Ultrasonic Vocalizations by the Spectral Tarsier, *Tarsius spectrum*

Sharon Gursky

Department of Anthropology, Texas A&M University, College Station, Tex., USA

Key Words

Ultrasonic vocalizations · Communication · Sulawesi · Prosimian · Haplorhine · Indonesia

Abstract

Although the vocalizations of spectral tarsiers have been studied for over 3 decades by numerous primatologists, the data in this paper represent the first evidence that this species communicates in the ultrasonic range. In addition, this paper characterizes the types of ultrasonic vocalizations by spectral tarsiers, *Tarsius spectrum*. Data were collected at Tangkoko Nature Reserve in Sulawesi, Indonesia, from January through April 2013. Recordings were made on a Wildlife Acoustics Ultrasonic Song Meter BAT2 from 10 groups of varying sizes and compositions. The ultrasonic recorder was placed at the base of the group's sleeping tree and recorded from 5.00 to 7.00 h using an omnidirectional microphone. The ultrasonic vocalizations fell into 5 main categories: chirps, twitters, choruses, doubles and whistles. Chirps were the most frequent ultrasonic vocalizations, followed by twitters, choruses, doubles and then whistles. While chirps, twitters and choruses extended from the audible to the ultrasonic range, the doubles and whistles were pure ultrasound. Currently, the function of these ultrasonic vocalizations is not yet clear and requires additional research.

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Introduction

Over the last several decades, primatologists have made tremendous strides in studying the behavior of the nocturnal primates [Harcourt and Nash, 1986; Bearder, 1999; Radespiel et al., 2003; Pimley et al., 2005; Gursky, 2007; Nekaris and Bearder, 2011]. One of the easiest modes of behavior to study among the nocturnal species has been their vocal communication system. Consequently, more attention has been giv-

en to their vocalizations than to other harder-to-study aspects of their behavior [Zimmermann and Lerch, 1993; Zimmermann et al., 2000; Ambrose, 2003; Becker et al., 2003; Merker and Groves, 2006; Rovero et al., 2006; Bearder, 2007; Braune et al., 2008; Méndez-Cárdenas and Zimmermann, 2009; Hilgartner et al., 2012; Kappeler, 2012; Ramsier et al., 2012; Gursky-Doyen, 2013]. In addition to providing a clearer understanding of taxonomy, the vocalization studies of the nocturnal primates have also been useful for understanding various aspects of predation [Gursky, 2006], mating behavior, territoriality and even paternity [Kessler et al., 2012].

The majority of these vocalization studies have focused their attention on various forms of loud calls. For example, acoustic studies of the tarsiers have predominantly focused on the duet call [MacKinnon and MacKinnon, 1980; Niemitz, 1984; Gursky, 1997, 2007; Nietsch and Kopp, 1998; Nietsch, 1999; Merker and Groves, 2006]. The duet call, which is in reality a family chorus, not only transmits the relative location of the signaler, but the call can be easily heard from the range of neighboring tarsier groups (300–500 m away). The duet call has been interpreted to be the principal means by which spectral tarsier groups reunite in the morning after a night of foraging, as well as advertising the integrity of the social group to neighboring groups [MacKinnon and MacKinnon, 1980; Niemitz, 1984; Gursky, 2007].

In all the previous studies of the duet call [MacKinnon and MacKinnon, 1980; Niemitz, 1984; Nietsch, 1999], the frequency range of the call has been limited to 0–20,000 Hz. This is in part a reflection of the fact that most acoustic recording devices only record to this upper frequency, but also reflects the fact that humans are incapable of hearing vocalizations above this level. Several recent studies suggest that the previously noted upper range of the duet call may in fact be an artifact of the limitations of the recording equipment and the human ear. For example, Ramsier et al. [2012] recently noted that Philippine tarsiers are not only capable of hearing frequencies as high as 90 kHz, but they have been recorded emitting vocalizations as high as 80 kHz [Ramsier et al., 2012; Gursky-Doyen, 2013].

The goal of this paper is to demonstrate that spectral tarsiers, *Tarsius spectrum*, (aka *Tarsius tarsier*) also utilize ultrasonic vocalizations while conducting their morning vocalizations (duets). The secondary goal of this paper is to remind primatologists that not all vocalizations fall within the range of human hearing as well as to present some new avenues for future study.

Methods

The island of Sulawesi is the largest island of the biogeographical region of Wallacea, a transition zone between the Australian and Asian zoogeographical regions [Audley-Charles, 1981; Whitmore, 1987]. Consequently, Sulawesi shows a blend of Asian and Australian elements in its fauna and flora. Sulawesi also exhibits very high levels of endemic species. Sulawesi is the home of more than 260 bird species, 80 of which are endemic. Of the 127 indigenous mammals, 79 (62%) are endemic [Musser, 1987]. Endemic species include: anoa *Bubalus depressicornis*, macaque *Macaca nigra*, spectral tarsier *Tarsius spectrum* and babirusa *Babirusa babirusa*.

I conducted this study at Tangkoko Nature Reserve on the easternmost tip of the northern arm of Sulawesi. The reserve exhibits a full range of forest types, including beach formation forest, lowland forests, submontane forests and mossy cloud forests on the summits of the Tangkoko crater [MacKinnon and MacKinnon, 1980; Whitten et al., 1987; Gursky, 1997]. The reserve is far from pristine due to heavy selective logging and encroaching gardens along its borders. The forest canopy is very discontinuous and contains a high proportion of *Ficus* trees [Gursky, 1997,

1998]. Rainfall averaged approximately 2,300 mm annually, with most rainfall occurring between November and April [World Wildlife Fund, 1980; Gursky, 1997]. Additional details concerning the habitat type at Tangkoko Nature Reserve can be found in Gursky [1997, 2007].

The following procedures were used to locate groups. Prior to dawn, my field assistant and I would stand on the periphery of a 1-ha plot. Plots were chosen randomly (following a block design) within the 1 km² of the trail system at Tangkoko Nature Reserve. As the tarsiers returned to their sleeping site, or at their sleeping site, they gave loud vocal calls for 3–5 min that could be heard from 300–500 m [MacKinnon and MacKinnon, 1980; Niemitz, 1984]. All groups that were heard vocalizing were then followed to their sleeping site. My field assistant and I then returned to the sleeping site prior to dawn the following morning to set up the recording device and microphone in an inconspicuous location near the sleeping tree. Groups residing in sleeping trees with no bats or tree shrews were specifically chosen to ensure that the ultrasonic vocalizations of only the spectral tarsier were recorded. Additionally, I am confident that the ultrasonic calls that were recorded were in fact given by tarsiers because ultrasonic calls attenuate quickly and over very short distances, and no other organisms besides the tarsiers were observed at the sleeping trees during the recording of the calls. In addition, all 5 vocalizations reported in this paper were recorded from all 10 spectral tarsier groups. It is unlikely that another organism was present and recorded emitting ultrasonic vocalizations at all 10 spectral tarsier sleeping trees.

The vocalizations were recorded on a Wildlife Acoustics Ultrasonic Song Meter BAT2. This passive ultrasonic recorder sampled data at a rate of 192 kHz and recorded with 16-bit resolution. The time resolution for the analysis is 1.3 ms (256 points divided by 192,000 points/s), and the frequency resolution is 750 Hz (= 1/time resolution). An omnidirectional ultrasonic vocalization microphone was attached to the Wildlife Acoustic Song Meter BAT2. The recordings consisted of a single file that contained many different calls. The calls were extracted from the large files, so they could be analyzed individually using BatSound 4.0. The batch-processing tools within this software were used to automatically identify individual vocalizations. Vocalizations were considered individual if more than 5 ms passed between recordable sound [Cui, 2002]. The batch-processing tools were then used to measure the minimum fundamental frequency, maximum fundamental frequency, peak frequency at the start point and end point, as well as the duration of each vocalization. The frequency range of the spectrographic analysis conducted using the batch-processing tools was 0–96 kHz. Vocal recordings were made from 10 spectral tarsier groups between January and April 2013.

Study Species

The spectral tarsier is a small nocturnal primate found exclusively on the island of Sulawesi, Indonesia. Although most groups exhibit a monogamous social system, a few exhibit a polygynous social system [Gursky, 1994, 1995]. They are known to exhibit long-term relationships with the same individual [Gursky-Doyen, 2010] but are also known to engage in occasional extra-pair copulations. The mating season is in May and November. Spectral tarsiers have a 191-day gestation period that is followed by a 78-day period of lactation. The mean interbirth interval is 12.7 months. Births are seasonal, with most occurring in April/May and a few in November/December [Gursky, 1997]. Infants are not continuously transported by the mother or other group members following birth. Rather, they adopt a cache-and-carry infant caretaking strategy. Spectral tarsier infants are transported in the mother's mouth and then parked on branches while the mother forages nearby [Gursky, 1997]. They are highly insectivorous, eating a wide variety of insects, but with a preference for orthopterans and lepidopterans [Gursky, 2000]. Spectral tarsiers at Tangkoko Nature Reserve are extremely territorial. They give early-morning family choruses, scent-mark preferentially along the boundaries of their territory and regularly engage in territorial disputes with neighboring groups. Consequently, they exhibit minimal overlap between neighboring territories [Gursky, 2003]. Spectral tarsier home ranges vary from 1.6 to 4.1 ha with an average of 2.3 ha for females and 3.1 ha for males [Gursky, 2003]. Spectral tarsiers also exhibit a tremendous amount of site fidelity. Both males and females are known to disperse from the natal territory, but males usually disperse much further and at an earlier age [Gursky, 2007; Gursky-Doyen, 2010]. Spectral tarsiers at Tangkoko Nature Reserve primarily utilized strangling *Ficus* trees for their sleeping sites [MacKinnon and MacKinnon, 1980; Gursky, 1997]. Most ranges contained 1–3 sleeping sites, but 1 site was used preferentially.

Fig. 1. Spectrographic illustrations of vocalizations given by spectral tarsiers, *T. spectrum*.
a Ultrasonic chirp.

Table 1. Acoustic characteristics of the ultrasonic vocalizations given by the Sulawesi tarsier *T. spectrum*

Variable	Vocalization				
	chirp	twitter	double	chorus	whistle
Frequency, kHz					
Mean	36	43	35	45	45
Maximum	80	71	35	80	80
Minimum	20	20	25	20	20
Mean duration, ms	1	162	5	625	350
Vocalizations, n	66,220	35,569	13,813	16,291	3,543

Results

A total of 10,707 min (178.45 h) of vocal recordings were obtained during this study. During this time frame, 143,898 vocalizations were produced above 20,000 Hz (table 1). This amounts to approximately 13.44 ultrasonic vocalizations every minute.

The ultrasonic vocalizations fell into 5 main categories that I am referring to as chorus, chirp, twitter, double and whistle. Chirps, twitters and choruses have both audible and ultrasonic components (albeit only the ultrasonic component is presented in this paper), whereas the doubles and the whistles are pure ultrasound. Approx-

Fig. 1. Spectrographic illustrations of vocalizations given by spectral tarsiers, *T. spectrum*.
b Ultrasonic twitter.

imately 8,000 calls were too variable to be placed into any category and thus are not presented in this paper. Chirps were the most frequent ultrasonic vocalization (fig. 1a). The total number of chirps emitted was 66,220. The mean duration for the chirps was 1 ms (SD 1.63) and ranged from 1 to 16 ms. The average frequency for the chirp was 36 kHz (SD 11.78) and ranged from 20 to more than 80 kHz.

The next most frequent class of ultrasonic vocalization given by the spectral tarsier was the twitter (fig. 1b). The total number of twitters emitted was 35,569. The mean duration of the twitter was 162 ms (SD 18.27) and ranged from 34 to 416 ms. The average frequency for the twitter was 42 kHz (SD 8.22) and ranged from 20 to 71 kHz.

Fig. 1. Spectrographic illustrations of vocalizations given by spectral tarsiers, *T. spectrum*.
c Ultrasonic chorus.

The next most frequent class of ultrasonic vocalization given by the spectral tarsier was the chorus (fig. 1c). The total number of choruses emitted was 16,291. The mean duration of the chorus was 625 ms and ranged from 70 to 915 ms. The average frequency for the chorus was 45 kHz and ranged from 20 to 80 kHz.

The next most frequent class of ultrasonic vocalization, and the most frequent pure ultrasonic vocalization given by the spectral tarsier was the double (fig. 1d). The total number of doubles emitted was 13,813. The mean duration of the double was 5 ms and ranged from 1 to 30 ms. The average frequency for the double was 35 kHz and ranged from 25 to 45 kHz.

Fig. 1. Spectrographic illustrations of vocalizations given by spectral tarsiers, *T. spectrum*.
d Ultrasonic double.

The least frequent ultrasonic vocalization, but a pure ultrasonic vocalization with the longest duration and highest frequency emitted by the spectral tarsiers, was the whistle (fig. 1e). The total number of whistles emitted was 3,543. The mean duration of the whistle was 350 ms (SD 12.25) and ranged from 250 to 520 ms. The average frequency for the whistle was 45 kHz (SD 15.27) and ranged from 20 to 80 kHz.

Fig. 1. Spectrographic illustrations of vocalizations given by spectral tarsiers, *T. spectrum*.
e Ultrasonic whistle.

Discussion

The results of this preliminary study clearly demonstrate that spectral tarsiers, like their sister species the Philippine tarsier, *Carlito syrichta*, vocalize outside the range of human hearing [Gursky-Doyen, 2013; Ramsier et al., 2012]. Specifically, this study demonstrates that the spectral tarsier uses two purely ultrasonic vocalizations within its morning duets and that much of the morning chorus extends from the audible range into the ultrasonic range.

Five different types of ultrasonic vocalizations were recorded. This is almost twice the total number of ultrasonic vocalizations that were observed as given by the

Philippine tarsiers. The greater number of ultrasonic vocalizations used by the spectral tarsier might reflect the greater social complexity exhibited by this species relative to the Philippine tarsier; vocal complexity has been linked to social complexity in numerous birds and mammals [Bergman, 2010].

At one level, the use of ultrasonic vocalizations by spectral tarsiers is not surprising. One of the most common antipredator strategies for the strepsirrhine primates is crypsis [Fichtel, 2007; Gursky and Nekaris, 2007]. Given that alarm calling often helps predators identify the location of their prey, using vocalizations that might be outside the range of hearing of the potential predator might work as another strategy to maximize their cryptic behavior [Klump and Shalter, 1984]. That is, by calling outside the hearing range of the potential predator, the spectral tarsier can effectively communicate with its conspecifics without the predator being able to discern the call. This is effectively a 'silent signal'. Unfortunately, it is not presently known whether the main predator species that prey on tarsiers – monitor lizards (*Varanus indicus*), snakes (*Python reticulatus*), the Malaysia civet (*Viverra zibetha*), and various birds of prey, including falcons (*Falco* spp.) – can hear at these frequencies [Gursky, 2006]. However, it is known that domestic dogs, coyotes, red foxes and the domestic cat are all capable of detecting frequencies as high as 48 kHz while most falcons, eagles and owls are insensitive to frequencies exceeding 15 kHz [Klump, 1986]. Thus, it is possible that the civet predators of tarsiers can detect the ultrasonic vocalizations (assuming they are close enough) while it is less likely that the birds of prey can detect these ultrasonic calls.

However, although the spectral tarsier is known to use crypsis as an antipredator strategy, it is also known to use other antipredator strategies including mobbing the predator [Gursky, 2007]. Spectral tarsiers are known to mob snakes, large birds of prey and civets. While this is an effective strategy for the most part, a mobbing spectral tarsier was captured by a mobbed predator (snake) [Gursky, 2007]. Thus, the ultrasonic vocalization as an antipredator strategy is in direct contrast to their mobbing antipredator strategy. That is, while mobbing helps the predator identify the precise location of the tarsier, ultrasonic vocalizations may prevent the predator from identifying where the tarsier is positioned.

Although this study has shown that spectral tarsiers use ultrasonic vocalizations, future studies will be necessary to demonstrate if they also use ultrasonic vocalization for specific functions. Most species do not use ultrasonic vocalizations for long-distance communication, but to communicate with nearby conspecifics. This is because high-frequency calls attenuate very quickly and cannot be transmitted very far [Catchpole and Slater, 1995].

Clearly more research on ultrasonic vocalization in nocturnal primates is warranted. In particular, it would be useful to learn whether the spectral tarsiers emit ultrasonic vocalizations throughout their nightly activity, and whether they use ultrasonic vocalizations when they encounter natural predators. Research also needs to be conducted on the vocalizations of the Bornean tarsier, *Cephalophacus bancanus*. Although Crompton and Andau [1986] did observe occasional vocal choruses during the night, they rarely heard this species vocalize. Thus, it is possible that Bornean tarsiers also communicate outside the range of human hearing. Another interesting avenue for future research concerns whether nocturnal primates use ultrasonic vocalizations to help them distinguish conspecifics from other closely related species.

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