Research

Social drive and the evolution of primate hearing

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The structure and function of primate communication have attracted much attention, and vocal signals, in particular, have been studied in detail. As a general rule, larger social groups emit more types of vocal signals, including those conveying the presence of specific types of predators. The adaptive advantages of receiving and responding to alarm calls are expected to exert a selective pressure on the auditory system. Yet, the comparative biology of primate hearing is limited to select species, and little attention has been paid to the effects of social and vocal complexity on hearing. Here, we use the auditory brainstem response method to generate the largest number of standardized audiograms available for any primate radiation. We compared the auditory sensitivities of 11 strepsirrhine species with and without independent contrasts and show that social complexity explains a significant amount of variation in two audiometric parameters—overall sensitivity and high-frequency limit. We verified the generality of this latter result by augmenting our analysis with published data from nine species spanning the primate order. To account for these findings, we develop and test a model of social drive. We hypothesize that social complexity has favoured enhanced hearing sensitivities, especially at higher frequencies.

Keywords: Strepsirrhini; hearing; auditory brainstem response; evoked potential audiogram; sensory ecology; acoustic communication

1. INTRODUCTION

Vocal communication is a hallmark of primate behaviour and a foundation for human language. A rich literature has therefore been focused on non-human primates and the structure and function of their vocal signals [1,2]. As a general rule, vocal communication functions to maintain social cohesion [3] and to alleviate some of the costs of group living by decreasing food competition and exposure to predation [4]. Accordingly, a substantial proportion of the vocal behaviour of primates is devoted to signalling social separation or the presence of predators [5]. The attendant motivational states of distress or fear often result in calls with a high-frequency acoustic structure [6]. Such a structure is expected to benefit both the signaler and intended receiver, as high frequencies are difficult for predators to localize [7,8] and conspicuous in the low-frequency ambient noise of most natural habitats [9,10]. For example, predators of primates such as large raptors and some felids are relatively insensitive to frequencies above 6 kHz [11,12], a pattern that might account for the high-frequency components in many primate alarm calls [7].

Primate alarm calls are often referential and function to elicit predator-specific evasive responses from group members [13–18]. Such findings are compelling evidence of signaler–receiver communication and a testament to the adaptive advantages of alarm signals. It therefore stands to reason that natural selection might have also favoured a correspondence between the properties of alarm calls and the hearing sensitivities of intended receivers. Yet, the hearing of most primate species is unstudied, and the extent to which primate vocal complexity has exerted a selective pressure on (or was constrained by) hearing sensitivity is unknown [19–21].

The comparative biology of primate hearing sensitivity is frustrated by limited data. Despite eight decades of research, comparable audiograms exist for only 16 species common to laboratory settings, and only 12 of these audiograms were derived from free-field conditions [22]. Variation in this limited
dataset is correlated with few socioecological factors, a finding that informs the prevailing model of hearing evolution in primates [23]. According to this model, enhanced high-frequency hearing sensitivity exists solely as a negative function of interaural distance because low-frequency sounds are likely to bypass smaller heads, thus leaving smaller species dependent on higher frequencies for sound localization. An implication of this scaling model—that large-headed, gregarious primes are deficient receivers of high-frequency alarm calls—is potentially profound, as it would challenge many assumptions concerning the form and function of primate vocal signals.

Here, we test the hypothesis that hearing sensitivity is influenced by socioecological factors and not solely constrained by interaural distance; we do so by estimating the auditory sensitivities of 11 primate species with varying head sizes and levels of social complexity. We draw attention to this latter variable in part because recent studies have suggested a causal positive correlation between social group size and vocal complexity among birds [24], cetaceans [25] and primates [26]. Although vocal complexity is difficult to define—it can be based on the acoustic structure of vocalizations [24,25] or the number of discrete vocalizations [26]—it is conceptually simple. As Changizi [27] put it, a 'system...is more complex if it can do more kinds of things'. Hence as group size increases, more complex vocalizations are required to facilitate a greater range of social and ecological interactions. For example, the ring-tailed lemurs (Lemur catta) emit frequencies that are higher and more modulated when attracting the attention of dispersed group members [28]. Accordingly, if primate group size did exert a selective pressure on, or 'drive', the evolution of vocal complexity [26], including high-frequency alarm calls [5–7], we predict that it has also driven variation in hearing sensitivity, especially at higher frequencies. This concept, which we term social drive, is also tested here.

2. MATERIAL AND METHODS

(a) Experimental procedure

(i) General method

To estimate the hearing sensitivities of primates, we used the auditory brainstem response (ABR) method [29]. In this minimally invasive method, brief tones are used to evoke neural activity from the ascending auditory pathway that is recorded with sensory electrodes placed on the scalp [30,31]. This technique, which was developed for use in human infants, requires ca 1 h to generate an audiogram. The ABR method is thus a viable alternative to traditional behavioural methods that require months of training in laboratory settings. Importantly, common parameters of auditory sensitivity such as the frequency of best sensitivity and the high-frequency limit are comparable between the two methods [29].

(ii) Study animals

We used the ABR method to estimate the auditory sensitivities of 11 species (n = 30 individuals) in the suborder Strepsirrhini (electronic supplementary material, table S1).

(iii) Anaesthetic procedure

To reduce interference from myogenic noise, all animals were anaesthetized for ca 1 h with intramuscular injections of telazol and either medetomidine or medazolam, supplemented with sevoflurane or isoflurane gas. The use of such anaesthetics during the ABR testing has been common across a wide variety of animals, and short-term exposure (i.e. 1 h) does not affect thresholds significantly [29]. The body temperatures of the animals were monitored and controlled with blankets and electric heating pads; after the procedure, all animals were returned to their enclosures unharmed and then monitored.

(iv) Animal placement

The animals were placed in a custom-built, portable sound-attenuating box (1.0 × 0.7 × 0.7 m) constructed of sound-deadening board lined with mass-loaded vinyl and pyramid-style acoustical foam (Pinta Acoustic, MN, USA). The front panel was constructed of safety glass and Plexiglas, and various openings allowed veterinary access. The animals were positioned in the box in a supine posture with the head elevated slightly to free the pinna from compression; the right (non-test) ear was plugged with a soft foam earplug rated at 33 dB attenuation.

(v) Stimuli

The ABR stimuli were 2-1-2 cycle tone pips (sinusoidal, 2-cycle linear rise/fall, 1-cycle plateau) delivered at a rate of 39.1 s⁻¹ with an alternating polarity. The stimuli were generated digitally with Evrest software [32,33] operating on a PC laptop equipped with a multi-function data acquisition card (NI-USB 6251, National Instruments, Austin, TX, USA). Stimuli were converted to analogue (500 kHz rate, 16-bit resolution), bandpass-filtered (3CD8TB-20/200k g-N1u1, Krohn-Hite, Brockton, USA), attenuated (PA5, Tucker-Davis, Alachua, FL, USA), and delivered free-field via a magnetic speaker (FF1/SA1 Tucker-Davis) or an electrostatic speaker (ES1/ED1, Tucker-Davis) placed ca 10 cm from the entrance to the left external acoustic meatus. Test stimuli were half-octaves between 500 Hz and 64 kHz, delivered in steps of 10 and 5 dB (2048 repetitions per condition). We calibrated the stimuli daily with a type-1 sound-level metre (840015, Sper Scientific, Scottsdale, AZ, USA) and a studio condenser microphone (MKH 800, Sennheiser, Old Lyme, CT, USA) connected to a PC running Raven Pro v. 1.3 (Cornell Laboratory of Ornithology, Ithaca, NY, USA) [29]. Higher frequencies had slightly greater spectral splatter than lower frequencies (owing to the more rapid stimulus onset), resulting in a more gradual roll-off on each side of the centre frequency (electronic supplementary material, figure S1); however, the total stimulus bandwidth agreed closely across frequencies, and the ABR-derived audiograms agreed well with behaviourally derived audiograms at high frequencies despite increased spectral spatter [29].

(vi) Auditory brainstem response acquisition

The tone pip stimuli evoked activity from the auditory nerve and auditory brainstem nuclei, which we recorded with minimally invasive 28-gauge stainless steel
Table 1. ABR-derived audiometric parameters, group size and interaural distances for strepsirrhine primates.

<table>
<thead>
<tr>
<th>species</th>
<th>mean threshold (dB SPL)</th>
<th>60 dB high-frequency limit (kHz)</th>
<th>frequency of best sensitivity (kHz)</th>
<th>species mean group size</th>
<th>interaural distance (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daubentonia madagascariensis</td>
<td>27.8</td>
<td>65.6</td>
<td>11.3</td>
<td>1.0</td>
<td>34.77</td>
</tr>
<tr>
<td>Eulemur coronatus crowned lemur</td>
<td>26.3</td>
<td>59.6</td>
<td>8.0</td>
<td>6.2</td>
<td>32.66</td>
</tr>
<tr>
<td>Eulemur fulvus collaris collared lemur</td>
<td>30.8</td>
<td>57.4</td>
<td>8.0</td>
<td>7.5</td>
<td>31.44</td>
</tr>
<tr>
<td>Eulemur fulvus rufus red-fronted lemur</td>
<td>25.1</td>
<td>63.7</td>
<td>11.3</td>
<td>8.7</td>
<td>25.85</td>
</tr>
<tr>
<td>Eulemur mongoz mongoose lemur</td>
<td>28.6</td>
<td>54.2</td>
<td>8.0</td>
<td>2.9</td>
<td>26.21</td>
</tr>
<tr>
<td>Eulemur rubriceror red-bellied lemur</td>
<td>35.4</td>
<td>45.1</td>
<td>5.7</td>
<td>3.0</td>
<td>30.51</td>
</tr>
<tr>
<td>Lemur catta ring-tailed lemur</td>
<td>23.7</td>
<td>62.2</td>
<td>11.3</td>
<td>14.5</td>
<td>30.12</td>
</tr>
<tr>
<td>Nycticebus coucang slow loris</td>
<td>40.6</td>
<td>42.6</td>
<td>16.0</td>
<td>1.0</td>
<td>24.60</td>
</tr>
<tr>
<td>Nycticebus pygmaeus pygmy slow loris</td>
<td>41.6</td>
<td>51.5</td>
<td>11.3</td>
<td>1.0</td>
<td>22.50</td>
</tr>
<tr>
<td>Propithecus coquereli Coquerel’s sifaka</td>
<td>38.5</td>
<td>49.7</td>
<td>11.3</td>
<td>6.0</td>
<td>32.15</td>
</tr>
<tr>
<td>Varecia rubra red-ruffed lemur</td>
<td>29.0</td>
<td>59.0</td>
<td>11.3</td>
<td>4.7</td>
<td>34.57</td>
</tr>
</tbody>
</table>

(a) Foraging group sizes were averaged from the literature [35–52].
(b) Interal irregular distances from Coleman [34].

subdermal needle electrodes (F-E3, Grass Instruments, West Warwick, RI, USA). We braided the electrode wires to reduce electrical artefacts and inserted the electrodes in the skin at the cranial vertex (positive), the ipsilateral mastoid (reference) and the contralateral mastoid (ground). The signals from the electrodes were recorded via a biopotential amplifier (Grass P511, Grass Instruments), amplified (100 000 ×), filtered (0.03–3 kHz, 60 Hz), digitized (10 kHz rate, 16-bit resolution), input into Everest (20 ms epochs, 12 μV reject level) and digitally filtered offline. See representative waveforms for each species in electronic supplementary material, figure S2a.

(b) Data analysis
(i) Auditory brainstem response thresholds and parameters
For each frequency, we used a linear regression method [29] to determine the auditory threshold (quietest detectable level). We set the criterion at 77 μV (average encephalographic background noise + 40 μV); at this level, the ABR was consistently distinct above random fluctuations in background noise (see example of an ABR waveform series in electronic supplementary material, figure S2b). For individuals wherein data were insufficient to determine the threshold for any given frequency, we estimated that threshold using the average rise/fall from adjacent frequencies in other individuals of the same species. For each species, we then computed the average threshold at each frequency (electronic supplementary material, table S2), which we used to calculate three audiometric parameters: (i) the frequency of best sensitivity (frequency with the lowest threshold); (ii) the high-frequency limit (highest frequency detectable at 60 dB SPL) and (iii) the mean ABR threshold (table 2). We defined the mean ABR threshold (a measure of the overall auditory sensitivity) as the average threshold for half-octave steps from 1.0 to 64 kHz; the 0.5 kHz thresholds were excluded from this average due to overlapping acoustical noise from a ventilation fan.

(ii) Comparative data
To test whether interaural distance—the maximum distance between the most lateral extent of the tympanic rings [34]—or social behaviour can better predict variation in our three audiometric parameters, we assembled published data on these variables and used average foraging group size as a proxy for social complexity (table 1). Foraging group size was used as a measure of social complexity because it represents a consistent measure that is widely reported, and because primates are expected to encounter more predators and engage in more vocal communication during foraging than during resting (especially in strepsirrhines that form relatively small sleeping groups) [35–52]. Insufficient data were available to estimate the average group size of Eulemur fulvus collaris, accordingly, we substituted data from Eulemur fulvus fulvus owing to its similar social behaviours [35–39,42].

To test whether a positive correlation between the 60 dB high-frequency limit and social complexity (reported below) extended across the primate order, we broadened the scope of our analysis to include comparable behaviourally derived free-field audiograms in the published literature [22,53]. Of the 12 non-human primates, we excluded Lemur catta and Nycticebus coucang because we report original ABR data for these species. We calculated the 60 dB high-frequency limits (table 2) mathematically on the basis of thresholds reported in the original sources. The 60 dB high-frequency limit is comparable between ABR- and
be behaviourally derived datasets [29]; however, at lower frequencies, absolute threshold levels may differ between methodologies [29]. We, therefore, omitted any consideration of absolute threshold level (i.e. mean overall sensitivity) in the extended analysis.

(iii) Statistical analysis
We applied a log10 transformation to all data prior to statistical analysis owing to non-normality in distribution; for parameters with values ≤ 1, we added a constant to all data points of those parameters prior to transformation. First, we explored relationships between auditory sensitivity, group size and interaural distance using a traditional ordinary least-squares regression analysis (JMP v. 9.0, SAS Institute, Cary, NY, USA). Given that interaural distance could be a confounding factor in our analysis [23], if any parameter was significantly correlated with interaural distance, we regressed that parameter against interaural distance to generate residuals for subsequent analysis. Second, to further explore variation within our ABR dataset, we performed a multivariate repeated measures analysis of variance (MANOVA) within JMP: We tested whether there were species differences in the auditory parameters for each subject or in the threshold at each frequency for each subject as a function of group size, interaural distance or interaural distance x group size. Finally, to reduce error associated with phylogenetic relatedness [55], we explored the relationships between auditory parameters, group size and interaural distance using phylogenetically independent contrasts (PIC) [56] with the PDAP:PDTREE module [57] of Mesquite (v. 2.72, build 528, Tucson, AZ, USA) [58]. We used the species-level phylogenies (consensus trees and chronograms) from the 10kTress project, v. 3 [59]. Within Mesquite, we applied a natural log transformation to branch length if they exhibited significant lack of fit to the tip data [7]. For all analysis, significance was set at $p < 0.05$ (two-tailed).

To explore the potential driving factors (or directionality) of correlated character states, we performed a concentrated changes character evolution test [60] in MacClade [61]. All data were analysed as discrete binary characters; a species was defined as social if the average foraging group size was greater than three individuals, indicating social interactions beyond mother–infant pairs. We used mean values of raw data to dichotomize the parameters of auditory sensitivity, set the ancestral state as non-social and either enhanced or unenhanced auditory sensitivity, and simulated 100 000 samples. Interaural distance was not controlled for in this analysis, as it was found to be uncorrelated with the auditory sensitivities or group sizes of the species in our dataset.

3. RESULTS
Here, we report the largest number of standardized audiograms available for any primate radiation (figure 1a). Although the basic shape of each audiogram agrees well with the overall pattern reported for mammals, including primates [22], we detected substantial variation between the 11 species with respect to three audiometric parameters (table 1). This variation was uncorrelated with interaural distance (electronic supplementary material, tables S3–S7), indicating that other factors may have contributed to the evolution of auditory sensitivity among the strepsirrhine primates in our dataset.

(a) Social complexity and overall auditory sensitivity
As predicted, we found that increased social complexity, as measured by average group size, explained a significant proportion of the variance associated with increased overall auditory sensitivity (i.e. decreased mean thresholds; $r^2 = -0.40; F_{1,9} = 5.94, p = 0.037$, electronic supplementary material, table S3). However, the strength of this relationship was weakened after controlling for the effects of phylogeny (PIC: $p = 0.106$, electronic supplementary material, table S4), which magnified the statistical leverage of the aye-aye (Daubentonia madagascariensis). Aye-ayes are an enigmatic nocturnal species in a monotypic family (Daubentoniidae); and, despite a relatively

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Table 2. Behaviourally derived audiometric parameters, group size and interaural distance across the primate order.

<table>
<thead>
<tr>
<th>species</th>
<th>60 dB high-frequency limit (kHz)</th>
<th>frequency of best sensitivity (kHz)</th>
<th>species mean group size</th>
<th>interaural distance (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aotus trivirgatus, owl monkey</td>
<td>44.5</td>
<td>10.0</td>
<td>2.9</td>
<td>28.49</td>
</tr>
<tr>
<td>Callithrix jacchus, common marmoset</td>
<td>44.9</td>
<td>7.0</td>
<td>11.0</td>
<td>20.1</td>
</tr>
<tr>
<td>Galago senegalensis, bushbaby</td>
<td>65.0</td>
<td>8.0</td>
<td>1.0</td>
<td>19.94</td>
</tr>
<tr>
<td>Homo sapiens, human</td>
<td>17.6</td>
<td>4.0</td>
<td>37.5</td>
<td>81.68</td>
</tr>
<tr>
<td>Macaca fascicularis, long-tailed macaque</td>
<td>—</td>
<td>16.0</td>
<td>27.5</td>
<td>38.3</td>
</tr>
<tr>
<td>Macaca fuscata, Japanese macaque</td>
<td>36.5</td>
<td>4.0</td>
<td>36.6</td>
<td>43.07</td>
</tr>
<tr>
<td>Macaca mulatta, rhesus macaque</td>
<td>—</td>
<td>16.0</td>
<td>35.5</td>
<td>40.8</td>
</tr>
<tr>
<td>Papio cynocephalus, yellow baboon</td>
<td>41.0</td>
<td>8.0</td>
<td>55.5</td>
<td>53.17</td>
</tr>
<tr>
<td>Perodicticus potto, potto</td>
<td>42.0d</td>
<td>16.0</td>
<td>1.0</td>
<td>26.6</td>
</tr>
<tr>
<td>Phaner furcifer, fork-marked lemur</td>
<td>60.0</td>
<td>16.0</td>
<td>2.0</td>
<td>20.47</td>
</tr>
<tr>
<td>Saimiri sp., squirrel monkey</td>
<td>42.5</td>
<td>12.0</td>
<td>23.0</td>
<td>27.28</td>
</tr>
</tbody>
</table>

*Published free-field behaviourally derived data [22,53].
*Interaural distances from Coleman [34].
*Based on the electronic supplementary material from Heffner, see http://homepages.utoledo.edu/rheffne/
*Species designation is uncertain for the auditory data, thus group size and interaural distance data are estimated from multiple species within the genus.
variation in the frequency of best sensitivity (PIC: \( r^2 = 0.35, F_{1,8} = 14.2**, p < 0.01 \)). We found that average foraging group size explained a significant proportion of the variance associated with 60 dB high-frequency limits (figure 1c), again indicating a strong predictive relationship between social complexity and auditory sensitivity.

The validity of these findings is supported by a multivariate repeated measures analysis of variance that explored variation in the parameters of auditory sensitivity for each subject, and in the thresholds at each frequency for each subject. The results indicate that within strepsirrhines, auditory sensitivity varies significantly as a function of group size (auditory parameters: \( F_{2,21} = 7.03, p = 0.005 \); individual thresholds: \( F_{12,11} = 3.00, p = 0.039 \), electronic supplementary material, table S7). Again, our sample showed insignificant variation as a function of interaural distance (\( F_{2,21} = 0.87, p = 0.435 \), electronic supplementary material, table S7).

To test whether this pattern extends across the primate order, we combined our results with comparable published data based on free-field behavioural testing (electronic supplementary material, tables S2, S8–S11). In this primate-wide dataset, the 60 dB

large head size and limited social complexity, at least two individuals demonstrated enhanced auditory sensitivities, especially to higher frequencies. On the grounds that such sensitivity can be associated with highly specialized acoustic foraging behaviours (see §4a), we excluded this audiogram from subsequent analyses focused on social complexity. As a result of this omission, social complexity explained almost half of the variance associated with increased overall auditory sensitivity both with and without controlling for phylogeny (figure 1b, electronic supplementary material, tables S5 and S6). *\( p < 0.05 \), **\( p < 0.01 \).

**Social complexity and high-frequency auditory sensitivity**

After controlling for the effects of phylogeny, we found that social complexity was marginally related to variation in the frequency of best sensitivity (PIC: \( r^2 = 0.35, F_{1,8} = 4.36, p = 0.070 \), electronic supplementary material, table S6). However, this audiometric parameter is limited by the selection of test frequencies and complicated by multiple frequencies having similar thresholds. Accordingly, the 60 dB high-frequency limit is a more practical measure of high-frequency auditory sensitivities; and, in primates, it has been linked to morphological variation within the bony ear [62–63].

Figure 1. ABR audiograms and relationships between audiometric parameters and foraging group size in strepsirrhine primates. (a) (i) Images and (ii) audiograms of 11 species. (b) Log\(_{10}\) mean ABR threshold (overall sensitivity) on log\(_{10}\) group size, excluding Daubentonia. For both (b,c), the plotted variables are log\(_{10}\) transformations of the raw data presented intable 1, and statistics are shown for both a traditional ordinary least-squares regression analysis (OLS, line shown) and phylogenetically independent contrasts (PIC); interaural distance was not controlled for in these analyses owing to an insignificant correlation with the auditory variables (electronic supplementary material, tables S5 and S6). *\( p < 0.05 \), **\( p < 0.01 \).
high-frequency limit was a confounding factor—it was negatively correlated with interaural distance (PIC: \( r^2 = 0.30; F_{1,17} = 7.34, p = 0.015 \), electronic supplementary material, tables S8 and S9), a result that is consistent with predictions of a negative relationship between head size and hearing sensitivity in mammals [23]. Accordingly, we controlled for interaural distance via partial correlation analysis and found that group size and 60 dB high-frequency limit are positively correlated [23].

Accordingly, we controlled for interaural distance between head size and hearing sensitivity in mammals consistent with predictions of a negative relationship [23]. The principles of sensory drive—that environmental parameters drive the evolution of sensory systems, which in turn drive the evolution of social signals [77,78]—establish the possibility that enhanced hearing is tuned to the acoustic constraints of habitats that coincidentally favour larger social groups. Sensory drive is difficult to test with our limited dataset; however, we consider it an unlikely explanation for our results. For example, the red-fronted lemur (Eulemur fulvus rufus; relatively enhanced hearing) is twice as social as the red-bellied lemur (Eulemur rubriventer; relatively poor hearing), although both species have the same body mass (ca 2 kg) and compete for virtually identical food resources in Ranomafana National Park, Madagascar [52]. Furthermore, a

Figure 2. Distribution of binary character states on phylogenetic trees as used for the concentrated changes character evolution test. Black lines mark the distinguished states (social, enhanced auditory sensitivity). Dashed lines indicate uncertain character state.

4. DISCUSSION

Here, we describe and compare audiograms from 11 primate species. We report analyses with and without phylogenetic contrasts and show that social complexity, as measured by average foraging group size, explains a significant amount of variation in two audiometric parameters—overall auditory sensitivity and 60 dB high-frequency limit. The addition of comparable data from the literature expanded the scope and power of our analysis and verified that interaural distance [23] and social complexity are both correlated with an increased sensitivity to higher frequencies. The exclusion of a species, the aye-aye (Daubentonia madagascariensis), improved the strength of these patterns, perhaps owing to the demands of its unique acoustic ecology.

(a) Aye-ayes

The aye-aye is a distinctive primate with elongated hands and a disproportionately long, thin and clawed third digit that has been described as villiform, filamentous, gracile and grotesquely attenuated [64–67]. This finger is not only independently mobile [68], but also multi-axial owing to a unique ball-and-socket metacarpophalangeal joint [69]. Such digital morphology aids percussive foraging or tap-scanning [70–73], acoustic behaviours that contribute to the detection of embedded beetle larvae and to the material assessment of foods [74]. Thus, aye-ayes are highly specialized foragers; indeed, their large pinnae [63,75] and expanded frontal cortex [76] appear to support their dependence on asocial acoustic cues. Accordingly, the good high-frequency auditory sensitivity of aye-ayes is perhaps best interpreted as a foraging adaptation.

(b) Sensory drive

The principles of sensory drive—that environmental parameters drive the evolution of sensory systems, which in turn drive the evolution of social signals [77,78]—establish the possibility that enhanced hearing is tuned to the acoustic constraints of habitats that coincidentally favour larger social groups. Sensory drive is difficult to test with our limited dataset; however, we consider it an unlikely explanation for our results. For example, the red-fronted lemur (Eulemur fulvus rufus; relatively enhanced hearing) is twice as social as the red-bellied lemur (Eulemur rubriventer; relatively poor hearing), although both species have the same body mass (ca 2 kg) and compete for virtually identical food resources in Ranomafana National Park, Madagascar [52]. Furthermore, a

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behavioural audiogram of the yellow baboon (Papio cynocephalus) indicates a relatively enhanced sensitivity to high frequencies compared with other Old World monkeys [22,63]. Such auditory sensitivity is suboptimal in the savannah–woodland habitats of this species [10], but consistent with its tendency to form large social groups [79]. Taken together, these few examples suggest that primate hearing sensitivity is more strongly associated with group size than it is to habitat acoustical constraints.

(c) Perceptual drive

Another potential explanation for our findings, based on the principles of perceptual drive [80], is that enhanced audition was preadaptive for the evolution of large social groups. Under this model, enhanced hearing sensitivity might have enabled the evolution of larger vocal repertoires that in turn allowed larger social groups to assemble and function efficiently. To explore whether increased hearing sensitivity was a driving factor in the evolution of larger groups, we performed a concentrated changes character evolution test. The results of this test were inconclusive (electronic supplementary material, table S12), indicating that social complexity and hearing sensitivity have evolved in close tandem [60]. Insofar that these results cannot rule out perceptual drive, they do support our hypothesis that complex social behaviour and hearing sensitivity are coevolved.

(d) Social drive

Another explanation for our findings is that complex social behaviour was a driving factor in the evolution of enhanced hearing sensitivity. The strength of this ‘social drive’ model is twofold; first, the link between social group size and vocal complexity appears to be a general biological pattern among birds and mammals, including primates [24–26]. Second, it predicts the dual outcome reported here—that social complexity can explain significant variation in two audiometric parameters: (i) increased overall sensitivity and (ii) increased 60 dB high-frequency limits. Increased overall sensitivity is expected to confer adaptive advantages to individuals in larger social groups because they must travel greater distances amid more variable habitats [81]; thus a receiver faces the acoustic challenge of detecting a large number of discrete vocal signals [26], some of which vary between individuals [82], across a wide range of habitat constraints [9,10]. Further, given that larger social groups form in part to deter predation [4], and that predator-specific alarm calls often have a high-frequency acoustic structure [6,7], signal receivers are expected to benefit from an enhanced sensitivity to high-frequencies (expressed by increased 60 dB high-frequency limits). To further explore this social drive hypothesis, we performed a concentrated changes character evolution test. Again, the results were inconclusive (electronic supplementary material, table S12). Thus, we cannot verify causation, only that social complexity and enhanced hearing sensitivity are coevolved.

(e) Predicting group size in the fossil record

The strength of our findings raises the possibility of predicting social group size on the basis of osteological characteristics preserved in the fossil record. Two recent studies have identified relationships between high-frequency auditory sensitivity and the morphology of the middle ear ossicles [63] and cochlear labyrinth [62,63]. Such findings, in tandem with the present results, suggest that it is plausible to estimate the group sizes of fossil species, including early human ancestors, on the basis of bony ear morphology. Further exploration of how our findings extend across the primate order and beyond will require additional data, such as a more detailed analysis of cochlear functional morphology, standardized auditory data, and studies of vocal acoustics at higher frequencies, particularly in the ultrasound.

Data were collected at the Duke Lemur Center (Durham, NC, USA) under protocols approved by the Institutional Animal Care and Use Committees of the University of California, Santa Cruz, Duke University, and the Duke Lemur Center (approval nos. Domin0805, A209-08-08, and M-5-08-1, respectively).

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