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Vocalizations of Aye-Ayes *(Daubentonia madagascariensis)* in Captivity

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Introduction

The aye-aye *(Daubentonia madagascariensis)* is perhaps the most peculiar of all primates. Although it retains features that link it phylogenetically with the lemurs [1], it exhibits many unprimate-like traits such as a coat overlain with coarse guard hair, enormous ears, a large bushy tail and continuously growing rodent-like incisors that are powered by highly developed gnawing muscles [2]. Most striking of all is the aye-aye's bony middle finger, which is used to extract the interiors of fruits and nuts, flick the contents of eggs into the mouth and probe wood for insect larvae [3–8]. Information on communication and other behavior of free-ranging aye-ayes is still quite limited, though social, reproductive and foraging behavior has recently been described for captive individuals [7–10].

From the brief field observations that have been published, aye-ayes encountered foraged alone, and they appear to be active for most of the night [4–6, 11–14]. All nocturnal strepsirhines studied so far live in systems of overlapping home ranges with a presumably species-specific pattern of overlap between males and females [15–20]. These taxa forage alone or in pairs, and, as a result, they encounter conspecifics less frequently than species that forage gregariously [19]. This appears to be true for aye-ayes as well. One could imagine that, to regulate and maintain their social relationships, the spatial distributions of nongregariously foraging primates places special demands on their communication systems.

When studying the spatial and social relationships of the less gregarious nocturnal species, vocalizations may be a useful tool for understanding their social interactions. The

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number and structural complexity of vocalizations, along with the contexts in which they are used, may provide information about how and what these species communicate. Ideally, such studies will be conducted in the field and will include experimental components (e.g. call playbacks). The logical first step in any study of vocal communication, however, is the description of the vocal repertoire. Studies in captivity possess the distinct advantage that subjects can be approached more closely than in the field, rendering vocalizers and contexts of calling readily identifiable.

The arrival of 4 wild-caught aye-ayes at the Duke University Primate Center (DUPC) in 1988 provided the opportunity for us to study the vocalizations of these animals. Through consultation with E. Sterling, who studied aye-ayes in the field, we were able to cross-validate our findings of vocal repertoire content and call usage with Sterling's observations of aye-aye vocal behavior under natural conditions.

Methods

We recorded vocalizations from 2 adult males, 1 adult female and her infant female offspring at the DUPC. These individuals were captured near Manara in Madagascar's eastern rain forest. Information on housing and maintenance at the DUPC is provided by Erickson [7]. Aye-aye vocalizations were recorded on a Uher Report Monitor tape recorder with a Monacor ECM 10 microphone and on a Sony TC/D5M tape recorder with a Sennheiser ME-88 'shotgun' microphone. Calls were digitized with an 8-bit digitizer at a sampling rate of 22.3 kHz and were saved as SoundEdit files (MacRecorder, Farallon, Inc.) on a Macintosh IIci. Durations of calls and call units were measured (± 0.05 ms) on the oscillogram panel in SoundEdit, except for 'start-to-peak' frequency duration which was measured (± 1.2 ms) from on-screen spectrograms in the program Canary (Cornell Laboratory of Ornithology). Frequency variables of the fundamental (± 12.5 Hz from 0 to 2.8 kHz) and call peak frequency (± 50 Hz from 0 to 11 kHz) were also measured with Canary. A 1,024-point fast Fourier transform was calculated near each call's midpoint (and at the start, midpoint and end of 'screams') using Signalyze (InfoSignal, Inc.) to obtain the frequency/amplitude profile (± 21.7 Hz) at this location.

Results

Adult Vocalizations

We recorded 6 different call types from adult aye-ayes at the DUPC. Because captive conditions limited the contexts in which vocalizations could occur, information regarding the vocal behavior of free-ranging aye-ayes was provided by Eleanor Sterling (unless noted otherwise).

Scream (fig. 1a; table 1). Screams are largely tonal, high-amplitude vocalizations. These harmonically rich calls exhibit varying degrees of amplitude modulation and are frequently accompanied by an upsweeping introductory note (i.e. 'double-unit screams'). Screams were produced in captivity only during restraint by DUPC technicians. Free-ranging aye-ayes also gave screams during capture and likewise emitted them during aggressive interactions just prior to biting (e.g. when females were actively resisting mounting attempts by males). Double-unit screams are structurally similar to the 'av-hi' alarm call of the indriid lemur *Avahi laniger* (fig. 2a, b).

Plea (fig. 1b; table 1). The plea is a structurally variable tonal vocalization that seems to be a lower-arousal, closed-mouth version of the scream. Like screams, pleas were recorded only from aye-ayes which were struggling to escape restraint. Pleas were heard in the same context in the field, as well as when an individual seemed startled by the sudden appearance of another at close proximity. The behavior of aye-ayes when emitting pleas suggested to us more of a 'protesting' motivation than one of fear or alarm.

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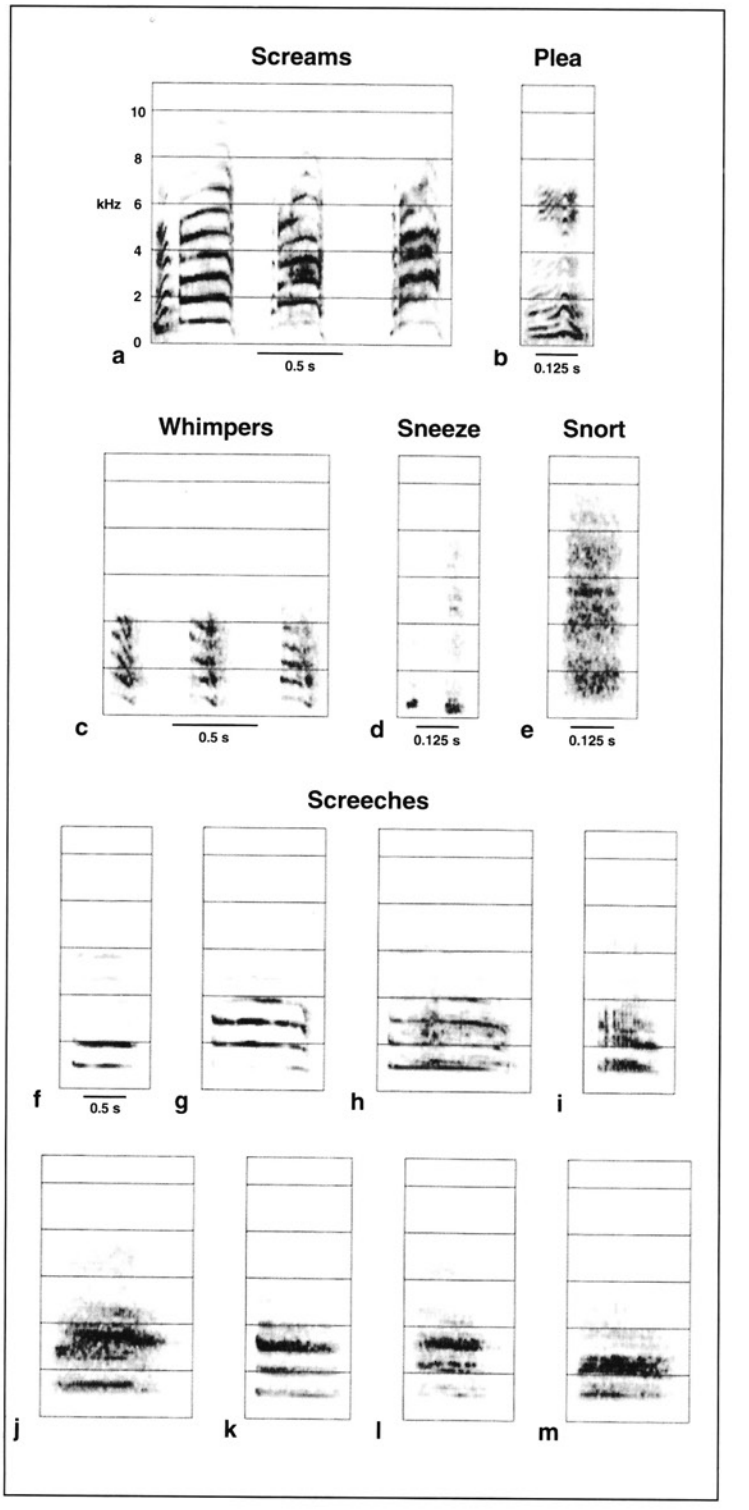

Fig. 1a–m. Vocalizations of adult aye-ayes.

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Table 1. Measurements for adult aye-aye vocalizations

A. *Screams, pleas, whimpers and screeches*

Call type	n	Duration	Peak frequency	Frequency/energy distribution			Fundamental frequency				
				strongest	second	third	start	peak	low	end	start-to-peak
Single-unit screams	3	327 (91)	8,580 (423)	3,253 (616)	2,941 (44)	2,182 (315)	929 (92)	1,169 (40)	325 (33)	376 (26)	134 (52)
Double-unit-screams	4	377 (42)	9,155 (461)	1,190 (172)	2,168 (744)	2,548 (506)	326 (32)	756 (22)	354 (34)	722 (13)	45 (12)
Unit 2				2,804 (328)	2,820 (389)	2,809 (857)	815 (40)	986 (21)	280 (10)	280 (10)	150 (14)
Pleas	2	209 (12)	8,750 (150)	467 (54)	1,423 (141)	2,804 (696)	291 (25)	525 (70)	206 (10)	278 (25)	103 (9)
Whimpers	40	105 (5)	6,045 (207)	812 (79)	1,688 (172)	2,588 (212)	697 (25)	835 (25)	215 (13)	368 (15)	15 (3)
Screeches	69	302 (8)	8,453 (120)	2,656 (91)	2,188 (118)	2,168 (126)	1,005 (13)	1,152 (20)	855 (16)	942 (30)	53 (7)

B. *Sneezes*

Call type	n	Call duration	Peak frequency	Interunit duration	Unit duration	Major energy distribution	
						high	low
Sneezes	49	207 (4)	7,276 (50)	64 (2)	1: 59 (2) 2: 83 (2)	662 (12) 704 (32)	292 (14) 129 (4)

Double-unit scream durations: unit 1: 72 (22); unit 2: 282 (21); interunit interval: 24 (8). Duration data in milliseconds; frequency data in hertz. 'Start-to-peak' is a duration measure. Figures in parentheses indicate standard deviation.

Whimper (fig. 1c; table 1). Whimpers are brief tonal calls with descending frequency sweeps. The number of consecutive whimpers produced was variable, but they were often uttered in sequences containing 3–4 calls. Whimper sequences were repeated over time such that they formed loose bouts. We recorded whimpers only during feeding, particularly in the context of competition for favored food items (e.g. mealworms). In Madagascar, whimpers were emitted by young aye-ayes when attempting to forage in a tree already occupied by an older conspecific and were also given in long series by females when seeking to terminate copulation.

Sneeze (fig. 1d; table 1). Sneezes consist of two structurally similar brief components, the second part being more broadband, noisy and of greater amplitude than the first (like that of a human sneeze). At the DUPC, sneezes were given in response to general disturbances (e.g. human observers, unusual sounds). Free-ranging aye-ayes emitted sneezes in response to the appearance of conspecifics, humans

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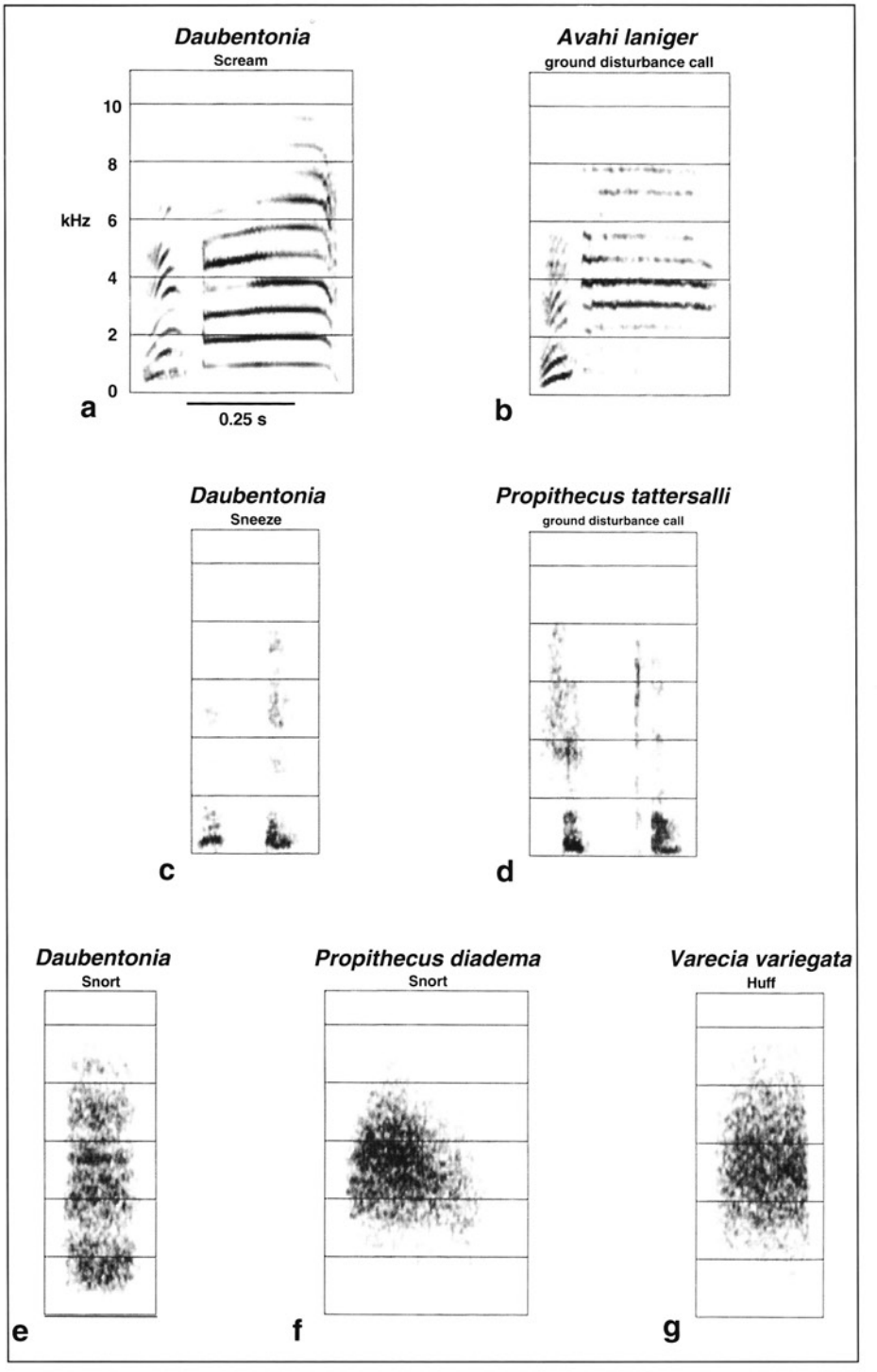

Fig. 2a–g. Some structurally similar vocalizations of *Daubentonia* and other lemur taxa.

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and other lemur species. The sneeze is structurally and functionally similar to the 'sifak' ground disturbance alarm of the indriid lemurs *Propithecus tattersalli* (fig. 2c, d) and *Propithecus verreauxi.*

Snort (fig. 1e, 2e; table 1). Other than being broadband and atonal, the structure of the snort has no definable form, although resonance zones are sometimes seen on the spectrograms. This sound appears to result from forced expulsion of air through the nostrils. Snorts were given singly by disturbed or aroused individuals but occurred also during exploration of arboreal pathways. Snorts were used similarly by free-ranging aye-ayes: agitated individuals produced snorts while pacing back and forth along branches, particularly during the approach of conspecifics. This sound may not necessarily have a communicative function and could be simply the acoustic result of clearing the nasal passages of air during olfactory sampling. Snorts are also produced by *Propithecus diadema* (fig. 2f) and *Varecia variegata* (fig. 2g: 'huff') in high-arousal disturbance contexts.

Screech (fig. 1f–m; table 1). The screech is the aye-aye's primary contact call [4], and it is their most structurally variable vocalization. Screeches form a graded series ranging from tonal, narrowband calls ('eeps': fig. 1f, g), through harsh, metallic-sounding ones ('aacks': fig. 1j–m) that contain frequency 'sidebands' [21], to rapidly amplitude-modulated (pulsed) calls (fig. 1i). These vocalizations can be produced loudly, softly and even voicelessly, and the major energy can be shifted to different harmonics and sidebands. Screeches were often exchanged antiphonally among the aye-ayes at the DUPC. In our captive setting we were not able to correlate structural variation in screeches with particular contexts. However, free-ranging aye-ayes tended to use brief tonal screeches ('eeps') in affiliative contexts (e.g. during close-contact foraging, just prior to moving to a new location) and brief noisy screeches ('aacks') in potentially aggressive contexts (e.g. maintaining interindividual distances). Low-amplitude emissions of 'aacks' were heard particularly during the breeding season when many individuals are in close proximity. In the field, screech duration and amplitude appeared to be correlated with interindividual distances: the greater the distance between callers, the longer and louder were their screeches.

Sterling observed additional aye-aye vocalizations in the field that we did not hear at the DUPC. One of these is the 'hai-hai' call from which *Daubentonia* gets its common name. This loud, two-part vocalization was given by individuals as they fled rapidly out of their nests during capture attempts. Individuals also were heard to produce a vocalization that sounded like the 'whirring' of a fishing reel during casting. This call was heard during feeding and sometimes when captured individuals were reviving from anesthesia.

Infant Vocalizations

Five call types were recorded from the captive infant (fig. 3, table 2), some of which were also given by the adults. All call types were recorded from the infant shortly after its arrival at the DUPC (approx. 1–2 months of age). Screams, pleas and sneezes were produced in the same contexts as the adults gave them, although the infant's calls were more variable in structure and intermediates between some call types occurred (fig. 3). Many of the infant's screams (fig. 3a, b) were strongly amplitude-modulated (pulsed), which would increase their localizability [22, 23]. Two call types not heard in the adults were given by the infant: grunts (fig. 3o, p) consist of a single broadband spike that is followed by a low-frequency tonal component. As in other lemur taxa that produce this call (e.g. *Varecia*

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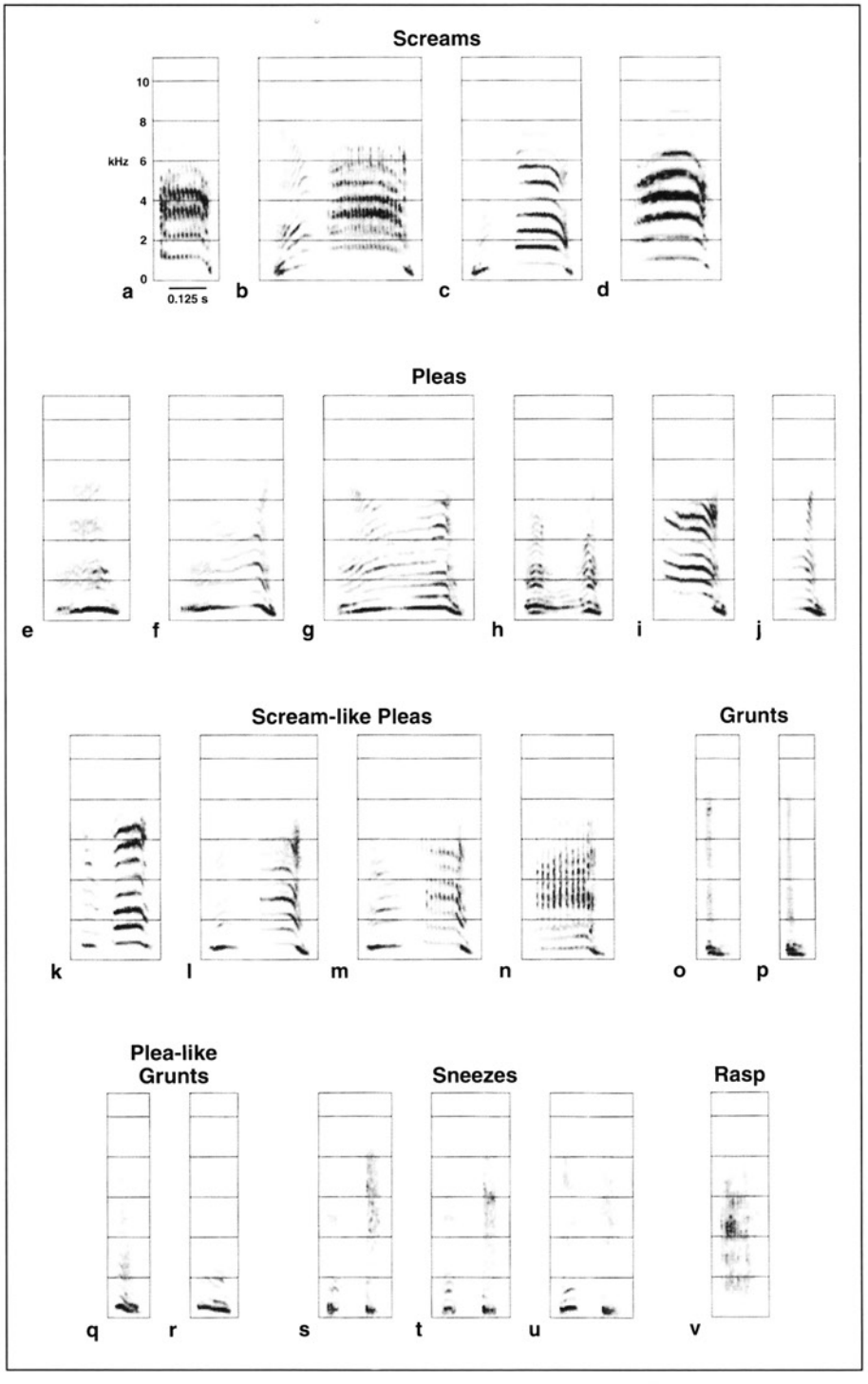

Fig. 3a–v. Vocalizations of an infant aye-aye.

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Table 2. Measurements for infant aye-aye vocalizations

A. *Screams and pleas*

Call type	n	Duration	Peak frequency	Frequency/energy distribution			Fundamental frequency				
				strongest	second	third	start	peak	low	end	start-to-peak
Single-unit screams	13	216 (10)	6,095 (287)	3,199 (237)	2,732 (359)	1,813 (377)	1,072 (18)	1,176 (21)	413 (20)	416 (21)	29 (11)
Double-unit screams	20	339 (10)	7,488 (106)	563 (17)	2,048 (358)	3,404 (506)	363 (32)	706 (17)	332 (26)	597 (30)	57 (9)
Unit 2				3,454 (182)	3,152 (265)	3,727 (338)	732 (22)	861 (17)	250 (15)	255 (15)	54 (12)
Pleas	13	248 (24)	7,396 (24)	911 (241)	2,939 (310)	2,678 (435)	425 (64)	663 (34)	174 (9)	228 (18)	110 (28)

B. *Grunts and sneezes*

Call type	n	Call duration	Peak frequency	Interunit duration	Unit duration	Major energy distribution	
						high	low
Grunts	13	63 (5)	7,108 (528)	n/a	n/a	692 (37)	167 (11)
Sneezes	10	196 (52)	7,860 (269)	82 (4)	1: 50 (5)	571 (32)	199 (18)
					2: 64 (3)	703 (71)	139 (9)

Double-unit scream duration data: unit 1: 87 (7); unit 2: 224 (10); interunit interval: 28 (17). For explanations, see table 1. n/a = not applicable.

and *Indri* [24]), grunts appear to express aggravation. Free-ranging adult aye-ayes have been heard to emit grunts as well. Secondly, a call we have labeled a 'rasp' (fig. 3v) was heard only once and occurred within a bout of screams and sneezes while the infant was restrained for examination.

Discussion

Prior to this report, only 3 types of sounds had been described spectrographically for aye-ayes. Petter and Petter [4] and Petter and Dominique [25] reported a 'creee' vocalization that seemed to function both as a long-distance vocalization and as an antiphonal-exchanged 'mother-infant cohesion call'. The 'creee' corresponds to our screech. The 'roo-tint' or 'ron-tsi' was given in response to disturbances by human observers, and this call corresponds to our sneeze. Finally, a 'hissing sound', corresponding to our snort, was described as being emitted by individuals who seemed agitated.

With only the 6 adult call types described here, plus 3 more types heard in the field, the aye-aye appears to exhibit a relatively small vocal repertoire for a primate. Given that most sightings of aye-ayes in Madagascar

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have been of solitary animals [4, 13] and that other nocturnal lemur species also have small vocal repertoires in captivity (*Microcebus:* 8 call types: *Mirza:* 10 call types; *Cheirogaleus:* 12 call types [26, 27]) in comparison to the diurnal species (recorded in the DUPC forested enclosures: 14 or more call types for *V. variegata* [28; Morland and Balko, pers. commun.]; 22 call types for *Lemur catta* [29]), a repertoire of 9 call types does not seem unusually small for a nocturnal prosimian.

When considering the enormous acoustic variation in the aye-aye's screech (fig. 1f–m) and the diversity of contexts in which it is emitted, it seems possible that this vocalization subsumes functions performed by several spacing-related calls in the vocal repertories of other nocturnal primates. It remains for future research to determine the precise relationships between structure and function in the aye-aye's screech and, hopefully, to gain some insight into why this species is unique among the lemurs in having evolved such a highly variable contact call.

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