A PRELIMINARY STUDY ON VOCAL COMMUNICATION IN THE GRAY'S BALD-FACED SAKI MONKEY, *PITHECIA IRRORATA*

THESIS

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DEDICATION

In loving memory of my beautiful daughter Dakota Benay...

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CHAPTER I

INTRODUCTION

Overview of Primate Vocal Communication

Primates live in a wide variety of social groups, thus the need to communicate with other group members, neighboring groups, and even unfamiliar solitary conspecifics is vital. Communicative signals may be olfactory (e.g., scent-marking), tactile (e.g., grooming), visual (e.g., gaze following), or vocal in nature (Epple 1974; Buchanan 1978; Owings & Morton 1998; Weber 2005). Indeed, nonhuman primate vocal communication has received a great deal of attention over the last half-century due to the phylogenetic similarities between humans and other primates. For this reason, nonhuman primates serve as potential models for studying the precursors to human language (Rendall 2003).

Rowell and Hinde were early pioneers in the field of primate vocal studies through their investigation of rhesus macaque (*Macaca mulatta)* vocalizations in 1962 (Rowell 1962; Rowell & Hinde 1962). Their study provided the first published primate vocal repertoire that included sound spectrograms (Rowell & Hinde 1962). Since then, the study of vocal communication has made an increased presence in the primate literature and includes studies on tamarins (e.g., *Saguinus geoffroyi,* Moynihan 1970), marmosets (e.g., *Cebuella pygmaea,* Pola & Snowdon 1975), gibbons (e.g., *Hylobates lar,* Raemaekers et al. 1984), lemurs (e.g., *Lemur catta,* Macedonia 1993), colobus monkeys (e.g., *Colobus guereza,* Harris et al. 2006), baboons (e.g., *Papio cynocephalus ursinus,* Kitchen et al. 2003*),* chimpanzees (e.g., *Pan troglodytes schweinfurthii,* Mitani et al. 1999), and many others. These studies demonstrate that vocal communication serves many functions and is essential to group survival. Vocalizations transmit important information regarding mediation of intergroup spacing (Ross & Geissmann 2007), group cohesion (Okamoto & Matsumura 1997), maintenance of long distance communication within and between groups (Jordan et al. 2004), mate attraction (Ruiz-Miranda et al. 2002), territory defense (Becker et al. 2003), predation avoidance (Fischer et al. 2002), and affiliative reinforcement (Oyakawa et al. 2007).

Past research on vocal communication has been concerned with the relationship between the context and function of call emissions. The "motivational-structural (MS) rules" hypothesis (Morton 1977) predicts that low frequency atonal vocalizations, such as the "wahoo" call of male baboons (*Papio cynocephalus*) (Fischer et al. 2002), are emitted in aggressive situations and high frequency tonal vocalizations, such as the "twitter" call of sooty mangabeys (*Cercocebus torquatus atys*) (Range &

Fischer 2004) in non-aggressive or fearful situations. The hypothesis assumes a negative correlation between the frequency of a vocalization and body weight; thus, larger animals tend to produce comparably lower-pitched vocalizations than smaller animals. Hauser (1993) attempted to test the MS rules hypothesis from data on 36 nonhuman primate species. His results confirmed Morton's prediction that body weight and frequency have a significantly negative relationship; however, they did not indicate a statistically significant relationship between motivational state and tonality. Researchers have continued to explore the relationship between call function and context in the construction of vocal repertoires.

A vocal repertoire can also provide information on specific environmental pressures that may have shaped a species' evolutionary history. For example, Marler (1976) argued that dense forest habitats tend to favor conventional (discrete) calls conveying simple messages that are less likely to suffer from transmission degradation, such as those exhibited in the vocal repertoire of common marmosets (*Callithrix jacchus jacchus)* (Agamaite 1997). Open habitats, however, tend to favor more complex (graded) acoustics that allow for additional contextual and visual information, such as those found in the vocal repertoire of Barbary macaques (*Macaca sylvanus*) (Hammerschmidt & Fischer 1998). Marler (1976) concluded that variables in the environment are capable of influencing the acoustic structure of particular calls.

Although primate vocal repertoires have traditionally been classified as discrete or graded, more recent studies have explored the inherent problems with this type of classification. Egnor et al. (2006) argue that a graded vocal system can easily appear to be a discrete system in studies with limited sample sizes (in regards to total number of vocalizations obtained and/or the complexity of behavioral contexts observed). Primate vocalizations also exhibit a wide array of variation within and between individuals. As a result, Egnor et al. question whether researchers can even determine when call variation is meaningful to the animals themselves. Recently, bioacousticians have begun to use mathematical models, such as multi-dimensional scaling (MDS) and principal component analysis (PCA) to examine subtle features in high dimensional acoustical data. However, this type of analysis is extremely time consuming and requires a large quantity of high quality vocal recordings. Despite the apparent problems in Marler's (1976) hypothesis regarding discrete and graded repertoires, it seems plausible that environmental factors may influence the acoustic structure of certain calls and, over time, this may lead to changes in a species' vocal repertoire.

More recently, McComb and Semple (2005) utilized a comparative approach to demonstrate that the size of the vocal repertoire in nonhuman primates evolved in association with increases in both group size and percentage of time spent grooming. Their results indicate a strong positive correlation between changes in repertoire size and group size, as well as in time spent grooming. Thus, the authors' findings indicate that changes in communication can facilitate changes in social behavior. Vocalization research on a lesser-known primate species, such as the Gray's Bald-faced saki (*Pithecia irrorata*), may further indicate how environmental pressures influenced the evolution of communication strategies.

Study Species

Saki monkeys (genus *Pithecia*) are medium-sized, diurnal primates found in the Amazonian forests of South America from Colombia south to Peru, including parts of Brazil and Bolivia. Little is known about the Pitheciidae in general (Kinzey 1997) and, despite their wide distribution, they are said to be the most under-studied genera of Platyrrhini (Norconk 2006). Traditionally, five species of *Pithecia* are recognized: *Pithecia pithecia* (white-faced saki), *P. monachus* (monk saki), *P. albicans* (white saki), *P. aequatorialis* (equatorial saki), and *P. irrorata* (Gray's bald-faced saki) (Hershkovitz 1986). The five species are separated into two groups, with the Pithecia group containing 2 subspecies (located north of the Amazon River) and the Monachus group containing 6 taxa in 4 species (located in the Central and Western Amazon Basin) (Norconk 2006).

Among the five *Pithecia* species recognized, long-term field research is almost completely restricted to *P. pithecia* (Setz 1994; Norconk 1996;

Setz & Gaspar 1997; Setz et al. 1999; Cunningham 2003; Norconk 2006). Although one long-term study has been conducted on *P. aequatorialis* (DiFiore et al. 2007), the relatively scarce data collected on saki species in the southern Amazonia region are mostly obtained from population surveys and short-term studies (*P. albicans,* Johns 1986 & Peres 1993; *P. monachus,* Freese et al. 1982, Happel 1982, Soini 1986, Heymann et al. 2002; *P. aequatorialis,* Heymann et al. 2002; *P irrorata,* Buchanan-Smith 1990b, Ferrari et al. 1999). Most early research on sakis focused on their ecology and feeding behavior (Mittermeier 1977). Recently, this focus has extended to examination of their locomotor behavior (Walker 2005), female reproduction (Norconk 2006), group composition (Lehman et al. 2001 & DiFiore et al. 2007), and habitat use (Vie et al. 2001).

The focal species of this study, *P. irrorata (*common name Gray's bald-faced saki or Gray monk saki*),* is perhaps the least studied of the pitheciin species and is only briefly mentioned in the primate literature (Hershkovitz 1986; Ferrari and Lopez 1995; Rowe 1996; Tarifa 1996; Fuentes 1998; Ferrari et al. 1999; Groves 2001). However, *P. irrorata* may have been referred to as *P. hirsuta* (Izawa & Bejarano 1981) or *P. monachus* (Hill 1960; Heltne et al. 1975; Pook & Pook 1982) prior to the 1986 taxonomic revision by Hershkovitz. Although they are not listed as endangered, Tarifa (1996) considered *P. irrorata* to be vulnerable due to their confined geographical range in Southeastern Peru, Western Brazil, and north of the Tahuamanu River in Northwestern Bolivia.

Sakis have been described as the most distinctive of all New World primates (Fleagle 1999), as evidenced by their coarse, fluffy hair and long, bushy non-prehensile tails. *P. irrorata* are moderately sexually dimorphic in body mass, with females weighing approximately 2160g and males 2920g (Rowe 1996). Unlike white-faced sakis, *P. irrorata* exhibit minimal sexual dichromatism in facial and body pelage. Males and females are uniform in their cryptic gray pelage coloration; however, females display a slightly more pronounced strip of white hair that extends from the inner corner of the eyes to the corners of the mouth. Additionally, females exhibit more rounded, bowl-shaped hair on the top of the head (Palminteri 2008, personal communication; Adams, personal observation).

Sakis can be found in a wide range of habitats, including highland and lowland forests, terra firma and seasonally flooded igapó forests, secondary forests, and even disturbed habitats (Kinzey 1997). *Pithecia* occupy the middle to lower levels of the canopy and travel primarily by leaping (Kinzey 1997); however, some species, like *P. irrorata*, appear to be more quadrupedal and often forage in the upper canopy (Peres 1993). Sakis, like most other platyrrhines, are primarily frugivorous with fruit comprising over 70% of their diet (Kinzey 1992). What makes them distinct from other New World frugivores, however, is that sakis feed on the seeds of hard, unripe fruits. These seeds provide them with a diet that is rich in lipids and high in fiber concentrations (Norconk et al. 2002). Sakis have developed small procumbent incisors and massive, outward flaring canines to aid in seed extraction (Kinzey 1992).

Most pitheciin species appear to live in small groups, which typically consist of a single breeding pair and their offspring (Buchanan et al. 1981; Shively & Mitchell 1986; Fuentes 1998; Vié et al. 2001; Lehman et al. 2001). As a result, many researchers have labeled sakis as monogamous (Buchanan et al. 1981; Robinson et al. 1987; Lehman et al. 2001; DiFiore et al. 2007). However, this assertion has recently been called into question. Several field reports have described groups containing more than one adult male or female, which may suggest a notable variation in group structure within sympatric groups of pitheciines (Setz and Gaspar 1997; Vié et al., 2001; Norconk, 2007). However, as DiFiore et al. 2007 point out, previous long-term studies of *Pithecia* have focused on isolated island populations or groups located in small forest fragments. As a result, there has been limited opportunity for data collection on natural changes in group composition. Therefore, according to DiFiore et al. (2007), it is possible that these larger groups with multiple reproductive-aged males or females are undergoing a transitional period of reproductive turnover. Indeed, variation in group size was evident in the *P. irrorata* populations at the field site where I conducted my study. While most groups contained only one adult breeding pair, some groups appeared to contain more than one adult female. However, I was unable to determine in the short period of my study whether or not these groups were undergoing a change in group composition or reproductive turnover.

Due to their cryptic nature, *Pithecia* are known to be one of the most difficult of the platyrrhines to habituate to human presence (Norconk 2006). For this reason, published data are limited on behavior and vocal communication in Pitheciin monkeys. However, Hill (1960) noted that bald-faced sakis make loud growl-grunts at human observers. Buchanan (1978) further established a preliminary vocal repertoire for *P. pithecia, P. monachus,* and *Cacajao rubicundus.* He reported a repertoire of 18 calls in five call groups (whistles, chucks, trills, purr, and moans and growls) for *P. pithecia* and 17 calls in five call groups (whistles, chucks, trills, squeal, and moans and growls) for *P. monachus.* All vocal recordings in Buchanan's study were obtained from captive individuals and few data were given on call function. Since this study, there has only been brief mention of vocalizations for *P. pithecia* in the literature (Robinson et al. 1987; Gleason & Norconk 2002; Norconk & Funk 2004). Interestingly, Gleason and Norconk (2002) documented a group of white-faced sakis that mobbed a small felid (which they speculated was an oncilla, *Leopardus tigrinus)* for over 20 minutes. The group made alarm calls while chasing the felid over 200 meters. According to Gleason and Norconk, the most frequent response by sakis to small arboreal, terrestrial, and perched avian predators was this type of mobbing behavior.

Purpose

As Snowdon et al. state, "An understanding of communication is necessary for successful analysis of social behavior in general (Snowdon et al. 1982: xvi)." Vocal communication is a fundamental component of sociality in primates and therefore plays a vital role in the primate behavioral repertoire. The scarcity of vocal studies on pitheciins, and the near absence of *P. irrorata* in the primate literature, clearly indicates the need for additional research. The objective of this study was to examine the vocal behavior of wild Gray's bald-faced saki monkeys (*P. irrorata*) to provide a preliminary vocal repertoire of the species. To achieve this goal I described and categorized calls, ascertained call function, and examined correlations between call structure and function.

Given the phylogenetic proximity of the pitheciins, and the vocal repertoires of *P. pithecia, P. monachus,* and *Cacajao rubicundus* already established by Buchanan (1978), I expected *P. irrorata* to exhibit a vocal repertoire of a similar range and size. Furthermore, following McComb and Semple's predictions, I predicted the number of vocalizations in the *P. irrorata* vocal repertoire to be akin to that of other species that share a similar group size (McComb and Semple 2005). I also expected that the *P. irrorata* vocal repertoire would conform to Morton's (1977) motivational-structural rules hypothesis, with the majority of affiliative calls exhibiting high, tonal frequencies and the majority of aggressive calls exhibiting low, atonal frequencies. Little is known about the social behavior of sakis and it is my hope that a preliminary analysis of vocal communication in *P. irrorata* will provide a foundation for future research regarding the evolutionary significance of their communication and social behavior.

CHAPTER II

GENERAL METHODS

Study Site

My study took place at the Los Amigos Biological Station (commonly known as CICRA or Centro de Investigación y Capacitación Río Los Amigos), which was established in 2000. The field station is located in southeastern Peru at 12°34'07"S 70°05'57" W on a high terrace above the Rio Madre de Dios near the confluence of the Los Amigos River (Figure 1 and Figure 2). The conservation area protects over 140,000 hectares of Amazonian lowland forests and encompasses a variety of habitats, including palm swamps, oxbow lakes, dense bamboo patches, and flooded and *terra firma* forests (Pitman 2008). Rainfall patterns at Los Amigos are seasonal with more than 80% of rainfall occurring during the wet season between October and May and little or no rainfall during the dry season between June and September. The average annual rainfall from 2000 to 2006 was between 2,700-3,000 mm and annual temperatures averaged 24.2° C (Pitman 2008).

Figure 1. Overview map of the Los Amigos Conservation Concession (Pitman 2008).

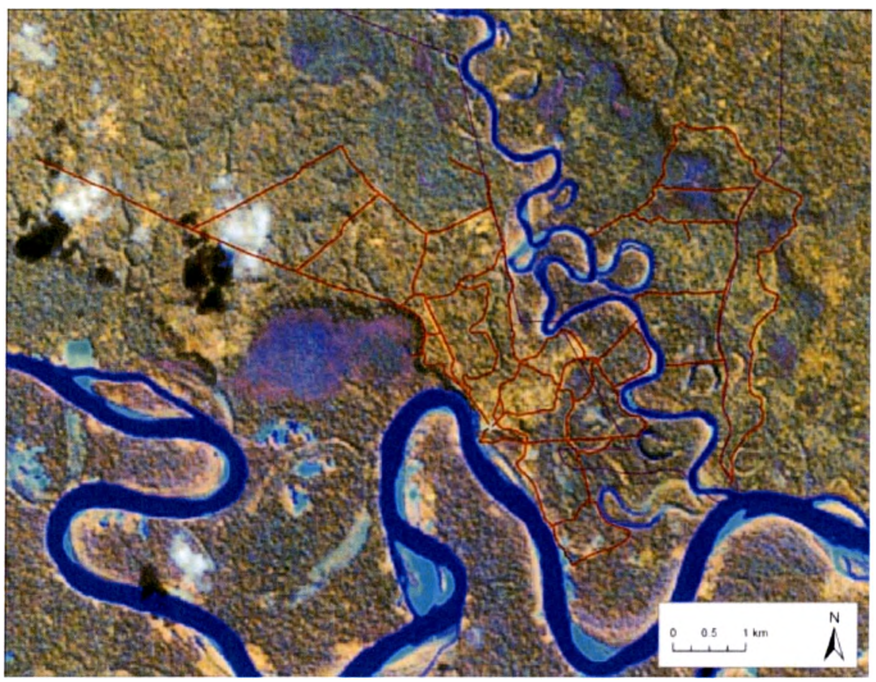

Figure 2. Satellite image of Los Amigos Research Station. The larger river is the Rio Madre de Dios and the smaller river running from North to South is the Rio Los Amigos. Red lines represent the main trail system at the research station. Floodplain forests are represented by dark green areas, the paler patchy spots away from the river represent upland forest, purple areas are palm swamps, and the yellow regions represent bamboo patches (Janovec & Glavan, accessed January 21st 2009 from http://cnx.org/content/m11555/1.1/).

Due to its protected status, the Los Amigos Biological Station has a high density and biodiversity of wildlife, with over 64 identified species of terrestrial and arboreal mammals. There are 11 species of nonhuman primates in the vicinity of the field station, including red howler monkeys (*Alouatta seniculus*), emperor tamarins (*Saguinus imperator*), saddleback tamarins (*Saguinus fuscicollis*), Goeldi's monkeys (*Callimico goeldii*), white-fronted capuchins (*Cebus albifrons*), brown capuchins (*Cebus apella*), squirrel monkeys (*Saimiri boliviensis*), spider monkeys (*Ateles chamek*), brown titi monkeys (*Callicebus brunneus*), owl monkeys (*Aotus nigriceps*), and Gray's bald-faced saki monkeys (*Pithecia irrorata*) (Pitman 2008). I observed all species at the field site with the exception of *Callimico*; *Cebus, Saimiri, Pithecia,* and the two species of *Saguinus* were the most common species observed in the area.

Study Groups

With the help of a research assistant, I collected behavioral and vocal data from May 31st to August 11th of 2008. Data were collected from three primary study groups of Gray's bald-faced sakis, which were referred to as Group 1, Group 2, and Group 3 (see Table 1). Groups 1 and 3 have been habituated since 2004 as part of a long-term study on *P. irrorata* feeding ecology conducted by Suzanne Palminteri and the World Wildlife Fund (Palminteri, personal communication). Group 2 was not previously habituated but was included in the study due to accessibility and frequency of sightings.

Table 1. Focal group compositions.

Group	Total individuals	Adult males	Adult females	Juveniles	Infants
1	6	1	2	2	1
2	4	1	1	2	0
3	4	1	1	2	0

I attempted to collect data from each group twice per week throughout the study; however, in instances where the scheduled group could not be located within the first three hours of the day, another group was located. Groups were located between 7:00-7:30 and were followed throughout the day until we lost sight of the group or until they chose a sleeping site, which usually occurred from 15:00-15:30. We utilized the well-established 61.4 kilometer trail system at the research station to locate and follow the groups whenever possible; however, I created additional trails where needed by marking every 25 meters with flagging tape.

Audio and Behavioral Recording

Vocal recordings were collected in the field from 31 May to 11 August 2008. Vocal recording was conducted opportunistically using a Sony PCM-D50 solid-state digital audio recorder and a Sennheiser ME66 shotgun microphone with a K6 power module. The PCM-D50 is capable of recording acoustics between 20 Hz to 40 kHz, which is well within the acoustical range of saki vocalizations (Buchanan 1978). Calls were recorded by standing approximately 10 to 20 meters from the focal group.

Immediately after the call sequence subsided, I spoke the following information into the audio recorder: the identity of the group being recorded, sex and age class of vocalizing individual if known, the type of movement, if any, on the part of the vocalizer (e.g., chasing, moving up or down canopy, etc), approximate distance between vocalizer and conspecifics, the identity of animals who responded to the vocalization, the type of response or movement of the responding individual(s), whether the subject was seen or only heard, and the activity or context of vocalization. My research assistant concurrently recorded contextual behaviors of each call by writing down the audio file number and context code in a field notebook (Table 2). If multiple behaviors were exhibited during the call emission, the dominant behavior was recorded. For example, if a saki emitted a CHUCK call while traveling in the canopy and it was obvious the call was emitted toward the presence of a sympatric primate, the behavior was not coded as "travel", but as "aggressive heterospecific". Additionally, a mini digital video camcorder with 300X optical zoom was used *ad libitum* to allow for closer examination of facial expressions, locomotive behavior, and other details to help provide contextual information to the vocalizations.

Acoustic Analysis

Recorded calls were transferred digitally from the audio recorder to the computer and individually edited and organized using Sony Sound Forge 7.0. Acoustic data were then analyzed via spectrographic software (Raven Pro 1.3) to identify vocal units and call sequences. All recorded vocalizations were viewed spectrographically; however, only those with good recording quality (i.e., where vocal emissions are clearly discernable from ambient noise) were analyzed. As a result, a small sample size was obtained for calls that were elicited primarily in movement or calls that were rarely emitted. These clear calls were then categorized into call categories (e.g. GROWL, PEE, SHRIEK, etc.) similar to the basic vocalization types previously established on *P. pithecia* (Buchanan 1978). The following variables were measured to identify trends and variation within the call categories: 1) duration of vocal emission in seconds, 2) frequency (in Hz) at the onset and termination of vocalization, 3) minimum and maximum frequency (in Hz) of a vocalization, 4) number of harmonics, and 5) the frequency range (Buchanan 1978; Macedonia 1990). Acoustic variables for *P. irrorata* vocalizations, as well as information on sex and age class of vocalizer (where available) and the context of vocalizations, were then entered into Microsoft Office Excel. Statistical analysis software, SPSS 16.0, was used to generate descriptive statistics (median and range) for all structural variables listed above. After completion of spectrographic analysis, calls were catalogued similar to the standardized format created by Macedonia (1990) for the vocal repertoire of *Lemur catta.*

Table 2. Behavioral ethogram. The ethogram shows the behavioral categories used to assign context to the vocalizations emitted by bald-faced sakis.

Context	Code	Definition
Travel	TRA	Movement from one place to another
Forage	FOR	Individual is consuming, manipulating, or actively searching for food
Inactive	INA	Sitting, laying, sleeping, not moving
Aggressive non-contact	AGN	aggressively chasing or threatening another with head bobs, stares, etc.
Aggressive contact	AGC	slapping, hitting, biting, or physically threatening another
Groom	GRO	picking through hair, removing objects from skin/hair with hands or mouth (includes auto- and allo-grooming
Contact sitting	COS	individuals are sitting side by side touching or within 1 meter from one another
Submission	SUB	fleeing from or relinquishing a feeding site to another individual
Aggressive intergroup	AGI	fighting with, lunging, displaying at a neighboring group
Aggressive heterospecific	AGH	aggressive actions, such as growling, lunging, displaying at another species (including humans)
Mob	MOB	to surround, lunge, chase, and display at a potential predator
Play	PLA	Includes wrestling, chasing, jumping, etc. (solitary or social)
Scent mark	SMA	urinating, rubbing on surfaces with chest or anogenital glands
Other	OTH	any action that does not fit into the above categories

CHAPTER III

RESULTS

The vocal repertoire of *P. irrorata* was determined from 133 hours of observations and recording in the field. Three general call classes (affiliative, distress/agonistic, and alerting/antipredator) and 13 individual calls were identified (Table 3). The calls ranged from simple tonal, single unit calls to complex multi-unit calls, and many of these calls were emitted in multiple contexts and in conjunction with other calls. I recorded a total of 1,845 calls, of which 1007 were of high enough recording quality to analyze.

The majority of analyzed calls, 51.54%, were emitted by sakis during affiliative activities, such as feeding, foraging, resting, and grooming. During these activities the sakis emitted the ZEE-TWITTER, TWITTER, FLUTTER, PEE, WHINY-PEE and HEE-HEE calls. The CHUCK, SHRIEK, GROWL, WAIL, and SCREECH accounted for 27.11% of analyzed calls and were uttered during agonistic encounter with heterospecifics and neighboring groups. Lastly, the CHIPPER and CHIPPER-CHUCK calls comprised 21.35% of all analyzed calls and were

Table 3. *P. irrorata* vocalizations. Columns represent the call types organized according to their call class, number of calls analyzed, number assigned a behavioral context, and the % of total vocalizations in which each type is emitted.

Call Type	Calls analyzed	# assigned behavioral context	% of Total Vocalizations
Affiliative			51.54
ZEE-TWITTER	74	71	7.35
TWITTER	59	57	5.86
FLUTTER	71	60	7.05
PEE	241	223	23.93
WHINY-PEE	42	41	4.17
HEE-HEE	32	26	3.18
Distress/Agonistic			27.11
SHRIEK	29	17	2.88
GROWL	32	32	3.18
WAIL	85	82	8.44
CHUCK	110	93	10.92
SCREECH	17	5	1.69
Alerting/Antipredator			21.35
CHIPPER	46	43	4.57
CHIPPER-CHUCK	169	169	16.78
Totals	1007	919	100%

emitted by the sakis when unexpectedly startled by human observers or unknown mammals, presented with audio playbacks of the harpy eagle (*Harpia harpyja*) and jaguar (*Panthera onca*), or upon the simulated visual presence of a feline predator.

The remainder of this chapter is divided into two sections. In the first section, I will present data collected on the behavioral context for the analyzed vocalizations. The data were then used in the second part of the chapter to present the vocal repertoire of *P. irrorata*.

Quantitative Analysis of Behavioral Data

I was able to assign behavioral contexts to 922 of the 1007 analyzed calls. Most calls were emitted by sakis while foraging, traveling, and engaging in mob behaviors during encounters with potential predators. Sakis also vocalized often during agonistic encounters with neighboring groups and heterospecifics. Table 4 shows the marginal percent of total vocalizations emitted in each context. Following Buchanan (1978), I calculated the percent of all times a vocalization was emitted in each context (Table 5) and the percent of all vocalizations given in one context (Table 6). The data in these tables provide a quantitative approach to context and allowed me to better determine the relationship between each vocalization and its context. These data, along with the *ad libitum* data collected for each vocalization, were used to determine call function. Examples of usage for each call and call function are given for each call type in the second part of this chapter.

Table 4. Percent of total vocalizations emitted in each context.

Context	**% of Total Vocalizations**
Travel	17.3
Forage	26.2
Inactive	4.0
Non-contact aggression	0.1
Contact aggression	0.0
Groom	2.4
Contact	2.0
Submission	0.1
Intergroup aggression	15.1
Heterospecific aggression	12.3
Alarm	19.3
Play	0.7
Scent Mark	0.2
Other	0.3

Table 5. Percent of contexts associated with each vocalization*.

Context	ZEE-TWITTER	TWITTER	FLUTTER	PEE	WHINY-PEE	HEE-HEE	SHRIEK	GROWL	SCREECH	WAIL	CHUCK	CHIPPER	CHIPPER-CHUCK
Travel	44	53	33	27	7	19	6				29	7	2
Forage	41	45	48	56	46	42							2
Inactive	12	2	4	7	15	16							
Non-contact aggression											1		
Contact aggression													
Groom	3		10	6	22								
Contact			5	3									
Submission									20				
Intergroup aggression					5	23	18	22		96	43	2	
Heterospecific aggression							65	53		4	27	89	10
Mob								25					86
Play				1	5				20			2	
Scent Mark							12						
Other									60				

*The table shows the percent of all times a vocalization was emitted in a specific context. For example, 96% of all WAILS were emitted during intergroup aggression. All columns amount to 100%.

Table 6. Percent of vocalizations in each context*.

Context	ZEE-TWITTER	TWITTER	FLUTTER	PEE	WHINY-PEE	HEE-HEE	SHRIEK	GROWL	WAIL	CHUCK	SCREECH	CHIPPER	CHIPPER-CHUCK
Travel	19	19	11	38	2	3	1			3		2	2
Forage	12	11	12	51	8	5							1
Inactive	24	3	5	41	16	11							
Non-contact aggression										100			
Contact aggression													
Groom	9		27	59	5								
Contact			17	39	44								
Submission											100		
Intergroup aggression				1	1	4	2	5	57	29		1	
Heterospecific aggression				1			10	15	3	23		34	14
Mob								5		13			82
Play			17	16	33						17	17	
Scent Mark							100						
Other											100		

*The table shows the percent of all calls given in one context. For example, 44% of all calls given during contact are WHINY-PEES. All rows amount to 100%.

The *Pithecia irrorata* Vocal Repertoire

In this section I describe the vocal repertoire of *Pithecia irrorata* quantitatively, spectrographically, and contextually. Each call type is presented in a standardized format (Table 7) created by Macedonia (1990), with emphasis on call function and context. The acoustic features of each call (see Table 8 for a summary of general acoustical features) are accompanied by one or more audiospectrograms. Each call type is accompanied by specific examples of use. Unfortunately, I was often unable to identify individual vocalizers or the vocalizers' sex due to the high canopy level occupied by the sakis and their lack of obvious sexually dimorphic traits. As a result, the vocal behavior of *P. irrorata*, like other previous studies conducted in difficult observational conditions (Byrne 1981a & Palombit 1992), was measured at the group level. Lastly, summary statistics are provided for measurements taken on structural features of the call, which include call durations and frequencies.

Table 7. Repertoire format*.

I. Vocalization Class: Each call type falls under one of three general classes – Class I: Affiliative Vocalizations; Class II: Agonistic and Distress Vocalizations; and Class III: Alerting and Antipredator Vocalizations.

II. Vocalization Descriptions

A. Vocalization: The name of a call type.

B. Synonyms: Call designations of previous author (Buchanan 1978) for *P. pithecia* and/or *P. monachus*.

C. Acoustic Structure

1. General Spectrographic Features of Vocalizations

   a. Simple tonal structure: A call containing one or more clear harmonic bands.

   b. Simple atonal structure: A call lacking clear harmonic bands.

   c. Complex Structure: Synchronous or asynchronous mixture of tonal and atonal sounds.

2. Frequency Modulation: Patterns of frequency modulation, if present.

3. Harmonics: Typical range of harmonic bands, if present.

4. Additional Characteristics: Any noteworthy structural features not covered previously.

5. Vocalizers: Sex and age-class of call emitter

6. Context of Emission: Specific context(s) during which a call type is emitted.

7. Function: Function of the given vocalization.

8. Structurally-related vocalizations: includes other calls in the repertoire that are most similar acoustically to the one being described.

9. Contextually-related vocalizations: includes other calls emitted in the same context as the one being described.

III. Descriptive Statistics. Sample size, median, and range are given for all structural variables. Additional statistics are given where appropriate. Variables measured for simple tonal and atonal calls include:

Table 7 continued.

A. Number of calls analyzed
B. Call duration in seconds
C. Number of units measured per call
D. Start, end, high, and low frequency in Hz

Variables measured for simple atonal calls:

A through D above

E. Major Energy (darkest continuous portion of the spectrogram) in Hz
1. lowest frequency
2. highest frequency

*Format created by Macedonia (1990) for the vocal repertoire of *Lemur catta.* Slight adjustments were made to fit the repertoire of *P. irrorata.*

Table 8. General acoustic characteristics of each call type.

Vocalization Type	Duration (sec) Mean	Duration (sec) SD	Minimum Frequency (Hz) Mean	Minimum Frequency (Hz) SD	Maximum Frequency (Hz) Mean	Maximum Frequency (Hz) SD	N
ZEE-TWITTER	1.428	.384	1532.6	340.6	4265.5	656.8	74
TWITTER	1.029	.437	1416.2	415.4	4327.8	863.7	59
FLUTTER	1.273	.396	1594.4	274.2	5014.3	1845.2	71
PEE	0.295	.313	543.3	381.3	3224.8	1051.7	241
WHINY-PEE	0.859	.764	787.1	177.3	3408.6	1360.4	42
HEE-HEE	5.751	.014	672.4	180.9	6123.4	3380.6	32
SHRIEK	3.399	.252	484.5	83.3	4890.9	3399.7	29
GROWL	2.587	.823	343.9	119.7	1971.0	998.3	32
WAIL	7.953	.281	596.9	129.6	5334.0	2802.8	85
CHUCK	0.205	.064	399.9	109.5	2823.7	803.0	110
SCREECH	3.099	1.602	627.1	156.2	12457.7	3517.6	17
CHIPPER	0.185	.059	675.1	153.3	3075.4	667.3	46
CHIPPER-CHUCK	0.917	.835	510.5	257.1	3319.1	851.3	169

CLASS I: AFFILIATIVE VOCALIZATIONS

Vocalization: ZEE-TWITTER
Synonyms: Similar in structure and context to the "cheeyeep" of *P. pithecia* and "gurgle cheeyeep" of *P. monachus* (Buchanan 1978).
Acoustic Structure
Spectrogram: Fig 3a,b.
General Structure: Simple, tonal structure; single unit.
Frequency Modulation: Rapid modulation present throughout call; slight downsweep is present at call onset and equivalent upsweep is present at the offset. Variation can be seen at the tail end of the call, with some calls exhibiting a lengthened even tone.
Harmonics: Typically 2 strong sinusoidal shaped bands.
Additional Characteristics: The ZEE-TWITTER appears very clear in most spectrographs and has a bird-like sound to the human ear.
General Contexts of Emission: Most often emitted as a contact call while foraging, traveling, and resting.
Examples of Usage: (a) given when foraging in close proximity to other group members; (b) emitted during group travel from one food location to the next; (c) commonly emitted in response to other contact calls (namely the PEE); occasionally heard when group members are resting or engaging in allogrooming.
Function: Promotes group cohesion in low arousal situations, such as traveling, foraging, and resting.
Vocalizers: All individuals except infant.
Structurally-Related Vocalizations: TWITTER; FLUTTER.
Contextually-Related Vocalizations: TWITTER; FLUTTER; PEE.

Number of Calls Analyzed: n = 74
Call Duration: (s) median = 1.466; range= .500-2.380
Call Frequency
Start Frequency (Hz): median = 2400; range = 1666-5070
End Frequency (Hz): median = 2427; range = 956-4296
Low Frequency (Hz): median = 1583; range = 754-3116
High Frequency (Hz): median = 4269; range = 1589-5827

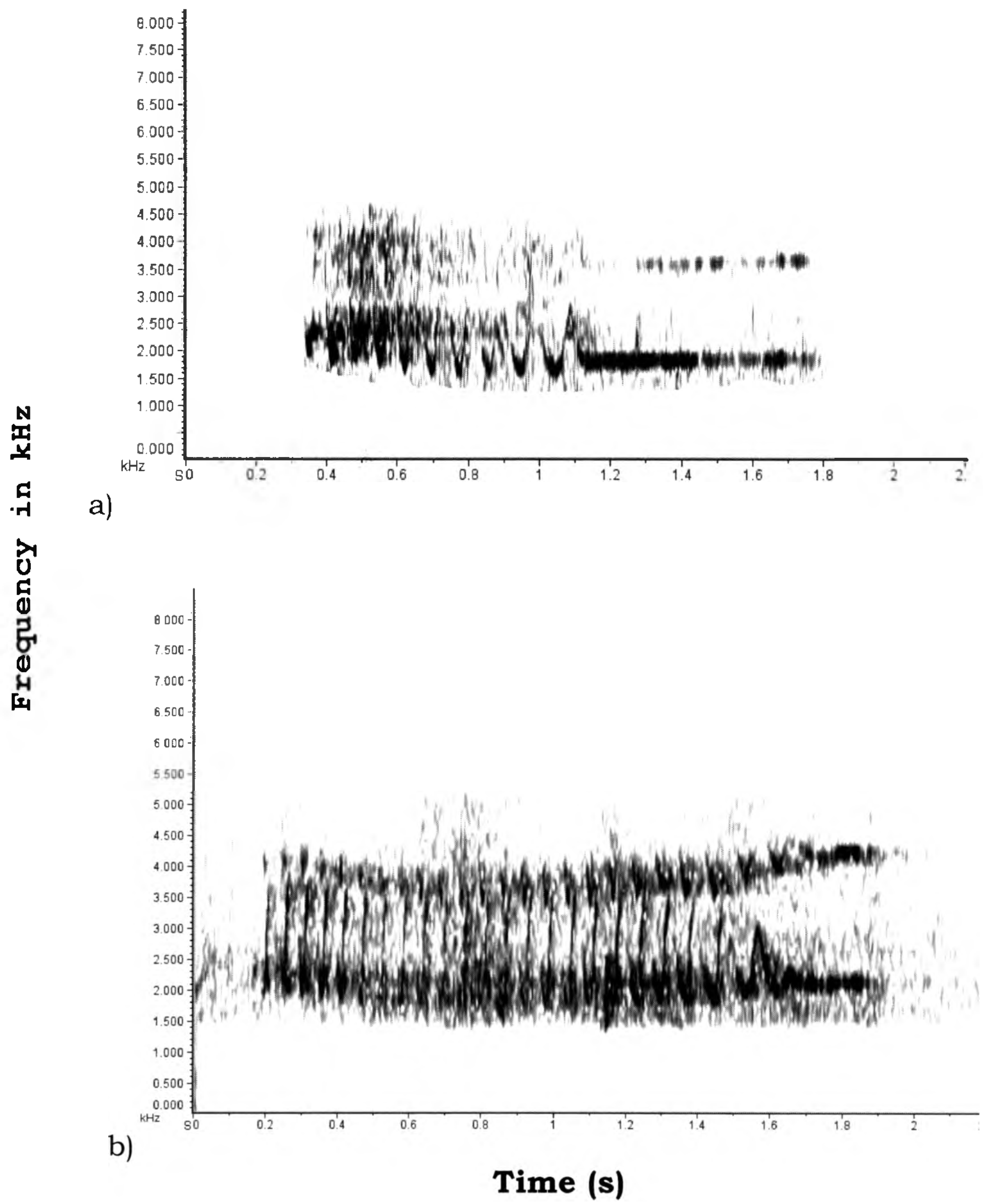

Figure 3. Spectrograms of the ZEE-TWITTER. ZEE-TWITTER (a) was emitted from an individual feeding approximately 3 meters from the group; ZEE-TWITTER (b) was given just after the emission of a PEE by another group member during travel from one feeding location to another.

Vocalization: TWITTER
Synonyms: Similar in structure and context to the "peeyeep" of *P. pithecia* and the "gurgle cheeyeep" of P. *monachus* (Buchanan 1978).
Acoustic Structure
Spectrogram: Fig 4a,b.
General Structure: Simple, tonal structure; single unit.
Frequency Modulation: Like the ZEE-TWITTER, the call exhibits rapid modulation with a sinusoidal wave shape; faint downsweep present throughout the duration of the call.
Harmonics: Like the ZEE-TWITTER, consists of 2 sinusoidal shaped bands.
Additional Characteristics: This call differs in structure and sound from the ZEE-TWITTER because it ends abruptly and lacks an elongated even pitch at the call offset.
General Contexts of Emission: The TWITTER is emitted most often during foraging and traveling. The call is often heard just before or after the emission of a ZEE-TWITTER by another group member. It is possible that the structural variation in the ZEE-TWITTER and TWITTER is a result of sex differences among vocalizers. Therefore, the ZEE-TWITTER AND TWITTER may indeed be the same call with sexually dimorphic characteristics; however, I was unable to collect sufficient data on the vocalizer's sex to make this determination.
Examples of Usage: (a) commonly given as a contact call when traveling short distances; (b) often emitted just prior to the group departing from one feeding location to the next; (c) frequently emitted when foraging within 1 to 3 meters of other group members.
Function: Encourages group cohesion in low arousal situations and possibly indicates the imminence of group relocation.
Vocalizers: All individuals except infant.
Structurally-Related Vocalizations: ZEE-TWITTER (similar sinusoidal structure, but lacks harmonic tails); FLUTTER.
Contextually-Related Vocalizations: ZEE-TWITTER; FLUTTER; PEE.

Number of Calls Analyzed: n = 59
Call Duration: (s) median = .991; range = .254-2.170
Call Frequency
Start Frequency (Hz): median = 2472; range = 1317-4952
End Frequency (Hz): median = 2222; range = 1212-4052
Low Frequency (Hz): median = 1297; range = 718-2740
High Frequency (Hz): median = 4432; range = 2782-6059

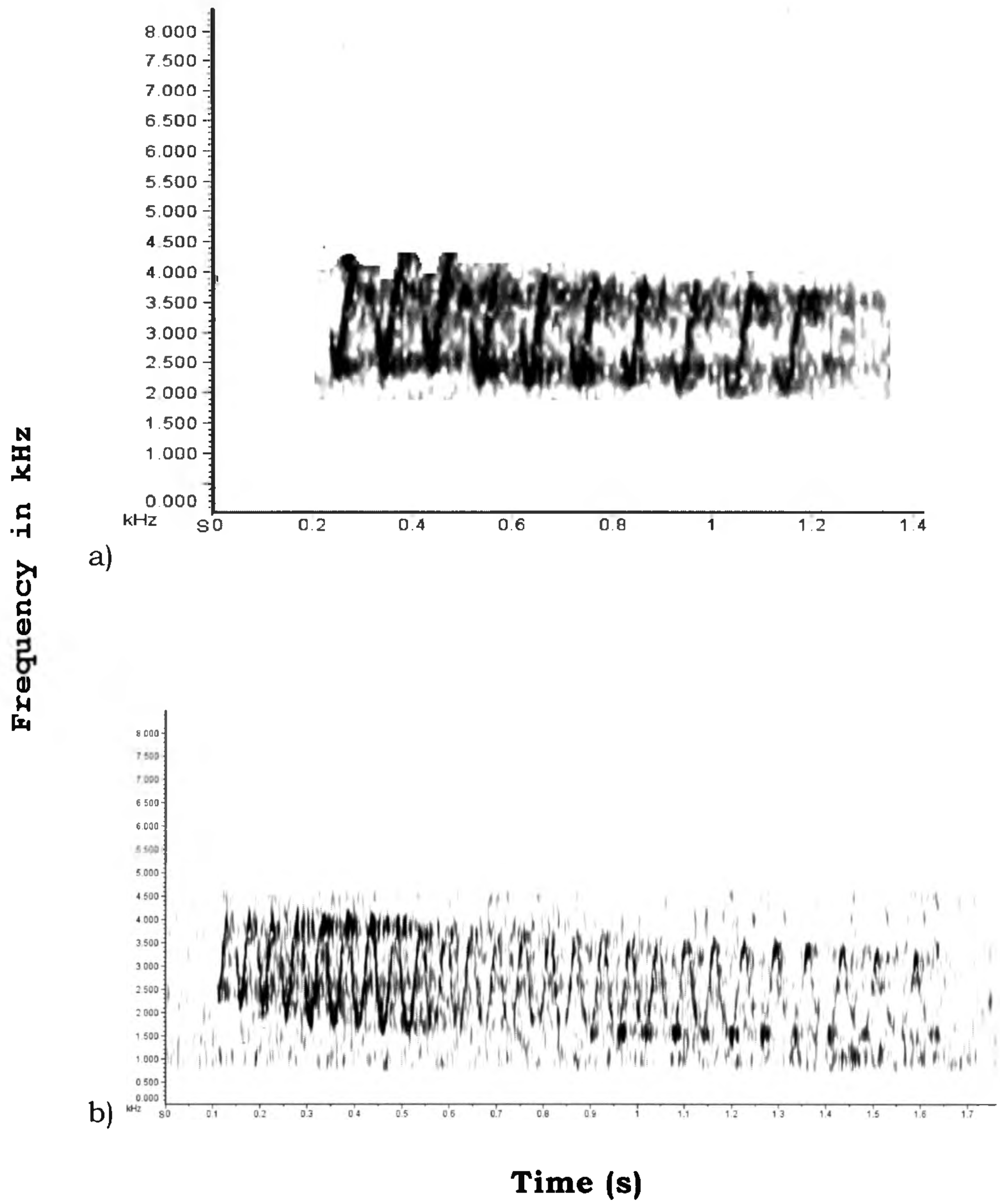

Figure 4. Spectrograms of the TWITTER. TWITTER (a) was emitted by a juvenile traveling within 2 meters of an adult; TWITTER (b) was given just after the emission of a ZEE-TWITTER by another group member during group foraging.

Vocalization: FLUTTER
Synonyms: none.
Acoustic Structure
Spectrogram: Fig 5a,b.
General Structure: Simple, tonal structure; single unit.
Frequency Modulation: Both bands begin from a single frequency at the onset of the call, but the lower band diverges with a sharp downsweep while the higher band occupies the same frequency throughout the duration of the vocalization.
Harmonics: 2 strong sinusoidal shaped bands (see above).
General Contexts of Emission: The FLUTTER is emitted most often during group foraging and traveling and less frequently during allogrooming and contact with conspecifics. Given seldomly when resting, playing, and during heterospecifics encounters.
Examples of Usage: (a) given by adult individual feeding near group on termites; (b) individual emitted FLUTTER then immediately moved over into a nearby feeding tree; (c) adult male grooming female and emitted FLUTTER, then female began to groom male.
Function: Encourages group cohesion in low arousal situations and possibly indicates the desire to maintain contact with conspecifics.
Vocalizers: All individuals except infant.
Structurally-Related Vocalizations: ZEE-TWITTER; TWITTER.
Contextually-Related Vocalizations: ZEE-TWITTER; TWITTER; PEE.

Number of Calls Analyzed: n = 71
Call Duration: (s) median = 1.285; range = .480-2.124
Call Frequency
Start Frequency (Hz): median = 3139; range = 1922-11391
End Frequency (Hz): median = 3342; range = 1108-4190
Low Frequency (Hz): median = 1645; range = 933-2173
High Frequency (Hz): median = 4464; range = 3086-12095

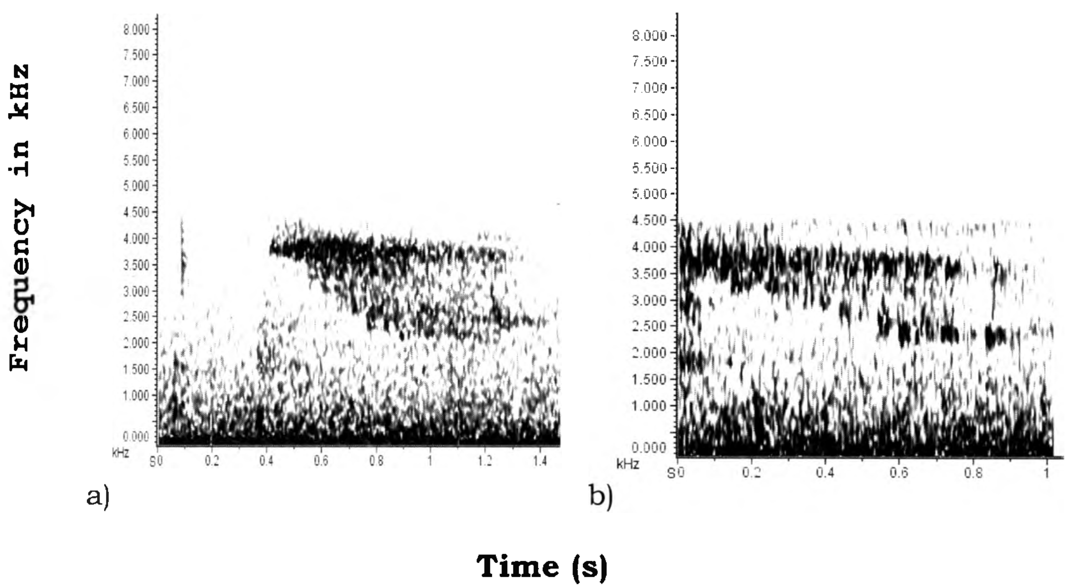

Figure 5. Spectrograms of the FLUTTER. FLUTTER (a) was given by a juvenile shortly after the end of a play bout with another juvenile; FLUTTER (b) was emitted by an adult male grooming an adult female just prior to switching grooming roles.

Vocalization: PEE
Synonyms: Similar in structure and context to the "mee" of *P. monachus* (Buchanan 1978).
Acoustic Structure
Spectrogram: Fig 6a,b.
General Structure: simple tonal; single unit.
Frequency Modulation: slight single frequency downsweep, with some calls falling more sharply than others.
Harmonics: Variable, typically 4 to 5 strong bands.
Additional characteristics: It is not uncommon to hear two or three PEES emitted in succession. Length can vary, with longer calls exhibiting more dramatic frequency downsweep.
General Contexts of Emission: This is the most commonly emitted call in the *P. irrorata* repertoire. It is emitted most frequently in close proximity (less than 1 meter) to other group members while foraging and less frequently given during close group travel. It is seldomly emitted when resting, grooming, and engaging in contact with a conspecific.
Examples of Usage:(a) emitted by individuals when most group members were feeding within 1 meter of each other in the same tree; (b) emitted by group members when traveling side by side; (c) used often when feeding on rarer food sources, such as termites and flowers; (d) occassionally given when resting within a meter of a conspecific and when engaging in allogrooming.
Function: Promotes group cohesion in relaxed, low-arousal situations, especially when group members are in close proximity (usually within 1m).
Vocalizers: Adults and juveniles.
Structurally-Related Vocalizations: WHINY-PEE.
Contextually-Related Vocalizations: ZEE-TWITTER; TWITTER; FLUTTER; WHINY-PEE.

Number of Calls Analyzed: n = 241
Call Duration: (s) median = .216; range= .067–2.889
Call Frequency
Start Frequency (Hz): median = 967; range = 376-3919
End Frequency (Hz): median = 661; range = 215-3486
Low Frequency (Hz): median = 632; range = 215-3842
High Frequency (Hz): median = 3274; range = 765–6785

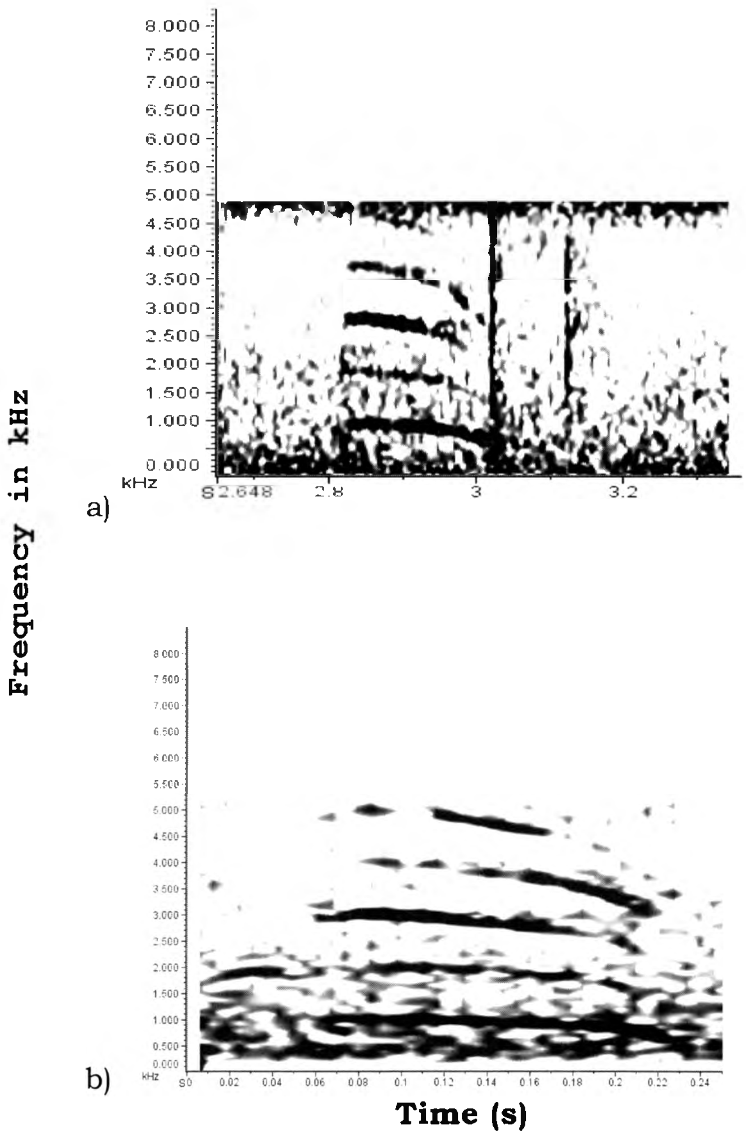

Figure 6. Spectrograms of the PEE. PEE (a) was emitted by an adult feeding on termites in close proximity to other group members; spectrogram (b) was one PEE in a sequence of PEES given by an individual feeding in the same tree as three other group members.

Vocalization: WHINY-PEE
Synonyms: Similar in structure to the "pee" of *P. pithecia* (Buchanan 1978).
Acoustic Structure
Spectrogram: Fig 7a,b.
General Structure: simple tonal; single unit.
Frequency Modulation: power is concentrated mostly in a single, long, narrow band that exhibits little variation in frequency throughout the duration of the call.
Harmonics: 1 strong band in the fundamental frequency and sometimes two or three higher, weaker bands.
Additional characteristics: The WHINY-PEE is similar in sound to the PEE; however, it is more dramatic because it sustains for a much longer duration and is higher in pitch.
General Contexts of Emission: Emitted most frequently by juveniles when foraging in close proximity to the group and by the infant when trying to elicit contact from its mother. Heard very seldomly from adults.
Examples of Usage: (a) emitted by juvenile foraging in the same tree as other group members; (b) given by a juvenile engaged in self-grooming within 1 meter of a conspecific; (c) repeated WHINY-PEES were emitted by the infant while attempting to climb onto its mother's back; however she was engaged in allogrooming with an adult male and ignoring his calls.
Function: Promotes group cohesion in low-arousal situations and may serve to maintain or elicit contact with a conspecific.
Vocalizers: Mostly by infant (over 2 months of age) and juveniles, rarely emitted by adults.
Structurally-Related Vocalizations: PEE.
Contextually-Related Vocalizations: ZEE-TWITTER; TWITTER; FLUTTER; PEE.

Number of Calls Analyzed: n = 42
Call Duration: (s) median = .623; range= .171-4.248
Call Frequency
Start Frequency (Hz): median = 1232; range = 685-3342
End Frequency (Hz): median = 1074; range = 449-3472
Low Frequency (Hz): median = 837; range = 331-1203
High Frequency (Hz): median = 3609; range = 1270-6785

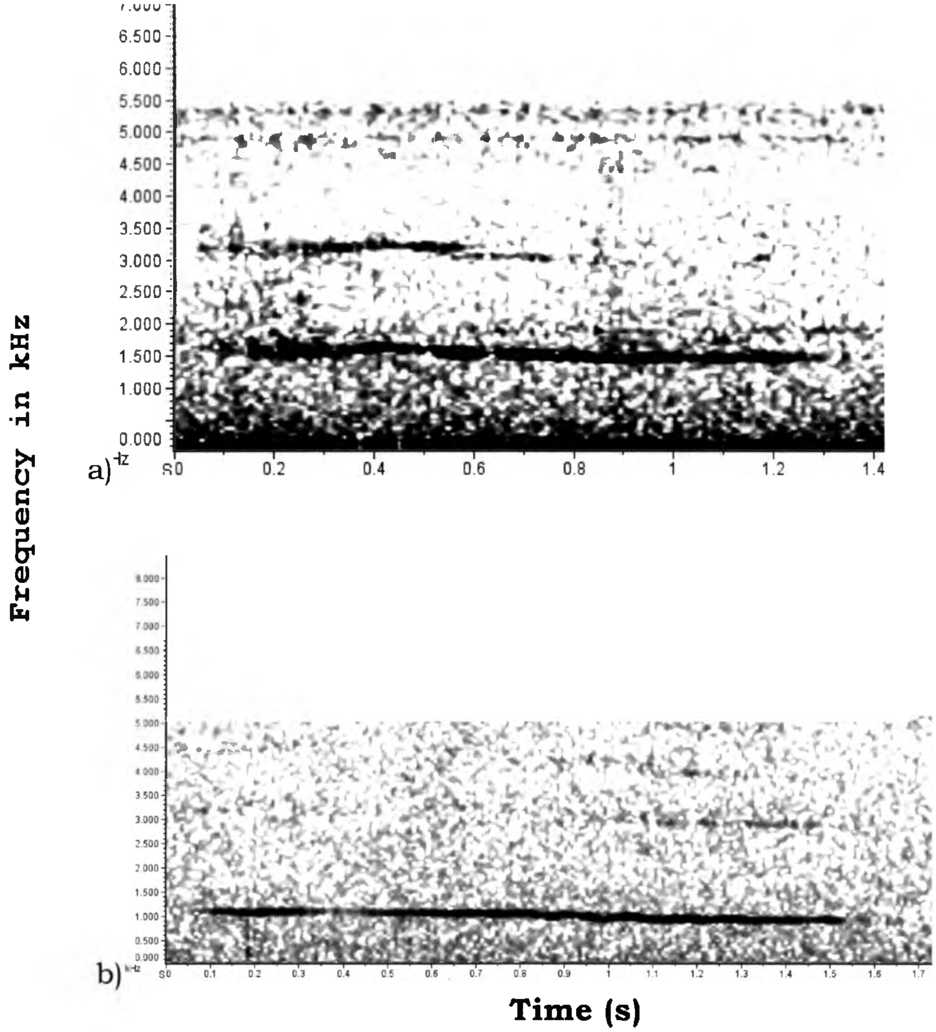

Figure 7. Spectrograms of the WHINY-PEE. WHINY-PEE (a) was given by a juvenile feeding within in 1 meter of a conspecific; WHINY-PEE (b) was emitted by a juvenile engaged in a play bout.

Vocalization: HEE-HEE
Synonyms: none.
Acoustic Structure
Spectrogram: Fig 8a,b.
General Structure: simple tonal; multi-unit.
Frequency Modulation: The HEE-HEE frequently descends sharply downward at call onset and is followed by repeated pulses of partial chevron shaped units.
Harmonics: Highly variable, typically 4 to 5 strong bands with up to 3 to 4 fainter bands in the upper register of the vocal range (above 5 kHz).
General Contexts of Emission: Emitted by individuals in high arousal situations, typically by individuals visually separated from the group. These call bouts usually last an average of 29.5 minutes.
Examples of Usage: (a) emitted by individuals visually separated from the group by 25 or more meters and often elicited a ZEE-TWITTER OR PEE in response from other group members;(b) present at the onset of territorial calls when one group detects the presence of a neighboring group over 25 meters away.
Function: To identify location of group when visually separated in high arousal situations.
Vocalizers: All individuals except infants.
Structurally-Related Vocalizations: WAIL.
Contextually-Related Vocalizations: WAIL.

Number of Calls Analyzed: n = 32
Call Duration: (s) median = 5.869; range= 1.765-9.947
Call Frequency
Start Frequency (Hz): median = 1181; range = 756-5379
End Frequency (Hz): median = 1320; range = 702-4009
Low Frequency (Hz): median = 656; range = 331-1286
High Frequency (Hz): median = 4795; range = 1110-13512

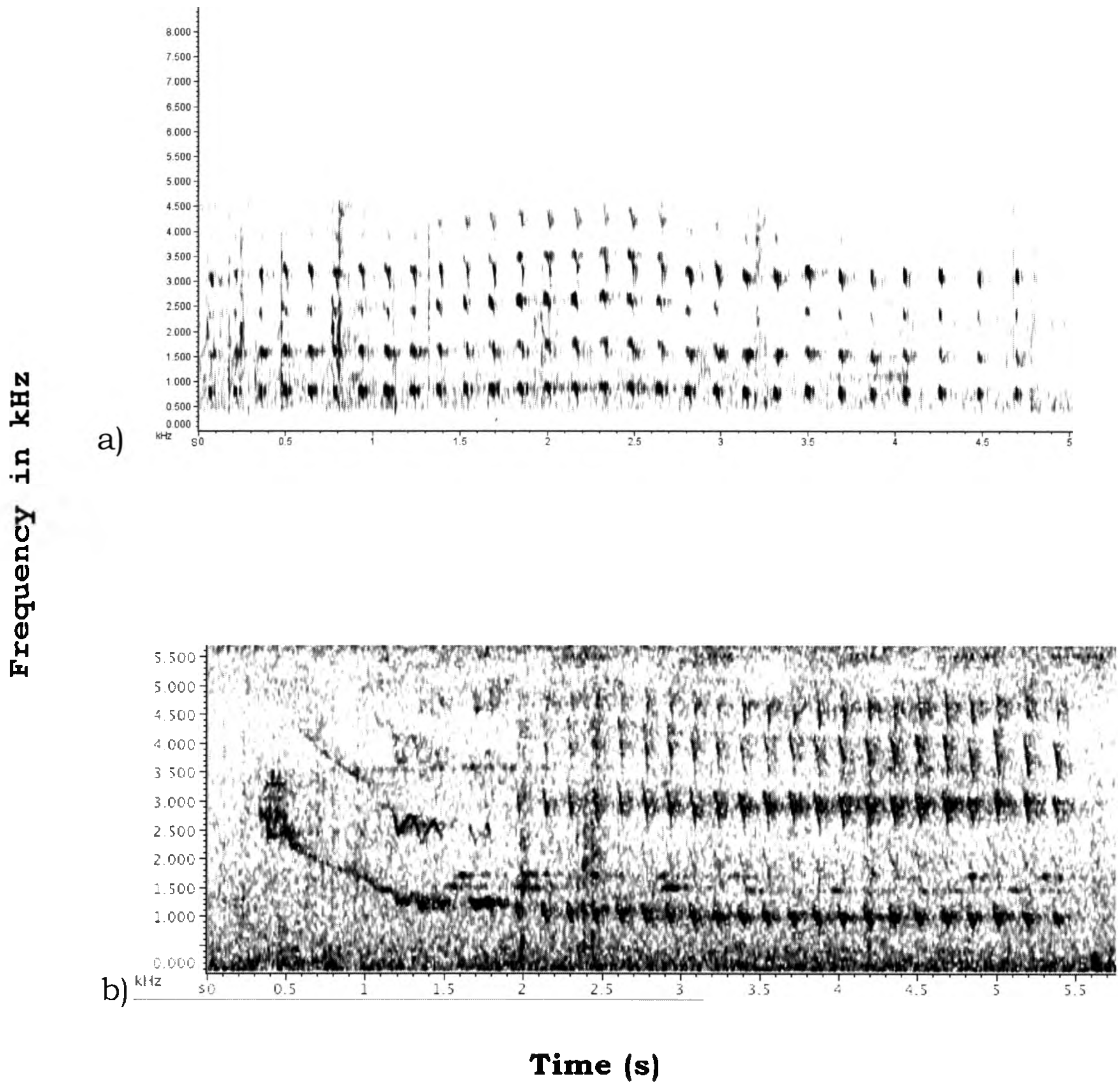

Figure 8. Spectrograms of the HEE-HEE. HEE-HEE (a) was emitted by an adult male visually separated from group by 30+ meters; HEE-HEE (b) was given by a juvenile who was foraging with one other group member while the remainder of the group was 20+ meters away.

CLASS II: DISTRESS AND AGONISTIC VOCALIZATIONS

Vocalization: SHRIEK
Synonyms: Similar in context and structure to the "throat rattle" of *P. pithecia* and the "hoo" of *P. monachus* (Buchanan 1978).
Acoustic Structure
Spectrogram: Fig. 9.
General Structure: simple, tonal; single unit.
Frequency Modulation: Call onset marked by a sustained and unmodulated glottal unit. Call offset either quavers abruptly and ends or quavers repetitively in a sequence of rounded chevron units.
Harmonics: generally 4 bands but can be highly variable, with anywhere from 3 to 12 bands.
General Contexts of Emission: Emitted during heterospecific and intergroup encounters.
Examples of Usage: (a) adult male emitted the SHRIEK during a territorial bout with a neighboring group; (b) given during the presence of a group of spider monkeys (*Ateles chamek*)that appeared to displace the sakis from their feeding tree.
Function: This call was only heard on a few occasions; however, it appears that it is used in high arousal situations to possibly defend territory and resources from sympatric primate species and neighboring groups.
Vocalizers: All individuals except infants, most often adult Males.
Structurally-Related Vocalizations: none.
Contextually-Related Vocalizations: GROWL.

Number of Calls Analyzed: n = 29
Call Duration: (s) median = 2.437; range= 1.030-9.765
Call Frequency
Low Frequency (Hz): median = 472; range = 351-684
High Frequency (Hz): median = 4088; range = 2673-14685
Major Energy (Hz)
Start Frequency (Hz): median = 752; range = 568-1002
End Frequency (Hz): median = 685; range = 518-2422

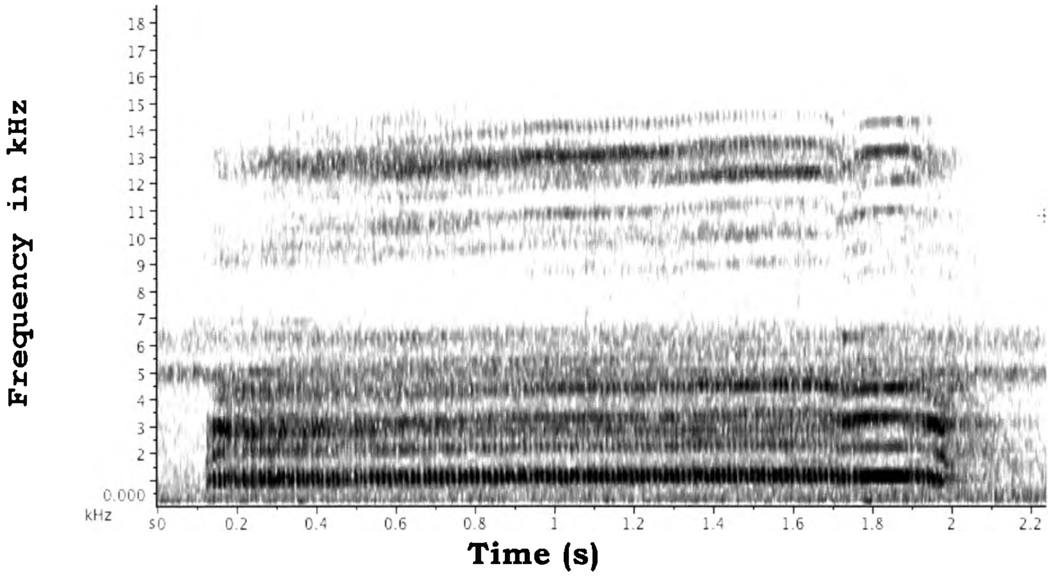

Figure 9. Spectrogram of a SHRIEK. This call was emitted from an adult male during a territorial bout with a neighboring group of sakis.

Vocalization: GROWL
Synonyms: Similar in context and structure to the "juvenile growl" of *P. pithecia* and "low throat rattle" of *P. monachus* (Buchanan 1978).
Acoustic Structure
Spectrogram: Fig 10a,b.
General Structure: simple atonal; single unit. Spectrographically viewed as a continuous guttural stream.
Frequency Modulation: n/a.
Harmonics: n/a.
Additional characteristics: A plosive wall of energy that is evenly distributed throughout the emitted frequencies and often followed by the CHUCK call.
General Contexts of Emission: Emitted in response to the presence of low to moderate level mammalian threats.
Examples of Usage: (a) adult males often emitted growls upon the sudden presence of human observers; (b) emitted at the nearby presence of heterospecifics, such as spider monkeys (*Ateles chamek*) and capuchins (*Cebus apella*); (c) frequently given during intergroup encounters; (d) also emitted during the presence of a jaguar decoy.
Function: To alert group of potential known and unknown threats.
Vocalizers: All individuals except infants.
Structurally-Related Vocalizations: none.
Contextually-Related Vocalizations: SHRIEK; CHUCK; CHIPPER.

Number of Calls Analyzed: n = 34
Call Duration: (s) median = 2.200; range= .787-8.366
Call Frequency
Low Frequency (Hz): median = 364; range = 142-635
High Frequency (Hz): median = 1787; range = 839-4365
Major Energy
Low Frequency (Hz): median = 579; range = 154-854
High Frequency (Hz): median = 616; range = 251-991

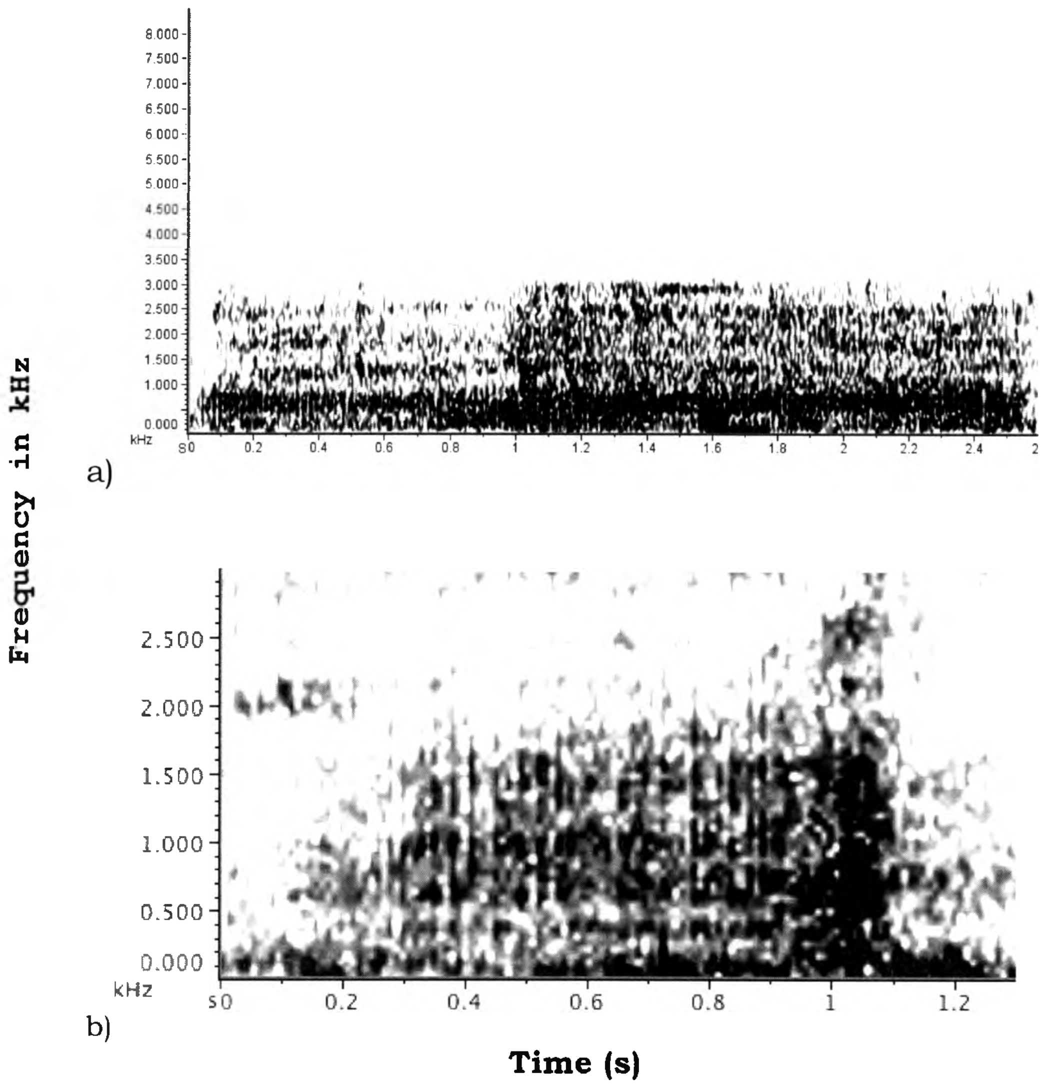

Figure 10. Spectrograms of the GROWL. GROWL (a) was emitted by an adult male upon the presence of a large group of capuchins moving into the same tree; GROWL (b) was followed by a CHUCK and was directed toward the simulated visual presence of a jaguar.

Vocalization: WAIL
Synonyms: none.
Acoustic Structure
Spectrogram: Fig 11a,b.
General Structure: simple tonal; multi-unit.
Frequency Modulation: Typically exhibits a long sequence of short modulated units at call onset. The call usually consists of two or three units with a brief pause between each unit. Each new segment begins with a sharp downsweep from a higher frequency into a pulsating sequence of chevron-shaped units.
Harmonics: Power is almost always concentrated in the first 3 bands; however, some calls exhibit up to 9 bands that become weaker in higher frequencies.
General Contexts of Emission: Emitted during inter-group encounters. WAILS are often accompanied by aggressive displays such as tail lashing, arching of the back, head bobbing, full body shaking, and quick back and forth movements across branches.
Examples of Usage: (a) emitted most often by adult males when attempting to drive away a neighboring group in overlapping home ranges.
Function: To establish territorial boundaries with neighboring groups and defend food resources and possibly mates.
Vocalizers: all individuals except infant, mostly adult and juvenile males.
Structurally-Related Vocalizations: HEE-HEE.
Contextually-Related Vocalizations: HEE-HEE; GROWL; SHRIEK.

Number of Calls Analyzed: n = 85
Call Duration: (s) median = 7.650; range= 2.504-16.800
Number of units measured per call: median = 3; range = 2-4
Call Frequency
Start Frequency (Hz): median = 992; range = 756-3207
End Frequency (Hz): median = 1036; range = 567-4252
Low Frequency (Hz): median = 601; range = 234-835
High Frequency (Hz): median = 4343; range = 2646-13606

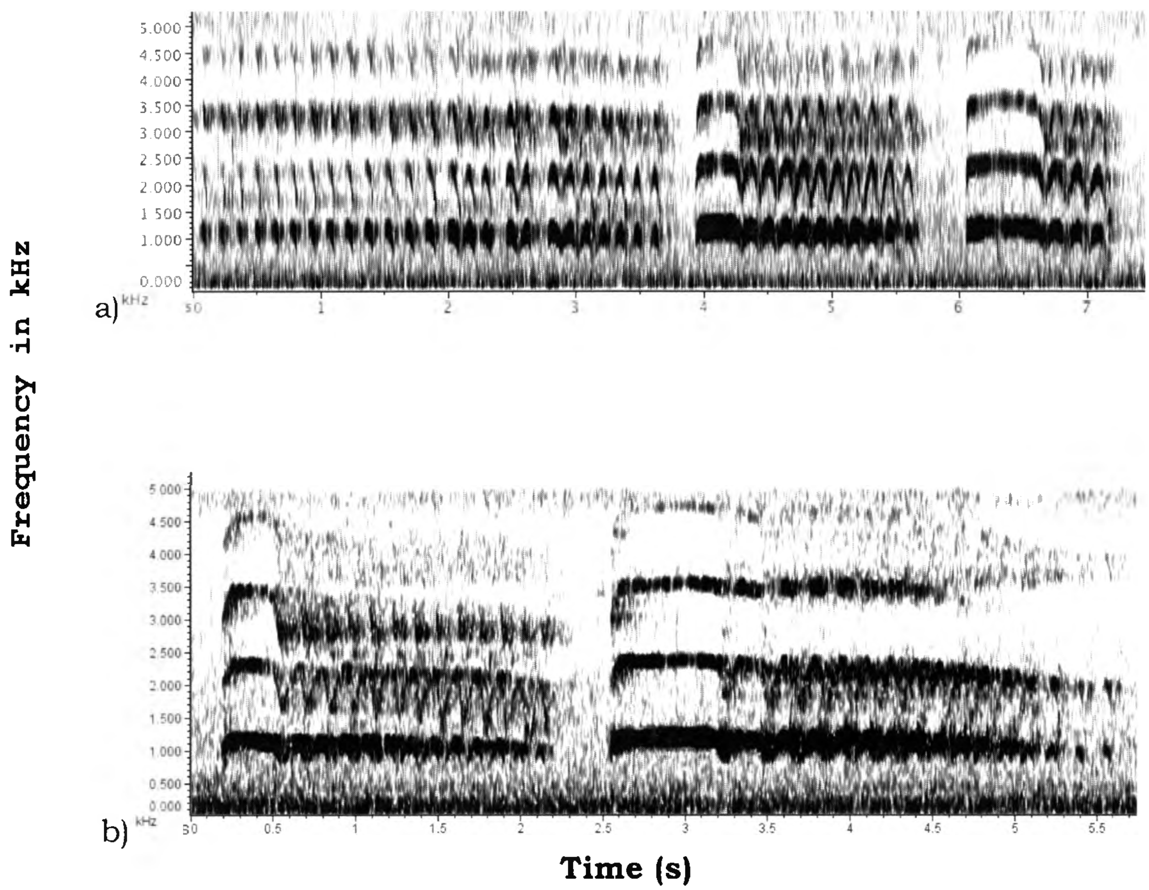

Figure 11. Spectrograms of the WAIL. WAIL (a) was emitted by an adult male during a surprise encounter with a neighboring group; WAIL (b) was given by an adult male during a territorial bout that lasted 39 minutes.

Vocalization: CHUCK
Synonyms: Similar in context to the "high chuck" and "intense chuck" of *P. pithecia* (Buchanan 1978).
Acoustic Structure
Spectrogram: Fig 12.
General Structure: simple atonal; single unit.
Frequency Modulation: n/a.
Harmonics: n/a.
Additional characteristics: Burst of power evenly distributed throughout the emitted frequencies.
General Contexts of Emission: The CHUCK is the shortest duration call in the *P. irrorata* repertoire. It is most often emitted in moderate to high arousal situations, such as intergroup interactions, interspecies interactions, and detection of a potential threat. CHUCKS were often emitted in a repeated sequence of highly variable intensity, with some chucks exhibiting a much shorter duration and lower frequency than others. This call was generally emitted at the end of prolonged bouts of unsuccessful attempts to ward off unwanted company. The vocalizers mouth appears to take the shape of an "O" when emitting CHUCKS.
Examples of Usage: (a) adult male emitted sequence of chucks at the end of a lengthy territorial bout with a neighboring group; (b) 2 to 3 group members (including 1 juvenile) emitted a series of chucks after detecting a tayra in a nearby tree.
Function: To alert group members and drive out potential threats.
Vocalizers: All individuals except infants.
Structurally-Related Vocalizations: CHIPPER.
Contextually-Related Vocalizations: GROWL; SHRIEK.

Number of Calls Analyzed: n = 110
Call Duration: (s) median = .202; range= .087-.394
Call Frequency
Low Frequency (Hz): median = 401; range = 200-835
High Frequency (Hz): median = 3003; range = 1512-3992
Major Energy
Low Frequency (Hz): median = 702; range = 402-2539
High Frequency (Hz): median = 902; range = 567-3007

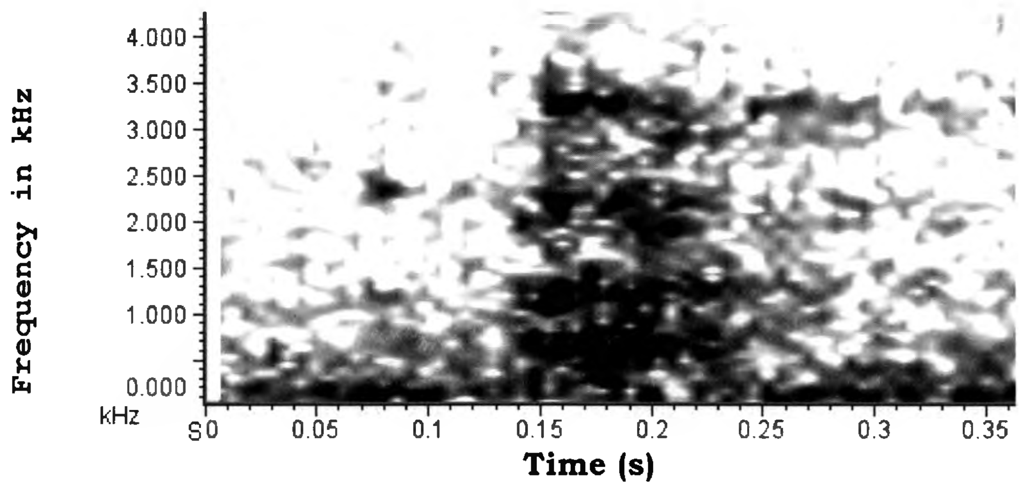

Figure 12. Spectrogram of the CHUCK. This call was emitted by an adult male after a prolonged bout of mobbing a jaguar decoy.

Vocalization: SCREECH
Synonyms: none.
Acoustic Structure
Spectrogram: Fig 13.
General Structure: simple atonal; single unit.
Frequency Modulation: n/a.
Harmonics: n/a.
General Contexts of Emission: Distress call emitted by infants and juveniles during stressful situations.
Examples of Usage: (a) infant emitted a succession of SCREECHS after an adult female removed infant from her back and traveled 15 meters away to forage; (b) juvenile emitted 2 loud SCREECHS after being displaced while feeding by a capuchin (*Cebus apella*); (c) juvenile emitted a succession of SCREECHS after falling a couple of meters in the tree during a play bout with a conspecific.
Function: The SCREECH was only heard on 5 separate occasions; however, it appears to indicate fear and may serve to elicit comfort or attention from other group members.
Vocalizers: Infants and juveniles.
Structurally-Related Vocalizations: none.
Contextually-Related Vocalizations: none.

Number of Calls Analyzed: n = 17
Number of Individuals Sampled: n = 3
Call Duration: (s) median = 3.301; range= .603-5.79
Call Frequency
Low Frequency (Hz): median = 589; range = 326-921
High Frequency (Hz): median = 13849; range = 4745-15918
Major Energy:
Low Frequency (Hz): median = 1798; range = 702-3968
High Frequency (Hz): median = 3907; range = 2450-8434

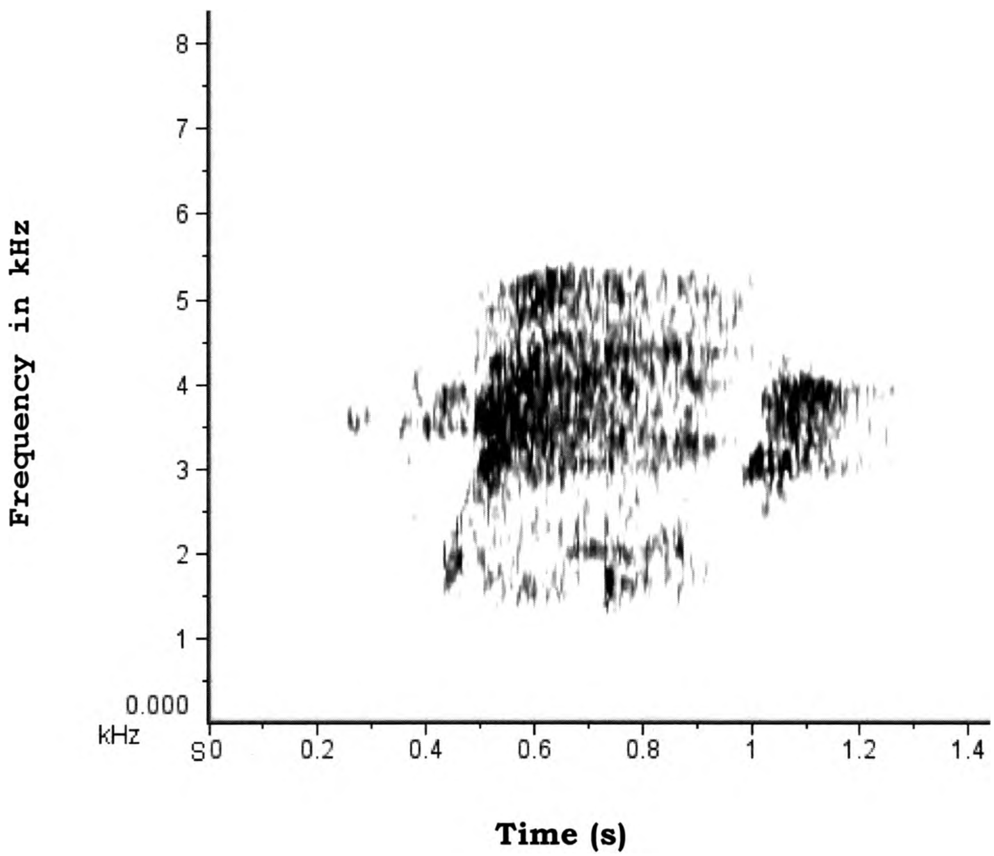

Figure 13. Spectrogram of the SCREECH. The SCREECH in this spectrogram was one of a succession of SCREECHS emitted by an infant after an adult female removed the infant from her back and quickly traveled several meters away to forage.

CLASS III: ALERTING & ANTIPREDATOR VOCALIZATIONS

Vocalization: CHIPPER
Synonyms: none.
Acoustic Structure
  Spectrogram: Fig 14a,b.
  General Structure: simple tonal; multi-unit.
  Frequency Modulation: 2 short continuous units, often emitted in a sequence with little modulation.
  Harmonics: Varies significantly from 2 to 5 strong bands; power is often evenly distributed among all bands, but with shorter duration in higher frequencies.
General Contexts of Emission: most frequently given at the presence of human observers.
Examples of Usage: (a) adult emitted call upon the sudden arrival of a small group of people; (b) multiple group members gave call when arriving at the edge of a cliff and detected our unexpected presence.
Function: Appears to be an alert call given when individuals are startled by the presence of humans and possibly other terrestrial mammals.
Vocalizers: All individuals except infants
Structurally-Related Vocalizations: n/a.
Contextually-Related Vocalizations: GROWL.

Number of Calls Analyzed: n = 46
Call Duration: (s) median = .187; range= .098-.335
Number of units measured per call: median = 2; range = none
Call Frequency
  Start Frequency (Hz): median = 1087; range = 768-2138
  End Frequency (Hz): median = 1512; range = 732-3165
  Low Frequency (Hz): median = 709; range = 267-969
  High Frequency (Hz): median = 3324; range = 1228-4142

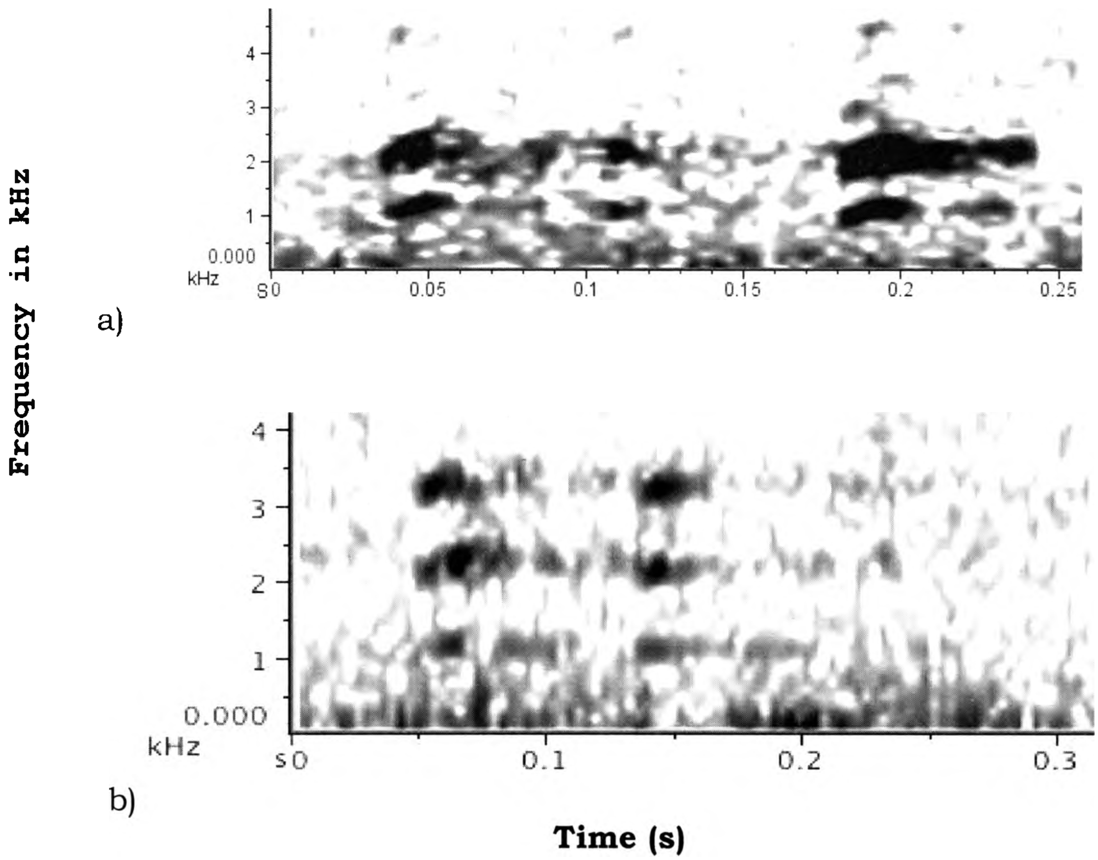

Figure 14. Spectrograms of the CHIPPER. Both spectrogram were emitted by adult individuals upon sighting the presence of human observers.

Vocalization: CHIPPER-CHUCK
Synonyms: none.
Acoustic Structure
Spectrogram: Fig 15a,b,c.
General Structure: Simple tonal to complex; multi-unit.
Frequency Modulation: Sequence of short modulated units, often followed by a burst of plosive energy that occupies all frequencies of the call.
Harmonics: 1 to 3 bands usually visible.
Additional characteristics: This call is similar to a sequence of CHIPPER calls ending with a CHUCK; however, it has a highly variable structure and the chuck is not always emitted at the end of the sequence. The call is usually emitted in repeated successions with a graded intensity.
General Contexts of Emission: Emitted by group members when mobbing large terrestrial predators.
Examples of Usage: (a) this call was only recorded when sakis were exposed to visual stimuli of a jaguar in conjunction with audio playbacks.
Function: May serve to alert terrestrial predators that their presence has been detected.
Vocalizers: All individuals except infants.
Structurally-Related Vocalizations: CHUCK.
Contextually-Related Vocalizations: CHUCK.

Number of Calls Analyzed: n = 169
Call Duration: (s) median = .579; range= .099-14.753
Fundamental Frequency
Low Frequency (Hz): median = 468; range = 84-1417
High Frequency (Hz): median = 3572; range = 1488-5462
Major Energy (Hz)
Low frequency (Hz): median = 992; range: 815-1786
High frequency (Hz): median = 1734; range: 806-2306

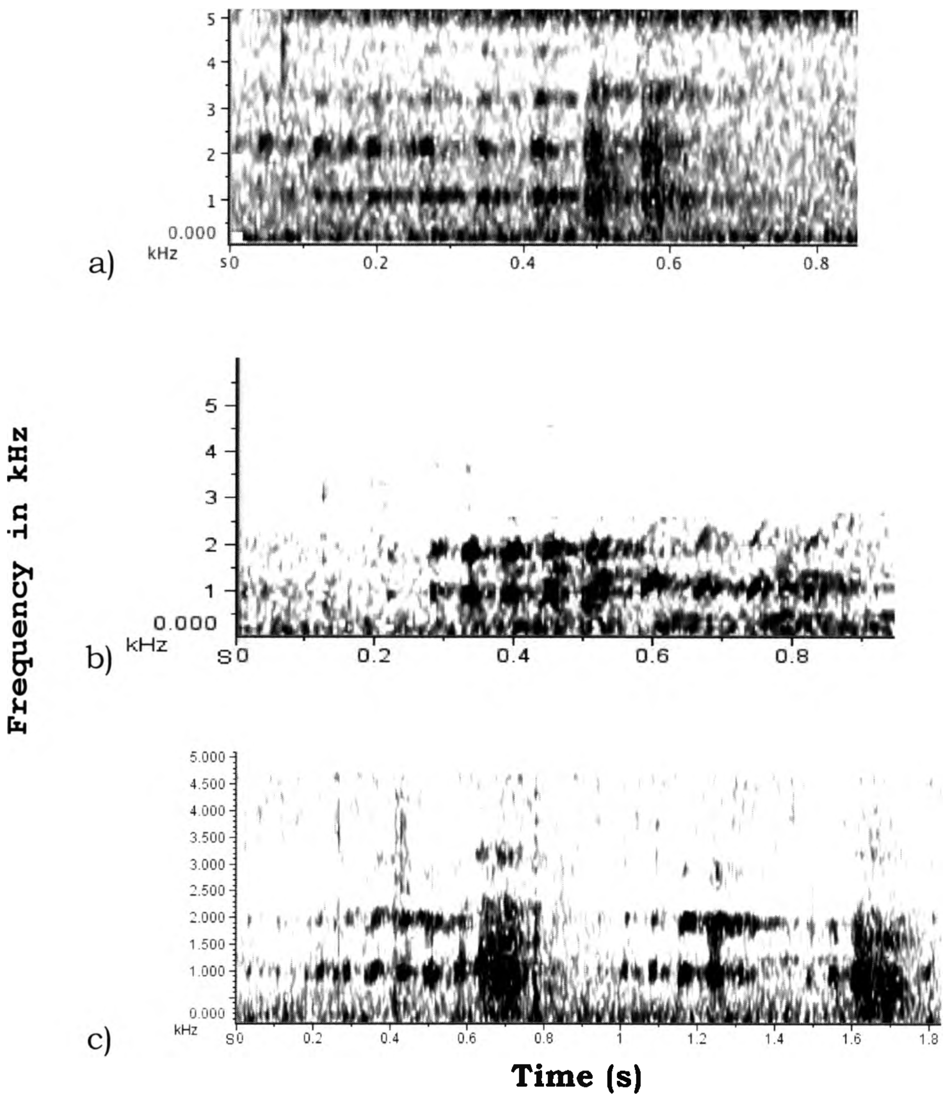

Figure 15. Spectrograms of the CHIPPER-CHUCK. Spectrograms a-c demonstrate the structural variation in the CHIPPER-CHUCK. CHIPPER-CHUCK (a) appears to be emitted in the highest arousal situations, most commonly when individuals appeared frustrated by the prolonged presence of a jaguar decoy; CHIPPER-CHUCK (b) is given in moderate arousal situations such as when presented with audio of a jaguar call without an accompanying visual; (c) is given in high arousal contexts, generally upon first sight of a jaguar decoy.

CHAPTER IV

DISCUSSION

The vocal repertoire of the adult bald-faced saki consists of 12 call types, with at least one additional call type seemingly emitted only by juveniles and infants. It is important to note that the number of call types in a species' repertoire is subject to the quantity and quality of recorded calls and the method of classification used by the researcher (i.e. "lumping" or "splitting"). There is no standard method for classifying call types and this makes it difficult to compare vocal repertoires across species. Additionally, the manner in which calls are categorized, according to either context or function, can be highly variable from one researcher to the next. For example, while Jolly (1966) determined that the vocal repertoire of *Lemur catta* contained 15 call types, Macedonia (1990) later reported between 18 and 22 call types. The reason for this discrepancy is that Macedonia (1990) classified calls more discretely and reported several low volume calls not included in Jolly's (1966) repertoire. Additionally, even in the most carefully constructed repertoires, it remains largely uncertain whether the call categories designated by the researcher are actually significant to the animals emitting the calls (Egnor et al. 2006). Despite these inherent problems, vocal repertoires can elucidate the most basic communicative patterns of a species and provide valuable insight into their social behavior.

Comparison To Other Pitheciids

Buchanan (1978) reported the vocal repertoire size of *P. pithecia* to contain 18 call types and *P. monachus* to contain 17 call types, whereas I identified 13 total call types for *P. irrorata.* The difference in repertoire size between my findings and Buchanan's may be due to our differing methods of classification. Buchanan classified his calls into call groups based on their acoustical sound (trills, whistles, moans, guttural sounds, etc.), whereas I separated calls according to their function (affiliative, agonisitic and distress, and alerting and antipredator). Additionally, Buchanan identified five discrete types of "chuck" calls for both *P. pithecia* and *P. monachus*, while I only identified one CHUCK call type for *P. irrorata.* I identified the CHUCK as a graded call, which can be slightly shorter or longer in duration and lower or higher in frequency depending on the intensity of the situation in which it is emitted. Buchanan also identified two call types that were unique to juveniles (the "juvenile warbled chuck" and the "juvenile growl"). I was able to identify only one call type unique to juveniles and infants (the SCREECH).

Buchanan (1978) identified one call in the "purr" call group for both *P. pithecia* and *P. monachus*. He stated that these uncommon calls were indistinguishable from one another and sounded like the purr of a cat. According to Buchanan, the "purr" call types were only emitted when he was in close contact with the vocalizer and they appeared to be directed toward him. I did not identify a call similar to this for *P. irrorata*. Buchanan may have been able to identify low-volume calls that I did not hear, such as the "purr", because he was able to record vocalizations in much closer proximity to his captive subjects. However, this may also be a species-specific call that was not evolutionarily selected for by the environment of *P. irrorata*.

Similar vocal repertoire sizes have been reported for other genera of Pitheciidae. Buchanan (1978) identified 8 calls in the vocal repertoire of *Cacajao rubicundus* and Robinson (1979) reported 11 calls in the vocal repertoire of *Callicebus moloch*. Interestingly, the vocal repertoire size for *P. irrorata,* at 13 total call types, falls exactly in the middle of the repertoire range for the Pitheciids discussed above.

Relationship Between Vocal Repertoire Size and Group Size

McComb and Semple (2005) conducted a comparative study across 42 non-human primates to assess the relationship between a species' vocal repertoire size and group size. The results of their study demonstrate that evolutionary changes in repertoire size are positively influenced by changes in group size. As group size increases, new social complexities arise that may call for increased communication. For example, larger groups may experience more agonism over resources, which may then lead to an increase in the number of agonistic calls in their repertoire. Furthermore, individuals may need to increase the contact calls in their repertoire to compensate for the greater traveling and foraging distance that occurs between individuals living in larger groups.

The mean group size of sakis in my study was 4.7, which is consistent with the *P. irrorata* mean group size of 4.4 documented by Kappeler and Heymann (1996). According to McComb and Semple's (2005) data, primate species with mean group sizes between 3.5 and 5.5 have an average adult repertoire size of 12.5 calls (see Appendix A). Thus, my results of 12 calls in the *P. irrorata* repertoire support McComb and Semple's hypothesis that changes in the repertoire size of nonhuman primates are positively correlated with changes in group size.

Evaluation of the Motivational-Structural Rules Hypothesis

As discussed briefly in the first chapter of this thesis, Morton (1977) proposed the "motivational-structural rules" hypothesis (hereafter referred to as MS rules). This hypothesis assumes an inverse relationship between body size and vocal frequency in birds and mammals. Morton

(1977) argued that, because larger animals generally dominate their smaller counterparts, animals favor low frequency calls in aggressive encounters to create the perception that they are larger and, perhaps, more dangerous to opponents. These calls also tend to be atonal, or noisy, because low frequency sounds cause the membrane on the glottis to vibrate during vocal emission. In contrast, Morton (1977) observed that animals emit tonal, high frequency sounds in fearful or friendly contexts. According to Morton, infants, due to their size, emit high frequency sounds that elicit attention from the parent. Therefore, animals will emit tonal, high frequency vocalizations as a means to suppress aggression and elicit comfort.

The GROWL, CHUCK, SHRIEK, and WAIL were almost always emitted by the sakis in aggressive situations and on many occasions they were accompanied by aggressive behaviors such as tail lashing, head bobbing, body arching, piloerection, and erratic movements in the canopy. The GROWL and CHUCK are both atonal, broadband calls that occupy the lowest frequencies in the *P. irrorata* repertoire (median low frequencies of 364 and 401 Hz respectively). Therefore, these two call types comply with the MS rules hypothesis.

On the other hand, although the SHRIEK had a median low frequency of 472 Hz, it is a highly variable tonal call with a median maximum frequency of 4134 Hz. The call was almost always emitted in aggressive encounters with neighboring groups or sympatric primate species. The WAIL is also a tonal, higher frequency call emitted solely during aggressive intergroup encounters. Thus, the defensive SHRIEK and WAIL calls do not seem to support Morton's hypothesis. Morton (1977) did however, state that MS rules mostly affects calls emitted by individuals when they are in close proximity to one another. In this case, the SHRIEK and WAIL would not necessarily fit Morton's hypothesis because they are usually emitted toward aggressors at a distance.

The SCREECH was the only call in the sakis' repertoire to exclusively signal fear or submission. The call had a median high frequency of 13849 Hz, which appears to conform to the MS rules hypothesis. However, this is a noisy, atonal call that was only emitted by infants and juveniles. Due to their smaller body size, it is not surprising that it has a higher frequency than those calls emitted by adults. It is also important to note that this call type had the smallest sample size of all recorded calls and, therefore, its acoustic features may not be as accurately represented. Out of the six affiliative or "friendly" calls in the *P. irrorata* repertoire, all are tonal and none of them exhibit sound frequencies as low as those calls emitted in aggressive situations. The ZEE-TWITTER, TWITTER, and FLUTTER seem to fit the MS rules hypothesis well because they all have median low frequencies above 1297 Hz. Additionally, Morton (1977) suggested that calls emitted in fearful or friendly motivational states will tend to exhibit an upsweep in frequency. The only affiliative call to show this upsweep is the ZEE-

TWITTER, while the TWITTER, FLUTTER, and PEE have slight downsweeps.

As part of the MS rules hypothesis, Morton (1977) suggested that mobbing calls were selected for in situations when an animal is indecisive or uncertain (i.e. should the animal move toward or away from the stimulus). Mobbing calls are generally accompanied by lunging and erratic, back and forth movements by the prey (Gursky & Nekaris 2006). As a result, Morton argued that mobbing calls tend to be chevron-shaped because they are emitted in a mixed motivational state of both fear and aggression. The CHIPPER-CHUCK was the only mobbing call heard in the *P. irrorata* repertoire but it does not have the chevron-shape predicted by Morton. It is also interesting to note that the ZEE-TWITTER and TWITTER, which are emitted during friendly motivational states, and the WAIL, which is emitted during aggressive motivational state, exhibit the up and down chevron-shape.

It appears that Morton's (1977) motivational-structural rules hypothesis only partially applies to the vocal repertoire of *Pithecia irrorata*. The hypothesis does not fully conform because the *P. irrorata* repertoire exhibited affiliative calls with slight downsweeps instead of upsweeps (TWITTER, FLUTTER, and PEE), a mobbing call that lacked the chevron-shaped pattern (CHIPPER-CHUCK), and the presence of the chevron-shape in affiliative and aggressive calls (ZEE-TWITTER, TWITTER, FLUTTER, WAIL).

CHAPTER V

CONCLUSION

This study is unique because it is the first study, to my knowledge, to examine vocal communication in the Gray's bald-faced saki, *Pithecia irrorata.* Additionally, it is the only vocal repertoire of a Pitheciinae species to be constructed solely from calls collected and recorded in the wild. My results indicate that the vocal repertoire of *P. irrorata* contains 12 adult call types and one additional call type exclusive to infants and juveniles. As expected, the repertoire size of *P. irrorata* falls in the middle of the repertoire size range for other Pitheciids (*Cacajao rubicundus,* 8 call types; *Callicebus moloch,* 11 call types; *Pithecia monachus,* 17 call types; and *Pithecia pithecia,* 18 call types). Additionally, the repertoire size of *P. irrorata* is comparable to other non-human primates with mean group sizes between 3.5 and 5.5 (McComb & Semple 2005). Thus, my findings support McComb and Semple's (2005) hypothesis that repertoire size and group size are positively correlated.

Lastly, my data show that the vocal repertoire of *P. irrorata* only partially conforms to Morton's (1977) MS rules hypothesis. While the majority of affiliative call types are tonal and higher in frequency, not all affiliative calls exhibit the call upsweep predicted by Morton (1977). Furthermore, the mobbing call in the *P. irrorata* repertoire does not exhibit the chevron-shaped structure predicted by Morton for calls elicited during mixed-motivational states.

My results reveal basic patterns in the *P. irrorata* vocal repertoire and are only meant to serve as a starting point in elucidating call function. A longer-term study that incorporates multivariate statistics is needed to create a more definitive catalogue of *P. irrorata* vocalizations. Expansion of this study to include detailed data on the sex and identity of the caller will prove invaluable in examining the range of variation present in their vocal communication. Data on the Gray's bald-faced saki monkey are virtually absent from primate literature and it is my hope that this study marks the first step toward discerning the link between communication and social behavior in the species.

APPENDIX

Relationship between repertoire size and group size. Table includes the repertoire size and group size for nonhuman primate species with mean group sizes between 3.5 and 5.5 (data from McComb & Semple 2005:382).

Species	Repertoire Size	Group Size*	Reference for repertoire size
Euoticus elegantulus	6	4	Charles-Dominique (1977)
Galagoides demidoff	8	3.5	Charles-Dominique (1977)
Petterus mongoz	9	3.5	Curtis (1997)
Callicebus Moloch	11	3.5	Robınson (1979)
Pithecia irrorata	12	4.4	Current study
Callimico goeldi	28	5	Masataka (1982)

*All data taken from Rowe (1996) except group size for *P. irrorata* (Kappeler & Heymann 1996).

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VITA

Dara Bethany Adams was born in Houston, Texas on April 19th, 1982. She grew up in San Antonio, Texas and graduated from William Howard Taft High School in 1999. Immediately following high school, she entered Texas State University-San Marcos to pursue a Bachelor of Science in Biology. After enrolling in introductory courses to cultural and physical anthropology, Dara soon realized that her fascination with non-human primates would be best pursued from an anthropological perspective. Dara was given the opportunity to participate in a field school through the Department of Anthropology at Texas State in the summer of 2006. It was during this field school that her future M.A. advisor, Elizabeth Erhart, opened her eyes and heart to the world of fieldwork and monkey chasing. She obtained her Bachelor of Arts in Anthropology from Texas State in May 2007 and immediately entered the graduate program in Anthropology to focus on physical anthropology and primatology. She received her Master of Arts in Anthropology from Texas State University-San Marcos in December 2009.

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