

**Vocal Repertoire of White-faced Sakis (*Pithecia pithecia*)**

**by**

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1995**

**Submitted to the Faculty of the Graduate School of  
Eastern Kentucky University  
in partial fulfillment of the requirements  
for the degree of  
MASTER OF SCIENCE  
December 2007**

## **ACKNOWLEDGMENTS**

I would like to thank and dedicate this thesis to my mother, Carol Anderson. Without her help and encouragement through the years, I would not be who I am today. I would also like to thank my committee members, Gary Ritchison, Charles Elliott, and Paul Cupp, for their input and assistance. I would like to thank Pat Calie for his support and encouragement, Margaret Lane and the staff at Academic Computing for the assistantship they created for me, and friends and family, all who have believed in me. I am grateful to Marilyn Norkonk of Kent State University for the guidance in the field. I am also grateful to Robert Mitchell of Eastern Kentucky University for use of his library.

Funding for this project was provided by the Eastern Kentucky University Department of Biological Sciences and the Explorers Club of New York, New York. Additional funding came from private sources.

## ABSTRACT

Little is known about the vocal behavior of Pitheciine monkeys and, specifically, of white-faced sakis (*Pithecia pitecia*). The objective of my study was to examine the vocal behavior of a free-living population of white-faced sakis in Venezuela and, specifically, to describe their vocal repertoire, ascertain call function, and examine possible relationships between call function and structure. Vocalizations of white-faced sakis were recorded on Isla Redonda, Lago Guri in Bolivar State, Venezuela, from 28 May-31 June 1999, and in captivity at the Cincinnati Zoo and Botanical Garden on 29 January and 11 March 1999 and at the Pittsburgh Zoo on 13-14 February 1999. On Isla Redonda, vocalizations were recorded using a cassette recorder with either a parabolic or directional microphone and the behavioral context, distance from other sakis, and the sex of the calling individual were noted. Sonograms of recorded calls were subsequently generated and, using differences in duration and frequency, calls were identified and categorized. I observed and recorded three adult males and four adult females on Isla Redonda for a total of 78 hours and, in captivity, recorded eight males and six females for a total of 21 hours. Analysis revealed five call groups (whistles, chucks, trills, purr, and moan and alarm calls) and 12 individual calls in the vocal repertoire of white-faced sakis. Sakis vocalized most often when within 3 m of conspecifics and when feeding, drinking, and engaged in activities such as object manipulation. In these contexts, calls were typically low volume and, as for many other species of primates, such calls apparently provide information about a caller's intentions and likely communicate an intent to behave peacefully. In addition, when a group of sakis was moving,

individuals sometimes vocalized, perhaps to help troop members remain in contact. Three calls in the vocal repertoire of white-faced sakis were uttered with greater volume than other calls. Similar loud calls have been reported in many other species of primates and such calls have been hypothesized to serve five possible functions, including predator avoidance, food advertisement, group coordination, mate attraction, and resource defense. The vocal repertoire of white-faced sakis (12 calls) appears to be similar in size to those of other primate species with similar group sizes. Such results support the hypothesis that vocal communication can facilitate or constrain increases in group size among primates and emphasize the importance of vocal communication in the social behavior of primate.

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## INTRODUCTION

White-faced sakis (*Pithecia pithecia*) are medium-sized diurnal monkeys found in southern Venezuela, the Guianas, and northern Brazil. They are members of the least-known family of South American primates (Pitheciidae; Kinzey 1997) and one of the least known primates in the Neotropics (Vie et al. 2001). Rowe (1996) noted that all Pithecines were either endangered or at risk.

Early research on white-faced sakis included a study of Suriname monkeys by Mittermeier (1977) that included a description of their ecology, distribution, populations densities, and conservation status. More recently, investigators have examined their food habits (Kinzey and Norconk 1990, 1993, Kinzey et al. 1990), locomotor behavior (Walker 2005), and distribution and habitat use (Vie et al. 2001). Few studies have been conducted with free-living individuals because locating and monitoring sakis is difficult (Kinzey 1997, Vie et al. 2001) and, therefore, most of what is known about their behavior is based on studies of captive individuals.

Little is known about the vocal behavior of white-faced sakis, with only one study of captive individuals (Buchanan 1978). More generally, little is known about the vocal behavior of Pithecine monkeys. Most species apparently have vocal repertoires that include high-pitched whistles used in social interactions, low volume chirp-like calls used when feeding, and loud alarm calls, but few additional details about other, less frequently-used calls, the sizes of vocal repertoires, or the possible



influence of context on the physical structure of calls are available (Moynihan 1976, Mittermeier 1977, Rowe 1996, Kinsey 1997).

Recent work on avian and mammal vocal communication (including non-primates) has focused on the selective forces that help shape the physical structure of vocal signals and create connections between context and function. Owings and Morton (1998) contended that communication was based on what it accomplished, and asserted that communication can replace fighting when individuals attempt to control access to resources. In addition, the motivational-structural (M-S) model (Morton 1977) predicts that non-human primate calls will follow two rules. Calls motivated by hostility or aggression will be low-pitched and noisy, and calls motivated by fear or appeasement will be high-pitched and tonal. This hypothesis is based on the assumptions that call frequency is inversely proportional to body mass, and larger animals are dominant to smaller ones.

Hauser (1993) attempted to apply motivational-structural rules to non-human primate vocal evolution and found a significant negative correlation between body mass and call frequency. Larger-bodied primates produced lower frequency calls and smaller primates produced higher-pitched calls. However, relationships between motivational state and call frequency were not apparent in all species, and no Pithecines were included in his study.

Given the lack of information about the vocal behavior of pithecines in the wild and the need to better understand relationships between call function and physical structure in primates, additional study is clearly needed. The objective of my study was to examine the vocal behavior of a free-living population of white-faced

sakis in Venezuela and, specifically, to describe their vocal repertoire, ascertain call function, and examine possible relationships between call function and structure.

## METHODS

Vocalizations of White-faced Sakis (*Pithecia pithecia*) were recorded in the wild on Isla Redonda (7° 46'N, 62° 53'W), Lago Guri in Bolivar State, Venezuela, and in captivity at the Cincinnati Zoo and Botanical Garden (Cincinnati, Ohio) and the Pittsburgh Zoo (Pittsburgh, Pennsylvania). The wild population was located on a 12.8-ha island created in 1984 by the damming of the Rio Caroni River and sakis on this island had been habituated to the presence of humans during 15 years of studies (Kinzey 1997). At the time of my study, the saki population on the island included one troop of five adults (two males and three females) and a one breeding pair. The saki population at the Cincinnati Zoo consisted of one adult breeding pair, and the population at the Pittsburgh Zoo included five males and six females. All individuals studied, both wild and captive, were adults. Recordings in the field were made from 28 May-31 June 1999, and recordings of captive sakis were made on 13-14 February 1999 at the Pittsburgh Zoo and on 29 January and 11 March 1999 at the Cincinnati Zoo. Animal enclosures at both zoos consisted of wire fence and concrete walls,

floors, and ceilings. Natural and synthetic perches and enrichment items were provided, and food and water were supplied daily.

In the field, a context coding system was used to record the behavior of focal individuals. Buchanan (1978) described categories of behaviors of white-faced sakis, and I used these categories to indicate the context during which vocalizations were uttered by sakis (Table 1). During observations of focal sakis, I noted the sex of the vocalizing individual and its distance from other sakis. I used four distance categories, with category 1 defined as when a vocalizing individual was close enough to another individual that physical contact could occur at the same time as the vocalization (e.g., hand touch or grooming), category 2 assigned when a calling individual was within a single leap from another individual (about 3 m), category 3 assigned when another saki was within 25 m, and category 4 assigned when the nearest saki was more than 25 m away.

Vocalizations were recorded by following sakis for 8 - 10 hours a day, five days a week. Sakis were located before waking (about 06:00) and followed by sight and sound until nesting (about 15:00). Most recordings were made from a distance of 2-4 m. After vocalizations were recorded, the context, distance from other sakis, and the sex of the individual were spoken into the microphone. Because sakis are sexually dimorphic, I noted, when possible, the sex of calling individuals. However, I was unable to identify particular individuals of the same sex because they were too similar in appearance. I noted the time at the beginning of each observation period, but did not note the specific time when each call was uttered.

Vocalizations recorded in captivity were obtained by placing either video or audio recorders outside the saki enclosures. All equipment could be seen by the sakis and no attempt was made to habituate them to the equipment. The recording equipment was placed near the enclosures with no people present. As a result, no behavioral data were collected along with the recordings.

All audio recordings were made using a Sony cassette recorder (TCM-59V, Sony, Tokyo, Japan) with either a parabolic (Dan Gibson) or a Sennheiser directional microphone. All analog audio and video recordings were digitized on a Pentium III 800-mHz computer using GoldWave software and saved as wav files at 22.1 kHz/8 bit/Mono. Waveforms and sonograms were generated from the wav files on an Apple Powerbook G4 computer using Raven software (version 1.2.1; Cornell Laboratory of Ornithology, Ithaca, NY) for Mac OS X. Using differences in duration and frequency, calls were identified and categorized using Buchanan's (1978) original classifications as a starting point. All calls of each call type that were of sufficient quality to obtain measurements were used to determine mean fundamental frequency and duration (Beeker et al. 2003). All context, sex, and proximity data for the calls identified were analyzed with using the Statistical Analysis System (SAS Institute 1999).

Table 1. Behavioral categories used to assign contexts to vocalizations given by white-faced sakis. Behaviors were described by Buchanan (1978).

<b>Category</b>	<b>Behaviors</b>
Inactive	Sitting, lying down
Locomotion	Walking, running, climbing, leaping
Alarm	Predator attack
Intergroup	Rival troop, conspecific
Heterospecific contact	Contact with non-saki species, including non-primates
<b>Social Proximity</b>	
SP-Parent-Offspring	Nursing, contact, allogrooming, lost young
SP-Social Cohesive	Greet, sniff, embrace, groom, approach
SP-Social Conflict	Open-mouth threat, pose, display, bite, lunge, flee
SP-Sexual	Present, chase, tease
<b>Solo individual</b>	
I-Food Related	Eating, drinking, carry food
I-Manipulate	Non-food object - inspect, finger, chew
I-Play	Swinging, wrestle object, splash, jumping
I-Groom	Scratch, nibble, bite, pick, hair parting, inspect

## RESULTS

The vocal repertoire of white-faced sakis was determined from 78 hours of observation and recording of three adult males and four adult females in the field. In captivity, eight males and six females were recorded for a total of 21 hours. Five call groups (whistles, chucks, trills, purr, and moan and alarm calls) and 12 individual calls were identified (Table 3). Calls ranged from simple pure tones to complex trills, and many were used in combination with other calls and in multiple contexts. All calls except the z-trill were recorded both in captivity and in the field. I identified a total of 263 calls (126 recorded in the field, and 137 in captivity), and was able to assign a behavioral context for 88 calls given by sakis in the field.

Most calls (64.8%; N = 57 of 88) were given when sakis were feeding, drinking, and engaged in solo activities, such as object manipulation. During these activities, sakis uttered see, pee, chew, cheeyeep, seeyeep, and peeyeep calls. Chuck, warbled trill, z-trill, and throat rattle calls were given by sakis when fighting, alarmed, and when providing conspecifics with information about the location of desirable food. All names of call groups and individual calls were derived or modified from Buchanan (1978), except for the z-trill described by Norconk (pers. comm.).

Table 2. Characteristics of the calls of white-faced sakis.

Call	Mean duration (sec)	Fundamental frequency (Hz) ( $\pm$ SD)	Harmonic structure and contour	Formant frequencies (Hz) ( $\pm$ SD)	Formant Structure
<b>Whistles</b>					
Pee	0.44	4758.8 $\pm$ 170.7	Single, straight	4758.8 $\pm$ 170.7, 6266.3 $\pm$ 170.1, 15766.5 $\pm$ 180.0, 17291.2 $\pm$ 89.1	Double paired
See	0.88	3282.4 $\pm$ 73.7	Flat	3282.4 $\pm$ 73.7, 7744.5 $\pm$ 72.0 14252.1 $\pm$ 89.1	Triple single, straight
Chew	0.63	3574.5 $\pm$ 61.9	Curved downward	3574.5 $\pm$ 61.9, 7450.5 $\pm$ 61.0, 14470.3 $\pm$ 121.8	Second mirrors fund. and third curved downward
<b>Chucks</b>					
Chuck	0.35	6707.6 $\pm$ 613.6	Nearly vertical slash, no modulation		
Churk	0.32	6306.7 $\pm$ 348.0	Nearly vertical slash, no modulation		
<b>Trills</b>					
Cheeyeep	1.03	6749.1 $\pm$ 534.3	Hat shaped sinusoidal	6749.1 $\pm$ 534.3	Hat shaped sinusoidal
Seeyeep	0.54	3253.8 $\pm$ 388.1	Modulated, but not sinusoidal		
Peeyeep	0.43	4995.7 $\pm$ 426.4	Flat sinusoidal	4995.7 $\pm$ 426.4	Flat sinusoidal
Warbled Trill	2.65	3038.6 $\pm$ 276.7	Sinusoidal swags followed by flat sinusoidal	3038.6 $\pm$ 276.7, 4575.1 $\pm$ 484.2,	Smaller, shorter flat sinusoidal somewhat

				6847.6 ± 657.2, 7988.8 ± 761.3	wispy with great variation
<b>Purr</b>					
Soft growl	0.60	1162.8 ± 182.7	Flat scattered	1162.8 ± 182.7, 3087.8 ± 225.4, 4263.55 ± 160.9, 5112.1 ± 118.2	Flat scattered
<b>Moans and alarms</b>					
Throat rattle	2.09	2890.2 ± 360.6	Thick flat scattered	2890.2 ± 360.6, 5137.2 ± 403.0, 6835.3 ± 502.0	Thick flat scattered not continuous
Z-trill	1.63	947.5 ± 74.6	Hat-shaped at start then flat scattered and back to hat- shaped	947.5 ± 74.6, 2928.2 ± 163, 4362.7 ± 113.4	Flat, can be broken

Table 2 Continued.



## Call descriptions

**Whistle group.** Whistle calls were clear, pure tones, relatively short in duration (0.4 – 1 sec), with harmonics and ranging in frequency from 3 – 5 kHz. Calls placed in the whistle group are the see, chew, and pee calls. Whistles were given frequently, accounting for 28.4% (N = 25 of 88) of all calls analyzed. Sakis sometimes gave single whistle calls, but also uttered whistles in series with other whistles and trills. They were uttered almost exclusively during feeding, drinking, non-food object manipulation, and solo grooming when near other sakis.

**See.** The see call was the longest duration whistle ( $\bar{x} = 0.88 \pm 0.19$  sec; N = 6), with a fundamental frequency of  $3.3 \pm 0.01$  kHz (N = 6) and prominent harmonics (Fig. 1a). These calls were given by sakis when feeding and moving. See and pee calls were sometimes given together, with pee calls followed quickly by a see call.

**Chew.** Chew calls, to the human ear, sounded like a slurring of the pee and the see calls. The fundamental and second harmonics were mirror images, with the fundamental exhibiting a decline in frequency (Fig. 1b). The third harmonic matched the form of the fundamental. The fundamental frequency of chew calls ( $\bar{x} = 3.6 \pm 0.01$  kHz; N = 8) and duration ( $\bar{x} = 0.63 \pm 0.07$  sec; N = 8) were between those of the pee and see calls.

**Pee.** The pee call was the simplest of the whistle calls. These high-frequency calls ( $\bar{x} = 4.7 \pm 0.02$  kHz; N = 20) had a mean duration of  $0.44 \pm 0.10$  sec (N = 20) and were most often given by sakis when feeding (58.3%) and moving (16.7%; Table

4). Pee calls were sometimes used at the beginning of a series of calls. Pee calls exhibited no frequency modulation and typically included two harmonics (Fig. 1c).

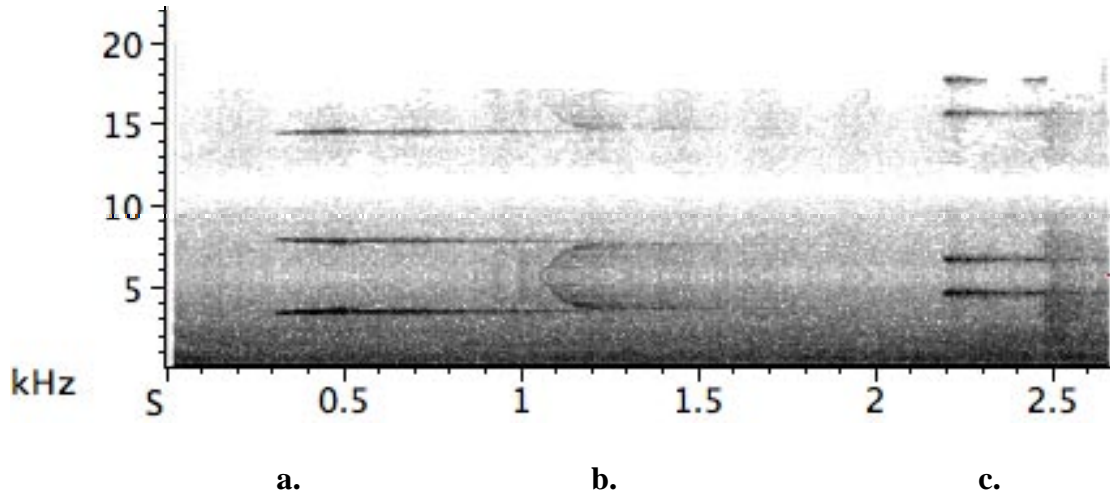


Figure 1. Sonograms of the see (a), chew (b), and pee (c) calls of white-faced sakis.

**Chuck group.** The chuck group included two different calls that differed sufficiently in frequency that I was able to tell them apart in the field. It was common to hear chucks given in a series by one individual, with conspecifics then responding with additional chucks. Chucks appeared to be used primarily in aggressive contexts or in response to undesired events, including unsolicited grooming by others, rain beginning to fall, and having food stolen.

**Chuck.** Chucks were short duration calls ( $\bar{x} = 0.35 \pm 0.07$  sec;  $N = 16$ ) that exhibited no frequency modulation and had a mean frequency of  $6.70 \pm 0.61$  kHz ( $N = 16$ ). It was not uncommon to hear one individual utter a series of chuck calls that varied in frequency and intensity (Fig. 2). Single chucks were given by sakis when

eating or manipulating objects. When used with the throat rattle, chuck calls appeared to signal aggression and were given during heterospecific or intergroup encounters.

**Churk.** The churk was a guttural chuck, with a high-frequency harmonic similar to that of chuck calls (Fig. 3). However, churk calls also included a lower harmonic not apparent in chuck calls. I determined the behavioral context for only one churk call, with a male saki giving the call when close to other sakis.

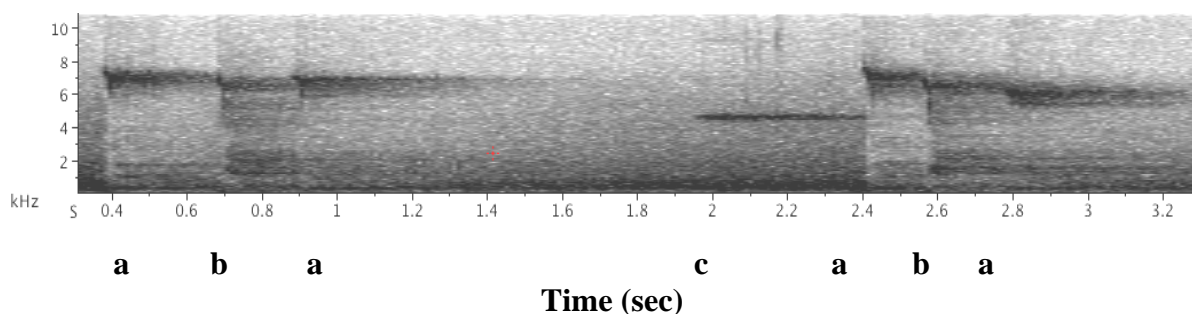


Figure 2. Sonagrams of a chuck call (a) and churk call (b). The first set of calls includes a chuck, a churk, and then another chuck in rapid succession. This is followed by a peeyep call (c), then another series of chuck, churk, and chuck calls. Note the lower frequency of the churk call. These calls were uttered by captive white-faced sakis.

**Trill group.** Trills were modulated calls and four types were identified, with only the cheeyeep having a strong sinusoidal structure. Saki trills ranged from low volume, melodic calls (cheeyeep) to harsh, noisy calls (warbled trill).

**Cheeyeep.** The cheeyeep call was the call used most frequently by sakis (32.95%, N = 29 of 88). This call exhibited pronounced frequency modulation and a

gradual decrease in both amplitude and frequency (Fig. 3a). The call was most often given during feeding (29.1%) and individual activities (37.9%; Table 4). A cheeyeep-like call was also given at the beginning of the warbled trill, and a combined seeeyeep-cheeyeep call was recorded three times. With a mean frequency of  $6.75 \pm 0.53$  kHz (N = 20), cheeyeep calls had the highest frequency of any saki vocalization. It was a clear, distinct call that, to the human ear, sounded bird- or cricket-like.

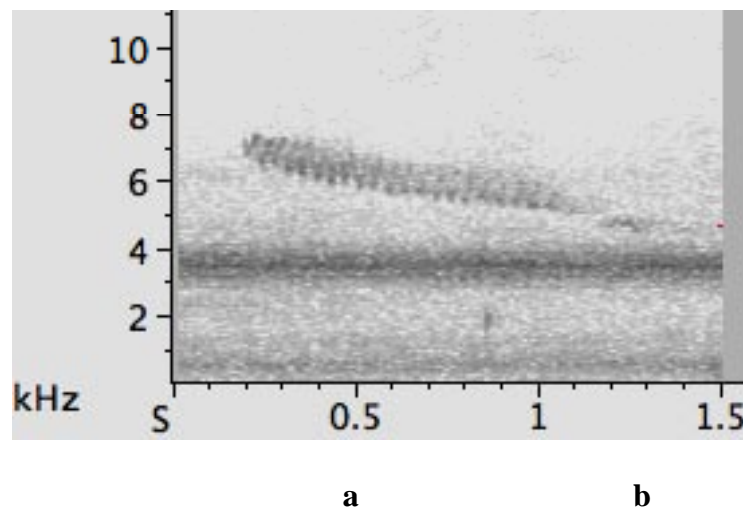


Figure 3. Sonograms of a cheeyeep call (a) and a seeeyeep call (b) of a white-faced saki.

**Seeeyeep.** The seeeyeep was a short trill ( $\bar{x} = 0.54 \pm 0.21$  sec; N = 5) with a mean frequency of  $3.25 \pm 0.39$  kHz (N = 5; Fig. 4). Seeeyeep calls were uttered infrequently and given by sakis during independent activity and feeding (60%) and when moving (20%; Table 4).

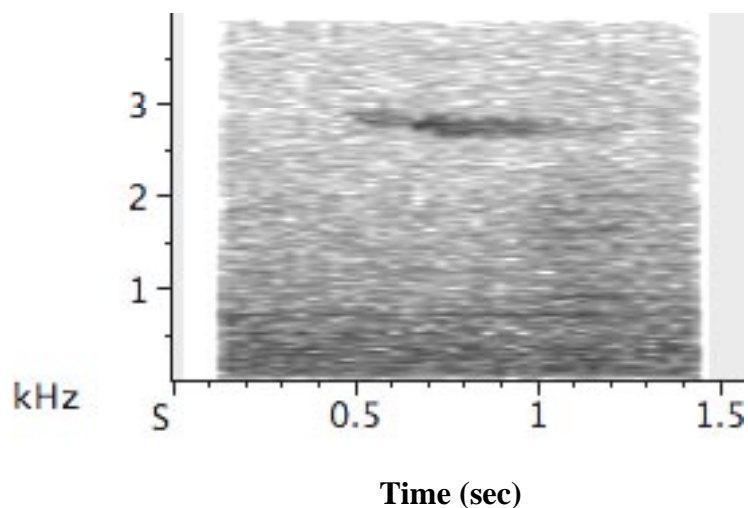


Figure 4. Sonogram of the seeyep call of a white-faced saki.

**Peeyep.** Peeyep calls were simple in structure, relatively short in duration, ( $\bar{x} = 0.43 \pm 0.19$  sec;  $N = 2$ ) with no harmonics and a mean frequency of  $3.04 \pm 0.04$  kHz ( $N = 2$ ). Peeyep calls exhibited slight frequency modulation (Fig. 5) and were easily heard because they were uttered at a relatively high volume. These calls were given primarily when sakis were feeding (44.4%) and during object manipulation (25%; Table 4). On one occasion, a female uttered multiple bouts of up to four peeyeps shortly after waking in the morning.

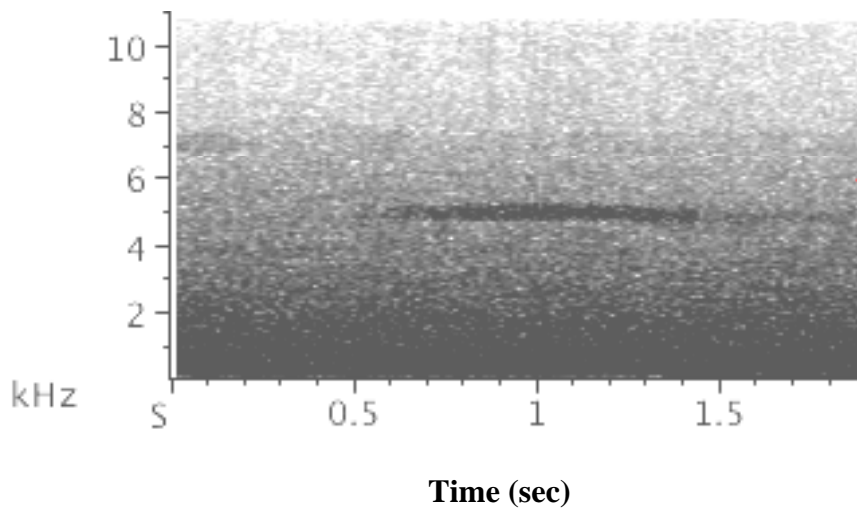


Figure 5. Sonogram of the peeyeep call of a white-faced saki.

**Warbled trill.** The warbled trill was a loud, distinctive call that was relatively long in duration ( $\bar{x} = 2.65 \pm 0.64$  sec;  $N = 8$ ). This trill started with a cheeyeep-like call, and then descended in frequency into a low, raspy call. This call sometimes exhibited brief gaps between successive components. However, the initial cheeyeep-like portion was never repeated. Warbled trills were given during a variety of what appeared to be stressful contexts, including heterospecific encounters, intergroup conflict, and feeding. On several occasions, sakis giving this call simultaneously arched their back and shook the branches on which they were perched. When a saki uttered a warbled trill, other sakis sometimes responded with chuck calls, arched-back posturing, head bobbing, and branch shaking.

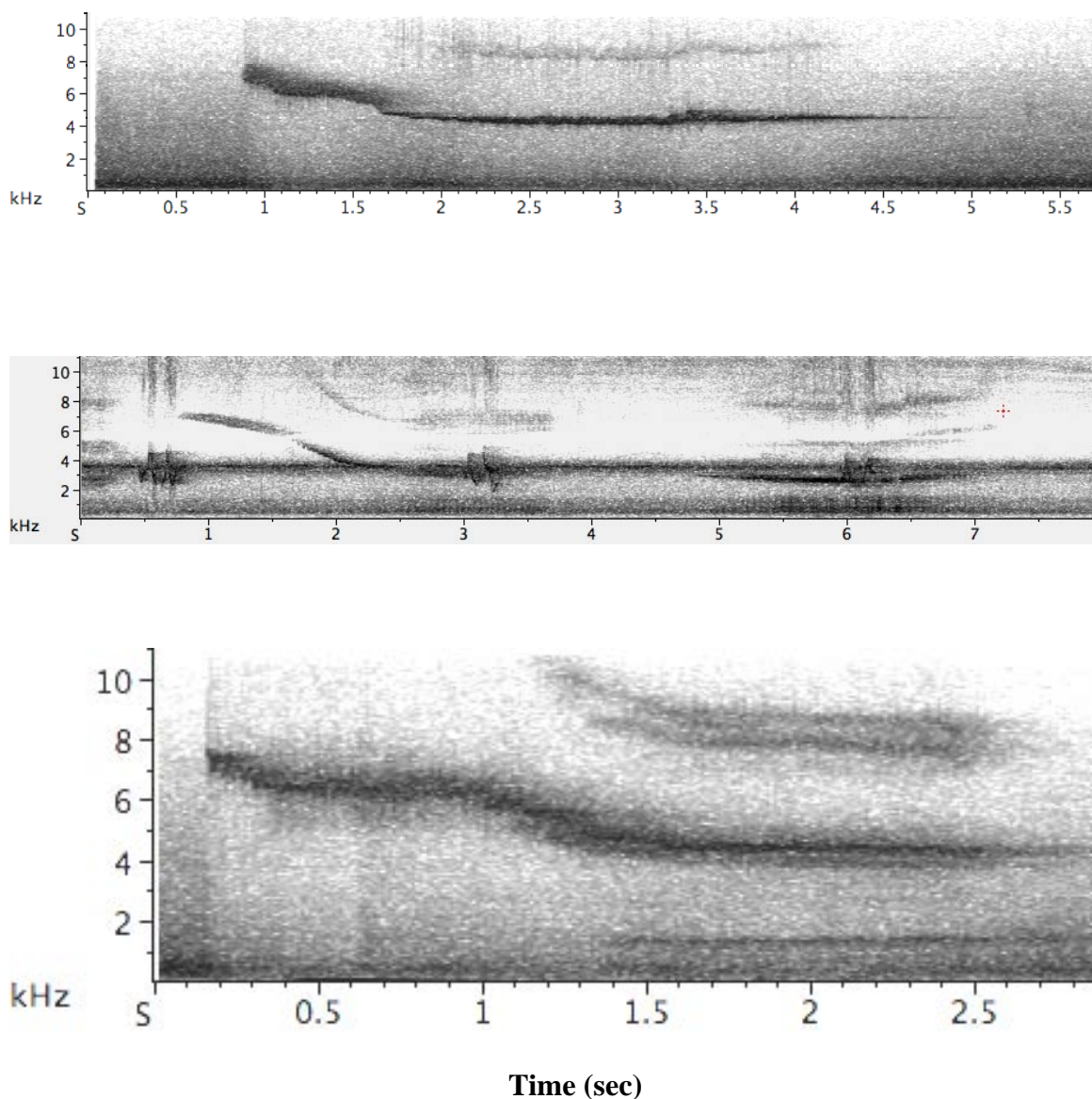


Figure 6. Sonagrams of three warbled trill calls of white-faced sakis.

**Purr group - soft growl.** The soft growl was a low frequency ( $\bar{x} = 1.62 \pm 0.18$  kHz;  $N = 3$ ), low volume call that, because of its low volume, was difficult to record. I heard the call given by sakis at other times, but was unable to record the calls due to ambient noise. The only behavioral data recorded for the soft growl was from a single male that was moving.

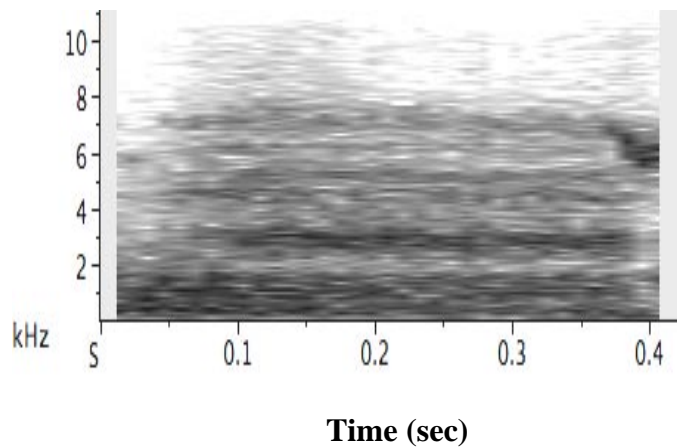


Figure 7. Sonogram of a soft growl call of a white-faced saki followed immediately by a chuck call.

**Moans and alarm call group.** The throat rattle and z trill were combined into a call group based on similarities in volume and call structure (low frequency, guttural sounds). Both calls were given at high volume and easily heard in the field, suggesting that both function in long-distance communication.

**Throat rattle.** The throat rattle covered wide range of frequencies (2.5 – 8 kHz; Fig. 8) and had a guttural sound. The mean fundamental frequency was  $2.89 \pm 1.83$  kHz (N = 9). One throat rattle was given during an intergroup encounter, suggesting that this calls conveys aggression. Throat rattles were also uttered during intragroup and heterospecific encounters. The heterospecific encounter involved an interaction between a group of white-faced sakis and a troop of red howlers (*Alouatta seniculus*).



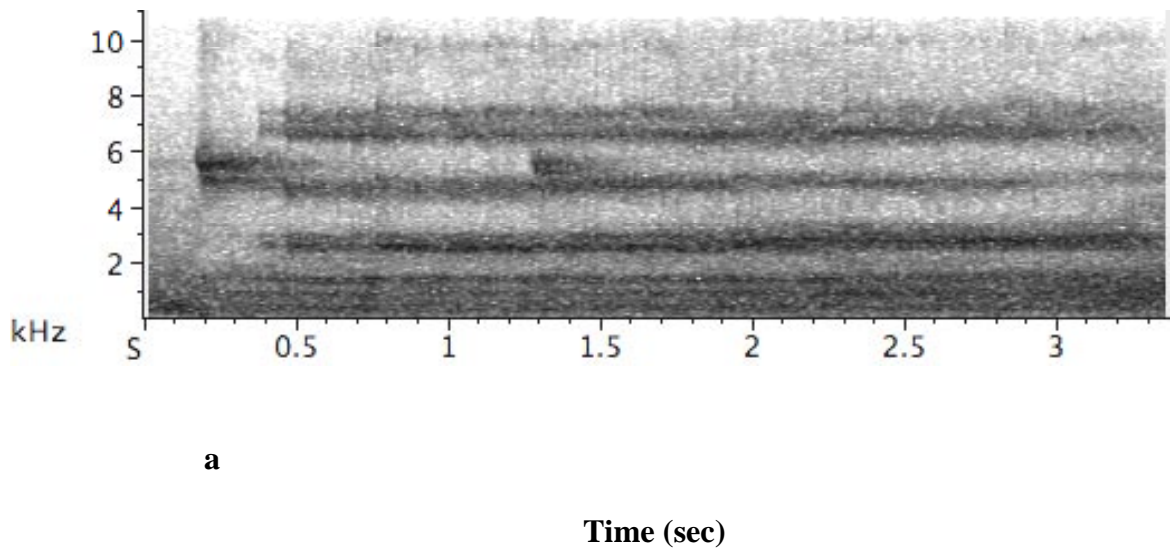


Figure 8. Sonogram of a throat rattle call of a white-faced saki preceded by a chuck call (a).

**Z-trill.** The z-trill was only heard and recorded in the wild. These calls were given by sakis separated from their troops, suggesting that the z-trill was a location call. When an isolated individual called, other members of the troop typically responded with peeyeeps and chuck calls. Z-trills had the lowest frequency of all call types identified, with a mean fundamental frequency of  $0.95 \pm 0.08$  kHz ( $N = 3$ ). I had behavioral context information for six z-trills, and all were given by individuals located more than 25 m from other members of the troop. In three cases, a z-trill was given by a saki moving back toward the rest of its troop.

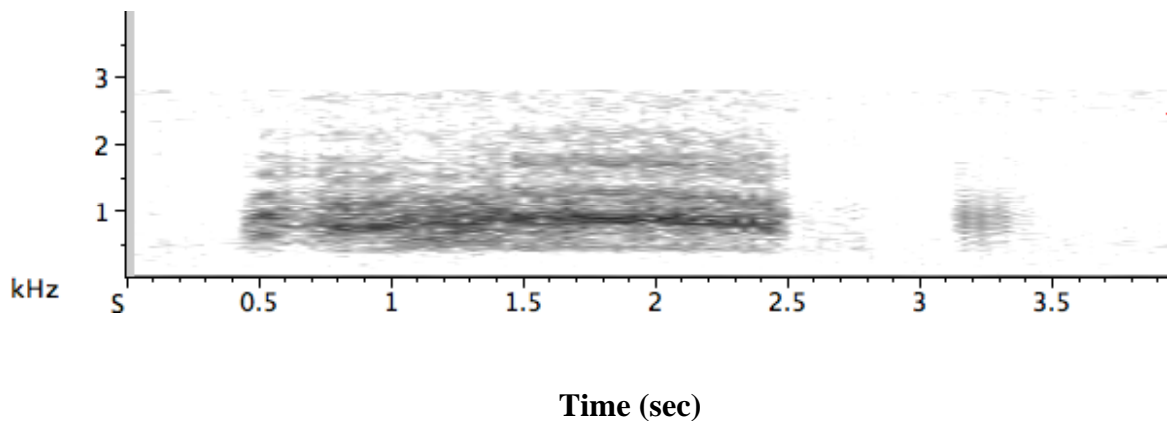


Figure 9. Sonogram of a z trill call of a white-faced saki.

**Behavioral context.** I was able to note a behavioral context for 88 calls. In addition, for 71 calls, I was able to determine the sex of the calling saki, with 33 given by males (46.5%) and 38 by females (53.5%; Table 3). For 61 calls, I knew the location of conspecifics, with more calls (36 of 61, or 59%) given when another saki was 1-3 m away than when they were located at other distances from the calling individual (Table 4).

Behavioral contexts noted when sakis vocalized included agonistic behavior (heterospecific and intergroup encounters), individual behavior feeding, solo object manipulation, and moving (alone or in a group; Table 5). Most calls were given by sakis engaged in individual behavior (57 of 88 calls, or 64.8%). Sakis also called when feeding (31 of 88 calls, or 35.2%) and manipulating various objects (26 of 88 calls, or 29.6). I also noted 15 calls (17.0%) given by sakis moving through the foliage, and five calls (5.7%) were given during agonistic encounters (two heterospecific encounters and three intergroup encounters).

For behavioral contexts relative to distance from conspecifics, sakis often uttered solo feeding calls (30 of 82, or 37.5%) when within 3 m of another saki (Figure 1). In addition, 86.7% (N = 13 of 15) of calls given by sakis that were moving and all (N = 3 of 3) agonistic (heterospecific and inter-group) calls were given when one or more conspecifics was within 3 m.

Table 3. Number of times each call was given by male and female white-faced sakis.

<b>Call type</b>	<b>Male</b>	<b>Female</b>	<b>Unknown sex</b>
Chew	3	3	0
Chuck	3	3	0
Churk	1	0	0
Cheeyeep	11	12	6
Pee	3	9	0
Peeyeep	4	2	3
See	2	4	1
Soft growl	1	0	0
Seeyeep	1	2	2
Throat rattle	0	0	1
Warbled trill	2	3	0
Z-trill	2	0	4
<b>Total</b>	33	38	17
	37.5%	43.2%	19.3%

Table 4. Number of times that the calls of white-faced sakis were given at various distances from conspecifics.

<b>Call type</b>	<b>&lt; 1 m</b>	<b>1 - 3 m</b>	<b>&gt; 3 - 25 m</b>	<b>Out of sight</b>
Chew	2	3	0	0
Chuck	1	2	0	0
Churk	0	1	0	0
Cheeyeep	2	15	1	1
Pee	4	3	0	1
Peeyeep	1	4	0	1
See	2	4	0	0
Soft growl	0	0	0	0
Seeyeep	3	1	0	0
Throat rattle	0	0	0	0
Warbled trill	0	3	0	0
Z-trill	0	0	6	0
<b>Totals</b>	15 24.6%	36 59.0%	7 11.5%	3 4.9%

Table 5. Number of times that calls of white-faced sakis were given in particular behavioral contexts.

Call type	Individual, but not food related	Individual, and food related	Moving	Agonistic
Chew	1	3	0	
Chuck	2	3	1	
Churk	0	0	0	
Cheeyeep	11	9	4	
Pee	3	7	2	
Peeyeep	2	4	1	Intergroup - 1
See	2	2	3	
Soft growl	0	0	1	
Seeyeep	1	2	1	
Throat rattle	0	0	0	Intergroup - 1
Warbled trill	0	1	1	Intergroup - 1, Heterospecific - 1
Z-trill	2	0	1	Intergroup - 1
<b>Totals</b>	24 29.6%	31 35.2%	15 17.04%	5 5.7%

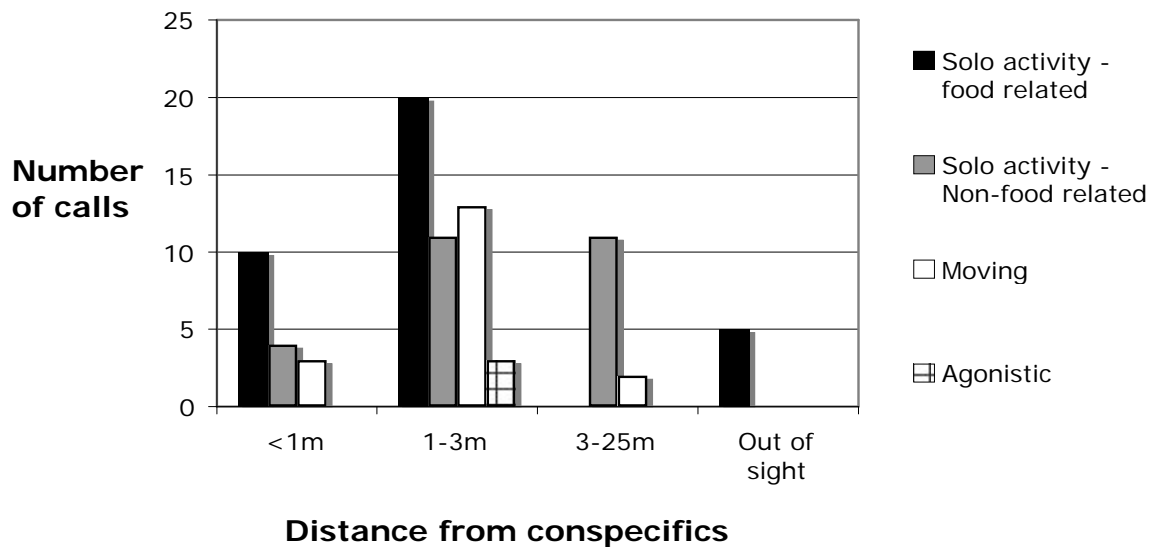


Figure 10. The number of times calls were given by white-faced sakis in different contexts relative to the distance of the calling individual from conspecifics.

## DISCUSSION

The vocal repertoire of white-face sakis in my study consisted of 12 calls in five call groups, whereas other investigators (Buchanan 1978, Roosmalen et al. 1981) reported a repertoire of 18 calls and five call groups. The primary reason for this difference is that previous authors (Buchanan 1978, Roosmalen et al. 1981) identified five distinct calls in the chuck group and I identified only two calls, with one being a graded series. In addition, based on similarities in their characteristics, I combined the cheep, chuck, high chuck, and intense chuck calls described by Buchanan (1978) as variants of a single call, the chuck call. I also renamed the squeal group (Buchanan 1978), calling it moans and alarms. The squeal group of Buchanan (1978) included only a screech call that I did not identify in my study. However, I did identify a call (z-trill or rattle roar) that was similar in form to the screech, but longer in duration (1.62 sec vs. 0.25 sec).

Additional differences between my results and those of Buchanan (1978) were in the mean duration and frequency of several calls. Among whistles, I found the pee call to be nearly twice as long in duration (0.44 sec vs. 0.23 sec) and higher in frequency (4759 Hz vs. 3930 Hz). I also found the chew whistle to be longer in duration (0.625 sec vs. 0.451 sec). For other calls, I found that churk calls (0.32 sec vs. 0.12 sec), cheeyeep calls (1.03 sec vs. 0.37 sec), peeyeep calls (0.43 sec vs. 0.15 sec), and warbled trills (2.65 sec vs. 0.37 sec) were longer in duration, and the throat rattle was lower in frequency (2890 Hz vs. 3350 Hz). Such differences in the



characteristics of calls may be due to individual variation, differences in context, differences between free-living and captive individuals, or some combination of these factors. Additional study will be needed to determine the extent to which the characteristics of calls are influenced or altered by differences in sex, age, context, and interactions among those factors.

White-faced sakis vocalized most often when feeding, drinking, and engaged in solo activities, such as object manipulation and, when engaged in such activities, they uttered see, pee, chew, cheeyeep, seeyeep, and peeyeep calls. In addition, most calls (83.6%) were uttered when within 3 m of one or more conspecifics. Other primates also utter a variety of low-volume calls in the company of conspecifics. For example, rhesus macaques frequently use two calls in affiliative contexts and they appear to signal the caller's intention of behave benignly (Silk 2002). Other investigators have also noted that the most common calls of non-human primates are low amplitude grunts, coos, or trills that are given during social interactions, e.g., vervet monkeys (*Cercopithecus aethiops*; Cheney and Seyfarth 1982a), cotton-top tamarins (*Saguinus oedipus*; Cleveland and Snowden 1982), squirrel monkeys (*Saimiri sciureus*; Boinski 1992), and baboons (*Papio cynocephalus*; Cheney et al. 1995). Such low-volume calls apparently provide information about the caller's intentions and, on most occasions, likely communicate intent to behave peacefully (Silk 2002). Gros-Louis (2004) suggested that food-associated calls given by white-faced capuchin monkeys (*Cebus capucinus*) may function to announce food ownership and reduce the likelihood of aggression from other individual.

White-faced sakis in my study were sometimes moving when see, pee, and seeyeep calls were given, suggesting that they may also serve as contact calls to help troop members remain in contact. In support of this conclusion, Norconk and Funk (2004) noted that white-faced sakis uttered 'trill calls' (e.g., seeyeep calls) at higher rates when a caller was located further from other group members. Other primates are also known to utter contact calls when groups of individuals are moving (e.g., Kudo 1987, Sigiura 1998, Ambrose 2003) and such calls may be particularly important for forest-dwelling primates where maintaining visual contact may be more difficult. Rendall et al. (1996) reported that the contact calls of rhesus monkeys provide information about the location of group members, but, in addition, also provide information about individual identity. Thus, rhesus monkeys are apparently able to monitor the location of specific individuals as they move. Such individual vocal recognition has been reported in many other species of primates (Cheney and Seyfarth 1982b, Butynski et al. 1992, Hammerschmidt and Todt 1995, Ceugniet and Izumi 2004, Miller et al. 2005). Although white-faced sakis may also use differences in the characteristics of calls to identify individuals, additional study is needed to test that possibility.

White-faced sakis in my study uttered warbled trills and throat rattle call in what appeared to be aggressive contexts. Throat rattle calls were given during both conspecific intergroup encounters and during an encounter with a troop of red howler monkeys. In addition, Norconk (2006) apparently observed white-faced sakis giving warbled trills in aggressive encounters within groups. Although the characteristics of the call were not provided, Norconk (2006) noted that, preceding a male-male chase,

sakis engaged in activities such as body shaking and branch sniffing and, in addition, uttered a vocalization heard only in this context. On several occasions, sakis giving warbled trills in my study arched their backs and shook branches, behaviors similar to those of sakis in Norconk's (2006) prior to vocalizing and chasing a conspecific.

For five warbled trill calls, I was able to determine the sex of the calling individual, with three calls uttered by females and two by males. Di Fiore et al. (2007) found that male equatorial sakis (*P. aequatorialis*) played a prominent role during intergroup vocal encounters, and also noted that males responded more strongly to playbacks of territorial vocalizations than females, typically vocalizing and approaching the speaker. Similar behavior has been reported for other saki species (Rosenberger et al. 1996). Clearly, additional observations and larger sample sizes are needed to determine if male white-faced sakis vocalize more than females during intergroup encounters.

Many species of primates exhibit territorial behavior and use vocalizations during encounters with conspecifics in adjacent territories. For example, male titi monkeys regularly call near territory boundaries to define and reinforce the location of those boundaries (Robinson 1981). Similar behavior has been reported for white-handed gibbons (Raemaekers and Raemaekers 1985). The calls uttered by white-faced sakis in aggressive contexts were relatively low in frequency compared to most other vocalizations in their repertoire, particularly the throat rattle. Hauser (1993) examined the relationship between body mass and call frequency for 36 primate species representing 23 genera and 474 vocalizations and found a statistically significant negative correlation between body mass and frequency, i.e., larger species

produce relatively lower-pitched vocalizations than smaller species. In addition, primates tended to produce lower frequency calls in aggressive contexts (Hauser 1993). Such results generally support Morton's (1977) hypothesis that the characteristics of calls, including frequency, convey information that caller's might use to manipulate receivers. To test this hypothesis, Fitch (1994) placed cages with white-faced sakis near each other in a laboratory setting to elicit aggressive behavior and found that the sakis increased their visually-apparent size by piloerection and, to lower the frequency of their calls, also tended to protrude their lips during vocalizations. Fitch (1994) suggested that such behavior was consistent with the hypothesis that sakis use vocal tract length to assess the body size of the vocalizer, assuming, of course, that lip protrusion effectively lengthens the vocal tract.

Most calls uttered by white-faced sakis in my study were given in proximity to conspecifics. Calls given when near conspecifics are typically low in volume, complex in structure, and offer the sender flexibility to personalize (Uster and Zumberbuhler 2001). Signalers personalize close proximity calls, allowing for gradation in call types such as the graded series of chucks and trills uttered by white-faced sakis.

The use of graded calls, such as the chuck calls of white-faced sakis, has been reported for several other species of primates (Palombit 1992, Fischer and Hammerschmidt 2002, Fichtel et al. 2005). Marler (1976) suggested that graded repertoires might be more common among species in open habitats where individuals interact frequently and at close range. Subsequently, many investigators have reported graded vocal signals that function over long distances (e.g., Fischer et al. 2001) and in

species in forested habitats (e.g., Schrader and Todt 1993). Clearly, no single factor determines the extent of gradation within call types, a variety of factors, including phylogeny and social structure, help shape a species' repertoire (Fischer and Hammerschmidt 2002).

Three calls of white-faced sakis in my study, the z-trill, throat rattle, and warbled trill, were uttered with greater volume than other calls in their repertoire. Such calls are referred to as loud calls and the loud calls of non-human primates have been hypothesized to serve five possible functions, including predator avoidance, food advertisement, group coordination, mate attraction, and resource defense (Rasoloharijaona et al. 2005). For example, the whoop gooble and the alarm calls of Sooty Mangabeys (*Cercocebus torquatus atys*) apparently play a role in predator defense and resource defense against conspecifics (Range and Fischer 2004). The loud calls of Edwards' Sportive lemurs (*Lepilemur edwardsi*) aide in troop cohesiveness and spacing (Rasoloharijaona et al. 2005), whereas Diana monkeys (*Cercopithecus diana diana*) use loud calls for predator defense and resource defense against conspecifics (Zuberbuhler et al. 1997).

The three loud calls of white-faced sakis (throat rattle, warbled trill, and z-trill) were all uttered during intergroup and heterospecific encounters and apparently play a role in resource defense. In addition, z-trills were only given by sakis located more than 25 m from conspecifics, suggesting that they function to coordinate the activities of group members out of visual contact and aid in intragroup cohesion. Several other primate species have calls that serve a similar function. For example, capuchin monkeys have a call (arrawh) with a loud form that can be heard for long

distances (Robinson 1982). This loud form is uttered by individuals separated from other group members whose vocal responses help the isolated individual locate its group (Robinson 1982).

Many other primates also have calls for communication over longer distances and, in addition to being high volume calls, these calls typically have low frequencies, with most energy below 1.5 kHz to promote long range transmission of acoustic signals (Mitani and Stuht 1998). Low-frequency sounds exhibit less signal degradation, or attenuation, than higher-frequency sounds in closed habitats and, therefore, are particularly effective for long-distance transmission in forest habitats (Morton 1975). Thus, primates found in forested habitats are more likely to have low-frequency, long-distance calls in their repertoires than those that occupy open (non-wooded) habitats (Wich 2002). The long-distance, z-trill call of white-faced sakis in my study had the lowest mean frequency of any call in their repertoire (mean = 947.5 Hz), further supporting the hypothesis that the z-trill serves as a long-distance call.

### **Repertoire size**

Based on my results and those of Buchanon (1978), and depending on how various calls are categorized, the vocal repertoire of white-faced sakis appears to consist of about 12 – 18 different calls. Among other pithecines, monk sakis (*P. monachus*), a close relative of white-faced sakis (*P. monachus*), reportedly have a vocal repertoire of 12 different calls (Buchanan 1978) and red uakaris (*Cacajao rubicundus*) are reported to use eight different calls (Buchanan 1978).

Other than Pithecines, the vocal repertoires of several other Neotropical primates have been described, including howler monkeys (*Alouatta palliata*) with 22 calls (Baldwin and Baldwin 1976), Titi monkeys (*Callicebus moloch*) with 11 calls (Robinson 1979), common marmosets (*Callithrix jacchus*) with 13 calls (Epple 1968), wedge-capped capuchin monkeys (*Cebus olivaceus*) with 11 calls (Robinson 1984), squirrel monkeys (*Saimiri sciureus*) with 21 calls (Winter et al. 1966), and cotton-top tamarins (*Sanguinus oedipus oedipus*) with 38 calls. Given the variability in the calls of many primates and the difficulty of categorizing such calls, other investigators working with these same species may not arrive at the same number of calls in their repertoires. However, many primates, including pithecines, do appear to have vocal repertoires consisting of anywhere from about eight to 20 calls.

McComb and Semple (2005) examined the vocal repertoires of 42 non-human primate species and found a positive relationship between repertoire size and social parameters. For the primates examined, repertoire size ranged from 2 – 39 calls and mean group size ranged from 1.5 to 125 individuals. White-faced sakis in my study area had a vocal repertoire of 12 calls (my study) and have a mean group size of 3.6 individuals (Norconk et al. 1996). For primate species surveyed by McComb and Semple (2005), those with mean group sizes between three and four had vocal repertoires of 11 (dusky titi, *Callicebus moloch*), six (western needle-clawed galago, *Euoticus elegantulus*), eight (Demidoff's galago, *Galagoides demidoff*), and nine (black lemur, *Petterus mongoz*) calls, respectively. Thus, the vocal repertoire of white-faced sakis appears to be similar in size to those of other primates with similar group sizes and consists of approximately the number of calls predicted by McComb

and Semple's (2005) analysis. Such results support the hypothesis that vocal communication can facilitate or constrain increases in group size among primates and emphasize the importance of vocal communication in the social behavior of primates (McComb and Semple 2005).

As with other species of primates, the vocalizations and vocal repertoire of white-faced sakis have been influenced by habitat, social behavior, and phylogeny. Sakis form small groups of about two to eight individuals (Norconk et al. 1996, Norconk 2006, Vié et al. 2001) that forage primarily on fruit and leaves (Norconk and Conklin-Brittain 2004). The size of group home ranges remains unclear. However, Vié et al. (2001) radio-tracked three white-faced sakis in French Guiana and reported ranges of 148 and 287 ha, respectively, for two groups. On my study site, the 12.8-ha Isla Redonda, saki ranges are much smaller (4 – 10 ha; Norconk and Conklin-Brittain 2004), likely because ranges are constrained by the size of the island. Vié et al. (2001) also found that sakis spent much time moving through their forest habitat, with the two groups they monitored traveling a mean distance of 1.88 km per day. Thus, small groups of sakis, at least those not located on small islands, apparently travel relatively long distances daily in search of suitable fruit and leaves and must remain in contact with other group members while traveling through the dense vegetation of rainforest habitats. As might be expected, therefore, many calls in the vocal repertoire of white-faced sakis appear to serve as contact calls. Such calls may serve additional functions, but they do provide information about a caller's position relative to other group members and help maintain group cohesion.



Other calls in the vocal repertoire of white-faced sakis appear to be food-related and may help reduce conflict between group members by announcing food ownership and reducing the likelihood of aggression between group members. Other calls serve aggressive functions and aid in long-distance communication. Although the vocal repertoire of white-faced sakis appears typical for arboreal primates that form small groups, additional study may reveal additional calls. For example, many, if not all primates, have predator alarm calls, and some species have multiple alarm calls that warn conspecifics about the presence of specific types of predators (e.g., Zuberbühler et al. 1997, Zuberbühler 2001). White-faced sakis likely have predator alarm calls as well, but I observed no interactions between sakis and potential predators in my study.

Additional study is also needed to better understand the specific functions of many of the calls in the vocal repertoire of white-faced sakis. I was able to discern some general functions, but additional, more detailed observations are needed to better understand the response of conspecifics to particular calls uttered by specific individuals because call function may differ depending on the sex or status of a calling individual. In addition, playback experiments would likely prove useful in better understanding the specific functions of certain call types.

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