Coevolution of vocal signal characteristics and hearing sensitivity in forest mammals

Benjamin D. Charlton¹, Megan A. Owen¹ & Ronald R. Swaisgood¹

Although signal characteristics and sensory systems are predicted to co-evolve according to environmental constraints, this hypothesis has not been tested for acoustic signalling across a wide range of species, or any mammal sensory modality. Here we use phylogenetic comparative techniques to show that mammal vocal characteristics and hearing sensitivity have co-evolved to utilise higher frequencies in forest environments – opposite to the general prediction that lower frequencies should be favoured in acoustically cluttered habitats. We also reveal an evolutionary trade-off between high frequency hearing sensitivity and the production of calls with high frequency acoustic energy that suggests forest mammals further optimise vocal communication according to their high frequency hearing sensitivity. Our results provide clear evidence of adaptive signal and sensory system coevolution. They also emphasize how constraints imposed by the signalling environment can jointly shape vocal signal structure and auditory systems, potentially driving acoustic diversity and reproductive isolation.

¹Institute for Conservation Research, San Diego Zoo Global, California, CA 92027-7000, USA. Correspondence and requests for materials should be addressed to B.D.C. (email: bencharlton829@gmail.com)
**Results**

**Hearing sensitivity versus habitat.** To quantify hearing sensitivity for each species we extracted the frequency of peak hearing sensitivity (in kHz) and calculated the mean hearing threshold values (in dB) for the frequency ranges 0–20 kHz and 10–20 kHz from published audiogram data (Supplementary Table 1). Relative high frequency hearing sensitivity was then calculated by subtracting the mean threshold value for 10–20 kHz from the overall mean (Fig. 2). Phylogenetic generalized linear mixed models (PGLMM) with Bayesian Markov chain Monte Carlo (MCMC) simulations revealed that forest living mammals have higher peak hearing sensitivity than other terrestrial mammals (PGLMM: model effective sample size (ESS) = 1090, phylogenetic heritability ($H^2$) = 0.09, parameter estimate ($\beta$) = −3.20, 95% Credible Interval (CI) = −5.96 to −0.47, $P_{\text{MCMC}} = 0.030$) (Supplementary Table 4). Relative high frequency hearing sensitivity was also significantly higher for forest mammals than those living in other terrestrial environments (PGLMM: $ESS = 1199$, $H^2 = 0.75$, $\beta = −5.82$, CI = −10.63 to −1.17, $P_{\text{MCMC}} = 0.021$) (Fig. 3b) and negatively correlated to log$_{10}$ functional head size (PGLMM: $\beta = −18.97$, CI = −27.06 to −10.98, $P_{\text{MCMC}} < 0.001$) (Supplementary Table 5). Taken together, these findings indicate that mammal species living in forest environments have better high frequency hearing than those living in more open habitats.
**Fig. 1** Diagrammatic summary of mammal vocal production. Mammal vocalisations typically consist of a source signal that is produced by the larynx and characterised by its fundamental frequency (F0), which corresponds to the rate the vocal folds in the larynx open and close, and a series of harmonic overtones that occur at multiple integers of F0 (labelled H1, H2, H3 etc.) (a). The supra-laryngeal vocal tract has its own set of natural resonance frequencies (a) that boost the amplitude of certain frequency bands and generate broadband frequency maxima in the sound spectrum termed formants (labelled F1, F2, and F3). The overall shape of the sound spectrum (a) is a linear combination of the source signal from the larynx and the filtering effect of the supra-laryngeal vocal tract. The first three formants and underlying harmonic structure of the resultant output spectrum are shown (a). Permission to use the red deer stag illustration was kindly provided by Tecumseh Fitch. The lower panels b and c show two sound spectrums with the same F0 (and harmonic spacing) of 100 Hz and the same formant pattern. SS spectral slope (see methods section for details). The red spectrum in panel c has relatively more high frequency energy than the spectrum in panel b, resulting in a shallower spectral slope. Note that vocalisations with the same F0 and formant patterns can have different spectral energy distributions.

**Fig. 2** Audiogram measures. Composite audiograms derived from the audiogram data for forest mammals (a) and mammals that live in other terrestrial habitats (b). Audiograms display audible thresholds for tones differing in frequency across a range of hearing, with lower values on the y-axis (dB) indicating greater hearing sensitivity (i.e. lower threshold values). The measures used to characterise the audiograms of different species are shown, and the values presented are derived from the raw data for forest mammals (n = 24) and those that typically live in other terrestrial habitats (n = 27): relHFHS relative high frequency hearing sensitivity. relHFHS is the mean threshold value for 10–20 kHz minus the overall mean threshold. PS peak sensitivity, the frequency of maximum hearing sensitivity in kHz. Source data are provided as a Source Data file.
Spectral energy distribution versus habitat. To determine whether forest mammals have relatively more high frequency acoustic energy in their vocalisations than other terrestrial mammals, we quantified the frequency distribution of 3701 vocalisations recorded from 116 different terrestrial mammal species by extracting the gradient (slope) of the line connecting spectral peaks, termed the spectral slope. Vocal signals with relatively more high frequency acoustic energy will have shallower spectral slopes (Fig. 1). The phylogenetic comparative analysis with MCMC simulations revealed that spectral slopes values were significantly higher for forest mammals than species with more open habitats (PGLMM: ESS = 1090, $H^2 = 0.18$, $\beta = -0.07$, CI = -0.11 to -0.02, $P_{MCMC} = 0.0033$) (Fig. 3c, Supplementary Table 6). Log$_{10}$ body mass was not significantly correlated with spectral slope values (PGLMM: $\beta = 0.00$, CI = -0.02 to 0.03, $P_{MCMC} = 0.8333$) (Supplementary Table 6). These findings indicate that mammal species living in forest environments produce vocal signals with relatively more high frequency sound energy than those living in other terrestrial habitats.

Spectral energy distribution versus hearing sensitivity. Our final phylogenetic comparative analysis with MCMC simulations sought to determine whether forest mammals optimise communication according to their high frequency hearing sensitivity, as predicted by sensory drive\cite{31,32}. For the 17 species with available audiogram and acoustic data we found that peak hearing sensitivity (PGLMM: ESS = 1090, $H^2 = 0.33$, $\beta = -0.02$, CI = -0.03 to -0.00, $P_{MCMC} = 0.012$) and relative high frequency hearing sensitivity (PGLMM: ESS = 1090, $H^2 = 0.24$, $\beta = -0.01$, CI = -0.02 to -0.00, $P_{MCMC} = 0.044$) were both negatively correlated with spectral slope values (Fig. 4, Supplementary Tables 7 and 8). These findings indicate that forest species with poorer high frequency hearing sensitivity produce vocal signals with more high frequency acoustic energy.

Discussion

In this study comparative analyses were used to test the complete sensory drive model of signal and sensory system coevolution on mammal vocal communication systems. Our phylogenetically-controlled analyses across a wide range of taxa (spanning nine mammalian orders) revealed that forest mammals have greater high frequency hearing sensitivity, and also produce vocal signals with more high frequency acoustic energy than mammals that live in more open habitats. We also revealed that poorer high frequency hearing sensitivity was predictive of shallower spectral slopes in forest mammal vocalisations. These findings suggest that hearing sensitivity and vocal signal characteristics have coevolved: firstly, to facilitate effective communication of information encoded in the upper frequency spectrum in forest environments, and then in the form of an evolutionary trade-off in forest mammals between high frequency hearing sensitivity and the production of calls with high frequency acoustic energy, with decreases in one creating a selection pressure for increases in the other. Although there is some evidence that mammal vocal
signals and visual capabilities are shaped by the signalizing environment, to our knowledge, the results of the current study constitute the first demonstration in mammals of adaptive signal and sensory system coevolution according to environmental constraints.

Our findings also demonstrate that sensory drive applies to vocal communication systems across a wide range of mammals. Comparative work on mammalian auditory anatomy indicates that high frequency hearing is an ancestral trait. Based on this premise, we suggest that it was retained in forest mammals to optimise sound localisation in a visually occluded environment, thereby helping animals to avoid predation, localise prey, and maintain social group cohesion. High-frequency hearing sensitivity could then open up a higher frequency band for auditory communication, leading to vocal signals with more high frequency acoustic energy via sensory drive. Boosting the amplitude of higher frequencies in vocal signals would help to counteract high frequency sound attenuation in forests, increase the perceptual salience of formants and any information that they encode, and place less emphasis on lower frequencies for information transfer in an environment with high levels of ambient noise at and below ~3 kHz. Broadband signals with wider frequency spectra are also thought to be easier to locate. Hence, this co-evolutionary process would not only facilitate the transfer of acoustic information encoded by the upper frequency spectrum (i.e. formants), but could also help animals locate vocalising conspecifics in densely forested environments with poor visibility. We suggest that the evolutionary trade-off within forest species reflects a minimal need to provide accurate (i.e. perceivable) information to receivers while avoiding the unnecessary production of more conspicuous signals that may incur a greater risk of predation.

Finally, our findings also accord well with recent comparative work that suggests hearing sensitivity in primates is not solely constrained by inter-aural distances. We suggest that future studies examine whether mammal vocal signals and sensory systems co-evolve in response to anthropogenic noise, or to utilise frequency ranges that are less likely to be perceived and eavesdropped upon by predators. Sensory drive acting on vocal signals to optimise the transfer of acoustic information in different ecological environments may prove to be an important driver of mammal vocal signal diversity. It may also explain why forest mammals sometimes produce vocal signals with higher frequency components than closely related species that live in more open habitats, despite the general consensus that lower frequencies should be favoured in acoustically cluttered habitats.

Furthermore, given that acoustic signals potentially contribute to reproductive isolation, our findings are also consistent with the notion that sensory drive has a wider role in the diversification of mammalian lineages. Future studies should investigate whether acoustic adaptation to forest versus open environments leads to corresponding divergence in mating preferences based on mammal vocal characteristics. A greater understanding of how vocal signal characteristics, auditory perception, and mating preferences based on vocal traits adapt to different local environments will illuminate whether sensory drive contributes to mammal vocal signal diversity and the early stages of reproductive isolation in natural mammal populations.

**Methods**

**Audiogram data.** For the comparative analyses of hearing sensitivity we collected audiogram data from the literature for 51 terrestrial mammal species (Supplementary Table 1). Functional head size (defined as the time taken for sound to travel between the two ears) is inversely related to high frequency hearing in mammals. It is thought that this inverse relationship exists because low-frequency sounds (with longer wavelengths) are likely to bypass smaller heads with more closely spaced ears. Smaller species (with smaller heads) are therefore more dependent on higher frequencies for sound localization, and thus, more sensitive to high sound frequencies. Accordingly, we took functional head size data from the same source as the audiogram data to control for this factor in the comparative analysis (Supplementary Table 1). We did not collect audiogram data for subtropical species or bats (Supplementary Table 1). Bats were excluded on the basis that they use very high frequencies that they (ultrasonic) echolocation in order to navigate via auto-communication, making it unclear whether their high frequency hearing capabilities are driven by selection pressures linked to navigation or vocal communication, or both. In addition, we restricted the dataset to adult individuals. To maximise our sample size we collected audiogram data generated from behavioural tests (n = 47 species) and auditory brainstem responses (n = 4 species). Importantly, common parameters of auditory sensitivity, such as the frequency of maximum hearing sensitivity, the frequency of maximum hearing sensitivity (peak sensitivity) in kHz and hearing threshold values were restricted to 0–20 kHz because it represented the maximum range that was available for all 51 terrestrial mammal species. Hearing threshold dB values at 20 kHz were estimated by interpolation between adjacent audiograms.
Acoustic analysis. All the sound human voices, cage rattling), so that a total of 3701 sound overlapping spectra, and/or sounds other than the targeted vocalisations (e.g., acoustic analyses

Nyquist frequency of 20 kHz that corresponded to our maximum hearing threshold script from GSU tools48. This script computes the spectral slope as a regression line of the separate recordings we measured the spectral slope using a Praat (v6.0.31) random effects. We ran each analysis for 11 million iterations with a burn-in of 100,000 and thinning interval of 10,000 to minimize autocorrelation in the chains.

Acoustic analyses. To quantify the relative distribution of spectral energy in each of the separate recordings we measured the spectral slope using a Praat script (v6.0.31) from GSU tools48. This script computes the spectral slope as a regression line fit to the amplitude peaks of frequency bins across the entire spectrum (for more details refer to supplementary methods). Vocalisations with more high frequency energy will have shallower gradients (or slopes) than those with relatively more low-frequency energy (Fig 1). The acoustic data was then averaged for each species for the statistical analysis.

Statistical analysis. The data were examined using phylogenetic generalized linear mixed models that generated Bayesian posterior probability distributions using Markov Chain Monte Carlo (MCMC) simulations. The Bayesian phylogenetic mixed models were implemented using the MCMCglmm package in R49,50, with Markov Chain Monte Carlo (MCMC) simulations. The Bayesian phylogenetic relationships among species as a random effect. For the analysis of the acoustic data we entered mean hearing threshold value for the frequency range 10 kHz and subtracted this from the overall mean sensitivity (0–20 kHz), to control for overall differences in hearing sensitivity values across studies (due to methodological differences) and create a standardised index of high frequency hearing sensitivity for each species: higher values indicate better high frequency hearing (Fig 2). The audio processing was conducted using Praat v5.1.32 (www.praat.org).

Recordings were initially segmented into separate vocalisations using the edit window and labelling facility in Praat and saved as individual sound files (.wav). We discarded recordings with excessive environmental noise, multiple callers with overlapping spectra, and/or sounds other than the targeted vocalisations (e.g., human voices, cage rattling), so that a total of 3701 sound files were retained for the acoustic analysis. All the sound files were down-sampled to 40 kHz, resulting in a Nyquist frequency of 20 kHz that corresponded to our maximum hearing threshold values. The mean intensity of all audio recordings was set to 60 dB prior to the acoustic analysis.

Data availability The data that support the findings of this study are available in the Supplementary Information. The source data underlying Figs. 2, 3 and 4 are provided as a Source Data file.

Code availability The R code used for the analyses is available from the corresponding author upon request.

Received: 10 December 2018 Accepted: 28 May 2019 Published online: 25 June 2019

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Acknowledgements

We would like to thank Karl-Heinz Frommolt and the Berlin Museum für Naturkunde for providing access to uncompressed recordings.

Author contributions

B.D.C. wrote the manuscript, collated the data, and conducted the analyses. B.D.C. R.R.S., and M.O. conceived and designed the study. R.R.S. and M.O. contributed to writing the manuscript and collecting the data.

Additional information

Supplementary Information accompanies this paper at https://doi.org/10.1038/s41467-019-10768-y.

Competing interests: The authors declare no competing interests.

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Peer review information: Nature Communications thanks the anonymous reviewers for their contribution to the peer review of this work. Peer reviewer reports are available.

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