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PROBOSCIS MONKEYS (*NASALIS LARVATUS* (WURMB, 1787)) HAVE UNUSUALLY HIGH-PITCHED VOCALIZATIONS

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ABSTRACT. **–** According to qualitative descriptions, proboscis monkeys have high frequency vocalizations, but no technical analysis of the calls is available because the species is rare, difficult to study in the field, and few zoological institutions have breeding populations. Here we analyse the high pitch vocalizations of captive proboscis monkeys in the Singapore Zoological Gardens. The monkeys produce very high frequency tonal vocalizations ranging from 1.4 kHz to 6.8 kHz. The calls are produced during acts of aggression or used as alarm calls and the pitch is higher than expected based on a comparative study for such a large primate. We discuss that the high frequency may be an adaptation for predator avoidance (crocodiles) and/or communication in dense vegetation.

KEY WORDS. **–** Primate calls; vocal communication; communication; Colobine; spectrograms; high frequency.

INTRODUCTION

The vocalizations of a large number of primate species have been studied since the early 1960s. Most major clades of primates have been well covered and species such as *Saimiri sciureus* (Linnaeus) (Biben & Symmes, 1986; Symmes & Goedeking, 1988; Boinski & Mitchell, 1997), *Callithrix pygmaea* (Spix) (Pola & Snowdon, 1975; de la Torre & Snowdon, 2009), *Macaca fuscata* (Blyth) (Masataka, 1983; Inoue, 1988), *Macaca mulatta* (Zimmermann) (Rowell, 1962; Hauser, 1993a), *Chlorocebus aethiops* (Linnaeus) (Owren & Bernacki, 1988; Brown *et al.*, 1992) and *Lemur catta* Linnaeus (Macedonia, 1986; Macedonia, 1993), are very well studied. However, the calls of the species in the species-rich clade of leaf monkeys (>32 species) remain poorly known, with detailed studies only available for four species, i.e., *Trachypithecus johnii* (Fischer), *Semnopithecus entellus* (Dufresne), *Presbytis thomasi* (Collett), and *Rhinopithecus roxellana* (Milne-Edwards) (Gurmaya, 1986; Hohmann, 1988; Tenaza et al., 1988; Wich et al., 2008). In particular, the odd-nosed leaf monkeys (Sterner et al., 2006) comprising nine species in four genera (IUCN Red List 2008) have been largely ignored (except for *Rhinopithecus roxellana*: Tenaza et al., 1988; Clarke, 1990). Often rare and shy, studying these leaf monkeys in the field presents major challenges. Since their ecology makes it likely that they rely heavily on vocal communication, studying their vocalizations could yield valuable contributions to the field of primate communication. Given the problems with studying leaf monkey vocalizations in the field, using captive populations is an alternative that can provide useful information about the species. This approach has the additional advantage of yielding high-quality recordings that can be analysed using quantitative techniques.

Proboscis monkeys (*Nasalis larvatus*) are arboreal leaf-eating monkeys that are found in Borneo, Brunei Kalimantan (Indonesia), Sabah, and Sarawak (Malaysia) where they inhabit swamp and mangrove forests (Bennet & Sebastian, 1988; Sha et al., 2008) (IUCN Red list 2008). A first and brief qualitative description of the vocalizations can be found in Kawabe & Mano (1972). The study discusses several vocalizations as being of high frequency. However, a quantitative description of the vocalizations has yet to be published and proboscis monkeys have thus been excluded from comparative studies of primate vocalizations. If confirmed, high frequency calls would be intriguing because among primates Hauser (1993b) documented a negative correlation between primate body mass and the frequency of vocalizations. *Nasalis larvatus* has a body mass of over 20 kg and is the largest species of colobine monkeys (Fig. 1; Murai, 2006; Smith & Cheverud, 2002). Here we describe the vocalizations of captive proboscis monkeys from the Singapore Zoological Gardens. Specifically, we analyzed the tonal calls, i.e., the vocalizations in which harmonics are integral multiples of the fundamental frequency.

METHODS

Recording of Vocalizations. **–** The study subjects were a family of two adult proboscis monkeys (one male and one female) and two juveniles kept in a single cage in the Singapore Zoological Gardens. The vocalizations were recorded during a two-month period (Jan – Feb.2010) between 1000–1700 hours using SongMeter 2.0 (Wildlife Acoustics Inc., Concord, MA) with 16-bit precision and a sampling rate of 48 kHz. The recording device was placed 2 m away from the cage. In order to distinguish the calls of the proboscis monkeys from ambient noise, the timing of each call was noted. This enabled the identification of the calls upon playback to the observer. This was done as the location of the captive setting was such that the calls could be mixed with the calls from the neighboring primate cages, or bird calls. We noted the behavioral context of the vocalizations of interest. The aspects noted included whether the individual responded to a threat/surprise ("alarm"), whether the individual was engaged in play ("aggression"), whether the call was food associated or any other behavior that may have been associated with the call. Other calls, such as low frequency calls, and associated behaviors were excluded from this study.

Analysis of the recordings. **–** SongScope 3.0 (Wildlife Acoustics Inc., Concord, MA) was used to analyse and identify the vocalizations. In order to measure the fundamental frequency values, we used PRAAT (Boersma, 2001) which includes two algorithms (auto-correlation, and cross correlation) for drawing the contours for the fundamental frequency of a call in a spectrogram. Both methods were tested for a subset of the data, and it was found that the autocorrelation algorithm detected the pitch of the calls better, and thus it was used henceforth. The parameters for the spectrogram analysis were as follows: window length 0.005 s, dynamic range 40 dB and frequency range 0–20kHz. The minimum, maximum and mean fundamental frequencies for each call were recorded. For noisy and complex vocalizations with strong tonal components, we characterized the lowest dominant frequency band to determine the pitch.

Fig. 1. A male proboscis monkey in the Singapore Zoological Gardens.

Jackknifing. **–** In our study we obtained 101 calls. Since most studies of primate vocalizations are based on a larger sample size [1000–10,000 calls, eg. *Lagothrix lagotricha* (Humboldt) (Casamitjana, 2002), *Rhinopithecus roxellana* (Clarke, 1990), *Cercopithecus campbelli* Waterhouse (Ouattara et al., 2009)], we were concerned whether our study yielded sufficiently robust data for obtaining reliable results. We thus performed a jackknife analysis (100 replicates). The premise behind such an approach is that, should a subset of the data set yield same results as the whole data set, no additional sampling would change the overall results. For each jackknife replicate we randomly removed e^{-1} (37%) of the sample as recommended for jackknife analyses in phylogenetics (Farris et al., 1996; Table 2). For each replicate we recorded the means, minima and maxima of vocalization frequencies. We used a t-test to test for comparing the distribution of each jackknife replicate with the distribution of original dataset.

RESULTS AND DISCUSSION

Twenty-eight hours of recording generated 211 vocalizations with complete spectrographic structures including 101 high pitch calls. These calls were made by the adults and juveniles. However, our conclusions pertain mainly to adult females and juveniles because they were the source of most calls. The high-pitched calls were similar to the "shriek" and certain other nasal vocalizations described by Kawabe & Mano (1972). They are associated with two types of situations encountered in captivity, i.e., "alarm" or "aggression". We considered the calls as "alarm calls" when they occurred in response to the sudden appearance of a human or a loud noise. This noise could originate from zoo visitors or animals (e.g., clanking sound from a nearby primate cage). These calls were also heard when the monkeys were excited during play and/or when an individual saw another primate or human in his vicinity and responded by approaching the cage boundary ("aggressive behaviour"). The mean pitch of these vocalizations range from 2.3 kHz to 6.1 kHz. The maximum frequency of the vocalizations varied from 2.7 kHz to 6.8 kHz (Table 1; see spectrogram in Fig. 2). These results are stable as revealed by the jackknife resampling regardless of whether all replicates were used or the extremes were removed (ca 6.5–6.7 kHz, see Table 2). None of the 100 jackknife replicates yielded a distribution that was significantly different from the original distribution based on all calls ($p>0.05$).

Table 1. Characteristics of the high-pitched vocalizations of *Nasalis larvatus*.

Feature	Low frequency limit	High frequency limit	Mean frequency of spectrogram
Average (Hz)	3307	4708	4020
Minimum (Hz)	1402	2681	2271
Maximum (Hz)	5666	6835	6145

Table 2. Jackknife analysis of the vocalizations: Low and high frequency limits of high-pitched vocalizations based on all replicates (a) and after removal of replicates with the 5% (b) or 10% (c) most extreme readings.

Characteristic of vocalization	(a) all replicates	(b) 95% cut-off	(c) 90% cut-off
Low frequency limit (Hz)*	1678	1668	1555
High frequency limit (Hz)*	6495	6743	6743

Approximately 10% of the 101 vocalizations had a maxima of >6 kHz and 35% had maxima >5 kHz (Fig. 3). These results support the previous, qualitative observation by Kawabe and Mano (1972) that the proboscis monkeys can vocalize at high frequencies. The high frequency limit of the vocalizations of proboscis monkeys is particularly interesting given its body size. A comparative study analysing the relationship between the fundamental frequency of vocalization and body size across nonhuman primate species found a negative correlation between high frequency limit and body size (Hauser, 1993b). Based on this correlation, a primate species with the body mass of *N. larvatus* (15.1 kg: Milton and May, 1976) would be expected to have a maximum frequency of vocalization of ca. 2 kHz. Even when the female body mass (10 kg) is considered, the expected maximum would be 2.3 kHz. Note, however, Hauser (1993b) used only adult vocalizations for his correlation study while we include juvenile vocalizations in our analysis because we lack information on which calls came from which individual. Fortunately, this does not affect our conclusion because all calls (including those of adults) were >2 kHz and most >3.5 kHz (Fig. 3). Future studies should nevertheless try to analyse the calls of adults and juveniles separately and focus on the high-pitched calls of the adult males.

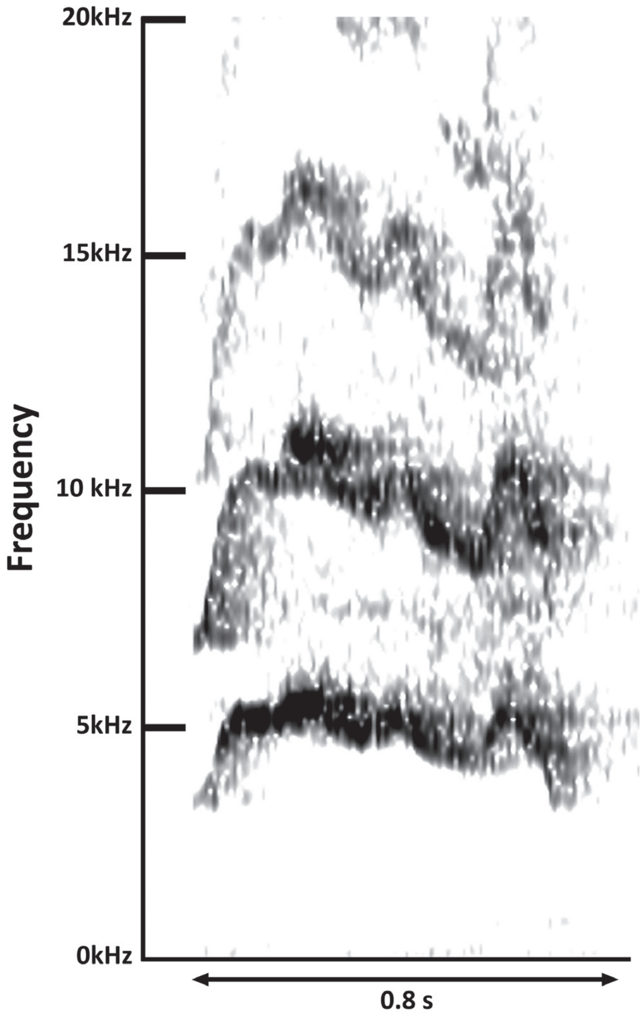

Fig. 2. A sample spectrogram of a high frequency vocalization of the proboscis monkey, *Nasalis larvatus*, that shows the harmonic structure of these calls. The fundamental frequency of this call ranges from 3.4–5.4 kHz and the mean frequency is 4.9 kHz.

The finding of unusually high-pitched vocalizations raises the question of their adaptive significance. We here consider two possible functions; i.e., predator avoidance and communication in a dense forest environment. Predator avoidance is a potential explanation especially if the frequencies can be shown to lie beyond the frequency range of the best hearing of relevant predators (Snowdon & Hodun, 1981). One of the main predators of proboscis monkeys is crocodiles, *Tomistoma schlegelii* (Müller) (Galdikas, 1985). Proboscis monkeys are known to sleep near river banks and

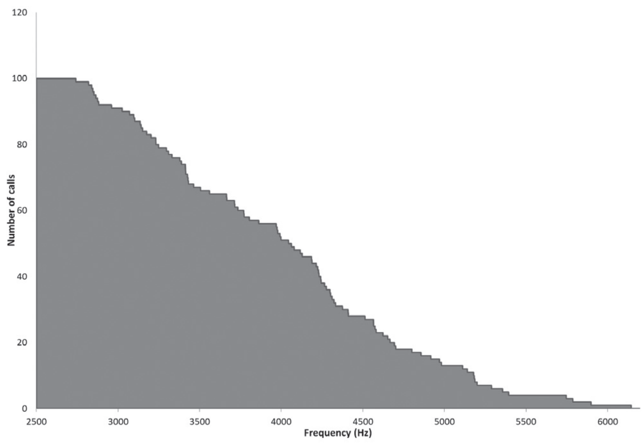

Fig. 3. Cumulative curve of mean frequencies of calls in the study. Graph omits the one call that has a frequency <2.7 kHz.

occasionally venture into the river (Galdikas, 1985); thus, they are exposed to predation by crocodiles. One defense mechanism are group movements across the river (Yeager, 1991) but another may be the use of high-pitch vocalizations which allows the monkeys to warn kin of danger without alerting crocodiles whose maximum auditory sensitivity lies between 0.3–2 kHz (Wever, 1971). Of course, this comes at the expense of not being able to use these vocalizations to harass the predator which, however, would not be adaptive while being within striking range of crocodiles. Another major predator of proboscis monkeys is the predominantly nocturnal clouded leopard *Neofelis diardi* (Cuvier) (Matsuda et al., 2008) and behavioural adaptation such as sleeping near river banks has been discussed in the literature as a predator avoidance mechanism (e.g. Matsuda et al., 2008). Unfortunately, no information is currently available for the hearing limits of this species. We are thus unable to determine whether the vocalizations of the proboscis monkey are outside of the frequency range of this predator.

A second factor that may explain the high frequency vocalizations in proboscis monkeys is their habitat, as acoustic communication can be challenging in forest environments (Waser & Waser, 1977). High frequency vocalizations have the advantage of being distinct from ambient environmental sounds (Snowdon & Hodun, 1981) and this can be particularly useful in dense vegetation, where high frequency tonal vocalizations retain their discernable nature. Because high frequency sounds attenuate at much shorter distances than low frequency sounds, animals which require communication over long distances generally use low-frequency vocalizations (Fletcher, 2010). But high-pitched calls can be used as alarm calls because the distances between monkeys are generally small. For long-distance communication, other types of calls may be used as suggested by certain low frequency calls by the males (see Fig. S1).

Now that the high frequency nature of captive proboscis monkey vocalization has been confirmed in a technical analysis, it would be important to conduct further field and zoo research that could reveal the precise use of the vocalizations. For example, in order to better characterise the vocalizations and understand the functions of these high frequency vocalizations, playback studies should carried out. It is also important to note that calls in captive conditions may not be fully representative of calls used in wild. Future studies should also use a larger number of individuals in order to address age- and sex-specific differences and their relationships to size.

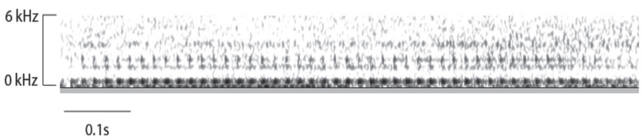

Fig. S1. Spectrogram of Call 2: Low frequency vocalization produced by adult male.

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