, $b = -0.28 \pm 0.04$, $F_{1,58} = 47.11$, $P < 0.001$; $\lambda = 0.47$) and minimum frequency (PGLS: $r^2 = 0.09$, $b = -0.29 \pm 0.10$, $F_{1,52} = 8.17$, $P = 0.006$; $\lambda = 0.63$) were inversely correlated with mass (Fig. 1). BW was also correlated significantly with body mass (OLS: $r^2 = 0.17$, $b = -0.19 \pm 0.06$, $F_{1,48} = 11.38$, $P = 0.001$; $\lambda = 0$). None of the acoustic variables differed significantly between habitats (MAX closed: 1.01 ± 0.06, open: 0.91 ± 0.05, $F_{1,58} = 1.41$, phylo-$P = 0.48$; MIN closed: 0.57 ± 0.10, open: 0.29 ± 0.11, $F_{1,52} = 3.11$, phylo-$P = 0.34$; BW closed: 0.77 ± 0.08, open: 0.49 ± 0.08, $F_{1,48} = 1.64$, $P = 0.21$). Similar results were obtained when computing the residuals of acoustic variables after discounting the effect of body size (MAX residuals: $F_{1,58} = 0.40$, phylo-$P = 0.70$; MIN residuals: $F_{1,52} = 6.78$, phylo-$P = 0.15$; BW residuals: $F_{1,48} = 0.71$, $P = 0.40$).

Table 2. Summary of comparisons of model fit to acoustic properties of alarm calls in Rodents

		Log (MAX frequency)		Log (MIN frequency)	
Model	k	Parameter	AICc	Parameter	AICc
BM	2		11.971		103.836
BM + λ	3	λ = 0.93	**0.222**	λ = 0.82	**80.863**
BM + κ	3	κ = 0.41	1.517	κ = 0.26	88.238
BM + δ	3	δ = 2.99	6.997	δ = 2.99	97.569
EB	3	$r \sim 0$	14.189	$r \sim 0$	106.081
OU	3	α = 0.04	3.213	α = 0.09	86.624

λ is a measure of phylogenetic signal, κ indicates gradual vs. punctuated evolution; δ determines whether trait evolution follows a pattern of adaptive radiation or species specialization, α is the strength of stabilizing selection, r determines how the rate of evolution of the trait changes over time (if $r = 0$, trait follows pure BM).

The models compared are: BM, pure Brownian motion (null model); BM + λ, Pagel's lambda; BM + κ, Pagel's kappa; BM + δ, Pagel's delta; EB, early-burst model; OU, Ornstein–Uhlenbeck model. The number of model parameters (k) and corrected Akaike information criterion (AICc) are provided. The best fitting model is shown in bold.

DISCUSSION

To date, much work on the factors affecting the evolution of acoustic signals has focused on birds, whereas the processes that shape variation in mammalian vocalizations are poorly understood. Most studies concerning the evolution of acoustic communication in mammals have focused on nonhuman primates (Ey & Fischer, 2009), whereas there is a relative paucity of broadscale studies in other taxa (Morton, 1975). In the present study, we assessed the effects of morphology and environment on the vocal displays of 65 rodent species. Our results indicate that body size plays a stronger role than habitat type in explanations of variation in the frequency of rodent alarm calls. We found a strong relationship between body mass and acoustic features, supporting the claim that small animals generally use higher frequencies in their calls than larger animals (Fitch, 2000). This appears to be a result of smaller and lighter tissues resonating most efficiently at higher frequencies, whereas larger acoustic source tissues resonate most efficiently at lower frequencies. Thus, at the interspecific level, potential information about body size is present (Fitch, 2006). The results of the present study are in accordance with previous studies in birds and frogs showing a strong correlation between body size and acoustic frequencies (Podos, 2001; Bertelli & Tubaro, 2002), which reinforces the view that body size is an important proximate factor in the evolution of animal signal structure.

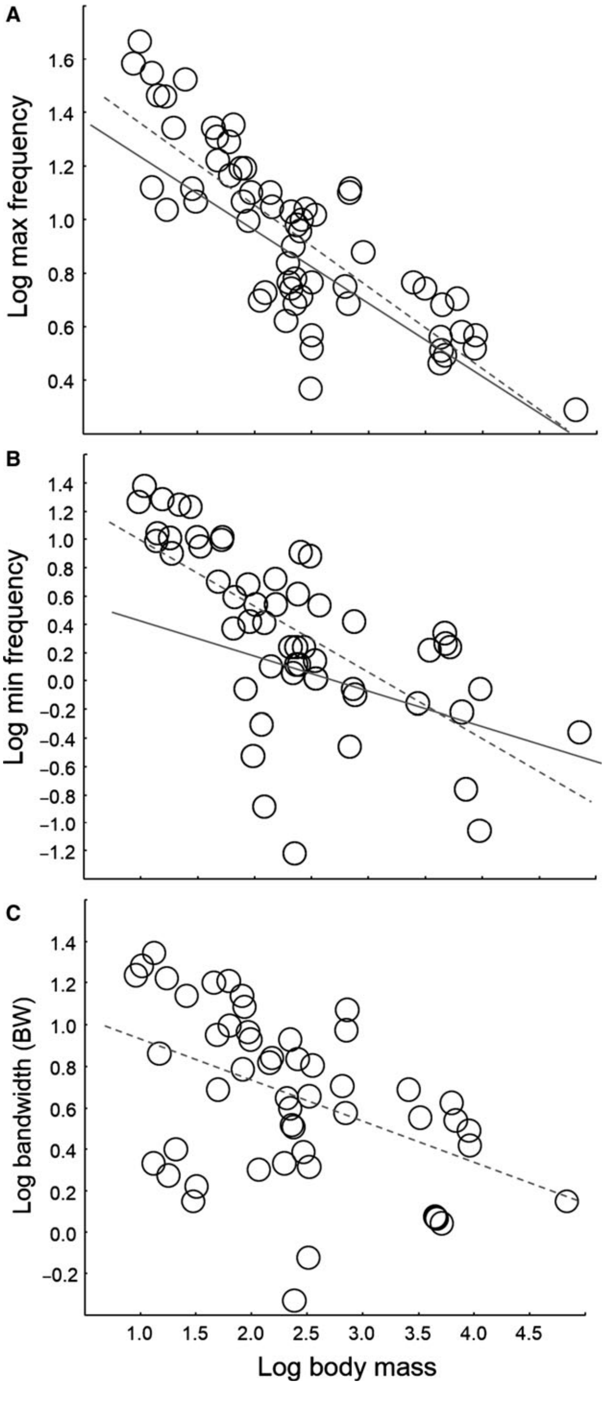

Figure 1. Relationship between male body mass and (A) maximum frequency, (B) minimum frequency, and (C) bandwidth across rodent species. The solid line represents the phylogenetic generalized least square regression line, and the dotted line represents an ordinary least square regression.

In addition to morphological constraints, conditions for sound propagation in the habitats of species are expected to affect the evolution of acoustic signals. By contrast to predictions of the AAH, we found no significant differences in call frequencies between species inhabiting open habitats and those living in acoustically cluttered environments (forests, woodlands). Thus, our results do not provide support for the AAH and add to the growing body of evidence suggesting that the effect size of the environment in the explanation of variation in acoustic structure is rather small (Shelley & Blumstein, 2004; Boncoraglio & Saino, 2007). Two factors may contribute to the lack of a relationship between acoustic frequencies and habitat openness in rodents. First, among species within this group, there are large differences in the height at which they emit their calls; some species are arboreal (tree squirrels, *Reithrodontomys* spp.), whereas others are terrestrial. This may create a confounding factor masking the existence of a habitat effect. In this sense, it is curious that, for example, arboreal *Reithrodontomys* species produce lower frequencies (9–13 kHz) than would be expected according to their body size. Second, in most terrestrial rodents, the height of the mouth of the signaller and the ears of the potential receiver are often relatively close to the ground (< 75 cm) where there is a ‘sound window’ through which low frequencies (1–3 kHz) propagate better irrespective of habitat (Marten & Marler, 1977). This constraint on where signals are used could mute any effect of habitat openness because terrestrial species might have similar acoustic environments.

The present study suggests that acoustic differences in terms of resonance and transmission properties among open and closed habitats do not impart strong selective pressures on the frequency characteristics of rodent vocalizations, for which interspecific differences are mainly driven by variation in body size. These results complement more limited studies of rodent acoustic transmission (Daniel & Blumstein, 1998; Perla & Slobodchikoff, 2002) and further reinforce the relatively limited effect size of the acoustic environment in the explanation of the evolution of acoustic structure in animal vocalizations (Boncoraglio & Saino, 2007).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

Figure S1. Phylogeny of rodent species included in this study (*sensu* Fabre *et al*. 2012), which was used to calculate the covariance structure in the phylogenetic generalized least square models.
Data S1. Supplementary References.