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Receiver bias and the acoustic ecology of aye-ayes (*Daubentonia madagascariensis*)

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The aye-aye is a rare lemur from Madagascar that uses its highly specialized middle digit for percussive foraging. This acoustic behavior, also termed tap-scanning, produces dominant frequencies between 6 and 15 kHz. An enhanced auditory sensitivity to these frequencies raises the possibility that the acoustic and auditory specializations of aye-ayes have imposed constraints on the evolution of their vocal signals, especially their primary long-distance vocalization, the screech. Here we explore this concept, termed receiver bias, and suggest that the dominant frequency of the screech call (~2.7 kHz) represents an evolutionary compromise between the opposing adaptive advantages of long-distance sound propagation and enhanced detection by conspecific receivers.

Keywords: *Daubentonia madagascariensis*, lemur, audiogram, auditory sensitivity, receiver bias, vocalization, sensory trap

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The aye-aye (*Daubentonia madagascariensis*) is a nocturnal primate endemic to Madagascar. It is an enduring source of fascination, both because of its many unique features and because it is the only survivor of a lineage with an origin ~70 million years ago.[1] As a result, *Daubentonia* is allocated to its own family (Daubentoniidae) and infraorder (Chiromyiformes). The aye-aye is perhaps best known for its acoustic foraging behaviors, termed percussive foraging or tap-scanning,[2-5] and suite of unusual anatomical specializations, particularly in the hand, skull, and central nervous system.[6-15] For example, aye-ayes have elongated hands with long, thin middle fingers that have been described as villiform, filamentous, gracile, or grotesquely attenuated.[6-9] This singular digit is highly mobile[10] due to a unique ball-and-socket metacarpophalangeal joint.[12] Such morphology enables rapid tapping and the detection, localization, and extraction of embedded foods such as the wood-boring larvae of cerambycid beetles.[13]

For aye-ayes, the importance of percussive foraging (5–41% of foraging time[13]) and the functional demands of integrating two sensory modalities -haptic touch and audition- appear to be linked with the evolution of large and elaborate ear structures[16-19] and the expansion of cerebral cortical regions associated with auditory processing, such as the inferior colliculus.[11] As a result, aye-ayes are relatively encephalized and reported to have high levels of sensorimotor intelligence.[20] Such attributes suggest that aye-ayes might also have exceptional hearing abilities, yet the auditory sensitivities of strepsirrhine primates are relatively unstudied.

Aye-ayes as Auditory Specialists

Recently, Ramsier et al.[21] used the auditory brainstem response (ABR) method to generate audiograms from 11 strepsirrhine primates, and they confirmed that aye-ayes have relatively enhanced auditory sensitivity between 2.8 and 22.6 kHz, with 2.8–15.9 kHz being the 10-dB bandwidth (the bandwidth across which thresholds are within 10 dB of the threshold of the frequency of best sensitivity).[22] Although ABR-derived thresholds are sometimes elevated in comparison with behavioral tests of primates, especially for frequencies ≤ 2.0 kHz, the two methods produce audiograms with similar shapes,

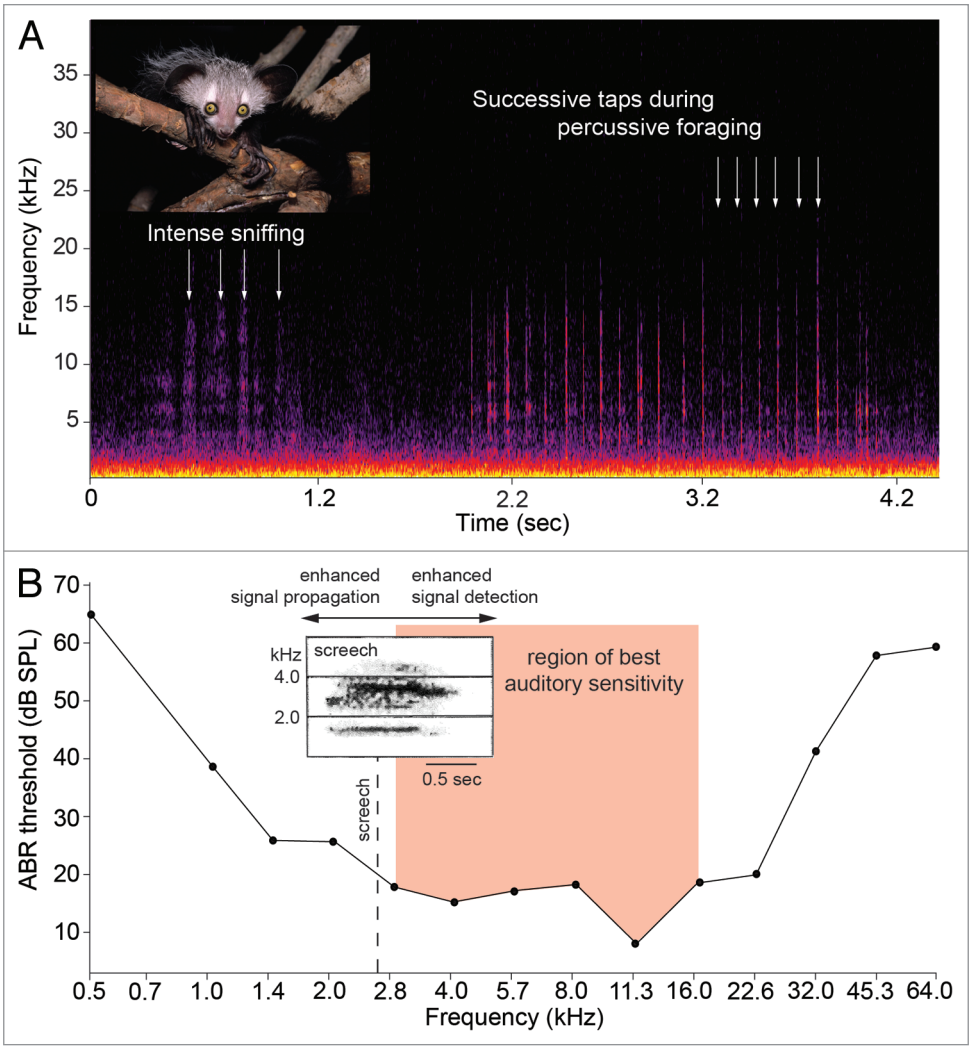

Figure 1. (A) Adult aye-aye and spectrogram of percussive foraging behavior. Each tap of the third digit is discernable with a dominant energy of 6–15 kHz. (B) Mean audiogram of two aye-ayes and the region of best auditory sensitivity (modified from Ramsier et al.[21]). Insert: spectrogram of the aye-aye's primary long-distance vocalization, the screech ('aack' variant), with a dominant frequency of 2.66 kHz (modified from Figure 1J in Stanger and Macedonia[30]). Photograph of aye-aye by D.M. Haring, reproduced with permission.

high-frequency limits, frequencies of best sensitivity, and upper-frequencies of the 10-dB bandwidth.[22] Our estimate for the low-frequency end of the 10-dB bandwidth of aye-ayes appears robust given the close agreement between two individuals for all low-frequency thresholds (0.2–1.6 dB difference, depending on frequency), and the very steep incline for frequencies ≤ 1 kHz (already > 30 dB above the threshold of best sensitivity at 1 kHz).[21]

If we accept this region of best auditory sensitivity, we must now ask if it corresponds with the acoustic properties of percussive foraging. To explore this premise, we used a studio condenser microphone (Sennheiser; frequency response 0.03–50 kHz) and a solid-state recorder (PMD-671, Marantz, Mahwah, New Jersey; sampling frequency 96 kHz, 24-bit) to analyze the percussive foraging of an adult male aye-aye, Merlin, housed at the Duke Lemur Center. We recorded tap-scanning on a typical stimulus used for enrichment purposes: 2x4-inch (5.1x10.2-cm) boards of Eastern white pine (*Pinus strobus*) permeated with food rewards. The rate of tapping was consistent across recordings (97.7 ± 19.9 ms) and each tap had a dominant energy of 6–15 kHz contained between 2 and 27 kHz (**Fig. 1A**). The percussive tapping of aye-ayes is thus a broadband sound that corresponds well to their frequency region of best auditory sensitivity (**Fig. 1B**); however, the acoustic attributes of a temperate softwood should be interpreted with caution. In the wild, extractive foraging is most strongly associated with the decaying stumps of trees, but aye-ayes do sometimes excavate living tissues (e.g., branches of *Protorhus* sp.; trees of *Anthocleista* spp.).[3] The acoustics of percussive foraging on these woods are unknown.

Receiver Bias and the Vocal Ecology of Aye-Ayes

Receiver bias, or preexisting bias, is a model of animal communication that emphasizes bias in the sensory systems of signal receivers.[23] For aye-ayes, the auditory demands associated with percussive foraging might drive, or bias, the

evolution of their vocal signals. According to this model, the dominant frequencies of aye-aye vocalizations are predicted to fall in the range of best auditory sensitivity, ca. 2.8–15.9 kHz (**Fig. 1B**). Yet aye-ayes are solitary foragers with extensive home ranges (females: 30–40 ha; males: 120–215 ha),[13] and population densities are sparse.[24] Thus vocal signals must propagate through relatively vast expanses of forest. Under these conditions, environmental noise can exert a significant selective pressure on the acoustic structure of vocal signals,[25] including those of primates.[26] In fact, most primates have evolved long-distance calls with dominant frequencies < 1.5 kHz,[27] probably because they propagate farther and are less susceptible to masking by forest noise.

The primary long-distance vocalization, or contact call, between aye-ayes has been described onomatopoetically (*creee* or *nee-a*) and prosaically (screech).[28-30] The screech is a variable signal with a dominant frequency of 2.66 kHz and a peak frequency of 8.45 kHz.[30] In addition, two types of alarm call, or screams, have dominant frequencies of 2.80 and 3.25 kHz and peak frequencies of 8.58 and 9.20 kHz.[30] The similar acoustic properties of these calls is puzzling given their different functions. Long-distance calls normally have low dominant frequencies,[27] whereas alarm calls have much higher dominant frequencies.[31] For aye-ayes, it is plausible that a dominant frequency close to ~2.7 kHz represents an evolutionary tradeoff between the opposing adaptive advantages of long-distance sound propagation and enhanced detection by conspecific receivers (**Fig. 1B**). Yet the elegance of this potential compromise is deceptive in part because it raises the possibility that aye-ayes are caught in a sensory trap.[23]

Sensory Traps and the Reproductive Ecology of Aye-Ayes

Sensory traps are part of a broader concept, the evolutionary trap,[32] which holds that animals can experience reduced fitness, or become "trapped", by their own sensory adaptations.[23] Here we hypothesize that the auditory demands of percussive foraging resulted in a receiver bias that precluded the evolution of lower-frequency contact calls. This constraint is expected to become increasingly suboptimal (i.e., contact calls will be increasingly inaudible) as aye-ayes become more widely dispersed as a result of habitat fragmentation. Indeed, the exceedingly low genetic diversity of aye-ayes is puzzling given their large geographic distribution.[33] These recent findings suggest that aye-ayes are quite vulnerable to extinction, not least, perhaps, because they have a limited ability to communicate over large distances.

In sum, we suggest that the unique acoustic ecology and auditory adaptations of aye-ayes have partly contributed to their low genetic diversity. Although speculative, this concept of a sensory trap invites testing; if true, it has profound conservation implications for a unique and highly endangered primate.

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