ACOUSTIC AND OLFACTORY COMMUNICATION IN EASTERN SIFAKAS (*PROPITHECUS SP*.) AND RHESUS MACAQUES (*MACACA MULLATA*)

A Dissertation
Presented to the Faculty of the Graduate School
of Cornell University
in Partial Fulfillment of the Requirements for the Degree of
Doctor of Philosophy

By
Erik R. Patel
January 2012

ACOUSTIC AND OLFACTORY COMMUNICATION IN EASTERN SIFAKAS (*PROPITHECUS SP.*) AND RHESUS MACAQUES (*MACACA MULLATA*)

Erik R. Patel, Ph. D.
Cornell University 2012

This dissertation contains three studies of acoustic and olfactory communication in several species of nonhuman primates. The first is a longitudinal study of “gecker” distress vocalizations in infant rhesus monkeys (*Macaca mullata*) during the first 24 months of life. Acoustic and behavioral analyses revealed age, sex, and maternal response differences across several temporal, spectral, and amplitude measures, but little context-specific acoustic differentiation. Female geckers showed higher spectral peaks and bout durations, while male geckers were higher in amplitude and less noisy. Developmentally, gecker usage peaked at four months of age for both sexes, with male geckers nonetheless tending to occur at younger ages than those of females. In sum, gecker acoustics appear to be well designed to draw the attention of mothers and other listeners, while also potentially becoming aversive.

The second study examines the acoustic structure and function of “zzuss” vocalizations in wild silky sifakas (*Propithecus candidus*) in northeastern Madagascar. Acoustically, the calls combined separate turbulent noise and tonal components, often including frequency jumps and rapid, highly frequency-modulated components. Although silky sifakas are sexually monomorphic, male and female zzuss calls were acoustically different, most importantly in fundamental frequency and amplitude-related features. All acoustic measures differed between individuals, with fundamental frequency related variables again playing the largest role. Overall, zzuss calls are multi-function vocalizations used both for terrestrial disturbance and group coordination. They are shaped for salience, localizability, and caller identification, rather than to have word-like meaning.

The final study examines non-nutritive tree gouging by wild silky sifakas (*P. candidus*) and Milne-Edwards' sifakas (*P. edwardsi*). Species differences were found in gouge mark morphology. Dominant males had longer gouge marks and gouged most frequently, with seasonal peaks just before and during the mating season. The resource gouging hypothesis was tested and supported in silky sifakas. A multiple regression analysis revealed that the number of gouges per tree species was predicted by the percentile rank of those species as food tree species and sleep tree species. Gouging appears to be an honest species specific signal of male status which may promote scent longevity and attract the visual attention of conspecifics.

BIOGRAPHICAL SKETCH

Erik Raj Patel was born in Chicago, IL. Both of his parents are retired college teachers who immigrated (from India and Germany) to the United States on academic fellowships to pursue graduate studies. Erik completed his B.A. in three years in Psychology at Earlham College.   While studying and traveling in India after college, he developed a strong interest in the behavior of nonhuman primates. After earning his M.A. in Anthropology (primatology) from the University of California at Berkeley, he participated in various research projects with zoo living bonobos (*Pan Paniscus*) and semi-free-ranging rhesus macaques (*Macaca mullata*). Since 2000, he has worked every year in Madagascar conducting the first long-term study of the behavioral biology of wild silky sifakas (*Propithecus candidus*) which are among the rarest mammals in the world. Several recent documentary films (including one by the BBC) have featured this work which was also featured on the front page of the Baltimore Sun newspaper and the cover of Smithsonian Magazine.

For my parents:

Dr. Chhaganbhai Kachardas Patel and Monika Dorothea Fischer Patel

ACKNOWLEDGMENTS

I would like to thank the members of my committee for their consistently thoughtful feedback over many years as well as their flexibility in allowing me to study lemurs in Madagascar. I feel very lucky to have three committee members with tremendous experience in animal communication and animal behavior: Robert Johnston, Michael Owren, and Adam Arcadi. If I had not had the opportunity to work at Ranomafana National Park initially (thanks to Debra Durham), I would not have become captivated by the communication system of eastern sifakas. Patricia Wright first suggested that the silky sifaka may be a suitable study species, a suggestion for which I am obviously grateful. Michael Owren's meticulous brilliance and his motto of "persistence, persistence, persistence" remains inspiring. Steve Goodman, Joerg Ganzhorn, Anne Mertl Millhollen, Michael Pereira, Steig Johnson, Mitch Irwin, Patricia Wright, and Ed Louis were kind enough to be accessible and helpful sources of information about all things lemur. My early coursework and research in Primatology, prior to my studies and work at Cornell University, was supervised by Katherine Milton, Dorothy Fragaszy, Irwin Bernstein, Edward Mulligan, and Christine Johnson. I thank them.

For permission to conduct research in Marojejy National Park and Anjanaharibe-Sud Special Reserve, I thank the government of the Democratic Republic of Madagascar. Particular thanks are due to Madagascar's Ad Hoc Committee for Fauna and Flora and Organizational Committee for Environmental Research (CAFF/CORE), Ministry of the Environment and Water and Forests, and National Association for the Management of Protected Areas (ANGAP) for granting permits. For logistical support, I thank Dr. Benjamin Andriamihaja, ANGAP Andapa Director J. H. Bakarizafy, the Malagasy Institute for the Conservation of Tropical

Environments (MICET), and the Institute for the Conservation of Tropical Environments (ICTE). Warm thanks are also due to Daniel and Berenice Rajaona for their permission and encouragement to study Milne-Edwards' sifakas at Ialatsara Forest Station.

Working in Marojejy National Park, with its steep cliffs, heavy rain, and remote location, requires a team of dedicated people. It has been a pleasure working with the following Malagasy individuals who have assisted greatly with tracking silky sifakas, identifying plant species, and with general logistics: Desire Rabary, Jean Nestor Randrianasy, Guy Irenel Raoliniaina, Lanto Andrianandrasana, Jean Chrysostome Bevao, Desire Kely, Janvier Rabe, Tonkasina Jacques Harson, Gerlain, Mahazandry Edouard, Honoré Andriamiarinoro, Alphonse, Donasien, Joseph, Dino, Momo, as well as cooks Primo, Seraphin, and Marcel.

A number of American and European volunteer field assistants tirelessly assisted with various aspects of habituation, data collection, and data entry including Claire Santorelli, Kristen Alldredge, Cedric Girard-Buttoz, Hannah Parathian, Andrew Ritchie, John Anderson, Casey Coke, Benjamin Stingle, Lucy Todd, Stacey Rosenbaum, Susan Longest, and Sarah Benson-Amram, and Daniela Herzog. A special thanks to those who survived leeches on their eyeballs, sprained knees, poisonous spider bites, dangerous river crossings, and almost sliding into the latrine!

TABLE OF CONTENTS

CHAPTER 5

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

Dissertation Overview

The chapters in this dissertation examine several issues that are of current interest in primate communication. Chapter 2 is a longitudinal study of vocal development of rhesus macaque (*Macaca mullata*) "gecker" distress vocalizations. These are amongst the loudest and mostly common produced infant vocalizations by this species. The study is unique because it was a twenty-four month long investigation which allowed a complete assessment of vocal usage, acoustic structure, and maternal responsiveness until the age at which the call is seldom emitted.

Infant age and call rate are known to influence the likelihood of macaque monkey mothers responding to their infants' calls (Maestripieri, 1995). In humans and nonhuman primates, extreme infant vocalizations can influence the quality of parental care received (Soltis, 2004). The "coos" of abused rhesus monkey infants have been found to differ in structure from the "coos" of nonabused infants (Maestripieri et al., 2000). However, little is known about which particular acoustic features of infant monkey calls are most effective at eliciting maternal response. Therefore, one of the main goals of the study was to determine how gecker acoustics influence maternal response.

A second major goal of this study was to determine the cues reflected in the acoustic structure of this vocalization, and make an informed decision about the function of gecker vocalizations based both upon acoustic structure and usage. Although many infant calls, like "geckers" are emitted during evident distress, spontaneous utterance is also quite common. The extent of co-occurrence of call context and acoustic structure has only been examined in a few studies of primate infant vocalization (Bayert et al., 1990; Jovanovic and Gouzoules, 2001; Kalin et al., 1992). Some debate exists about the extent to which calls of infant monkeys or the cries of human infants are state-specific (e.g. "hunger" cries, "pain cries" etc…), though little evidence exists for acoustically distinct cry types that reflect specific needs (Gustafson et al., 2000; Soltis, 2004). Sex differences have been found in infant macaque call rate and duration (Green, 1981; Wallen, 2005), though it is unknown whether the overall frequency structure varies according to caller age and sex. If so, such acoustic cues could allow mothers to adjust their responsiveness based upon these infant characteristics. Therefore, the second set of goals was to examine variation in the acoustic structure of "gecker" vocalizations as a function of call context as well as caller age and sex.

Chapter 3 examines the structure and function of wild silky sifaka (*Propithecus candidus*) "zzuss" vocalizations. These lemurs are among the rarest mammals in the world, and little has previously been reported about their behavior, ecology, or communication system (Mittermeier et al., 2010; Patel, 2009). Zzuss vocalizations are generally considered an alarm call (Petter and Charles-Dominique, 1979; Wright, 1998). However, neither the zzuss nor any other alarm calls of the genus *Propithecus* have as yet received detailed acoustic analysis.

Six major functions have been proposed for primate "loud" calls, a category that includes the zzuss vocalization. These functions include mate attraction and mate defense (Semple *et al.*, 2002), territory defense (Mitani, 1985a,b), food advertisement (Clark and Wrangham, 1993, 1994), auditory impact (Owren and Rendall, 2001; Rendall *et al.*, 2009), predator alarm (Cheney and Seyfarth, 1990; Macedonia and Evans, 1993), and group coordination (Trillmich et al., 2004; Rasoloharijaona *et al.*, 2006).

Zzuss vocalizations have most often been hypothesized to function as group coordination calls or anti-predator calls against predation by the civet-like fossa, Madagascar's largest carnivore. Several outcomes are expected if the zzuss is a specialized, terrestrial anti-predator call. First, its acoustic structure and usage are predicted to be specific to terrestrial predation contexts. Associated anti-predator behavior is also expected, which for the arboreal silky sifaka should include movement upward in the trees with downward staring (Fichtel and Kappeler, 2002; Karpanty and Wright, 2007; Macedonia and Evans, 1993; Sauther, 1989). Finally, rates of occurrence are predicted to show both seasonal and circadian peaks congruent with fossa hunting patterns.

Alternatively, if the zzuss call is primarily a group-coordination vocalization, most instances would be expected in response to the howl vocalizations of spatially separated or lost group members. In this case, usage should be evenly distributed across seasons and times of day. Those outcomes have been observed for the roar and shriek choruses of ruffed lemurs (*Varecia spp.*), which function both as general alarm and group-coordination vocalizations (Geissman and Mutchler, 2006; Pereira *et al.*, 1988; Vasey, 2003). Finally, given a group-cohesion function, these sounds can be expected to include reliable acoustic cues to caller sex and identity, helping identify separated group members to one another while also advertising group size and composition to neighboring groups.

Finally, chapter 3 also examines the acoustic measures that most distinguish males and females and individuals from one another. There is some debate on this topic with some considering duration and fundamental frequency to seldom distinguish individuals, particularly in broadband noisy calls (Gamba, 2011); while others report that fundamental frequency and duration do frequently vary between individuals and the sexes, particularly for high frequency tonal harmonically structured calls (Leliveld et al., 2011; Rasoloharijaona et al., 2006). Zzuss vocalizations contain both noisy and harmonic elements, and are therefore well suited to test this question.

Chapter 4 examines tree gouging behavior in silky sifakas (*P. candidus*) and Milne-Edwards' sifaka (*P. edwardsi*). This frequent behavior is performed only by males just before chest scent marking. The scent marks are placed directly over the large, visible gouge marks made by biting tree trunks and removing bark using their tooth combs. Details of the form and function of this behavior are unknown, although male tree gouging is believed to serve a communicative function since eastern sifakas are believed to seldom eat bark. The first goal of the study was to determine the diet of silky sifakas, and confirm that bark was never consumed since western sifakas, such as Verreaux's sifakas, do regularly consume bark (Richard, 1978, 1985).

Tree gouging may function as a visual-olfactory signal of resource ownership and signal willingness to defend high value resources. Amongst primates, several exudativorous species (e.g., marmosets, *Callithrix* sp.; slow lorises, *Nycticebus* sp.; galagos, *Galago* sp.) scent mark while gouging trees for food resources such as gum, sap, and nectar (Bearder and Doyle, 1974; Nekaris et al., 2010; Rylands, 1985). Weasel sportive lemurs (*Lepilemur mustelinus*) frequently gouge trees near their sleeping sites. They do not consume bark or tree exudates; therefore such gouging, which may be accompanied by olfactory cues in their saliva, is believed to signal sleeping site ownership (Rasoloharijaona et al., 2010).

Food and sleeping trees are limited resources that are frequently visited by other group members, which may lead to a large audience for these gouges and the scent marks which accompany them. Sleep trees and food trees are often along travel routes, and gouging these trees may lead to a "bulletin board" (Johnston et al., 1994) and increase the likelihood of receivers detecting them (Gosling and Roberts, 2001).

Two specific predictions are tested in Chapter 4: 1) The percentiles of tree species in the diet of silky sifakas (food tree percentile) is a significant predictor of the number of gouges on food tree species, 2) The percentiles of tree species among sleeping trees (sleep tree percentile) is a significant predictor of the number of gouges on sleep tree species.

Gouge marks may also be a male status signal. In many sifaka groups, there is only one breeding male even though the group may contain several males (Kappeler and Schäffler, 2008; Morelli and Wright, 2006). Dominant male sifakas are known to scent mark at higher rates than subordinate males (Lewis, 2005; Pochron et al., 2005), have higher testosterone levels (Kraus et al., 1999; Lewis, 2009), and more darkly stained chests due to increased secretion and marking with the sternal gland (Lewis 2009). It is therefore predicted that one sifaka male will gouge most and perhaps have the largest gouges.

Gouge marks are a long lasting trace of a sifaka's presence and may be useful tools during population surveys for critically endangered primates, such as the silky sifaka. A final goal of Chapter 4 is to determine the species specific characteristics of gouge marks while examining differences in gouge mark morphology between silky sifakas and Milne-edwards' sifaka.

Chapter 5 reviews the results of the questions posed and the predictions tested in this dissertation, while discussing the broader implications of these findings.

REFERENCES

Bayart, F., Hayashi, K. T., Faull, K. F., Barchas, J. D., and Levine, S. (**1990**). "Influence of maternal proximity on behavioral and physiological responses to separation in infant rhesus monkeys (*Macaca mulatta*)," Behav. Neuro. 104, 98-107.

Bearder, S.K. and Doyle, G.A. (**1974**). "Field and laboratory studies of social organization in bushbabies (*Galago senegalensis*)," J. Hum. Evol. **3**, 37-50.

Cheney, D. L. and Seyfarth, R. M. (**1990**). *How Monkeys See the World* (University of Chicago Press, Chicago).

Clark, A. and Wrangham, R. (**1993**). "Acoustic analysis of wild chimpanzee pant hoots: Do Kibale Forest chimpanzees have an acoustically distinct food arrival pant hoot?" Amer. J. Primat. 31, 99-109.

Clark, A. and Wrangham, R. (**1994**). "Chimpanzee arrival pant hoots: Do they signify food or status?" Int. J. Primat. **15**, 185-206.

Fichtel, C. and Kappeler, P. M. (**2002**). "Anti-predator behaviour of group-living Malagasy primates: Mixed evidence for a referential alarm call system," Behav. Ecol. Sociobiol. **51**, 262-275.

Gamba, M., Colombo, C., and Giacoma, C. (**2011**). "Acoustic cues to caller identity in lemurs: A case study," Ethology. http://dx.doi.org/10.1007/s10164-011-0291-z

Geissmann, T., and Mutschler, T. (**2006**). "Diurnal distribution of loud calls in sympatric wild indris (*Indri indri*) and ruffed lemurs (*Varecia variegata*): implications for call functions," Primates **47**, 393-369.

Gosling, L.M. and Roberts, S.C. (**2001**). "Scent marking by male mammals: Cheat-proof signals to competitors and mates," Adv. Stud. Behav. **30**, 169-217.

Green, S. M. (**1981**). "Sex differences and age gradations in vocalizations of Japanese and lion-tailed monkeys (*Macaca fuscata* and *Macaca silenus*)," Amer. Zool. **21**, 165-183.

Gustafson, G. E., Wood, R. M. & Green, J. A. (**2000**) "Can we hear the causes of infants' crying?" In *Cry as a sign, a symptom, and a signal. Clinical, emotional and developmental aspects of infant and toddler crying*, edited by R. G. Barr, B. Hopkins & J. A. Green. MacKeith Press. Pp. 8-22.

Johnston, R.E., Chiang, G. and Tung, C. (**1994**). “The information in scent over-marks of golden hamsters,” Anim. Behav. **48**, 323-330.

Jovanovic, T., and Gouzoules, H. (**2001**). “Effects of maternal restraint on the vocalizations of infant rhesus monkeys (*Macaca mulatta*),” Amer. J. Primat. **53**, 33 -45.

Kalin, N. H., Shelton, S. E., and Snowdon, C. T. (**1992**). “Affiliative vocalizations in infant rhesus macaques (*Macaca mulatta*),” J. Comp. Psychol. **106**, 254 – 261.

Kappeler, P.M. and Schaeffler, L. (**2008**). “The lemur syndrome unresolved: extreme male reproductive skew in sifakas (*Propithecus verreauxi*), a sexually monomorphic primate with female dominance,” Behav. Ecol. Sociobiol. **62**, 1007-1015.

Karpanty, S. M. and Wright, P. C. (**2007**). “Predation on lemurs in the rainforest of Madagascar by multiple predator species: observations and experiments,” In *Primate Anti-Predator Strategies,* edited by S. L. Gursky and K. A. I. Neckaris (Springer: New York), pp. 77-99.

Kraus C, Heistermann M, Kappeler PM. (**1999**). “Physiological suppression of sexual function of subordinate males: a subtle form of intrasexual competition among male sifakas (*Propithecus verreauxi*)?” Physiol. Behav. **66**, 855-861.

Leliveld, L., Scheumann, M., and Zimmermann, E. (**2011**). “Acoustic correlates of individuality in the vocal repertoire of a nocturnal primate (*Microcebus murinus*),” J. Acoust. Soc. Amer. **129**: 2278-2288.

Lewis, R.J. (**2005**). “Sex differences in scent marking in sifaka: Mating conflict or male services?” Amer. J. Phys. Anthro. **128**, 389-398.

Lewis, R.J. (**2009**). “Chest staining variation as a signal of testosterone levels in male Verreaux’s sifaka,” Physiol. Behav. **96**, 586-592.

Macedonia, J. M., and Evans, C. S. (**1993**). “Variation among mammalian alarm call systems and the problem of meaning in animal signals,” Ethology **93**, 177-197.

Maestripieri, D. (1995). “Maternal responsiveness to infant distress calls in the stumptail macaque,” Folia Primatol. **64**, 201-206.

Maestripieri, D., Jovanovic, T., and Gouzoules, H. (**2000**). “Crying and infant abuse in rhesus monkeys,” Child Develop. **71**, 301-309.

Mitani, J. C. (**1985a**). “Location-specific responses of gibbons (*Hylobates muelleri*) to male songs,” Zeitschr. Tierpsychol. **70**, 219-224.

Mitani, J. C. (**1985b**). "Responses of gibbons (*Hylobates muelleri*) to self, neighbor, and stranger song duets," Int. J. Primat. **6**, 193-200.

Mittermeier, R. A., Louis, E. E., Richardson, M., Schwitzer, C., Langrand, O., Rylands, A. B., Hawkins, F., Rajaobelina, S., Ratsimbazafy, J., Rasoloarison, R., Roos, C., Kappeler, P. M., and MacKinnon, J. (**2010**). *Lemurs of Madagascar*, 3rd Ed. (Conservation International, Washington, DC).

Morelli, T.L. and Wright, P.C. (**2006**). "Expect the unexpected: mating monogamy in a purportedly polygamous prosimian," Int. J. Primatol. **27**, Abstr. #497.

Nekaris, K.I., Starr, C.R., Collins, R.L., and Wilson, A. (**2010)**. Comparative ecology of exudate feeding by lorises (*Nycticebus, Loris*) and Pottos (*Perodicticus, Arctocebus*). In *The Evolution of Exudativory in Primates* edited by Burrows, A.M and Nash, L.T. Springer. Pp. 155-168.

Owren, M. J., and Rendall, D. (**2001**). "Sound on the rebound: Bring form and function back to the forefront in understanding nonhuman primate vocal signaling," Evol. Anthropol. **10**, 58-71.

Patel, E. R. (**2009**). Silky Sifaka, *Propithecus candidus*, 1871. In *Primates in Peril: The World's 25 Most Endangered Primates 2008-2010,* edited by R. A. Mittermeier, J. Wallis, A. B. Rylands, J. U. Ganzhorn, J. F. Oates, E. A. Williamson, E. Palacios, E. W. Heymann, M. C. M. Kierulff, L. Yongcheng, J. Supriatna, C. Roos, S. Walker, L. Cortés-Ortiz, and C. Schwitzer (Conservation International, Arlington, VA), pp. 23-26.

Pereira, M. E., Seeligson, M. L., and Macedonia, J. M. (**1988).** "The behavioral repertoire of the black-and-white ruffed lemur, *Varecia variegata variegata* (*Primates: Lemuridae*)," Folia Primatol. 51, 1-32.

Petter, J. J., and Charles-Dominique, P. (**1979**). "Vocal communication in prosimians," In The Study of Prosimian Behavior, edited by G. A. Doyle and R. D. Martin (Academic Press, New York), pp. 247-305.

Pochron, S.T., Morelli, T.L., Terranova, P., Scirbona, J., Cohen J., Kunaperredy G., Rakotonirina G, Ratsimbazafy, R., Rakotosoa, R., Wright, P.C. (**2005**). "Patterns of male scent-marking in *Propithecus edwardsi* of Ranomafana National Park, Madagascar," Amer. J. Primatol. **65**,103–115.

Rasoloharijaona, S., Randrianambinina, B., Braune, P., and Zimmermann, E. (**2006**). "Loud calling, spacing, and cohesiveness in a nocturnal primate, the Milne Edwards' sportive lemur (*Lepilemur edwardsi*)," Amer. J. Phys. Anthropol. **129**, 591-600.

Rasoloharijaona, S. Randrianambinina, B., and Joly-Radko, M. (**2010**). "Does nonnutritive tree gouging in a rainforest-dwelling lemur convey resource ownership as does loud calling in a dry forest-dwelling lemur?" Amer. J. Primatol. **72**, 1062-1072.

Rendall, D., Owren, M. J., and Ryan, M. J. (**2009**). "What do animal signals mean?" Anim. Behav. **78**, 233-240.

Richard, A.F. (**1978**). "Variability in the feeding behavior of a Malagasy prosimian, *Propithecus verreauxi*: Lemuriformes," In *The Ecology of Arboreal Folivores* edited by G.G. Montgomery. Smithsonian Institution Press: Washington, D.C. pp. 519-533.

Richard, A.F. (**1985**). *Primates in Nature* (Freeman and Company: New York).

Rylands, A. B. (**1985**) "Tree-gouging and scent-marking by marmosets," Anim. Behav. **33**, 1365–1367.

Sauther, M. L. (**1989**). "Antipredator behavior in troops of free-ranging Lemur catta at Beza Mahafaly Special Reserve, Madagascar," Int. J. Primatol. **10**, 595-606.

Semple, S., McComb, K., Alberts, S., and Altmann, J. (**2002**). "Information content of female copulation calls in yellow baboons," Amer. J. Primatol. **56**, 43-56.

Soltis, J. (**2004**). "The signal functions of early infant crying," Behav. Brain Sci. **27**, 443 – 490.

Trillmich, J., Fichtel, C., and Kappeler, P.M. (**2004**). "Coordination of group movements in wild Verreaux's sifakas (*Propithecus verreauxi*)," *Behav.* **141**, 1103-1120.

Vasey, N. (**2003**). "*Varecia*, ruffed lemurs," In *The Natural History of Madagascar*, edited by S.M. Goodman and J. Benstead (U. Chicago Press, Chicago), pp. 1332–1336.

Wallen, K. (**2005**). "Hormonal influences on sexually differentiated behavior in nonhuman primates," *Front. Neuroendocrin.* **26**, 7-26.

Wright, P. C. (**1998**). "Impact of predation risk on the behaviour of *Propithecus diadema edwardsi* in the rainforest of Madagascar," *Behaviour* **135**, 1-30.

CHAPTER 2

Acoustics and behavioral contexts of “gecker” vocalizations in young rhesus macaques (*Macaca mulatta*)

Erik R. Patel[1,2] and Michael J. Owren[3]

ABSTRACT

Loud, pulsed “gecker” vocalizations are commonly produced by young rhesus macaques in distressful circumstances. The acoustics, usage, and responses associated with these calls were examined using audio recordings and observational data from captive, socially living rhesus up to 24 months old. One-hundred-eleven gecker bouts were recorded from ten individuals (six males, four females), with most geckers produced during the first 6 months of age. A gecker call consisted of a bout of up to 28 pulses of spectrally structured noise with a single prominent frequency peak. Nine contexts of calling were identified, but little evidence of context-specific acoustic variation was found. While geckering often triggered responses by the vocalizer's mother, the most common outcome was the absence of any reaction. Females geckered longer and at higher rates than did males, while also showing acoustic evidence of greater vocal effort. Mothers nonetheless responded more often and more positively to males. Overall, results show that gecker acoustics vary somewhat with vocalizer sex, age, and likely arousal level, but do not reflect detailed aspects of behavioral context. Circumstances of production suggest that geckers function

---

[1] Author to whom correspondence should be addressed. Electronic mail: patel.erik@gmail.com

[2] Department of Psychology, 211 Uris Hall, Cornell University, Ithaca, New York, 14853

[3] Michael J. Owren is now at the Department of Psychology, Georgia State University, PO Box 5010, Atlanta, Georgia 30302-5010.

primarily to draw the attention of mothers, who in turn are selective in responding. ©2007 *Acoustical Society of America*[4]

INTRODUCTION

Young nonhuman primates produce a variety of vocalizations when in distress, which in rhesus macaques (*Macaca mulatta*) include “coos,” “squeaks,” “screams,” “pant threats,” “girneys,” and “geckers” (Maestripieri and Call, 1996; Maestripieri *et al.*, 2000; Tomaszycki *et al.*, 2001). Geckers in particular have been described as a distress-related vocalization in rhesus monkeys, occurring in large numbers when infants are ignored, rejected, or otherwise separated from their mothers. Often accompanied by dramatic, convulsive bodily jerking, these loud, explosive, and distinctive-sounding vocalizations have received some attention and mention from a variety of researchers, but predominantly through qualitative rather than quantitative description. Thus, while geckers have also been documented in a number of other macaque species, details of their form and function remain unclear (Newman, 1995; Green, 1981).

Altmann (1962) first named geckers onomatopoetically as “ik, ik, ik.” He noted that the call is accompanied by spasmodic jerking and occurs during weaning and other circumstances of evident infant distress. The sounds were subsequently referred to as “geckers” and “geckering screeches” by Rowell (1962; Rowell and Hinde, 1962), who described them as a series of 0.1 s squeaks separated by 0.5–1.0 s intervals (illustrated in Figure 2.1). Several subsequent studies have shown geckers to be among the most common vocalizations produced by young rhesus. For example,

---

[4] Reprinted with permission from Patel, E.R. and Owren, M.J. (2007). Acoustics and behavioral contexts of “gecker” vocalizations in young rhesus macaques (Macaca mullata). Journal of the Acoustical Society of America 121(1): 575 - 585. Copyright 2007, American Institute of Physics.

Owren *et al.* (1993) reported that geckers comprised approximately 38% of the total number of vocalizations produced by rhesus monkeys during the first year of life, and 12% in the second year. Figures from Maestripieri *et al.* (2000) were comparable, with geckers making up 43.3% of all vocalizations in the first three months of life. Tomaszycki *et al.* (2001) similarly noted that geckers were the most common vocalization over the first 8 months, accounting for 34% of vocal output.

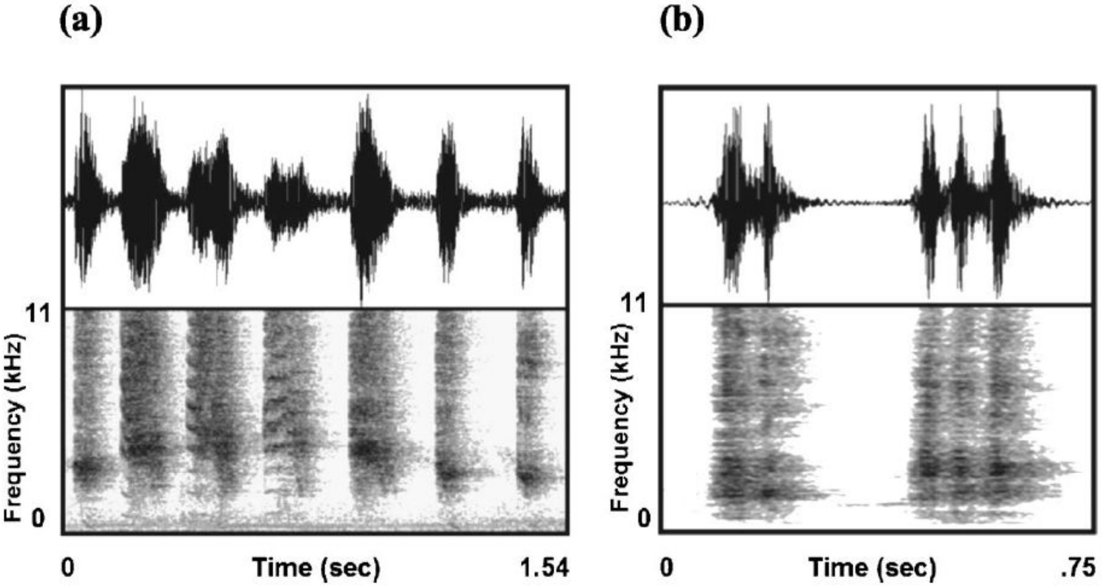


Figure 2.1 (a) A representative gecker bout consisting of seven pulses, shown as (top) a wave form and (bottom) a narrowband FFT spectrogram (20 ms Hanning analysis window, 22.05 kHz sampling rate). The third and fourth pulse shown produced higher HNR values than elsewhere, but are nonetheless still likely to reflect deterministic chaos in underlying vocal-fold vibration. (b) A gecker bout illustrating pulse reduplication in the wave form and a narrowband FFT spectrogram. Pulses are first doubled and then tripled.

In spite of the prevalence of these sounds, little quantitative information is available concerning their acoustics or function. On the one hand, Newman (1995) notes that geckers can routinely occur without apparent cause, and suggests that they “may largely be a reflection of the immature state of the central nervous systems underlying vocal expression” (p. 79). On the other hand, many researchers are likely to agree with Maestripieri and Call's (1996) characterization that geckers, like most primate infant distress calls, occur “when the infant is not in contact with its mother” and “signal the infant's need for nursing, transport, or protection” (Maestripieri and Call, 1996, p. 620). Critical issues thus include whether rhesus geckers are in fact occurring primarily or exclusively in instances of distress, whether geckers have specific, context-dependent signaling value, and how other animals respond to these sounds.

Relatively few studies of primate infant vocalization have examined the co-occurrence of call acoustics and context (e.g., Kalin *et al.*, 1992; Jovanovic and Gouzoules, 2001), or found evidence of context-specific vocal subtypes (e.g., Bayart *et al.*, 1990). Although also limited, some information is available concerning responses to geckers and other distress-related calls. Across primate species, for instance, it has generally been found that mothers are most responsive to young infants that vocalize at relatively low rates (Maestripieri, 1995; Hauser, 1993). Furthermore, females in several species have been reported to produce distress-related calls comprised of more call types, emitted at higher rates, and for longer durations than males (Locke and Hauser, 1999; Wallen, 2005; Green, 1981). Overall, rhesus females do show greater volubility than males, not only in infancy (Newman *et al.*, 1990; Tomaszycki *et al.*, 2001), but also in adolescence and adulthood (Erwin, 1975). Thus, while sex differences in maternal treatment of primate infants tends to be rare (Wallen, 2005), Tomaszycki *et al.* (2001) have nonetheless reported that rhesus mothers are more likely to respond to vocalizations by male than by female infants. Despite this evidence, rather little is as yet known about the ontogeny or extent of sex differences in vocal behavior (Gautier and Gautier 1977; Green, 1981). Furthermore, the few studies that are available have typically examined time periods of less than a year

(Hammerschmidt *et al.*, 2000; Hammerschmidt *et al.*, 2002; Seyfarth and Cheney, 1986; Newman, 1995; Snowdon *et al.*, 1997; Owren *et al.*, 1993).

The current study sought to extend previous work on rhesus geckers by examining the acoustics and contexts of these vocalizations as systematically as possible in animals up to 24 months of age. The work began with a detailed characterization of gecker acoustics and the contexts in which infants produce these calls. The data were then used to test for possible specificity in acoustics and contexts, age and sex-related differences, and factors that might affect the likelihood of responding by mothers or other animals. These questions were examined using a large database of calls recorded during a long-term study of two groups of socially housed rhesus monkeys living in outdoor cages at a national primate center.

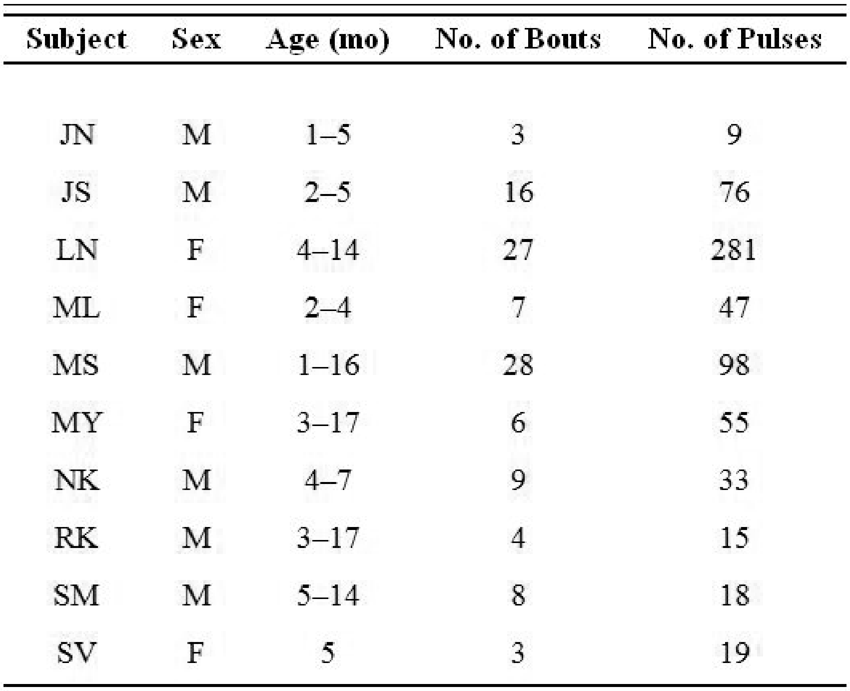
METHODS

Study site and subjects

Data were collected during the course of a long-term project on vocal development (Owren *et al.* 1992a, 1992b; Owren *et al.*, 1993). The subset analyzed here drew on audio recordings and behavioral data collected between 1986 and 1989 from ten rhesus macaques (six males and four females) ranging in age from newborn to 24 months of age (see Table 2.1). The overall project involved cross fostering a small number of neonatal infants between different-species foster mothers (Owren and Dieter, 1989), but no such offspring are represented in the data analyzed here. The ten subjects included here represented all the rhesus offspring born into the study groups during the course of the project from whom there were any usable gecker recordings. The subjects were offspring of a total of seven different mothers, all of whom were multiparous. Five mothers were represented by a single study subject, one by two study subjects, and one by three study subjects. All animals were located at the

California National Primate Research Center (CNPRC; University of California, Davis), as part of two socially living groups. Group composition varied somewhat over time, with each of the two cages including 1- 2 adult males, one or no unrelated juvenile males, 4 - 6 adult females, and 6 - 8 offspring of those females.

Table 2.1 Subject demographics and representation in the gecker sample.



Subject	Sex	Age (mo)	No. of Bouts	No. of Pulses
JN	M	1–5	3	9
JS	M	2–5	16	76
LN	F	4–14	27	281
ML	F	2–4	7	47
MS	M	1–16	28	98
MY	F	3–17	6	55
NK	M	4–7	9	33
RK	M	3–17	4	15
SM	M	5–14	8	18
SV	F	5	3	19

Each group was housed outdoors in a separate cage constructed from two modified commercial corn cribs connected by a rectangular inter-cage unit (Hoffman and Stowell, 1973). The cages were approximately 13.6×4.3×3.0 m (with additional space created by conical roofs), and contained capture chutes, perches, and pea gravel used as replaceable ground cover. During the winter months, screens were installed as wind shields and infrared lamps provided heat. The monkeys had continuous access to fresh water and received Purina monkey chow twice daily in quantities that ensured a plentiful supply for all. Detailed physical examinations of the animals were conducted three times per year by the CNPRC veterinary staff and general health was checked daily.

Apparatus and procedure

Behavioral observations were conducted in 10 min continuous focal sessions (Altmann, 1974) occurring in the morning (7:30 AM to noon) in the spring, summer, and fall, and in the afternoon (noon to 5 PM) in winter, up to six days per week. The daily sampling order was determined quasi-randomly. During sampling, behaviors exhibited by the focal animal and others it interacted with were entered as codes on a handheld computer, with each entry noting animal identities, any one or more of 63 concomitant behaviors, as well as the onset time of occurrence. This approach allowed documentation of all vocalizations produced by a focal animal during the session, as well as the behavior associated with these calls.

Audio recording was conducted with a four-channel Tascam 234 cassette deck (Teac Corporation, Tokyo), and two Sennheiser ME88 microphones (Sennheiser Electronic, Old Lyme, CT) placed on stands in fixed positions outside the cage. Calls from all animals were routinely recorded, including ad libitum samples that were described through supplementary commentary using a lapel microphone connected to a separate channel of the cassette deck. Vocalizations were later transferred to .25 in. audio tape using either a Uher 4200 Report Monitor (Uher Werke Munchen, Munich) or a Fostex A-2 reel-to-reel deck (Fostex America, Norwalk, CA). Calls were separated, numbered, and annotated during this process using the coded behaviors and any additional, audio-recorded comments.

Call selection and analysis

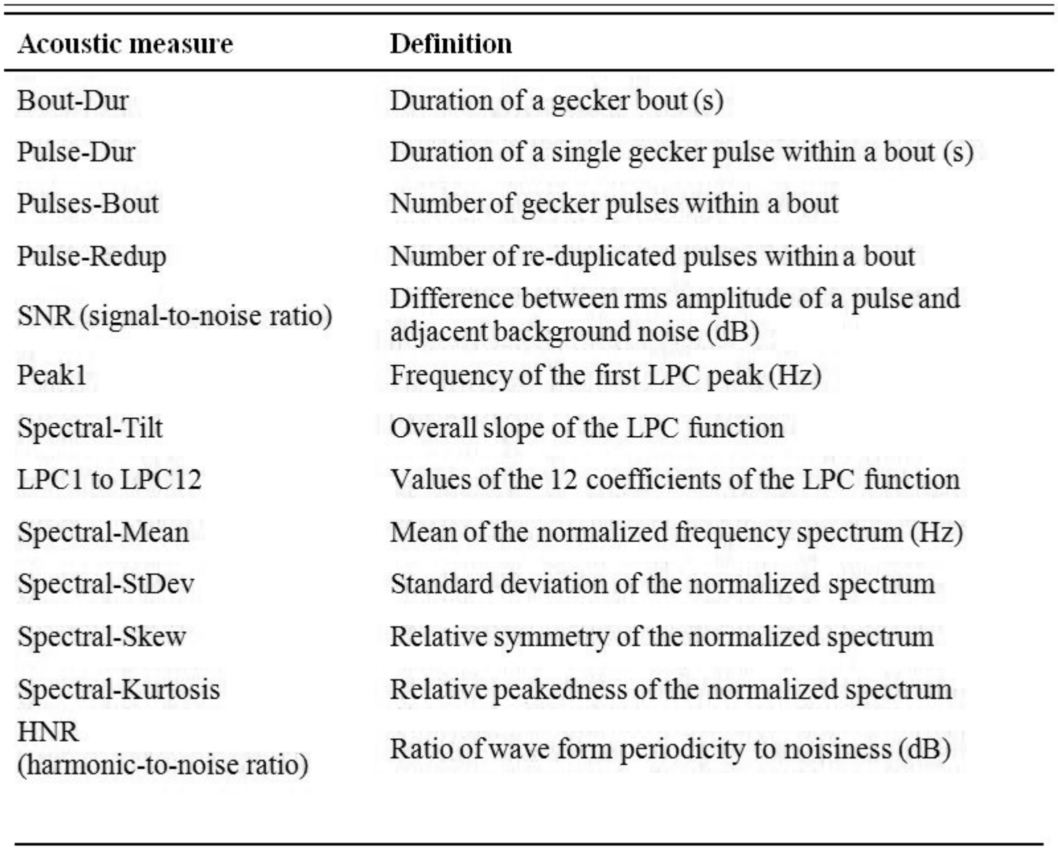
The vocalization sample was identified by examining the entire database of more than 10,000 separately cataloged calling episodes available from the project. Gecker vocalizations were identified based on previous annotations in the database (Owren *et al.*, 1992a), by matching acoustic features to published descriptions of gecker calls (e.g., Rowell and Hinde 1962; Jovanovic and Gouzoules 2001), and by ear. A total of 111 analyzable gecker bouts comprising 651 individual gecker pulses from the ten vocalizers were identified in this manner (see Table 2.1). A bout was defined an as uninterrupted emission of pulsed vocalization by a single animal with less than a 5 s pause between pulses.

Vocalizations were digitized and archived using a sampling rate of 44.1 kHz with 16 bit accuracy. Calls were subsequently downsampled to 22.05 kHz for analysis, which was conducted using the ESPS/waves+ 5.3 “xwaves” package (Entropic Research, Washington, DC), running on an SGI O2 workstation (Silicon Graphics Incorporated, Mountain View, CA). The Praat speech analysis package was also used in some analyses (Boersma, 2001; available at www.praat.org). Statistical analyses were conducted using NCSS 2004 (Jerry Hintze, Kaysville, UT) and SPSS 13.0 (SPSS Inc., Chicago, IL).

Acoustic variables

Twenty-four acoustic measures were extracted (definitions are provided in Table 2.2), spanning temporal, amplitude, and frequency-spectrum aspects of the calls. Temporal measures of geckering at bout and pulse levels included absolute durations (Bout-Dur, Pulse-Dur), and number of pulses per bout (Pulses-Bout). As illustrated in Figure 2.1(b), gecker pulses sometimes occur in doubled, tripled, quadrupled, and even quintupled form without intervening silent intervals. This phenomenon was referred to as “twinning” by Maestripieri *et al.* (2000), and here is considered as a single phenomenon labeled “reduplication” (Pulse-Redup). Call amplitude was characterized based on calculating a signal-to-noise ratio (SNR) for individual bouts,

Table 2.2 The 24 variables used in acoustic analysis.



Acoustic measure	Definition
Bout-Dur	Duration of a gecker bout (s)
Pulse-Dur	Duration of a single gecker pulse within a bout (s)
Pulses-Bout	Number of gecker pulses within a bout
Pulse-Redup	Number of re-duplicated pulses within a bout
SNR (signal-to-noise ratio)	Difference between rms amplitude of a pulse and adjacent background noise (dB)
Peak1	Frequency of the first LPC peak (Hz)
Spectral-Tilt	Overall slope of the LPC function
LPC1 to LPC12	Values of the 12 coefficients of the LPC function
Spectral-Mean	Mean of the normalized frequency spectrum (Hz)
Spectral-StDev	Standard deviation of the normalized spectrum
Spectral-Skew	Relative symmetry of the normalized spectrum
Spectral-Kurtosis	Relative peakedness of the normalized spectrum
HNR (harmonic-to-noise ratio)	Ratio of wave form periodicity to noisiness (dB)

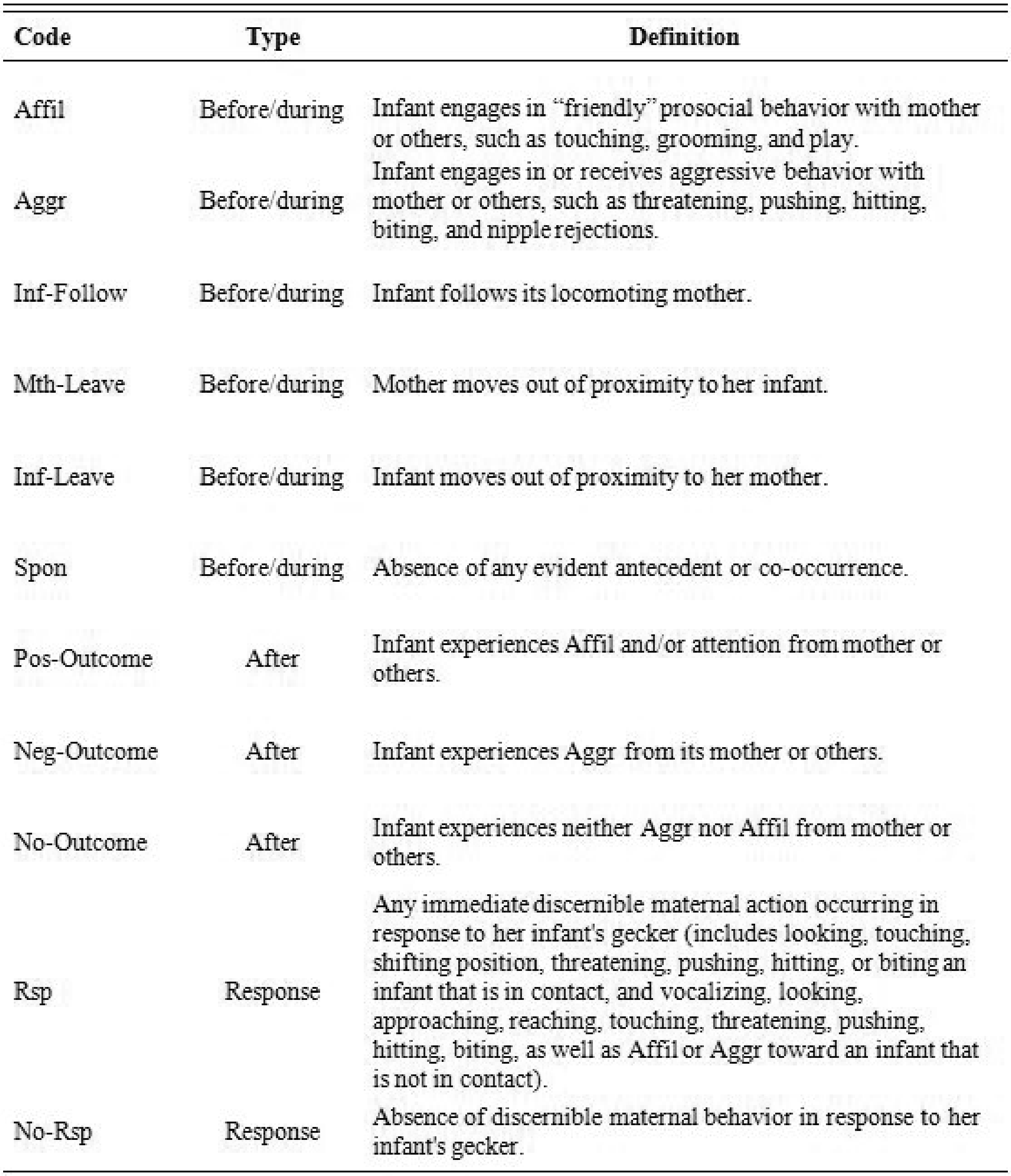
defined as the root-mean-square (rms) amplitude of the pulse minus the rms amplitude of a representative, adjacent segment of background noise. No attempt was made to measure the absolute amplitude of calls. This indirect approach was used as an attempt to obtain relative amplitude information for comparisons such as possible age-, sex-, and context-related differences. It was arguably justified by the fact that microphones were placed in the same locations outside the cages for every session, and based on the assumption that general background noise levels remained roughly constant over time. Sources of error for SNR measurements would then be any moment-to-moment variation in background noise, and the vocalizer's distance from and relative orientation to the microphone.

Frequency-spectrum (spectral) measurements were made from all 651 total pulses in the sample, based on a spectral slice located midway through each pulse. This slice was characterized by overlaying a ten-coefficient, autocorrelation-based linear predictive coding (LPC) function (0.023 s Hanning window) on a 512-point fast Fourier transform (FFT) spectrum (Hanning window) of the same segment (further described by Owren and Bernacki, 1998), with frequency and amplitude values recovered from the LPC envelope through cursor-based measurement. Variables used were the first LPC peak (Peak1), the overall slope of the LPC spectrum (Spectral-Tilt), values of each of the 12 coefficients used in the LPC function (LPC1 to LPC12), and the first four spectral moments of the Fourier spectrum (Spectral-Mean, Spectral-StDev, Spectral-Skew, Spectral-Kurtosis). Spectral-moment measures are particularly well suited to characterizing global features of noisy, broadband frequency spectra (Forrest *et al.*, 1988), and are computed by normalizing the Fourier power spectrum and treating it as a statistical distribution. The first four moments of this distribution are its mean, standard deviation, skewness, and kurtosis, in the normal sense of these terms. The last measure was the harmonic-to-noise ratio (HNR) of each pulse, extracted using Praat's pitch-based algorithm (Boersma, 1993).

Behavioral variables

The behavioral contexts of each of the 111 gecker bouts were coded in binary fashion according to whether the offspring's mother exhibited any discernible response to the vocalizations (Rsp/No-Rsp), as well as being scored as to which of six possible behaviors were occurring just before or during the bout (Before/During) and whether vocalizing was followed by aggression, affiliation, or neither (After). Behavioral codes are defined in Table 2.3. Coding for Before/During and After variables was based on

Table 2.3 Codes used to characterize behavior occurring before/during and after a geckering event.



Code	Type	Definition
Affil	Before/during	Infant engages in "friendly" prosocial behavior with mother or others, such as touching, grooming, and play.
Aggr	Before/during	Infant engages in or receives aggressive behavior with mother or others, such as threatening, pushing, hitting, biting, and nipple rejections.
Inf-Follow	Before/during	Infant follows its locomoting mother.
Mth-Leave	Before/during	Mother moves out of proximity to her infant.
Inf-Leave	Before/during	Infant moves out of proximity to her mother.
Spon	Before/during	Absence of any evident antecedent or co-occurrence.
Pos-Outcome	After	Infant experiences Affil and/or attention from mother or others.
Neg-Outcome	After	Infant experiences Aggr from its mother or others.
No-Outcome	After	Infant experiences neither Aggr nor Affil from mother or others.
Rsp	Response	Any immediate discernible maternal action occurring in response to her infant's gecker (includes looking, touching, shifting position, threatening, pushing, hitting, or biting an infant that is in contact, and vocalizing, looking, approaching, reaching, touching, threatening, pushing, hitting, biting, as well as Affil or Aggr toward an infant that is not in contact).
No-Rsp	Response	Absence of discernible maternal behavior in response to her infant's gecker.

after the vocalization, but rarely exceeded a few seconds on either side. In four cases, data were insufficient to determine the Before/During context and those gecker bouts included as the context of each vocalization event were determined by the observer, behavioral codes recorded just before, during, and after each gecker bout. Behaviors who also transcribed the relevant codes for each episode on a daily basis during the course of the project. Contexts were thus not inherently limited in time either before or were excluded from analyses involving this variable. In 34 cases, mothers were out of view, and Rsp/No-Rsp could not be coded.

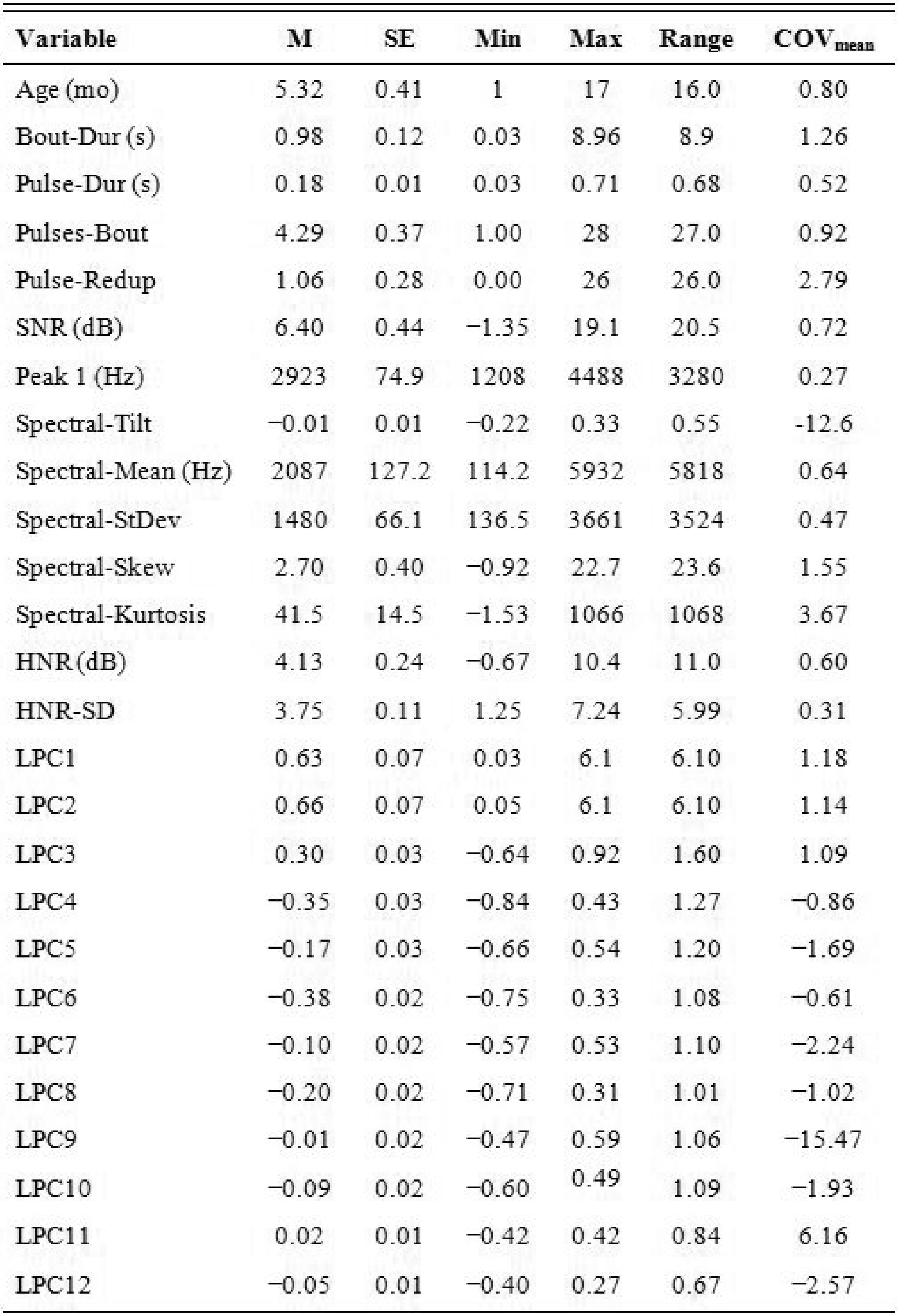
RESULTS

Gecker acoustics: General features

Descriptive statistics for the acoustic features of gecker vocalizations are shown in Table 2.4. On average, geckers were emitted in 1 s bouts of four pulses, though both bout duration (Bout-Dur) and number of pulses per bout (Pulses-Bout) were highly variable. The longest bout observed was nearly 9 s in duration, and as many as 28 pulses were observed in a single bout. Reduplication (Pulse-Redup) occurred in 34% of all bouts, could include as many as five pulses, but usually consisted of just two (72% of total reduplication events). Pearson's correlation coefficients revealed that Pulse-Redup was strongly correlated with Bout-Dur ($r=0.83$, $p<0.001$) and Pulses-Bout ($r=0.78$, $p<0.001$).

Although geckers are likely among the loudest vocalizations emitted by young rhesus macaques, mean SNR values were relatively modest (just over 6 dB), while showing high overall variability with the loudest geckers at 19.1 dB. The broadband noisiness of the sounds was reflected in generally low HNR values and spectral slopes that were virtually flat. HNR values did become significantly higher in a few cases (see, for example, the third and fourth pulses shown in Figure 2.1(a)), but were never

Table 2.4 Descriptive features of gecker vocalizations, based on 111 total bouts and 651 total pulses.



Variable	M	SE	Min	Max	Range	COV_{mean}
Age (mo)	5.32	0.41	1	17	16.0	0.80
Bout-Dur (s)	0.98	0.12	0.03	8.96	8.9	1.26
Pulse-Dur (s)	0.18	0.01	0.03	0.71	0.68	0.52
Pulses-Bout	4.29	0.37	1.00	28	27.0	0.92
Pulse-Redup	1.06	0.28	0.00	26	26.0	2.79
SNR (dB)	6.40	0.44	−1.35	19.1	20.5	0.72
Peak 1 (Hz)	2923	74.9	1208	4488	3280	0.27
Spectral-Tilt	−0.01	0.01	−0.22	0.33	0.55	-12.6
Spectral-Mean (Hz)	2087	127.2	114.2	5932	5818	0.64
Spectral-StDev	1480	66.1	136.5	3661	3524	0.47
Spectral-Skew	2.70	0.40	−0.92	22.7	23.6	1.55
Spectral-Kurtosis	41.5	14.5	−1.53	1066	1068	3.67
HNR (dB)	4.13	0.24	−0.67	10.4	11.0	0.60
HNR-SD	3.75	0.11	1.25	7.24	5.99	0.31
LPC1	0.63	0.07	0.03	6.1	6.10	1.18
LPC2	0.66	0.07	0.05	6.1	6.10	1.14
LPC3	0.30	0.03	−0.64	0.92	1.60	1.09
LPC4	−0.35	0.03	−0.84	0.43	1.27	−0.86
LPC5	−0.17	0.03	−0.66	0.54	1.20	−1.69
LPC6	−0.38	0.02	−0.75	0.33	1.08	−0.61
LPC7	−0.10	0.02	−0.57	0.53	1.10	−2.24
LPC8	−0.20	0.02	−0.71	0.31	1.01	−1.02
LPC9	−0.01	0.02	−0.47	0.59	1.06	−15.47
LPC10	−0.09	0.02	−0.60	0.49	1.09	−1.93
LPC11	0.02	0.01	−0.42	0.42	0.84	6.16
LPC12	−0.05	0.01	−0.40	0.27	0.67	−2.57

clearly or purely harmonically structured. LPC analysis revealed a one consistent frequency peak just below 3000 Hz (Peak1), with the spectral-moment mean falling just above 2000 Hz. LPC analysis revealed a second peak occurring above 7000 Hz in some cases, but associated frequency values were highly variable. This peak was not discernible in the majority of bouts, and therefore was also not included as a reliable component of gecker acoustic structure. When it did occur, the peak was not harmonically related to Peak1.

Gecker acoustics: Age and sex

The effects of age and sex on geckering are shown in Figure 2.2, based on 2-mo age blocks during which gecker bouts were available from at least three different individuals (i.e., months 1–2, 3–4, 5–6, 7–8, and 13–14, respectively). Repeated-measures General Linear Model analysis of variance (ANOVAs) were used to test for possible age effects on acoustics, but independent of individual variation. Results revealed that younger infants emitted the fewest pulses per bout, $F(4,96)=6.75$, $p<0.05$, the shortest pulses, $F(4,96)=8.39$, $p<0.05$, and the shortest bouts, $F(4,96)=7.55$, $p<0.01$. Results from associated Tukey-Kramer multiple-comparison posthoc tests are displayed in Figure 2.2.

A number of sex differences were also found, even when controlling as well as possible both for body-size differences between males and females, and for differences among individuals. As could be expected, analysis of covariance (ANCOVA) with vocalizer age entered as a covariate showed males ($M=1.62$ kg) to be significantly heavier than females ($M=1.41$ kg), $F(1,110)=14.2$, $p<0.001$. Infant body weight was therefore entered as a covariate in further repeated-measures ANCOVAs. With vocalizer sex as the independent variable, these tests revealed sex differences in four temporal, amplitude, and frequency-spectrum aspects of the calls

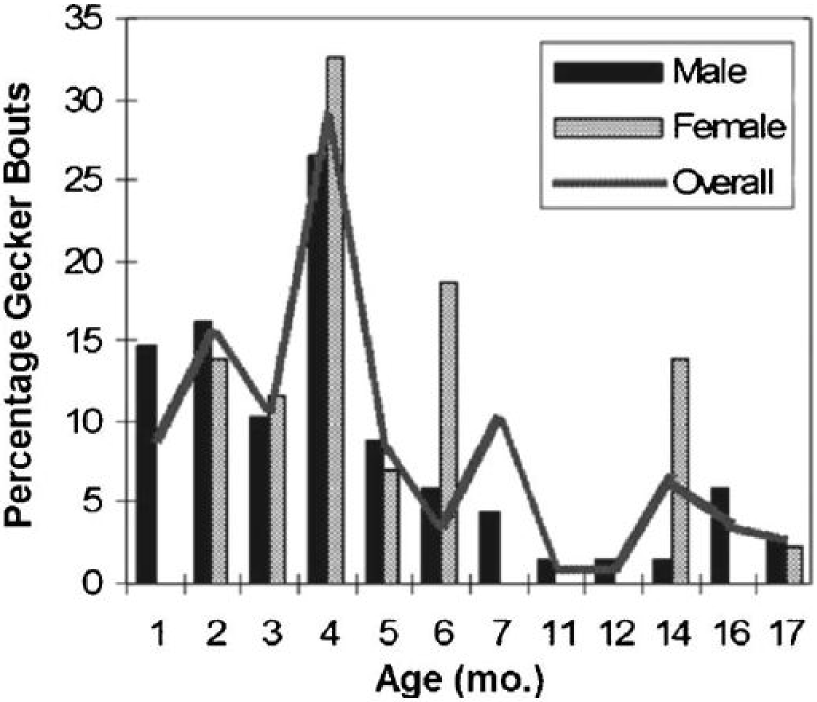


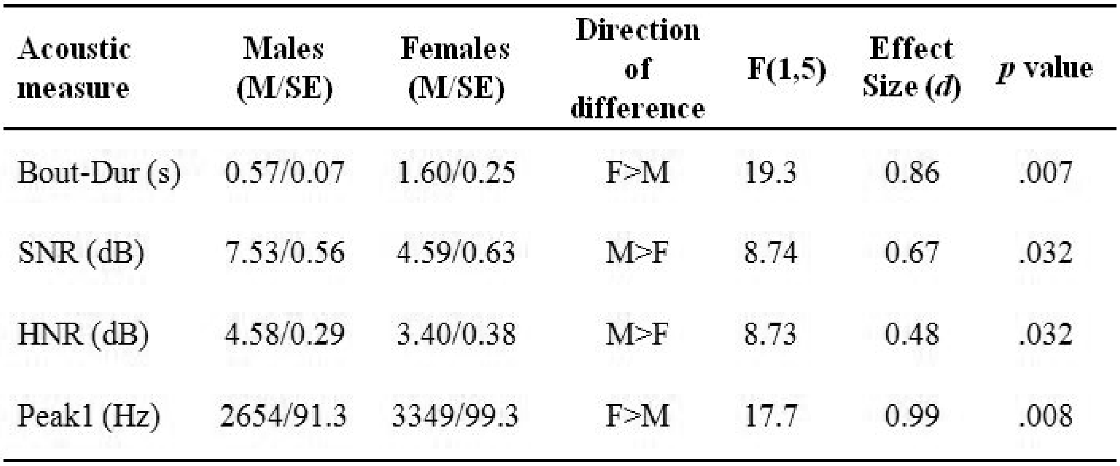
Figure 2.2 Mean percentage of gecker bouts occurring by sex and age, based on 2 month age blocks, tallied separately for each individual caller

(see Table 2.5). The strongest effect sizes were found for Peak1, with frequency peaks in female being almost 700 Hz higher than in male calls, and for Bout-Dur, where female bouts were more than twice as long as male bouts. Other outcomes showed male geckers to be higher in amplitude (SNR), and also less noisy (HNR).

Gecker usage: Age and sex

During the first two years of life, gecker bouts were emitted by infants from 1 to 17 months of age. Over this period, 75.7% of all gecker bouts occurred during the first 6 months of life (see Figure 2.3). Gecker usage peaked at 4 months in both males,

Table 2.5 Statistically significant ANCOVA tests for sex differences in gecker acoustics with body weight entered as a covariate.



Acoustic measure	Males (M/SE)	Females (M/SE)	Direction of difference	F(1,5)	Effect Size (*d*)	*p* value
Bout-Dur (s)	0.57/0.07	1.60/0.25	F>M	19.3	0.86	.007
SNR (dB)	7.53/0.56	4.59/0.63	M>F	8.74	0.67	.032
HNR (dB)	4.58/0.29	3.40/0.38	M>F	8.73	0.48	.032
Peak1 (Hz)	2654/91.3	3349/99.3	F>M	17.7	0.99	.008

26.5% (X^2 = 51.7, d.f. = 6, p<0.001), and females, 32.6% (X^2 = 16.7, d.f. = 6, p<0.05). However, the percentage of gecker bouts used in each month differed between the sexes (X^2=25.1, d.f. = 11, *p*<0.01), with male geckers tending to occur at younger ages. The greatest proportions of male gecker bouts occurred during months four (26.5%), two (16.2%), and one (14.7%), respectively. Females produced the most gecker bouts during months four (32.6%), two (14.0%), and 14 (14.0%), respectively.

Gecker usage and contexts

The behavior occurring immediately before or during a gecker bout was clear in all but four of the 111 total cases. Although none of the six categories of Before/During behavior could be considered predominant, relative proportions did show statistically significant heterogeneity (X^2 = 26.7, d.f. = 5, *p*<0.001). Inf-Follow (25.2%) was the most prevalent, followed by Aggr (22.3%) and Spon (22.3%), Mth-Leave (18.7%), and Affil (9.4%). Inf-Leave (1.9%) could also occur before or during a gecker bout, but was rare. Males and females were found to differ in the proportion of geckers emitted across these categories (X^2 = 23.9, d.f. = 5, *p*<0.001). Male geckers were most common in Affil (male: 15.4%, female: 0%) and Aggr (male: 27.7%, female: 14.3%) contexts, while female geckers were most common in the Inf-Follow

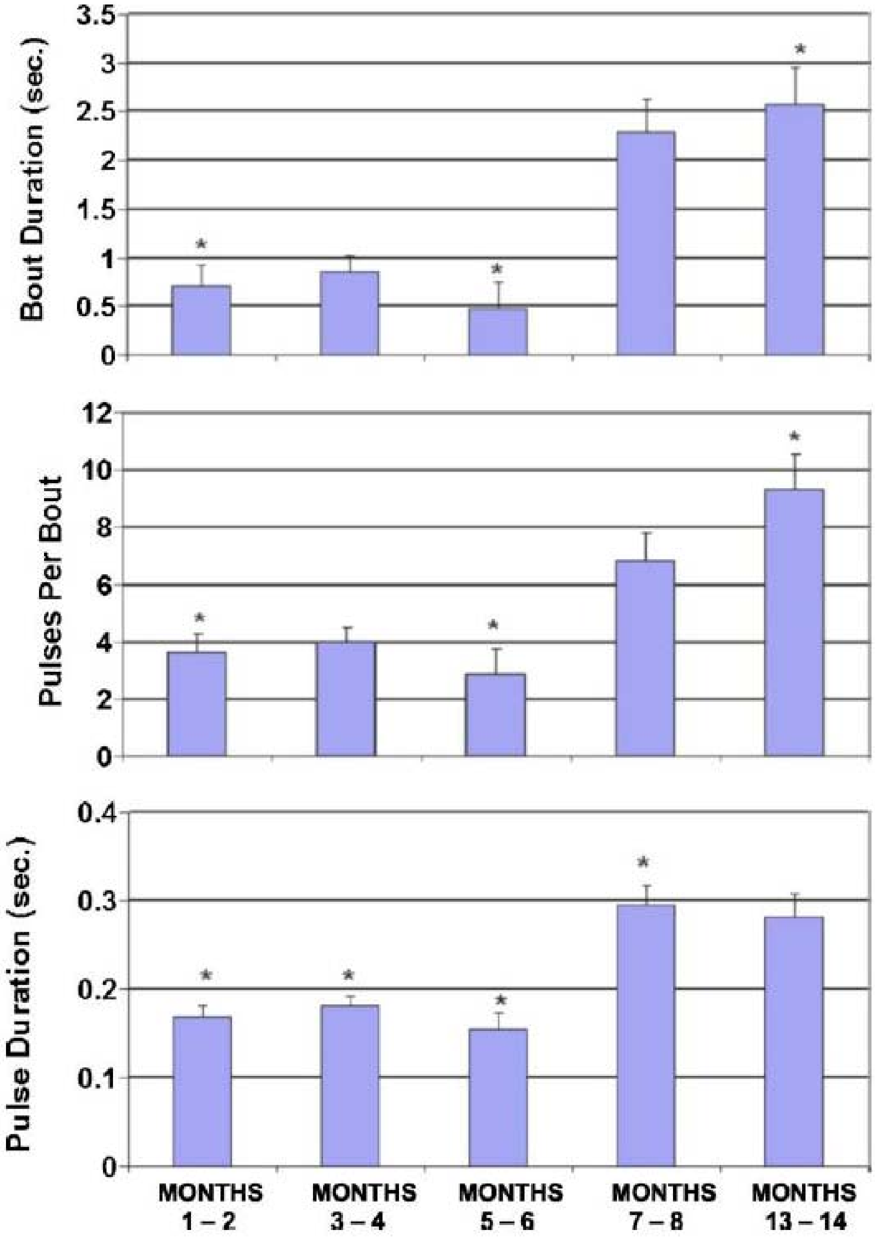


Figure 2.3 (Color online) Bout duration (Bout-Dur), the number of pulses per bout (Pulse-Bout), and pulse duration (Pulse-Dur) are shown as a function of offspring age in 2 month blocks. Asterisks signify Tukey-Kramer posthoc tests in which at least one comparison to other outcomes shown in the panel was statistically significant.

context (male: 10.8%, female: 47.6%). Differences in the Inf-Leave, Mth-Leave, and Spon categories were all less than five percentage points. The influence of infant age on sex differences in Before/During gecker usage was examined in infants up to 6 months old, and results paralleled the overall pattern of sex differences ($X^2 = 22.0$, d.f. = 5, $p<0.001$). Males geckered most in the Affil (male: 17.0%, female: 0%) and Aggr (male: 28.3%, female: 14.3%) contexts, while females geckered most in the Inf-Follow (male: 5.44%, female: 10.3%) context. However, the male-female difference in the Inf-Follow context was less pronounced in these younger infants.

Acoustics and contexts

A cross-validated, multinomial discriminant-function analysis was conducted with Before/During as an independent variable to determine whether the acoustic measures considered collectively could be used to discriminate among the six contexts associated with geckering. Only 34.8% of the 107 available cases were successfully classified, which was nonetheless statistically significant, $F(52,343)=2.10$, $p<0.001$. Canonical discriminant analysis (Tabachnik and Fidell, 2001) revealed that the first canonical correlation ($r_C=0.59$) was significant, $F(52,343)=2.06$, $p<0.0001$, with Pulse-Redup (1.02), SNR (0.91), and Bout-Dur (−0.67) being the most influential in discriminating among the contexts.

A cross-validated, multinomial discriminant-function analysis was conducted with After as an independent variable to determine whether the acoustic measures considered collectively could be used to discriminate among the three outcome categories associated with geckers. Only 26.6% of the 111 cases were correctly classified, which was not a statistically significant proportion, $F(26,184)=0.94$, $p>0.55$. One-way ANOVA did reveal that the means of some acoustic measures differed as a function of the After context, including HNR, *F*(2,104)=3.95, $p<0.05$, Bout-Dur, *F*(2,104)=3.91, $p<0.05$, and Pulse-Dur, *F*(2,104)=4.0, $p<0.05$. Tukey posthoc tests demonstrated that the geckers with the longest Bout-Dur and Pulse-Dur values were associated with negative outcomes significantly more often than either positive outcomes or no outcomes. Geckers with higher HNR values were more often associated with positive outcomes than no outcome.

Responses to geckers

Immediate maternal response coding (Rsp/No-Rsp) was available for 76 geckering episodes, with mothers found to respond in only 38.2% of these cases, and doing so predominantly when the vocalizers were relatively young (*M*=3.52 mo). Although offspring as old as 17 months were still producing geckers, no responses were noted to individuals older than 12 months (see Figure 2.4). A clear sex difference also emerged, with 47.2% of the gecker bouts emitted by males eliciting an immediate maternal response (25/53), compared to only 17.4% from females (4/23), $X^2 = 6.03$, d.f. = 1, $p<0.014$. Male geckers were also responded to (*M*=3.32 mo) earlier in life than females (M=4.75 mo), Mann-Whitney *U*, $z=2.44$, $p<.02$.

Gecker usage did not deviate significantly from expected proportions across the three outcome categories scored for geckers ($X^2 = 2.65$, d.f. = 2, $p>0.25$). Furthermore, no sex difference was found in the outcomes experienced when examining offspring across the entire 24 months, $X^2 = 0.72$, d.f. = 2, $p>0.68$. However,

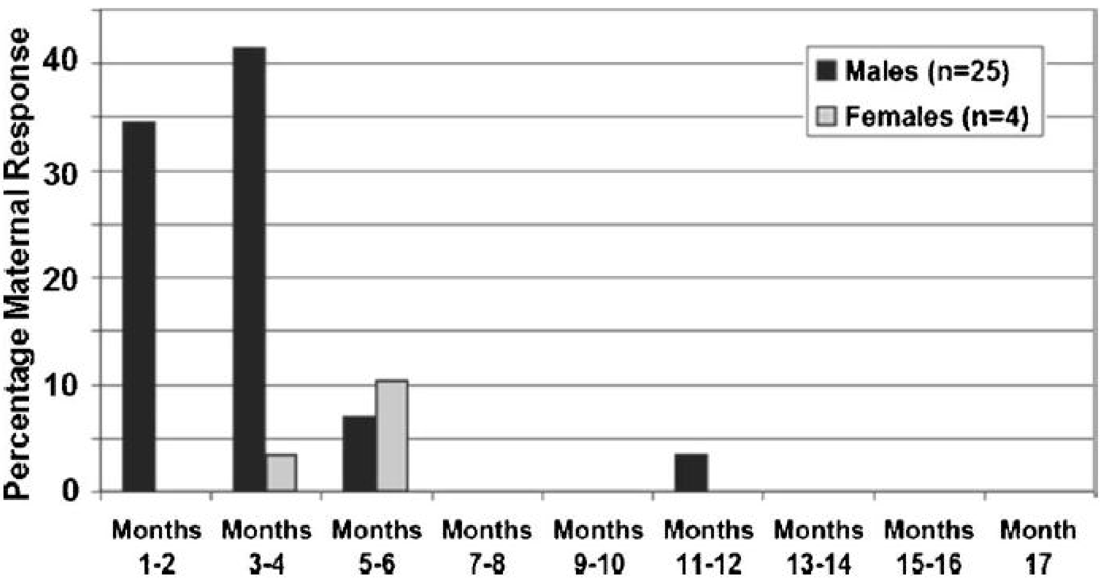


Figure 2.4 Percentage occurrence of immediate maternal response by infant age block (mo.) to each gecker bout that received an immediate maternal response. Percentages shown sum to 100%, representing all instances that the mother showed an immediate response to her offspring's geckering (scored as Rsp, as described in Table 2.3).

significant differences were apparent for infants that were 7 months of age or older. Here, 50% of male bouts were ultimately associated with positive outcomes, but only 26.7% of female bouts. Conversely, 66.7% of female bouts but only 8.3% of male bouts ultimately resulted in negative outcomes, $X^2 = 10.2$, d.f. = 2, $p<0.01$.

Multivariate logistic regression analysis was used to identify independent acoustic predictors of maternal response as coded through Rsp/No-Rsp. Two subjects, female infant LN and male infant MS, contributed a disproportionately high number of bouts to this sample, 17 and 23 bouts, respectively. Using a random number generator, 15 bouts from each were selected for analysis, which reduced the sample to 66 bouts from nine individuals (six males, three females), with equivalent numbers of male (*M*=7.7, SD=6.68, range 1–15) and female bouts (*M*=7.0, SD=6.93, range 3–15). All variables that achieved univariate statistical significance at the 0.2 level were entered into a forward stepwise model selection procedure for the multivariate logistic regression analysis. Two variables, HNR and Peak1, were determined to be statistically significant predictors of maternal response in a multivariate model. Like HNR, Peak1 can be interpreted as a measure of relative noisiness, as this LPC coefficient tends to co-vary with the overall slope of the LPC function. However, the measures were nonetheless largely independent. After adjusting for Peak1, the odds of a maternal response were 1.42 times greater for each unit increase in HNR (95% confidence interval 1.2–2.1). After adjusting for HNR, the odds of a maternal response were 3.3 times greater for each unit increase in Peak1 (95% confidence interval 1.2–9.1). Overall, the likelihood of a maternal response significantly increased for vocalizers with higher HNR and Peak1 values. The multivariate logistic regression model correctly predicted the presence or absence of maternal response in 80.3% of cases, although prediction accuracy was substantially higher for instances of no response (92.9%) compared to when a response did occur (58.3%).

DISCUSSION

Acoustic analyses of rhesus monkey gecker vocalizations during the first 24 months of life revealed age, sex, and maternal response differences across several temporal, spectral, and amplitude measures, but little context-specific acoustic differentiation. Geckers of the youngest infants had the shortest bout durations, pulse durations, and fewest pulses per bout. Female geckers showed higher spectral peaks and bout durations, while male geckers were higher in amplitude and less noisy. Developmentally, gecker usage peaked at four months of age for both sexes, with male geckers nonetheless tending to occur at younger ages than those of females. More than 75% of gecker bouts were produced by infants 6 months of age or less, but offspring as old as 17 months could also gecker. Over 20% of gecker bouts appeared to be spontaneous, while the majority of these calls were emitted when the offspring were following their mothers, receiving aggression from their mothers, or had been left behind. Acoustic measures showed some statistical power in discriminant-function classification of calls according to six different behavioral contexts associated with geckering, but modestly so. The measures discriminating most among these contexts were bout duration, pulse reduplication, and signal-to-noise ratio. Mothers responded most, and most positively to the geckers of young infants, while also clearly favoring males. Maternal response was also more likely when geckers showed a pronounced spectral peak and less noisiness.

Acoustics: Structure and function

Acoustic analysis confirmed that geckers are composed solely of multiple short pulses. With just one reliable frequency peak (at just below 3000 Hz), geckers can be considered “spectrally structured noise” (Beeman, 1998). The noisiness of gecker pulses was reflected in a virtually flat spectral slope (Spectral-Tilt), low tonality (HNR), and high spectral standard deviation (Spectral-StDev) relative to spectral mean (Spectral-Mean). While the absolute amplitude of geckers was not measured, they are likely among the loudest vocalizations produced by young rhesus. Their noisiness therefore almost certainly reflects chaotic vocal-fold vibration (e.g., Tokuda *et al.*, 2002) rather than simple airflow turbulence. The occasional occurrence of periodic components within this noise-based spectral structure is also consistent with interpreting the sounds as example of deterministic chaos (Wilden *et al.*, 1998). This kind of chaos is often a hallmark of elevated vocal effort, for example, occurring as subglottal air pressures and vocal-fold tensions increase during vocal production (Wilden *et al.*, 1998; Fitch *et al.*, 2002; Brown *et al.*, 2003; Riede *et al.*, 2004). The occurrence of pulse reduplications in 34% of all gecker bouts can thus be taken as an indicator of additional vocal-fold instability due to vocal effort, with these events being particularly prevalent in longer geckers with a large number of pulses.

This acoustic structure suggests that geckers are both salient and localizable to listeners. Several features, including their abrupt, high-amplitude pulses and broadband atonal spectra, likely make geckers particularly difficult to ignore as an auditory event (see Owren and Rendall, 1997, 2001). These same features also suggest that geckers should be easy to localize in both vertical and horizontal dimensions (Brown, 1982; Heffner, 2004; Recanzone and Beckermann, 2004). Moreover, auditory localization is facilitated when sounds are produced in conjunction with salient visual events (e.g., Heffner, 2004), such as the dramatic, spasmodic whole-body jerking that can accompany geckering. Geckers are thus well designed to serve as signals of distress, and communicative significance likely adds additional salience for species-specific listeners. However, these same perceptual features can contribute to these sounds becoming annoying as well, particularly with prolonged use (e.g., Todt, 1988). In humans, for instance, there is ample evidence both that infant distress vocalizations are aversive to caregivers, and that the sounds become significantly more noxious when produced in long bouts (Frodi and Senchak, 1990; Levitzky and Cooper, 2000; Soltis, 2004). Noisy, so-called “dysphonia” is also prominent among the features found to have the greatest negative impact in human infant cries (Wood and Gustafson, 2001; Gustafson and Green, 1989; Dessureau *et al.*, 1998), a phenomenon now shown to be chaotic vocal-fold vibration (Herzel, 1993).

Acoustics: Age and sex

Ontogenetic trends mainly involved producing longer pulses, longer bouts, and more pulses per bout. Consistent with previous work on primate vocal production, these changes likely reflect maturational and growth processes rather than vocal learning per se (Hammerschmidt *et al.*, 2000; Hammerschmidt *et al.*, 2002). Sex differences, such as female gecker bouts lasting more than twice as long as those of males, were similar to outcomes reported for other distress calls in rhesus (Tomaszycki *et al.*, 2001; Erwin, 1975) and Japanese macaques (Green, 1981). The single characteristic spectral peak in geckers was also nearly 700 Hz higher in females than in males. Male geckers were somewhat less noisy (HNR), as well as being substantially higher in amplitude (SNR). These differences were apparent even after statistically controlling for body weight, suggesting that the critical factors may involve neuroanatomy, hormones, or vocal-fold size and shape, rather than body size and associated differences in vocal-tract length (Fitch, 1997).

Gonadal sex steroids are particularly likely to play a critical role, with Tomaszycki *et al.* (2001) finding that female rhesus up to 8 months emitted longer call bouts and used a greater variety of call types than did males of comparable age. However, when female fetuses were treated with androgen during the second trimester of gestation, the sex difference in later calling behavior was eliminated. The hormone treatment was likely to be operating via effects both on inferior temporal cortex (Newman and Bachevalier, 1997; Newman *et al.*, 1990) and on the vocal folds themselves (Aufdemorte *et al.*, 1983; Saez and Martin, 1976; Hollien *et al.*, 1994). Vocal-fold dimensions are largely unrelated to overall body size (Fitch, 1997; Rendall *et al.*, 2005), consistent with the current finding that sex differences in gecker acoustics persisted after statistically controlling for body size.

Usage: Age and sex

Although rhesus from 1 to 17 months of age emitted geckers, 75.7% of these calls occurred during the first 6 months of life. Geckering peaked at 4 months of age in both males and females, similar to results from Berman *et al.*'s (1994) more general study of rhesus distress calling. Ontogenetic peaks have also been found in other primate infant distress calls: stumptail macaque “trilled whistles” at 8 weeks (Maestripieri *et al.*, 1995), vervet monkey “care-elicitation” calls at 8–10 weeks (Hauser, 1993), chimpanzee “crying” at 6–8 weeks (Bard, 2000), and human infant crying at 6 weeks (Barr, 1990).

The time course involved may reflect the changing quality of the mother-infant relationship, with both free-ranging and captive rhesus infants beginning to spend time away from their mothers at about 4 months of age (Berman, 1980). A mother's first postpartum estrus also occurs around the same point, potentially causing significant increases in separation, distress calling and infant tantrums (Berman *et al.*, 1994). Males both began and stopped geckering earlier than females (also see Green, 1981), consistent with Newman *et al.*'s (1990) finding that female rhesus vocalize more than males during social separation in the second half of their first year. Erwin (1975) has argued that this sex difference in rhesus vocalization rates is very general, extending to “every age other than the period when the females have reached puberty and the males have not” (p. 376).

Accompanying context

Gecker production was not associated with any single behavioral context, with most geckers occurring when an offspring received maternal aggression (22%), when there was a proximity change such as mother moving away (19%), or when the vocalizer was following its mother (25%). Spontaneous geckers (22%) were also common. This finding is compatible with Newman's (1995) argument that at least some geckers are artifacts of basic nervous-system development rather than having signaling function per se. In a similar vein, Blass (1994) argues that human infant crying may function to maintain ideal levels of brain activation during early development. Nonetheless, spontaneous geckers may also reflect distress with purely internal causes, or could be related to external circumstances that the observer cannot readily see. At present, this issue must be considered unresolved.

Male geckering was found to be significantly more likely in the context of experiencing either aggression or affiliative behavior than was female geckering. However, the most striking sex difference appeared for offspring following their mothers, a context that accounted for almost half of all gecker bouts in females, but only 11% in males. One interpretation of this discrepancy is that females are less independent of their mothers than are males, particularly in early infancy (Lindell *et al.*, 2003; Simpson *et al.*, 1986; although see Brown and Dixon, 2000). If so, females might also become more distressed and vocal when following an inattentive mother (Lovejoy and Wallen, 1988).

Acoustics and context

The contexts found to be associated with geckering are consistent with interpreting these sounds as “separation-rejection” vocalizations, but the lack of context-specificity suggests they are not differentiated signals of specific need. While gecker acoustics supported statistically significant discriminant-function classification according to preceeding or co-occurring context, categorization success was only 35% correct overall. The upshot is that the degree of acoustic differentiation is unlikely to attain the “just noticeable difference” (sensu Nelson and Marler, 1990) necessary for conspecifics to reliably infer the context of calling from acoustics alone. Gecker variation appears more likely to reflect differences in vocalizer arousal, particularly as pulse reduplication, signal-to-noise ratio, and bout duration were the primary variables contributing to successful statistical classification. Each of these measures probably reflects overall vocal effort, with increasing arousal plausibly associated with higher subglottal air pressures, greater vocal-fold tension, and more prolonged calling. This interpretation is consistent with Bayart *et al.*'s (1990) compelling results with coo calls produced by rhesus infants being separated from their mothers. Both infant behavior and associated coo acoustics were differentially affected by the degree of isolation, with concomitant effects found on hormone levels, monoamine neurotransmitter measures, and behavioral arousal. Total isolation produced increases in each of these domains, and triggered coos that were longer, harmonically richer, and more frequency modulated than those produced when mothers were visible to the infants in an adjacent cage.

Maternal response

Mothers showed an immediate response to only 38% of gecker bouts, and these reactions depended on a combination of gecker acoustics, offspring age, and whether the vocalizers were male or female. Mothers were most responsive to infants aged 4 months or less, and mothers were never observed to react to offspring older than 12 months. Maestripieri (1995) and Hauser (1993) have reported similar outcomes for stump-tailed macaques (*Macaca arctoides*) and vervet monkeys (*Cercopithecus aethiops*), respectively. Overall maternal responsiveness here was lower than in those studies, but probably because the current subjects were observed over a wider age range. Mothers were also more likely to react to male than to female geckers, and began to show responses earlier in the infant males' lives. Tomaszycki *et al.* (2001) similarly found that rhesus mothers responded more to males than to females across a variety of distress vocalizations, consistent with a general pattern of rhesus females showing somewhat greater parental investment toward sons than daughters (Bercovitch *et al.*, 2000).

Overall, the outcomes experienced by geckering infants were about equally likely to be positive or negative, and based again on discriminant-function analysis, gecker acoustics could not be used to predict the nature of the outcome, or whether there would be any discernible outcome. However, univariate analyses did show that geckers with longer bout and pulse durations tended to be associated with more negative outcomes such as aggression, while less noisy geckers were associated with more positive outcomes. An additional, striking difference was that for offspring 7 months or older, geckering was followed by aggression from mothers or other group members more than 50% of the time for females, but less than 10% of the time for males. Similarly, about half the gecker bouts from older male infants were associated with positive outcomes such as affiliation and attention, while the comparable figure for females was only about one-quarter.

These differences probably reflect a combination of factors, including the vocalizer's age and sex, as well as the potential aversiveness of geckers as auditory events. On the one hand, rhesus mothers could be less responsive to, but more negative toward females due to their higher calling rates, noisier geckers, and older ages when calling. Reinforcement learning has often been proposed as the mechanism by which rat pups (D'amato *et al.*, 2005), bird nestlings (Lotem, 1998; Stamps *et al.*, 1989), or rhesus monkey infants (Berman *et al.*, 1994) adjust their vocalizing towards optimal rates of effectiveness. Female rhesus infants may vocalize more often and intensively than males because mothers are rarely responding. Mothers may respond less to females because females are geckering excessively beyond the ages at which maternal response to geckers is crucial to offspring well being.

On the other hand, females may be more likely to exhibit these calling characteristics precisely because their mothers are less responsive and behave less positively toward them. If the latter, mothers are behaving differently toward males and females for other reasons, and can in fact likely distinguish their respective geckers due to differences such as spectral peak frequencies. In addition, mothers were simply less likely to respond to calls from older individuals, which in most instances of which were females. Overall, then, while sex differences in both geckering and maternal responsiveness are apparent in these animals, the direction of causality involved between remains unclear.

CONCLUSIONS

Taken together, gecker vocalizations are likely to be highly salient and localizable to receivers. Gecker acoustics appear to be well designed to draw the attention of mothers and other listeners, while also potentially becoming aversive. These sounds become even more salient by virtue of regularly being accompanied by spasmodic jerking, occurring in lengthy bouts, and being associated with situations of evident vocalizer distress. While thus potentially being an effective distress cue, geckers are not highly specific to particular circumstances, and only infrequently elicit maternal response. The likelihood of maternal response was greatest when geckers exhibited pronounced spectral peaks and less noisiness (HNR).

Most gecker bouts were emitted within the first 6 months of life, with peak occurrence when infants were 4 months of age and mothers were experiencing their first postpartum estrus. After this age, maternal responsiveness diminished markedly. Male infants both began and stopped geckering earlier in life than females, and mothers responded more to their calls. Sex differences were also found in gecker acoustics, albeit based on an imperfectly balanced sample. Female vocalizations were characterized by longer durations and higher-frequency spectral peaks, while male geckers were generally less noisy (HNR) and higher in amplitude. Differences in neuroanatomy, hormones, and vocal-fold size and shape are all likely to contribute to these acoustic differences. Sex-biased maternal responsiveness is likely attributable to sex differences in gecker acoustics as well as the fact that females are emitting geckers at older ages than males.

ACKNOWLEDGMENTS

This research was supported in part by NIH Grant No. RR00160 to the California National Primate Research Center, by NICHHD Grant No. NS 19826 to Robert M. Seyfarth, Dorothy L. Cheney, and Michael J. Owren, by postdoctoral fellowship 5 F32 HD06878-03 to Michael J. Owren, and by NIMH Grant No. R01MH65317 to Robert D. Hienz, Michael J. Owren, and Drew Rendall. We thank C. Cornelius, R. Henrickson, A. Hendrickx, and W. A. Mason for facilities and support provided throughout the cross-fostered macaque vocal development project, and to J. Adams, A. Cabrera, P. Telfer and other members of the technical staff for expert assistance. Thanks to Rachel Pulverman for digitizing sound files, Steve Creech for lending his statistical expertise, Nick Lerche for finding crucial information about the rhesus mothers involved in the project, and two anonymous reviewers for providing thoughtful and constructive comments on the initial manuscript.

REFERENCES

Altmann, J. (**1974**). “Observational study of behavior: Sampling methods,” Behav. 49, 227-265.

Altmann, S. (**1962**). “A field study of the sociobiology of rhesus monkeys (*Macaca mulatta*),” Annal. N.Y. Acad. Sci. **102**, 338-435.

Aufdemorte, T. B., Sheridan, P. J., and Holt, G. R. (**1983**). “Autoradiographic evidence of sex steroid receptors in laryngeal tissues of the baboon,” Laryngoscope **93**, 1607-1611.

Bard, K. A. (**2000**). “Crying in infant primates: Insights into the development of crying in chimpanzees,” In *Crying As a Sign, a Symptom, & a Signal: Clinical Emotional and Developmental Aspects of Infant and Toddler Crying*, edited by R. G. Barr, B. Hopkins, and J. A. Green (Cambridge University Press, New York), pp. 157–175.

Barr, R. G. (**1990**). “The normal crying curve: What do we really know?” Develop. Med. Child Neurol. **32**, 356 – 362.

Bayart, F., Hayashi, K. T., Faull, K. F., Barchas, J. D., and Levine, S. (**1990**). “Influence of maternal proximity on behavioral and physiological responses to separation in infant rhesus monkeys (*Macaca mulatta*),” Behav. Neuro. **104**, 98 – 107.

Beeman, K. (**1998**). “Digital signal analysis, editing and synthesis,” In *Animal Acoustic Communication: Sound Analysis and Research*, edited by S. L. Hopp, M. J. Owren, and C. S. Evans (Springer-Verlag, Berlin), pp. 59–104.

Bercovitch, F. B., Widdig, A., and Nuernberg, P. (**2000**). “Maternal investment in rhesus macaques (*Macaca mullata*): Reproductive costs and consequences of raising sons,” Behav. Ecol. Sociobiol. **48**, 1-11.

Berman, C. M. (**1980**). “Mother infant interaction among free ranging rhesus monkeys: A comparison with captive pairs,” Anim. Behav. **28**, 860-873.

Berman, C. M., Rasmussen, K. R., and Suomi, S. J. (**1994**). “Responses of free ranging rhesus monkey infants to a natural form of social separation: Parallels with mother infant separation in captivity,” Child Develop. **65**, 1028-1041.

Blass, E. M. (**2004**). “Changing brain activation needs determine early crying: A hypothesis,” Behav. Brain Sci. **27**, 460-461.

Boersma, P. (**1993**). “Accurate short-term analysis of the fundamental frequency and the harmonics-to-noise ratio of a sampled sound,” Proc. Instit. Phon. Sci. Amster. **17**, 97-110.

Boersma, P. (**2001**). “PRAAT, a system for doing phonetics by computer,” Glot. Internat. **5**, 341-345.

Brown, C. H. (**1982**). "Auditory localization and primate vocal behavior," In *Primate Communication*, edited by C. T. Snowdon, C. H. Brown, and M. R. Peterson (Cambridge University Press, New York), pp. 144–164.

Brown, C. H., Alipour, F., Berry, D. A., and Montequin, D. (**2003**). "Laryngeal biomechanics and vocal communication in the squirrel monkey (*Saimiri boliviensis*)," J. Acoust. Soc. Amer. **113**, 2114-2126.

Brown, G. R., and Dixon, A. F. (**2000**). "The development of behavioural sex differences in infant rhesus macaques (*Macaca mullata*)," Primates **41**, 63-77.

D'amato, F. R., Scalera, E., Sarli, C., and Moles, A. (**2005**). "Pups call, mothers rush: Does maternal responsiveness affect the amount of ultrasonic vocalizations in mouse pups?" Behav. Genet. **35**, 103-112.

Dessureau, B. K., Kurowski, C. O., and Thompson, N. S. (**1998**). "A reassessment of the role of pitch and duration in adults' responses to infant crying," Infant Behav. Develop. **21**, 367-371.

Erwin, J. (**1975**). "Rhesus monkey vocal sounds," In *The Rhesus Monkey, Vol.1: Anatomy and Physiology*, edited by G. H. Bourne (Academic, New York), pp. 365–380.

Fitch, W. T. (**1997**). "Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques," J. Acoust. Soc. of Amer. **102**, 1213-1222.

Fitch, W. T., Neubauer, J., and Herzel, H. (**2002**). "Calls out of the chaos: The adaptive significance of nonlinear phenomena in mammalian vocal production," Anim. Behav. **63**, 407-418.

Forrest, K., Weismer, G., Milenkovic, P., and Dougall, R. N. (**1988**). "Statistical analysis of word-initial obstruents: Preliminary data," J. Acoust. Soc. Amer. **84**, 115-123.

Frodi, A., and Senchak, M. (**1990**). "Verbal and behavioral responsiveness to the cries of atypical infants," Child Develop. **61**, 76-84.

Gautier, J. P., and Gautier, A. (**1977**). "Communications in old world monkeys," In *How Animals Communicate*, edited by T. A. Sebeok (Indiana University Press, Bloomington), pp. 890–964.

Green, S. M. (**1981**). "Sex differences and age gradations in vocalizations of Japanese and lion-tailed monkeys (*Macaca fuscata* and *Macaca silenus*)," Amer. Zool. 21, 165-183.

Gustafson, G. E., and Green, J. A. (**1989**). "On the importance of fundamental-frequency and other acoustic features in cry perception and infant development," Child Develop. **60**, 772-780.

Hammerschmidt, K., Newman, J. D., Champoux, M., and Suomi, S. J. (**2000**). "Changes in rhesus macaque `coo' vocalizations during early development," Ethology **106**, 873-886.

Hammerschmidt, K., Freudenstein, T., and Juergens, U. (**2002**). “Vocal development in squirrel monkeys,” Behav. **138**, 1179-1204.

Hauser, M. D. (**1993**). “Do vervet monkey infants cry wolf?” Anim. Behav. **45**, 1242-1244.

Heffner, R. S. (**2004**). “Primate hearing from a mammalian perspective,” Anatom. Rec. **218A**, 1111-1122.

Herzel, H. (**1993**). “Bifurcation and chaos in voice signals,” App. Mechan. Rev. **46**, 399-413.

Hoffman, R. A., and Stowell, R. E. (**1973**). “Outdoor housing of nonhuman primates,” Lab. Anim. Sci. **23**, 74-83.

Hollien, H., Green, R., and Massey, K. (**1994**). “Longitudinal research on adolescent voice change in males,” J. Acoust. Soc. Amer. **96**, 2646 – 2654.

Jovanovic, T., and Gouzoules, H. (**2001**). “Effects of maternal restraint on the vocalizations of infant rhesus monkeys (*Macaca mulatta*),” Amer. J. Primatol. **53**, 33-45.

Kalin, N. H., Shelton, S. E., and Snowdon, C. T. (**1992**). “Affiliative vocalizations in infant rhesus macaques (*Macaca mulatta*),” J. Comp. Psychol. **106**, 254 – 261.

Levitzky, S., and Cooper, R. (**2000**). “Infant colic syndrome, maternal fantasies of aggression and infanticide,” Clin. Pediat. **39**, 395 – 400.

Lindell, S. G., Shannon, C., Suomi, S. J., and Higley, J. D. (**2003**). “Sex differences in rhesus macaque mother-infant behavior,” Amer. J. Primatol. **60**, 130 – 131.

Locke, J. L., and Hauser, M. D. (**1999**). “Sex and status effects on primate volubility: Clues to the origin of vocal languages?” Evol. Human Behav. **20**, 151 – 158.

Lotem, A. (**1998**). “Differences in begging behaviour between barn swallow, *Hirundo rustica*, nestlings,” Anim. Behav. **55**, 809 – 818.

Lovejoy, J., and Wallen, K. (**1988**). “Sexually dimorphic behavior in group-housed rhesus monkeys (*Macaca mulatta*) at 1 year of age,” Psychobiol. **16**, 348–356.

Maestripieri, D. (**1995**). “Maternal responsiveness to infant distress calls in the stumptail macaque,” Folia Primatol. **64**, 201 – 206.

Maestripieri, D., and Call, J. (**1996**). “Mother-infant communication in primates,” Adv. Study Behav. **25**, 613 – 642.

Maestripieri, D., Jovanovic, T., and Gouzoules, H. (**2000**). “Crying and infant abuse in rhesus monkeys,” Child Develop. **71**, 301 – 309.

Nelson, D. A., and Marler, P. (**1990**). “The perception of birdsong and an ecological concept of signal space,” In *Comparative Perception, Vol. 2, Complex Signals,* edited by W. D. Stebbins and M. A. Berkley (Wiley, New York), pp. 443–478.

Newman, J. D. (**1995**). “Vocal ontogeny in macaques and marmosets: Convergent and divergent lines of development,” In *Current Topics in Primate Vocal Communication*, edited by E. Zimmermann, U. Jürgens, and D. Symmes (Plenum, New York), pp. 73–97.

Newman, J. D., and Bachevalier, J. (**1997**). “Neonatal ablations of the amygdala and inferior temporal cortex alter the vocal response to social separation in rhesus macaques,” Brain Res. **758**, 180 – 186.

Newman, J. D., Bachevalier, J., Michjeda, M., and Suomi, S. J. (**1990**). “A possible neural substrate for gender differences in vocal behavior by rhesus macaque infants during brief periods of social separation,” Soc. Neurosci. Abs. **16**, 599.

Owren, M. J., and Bernacki, R. H. (**1998**). “Applying linear predictive coding (LPC) to frequency-spectrum analysis of animal acoustic signals,” In *Animal Acoustic Communication: Sound Analysis and Research*, edited by S. L. Hopp, M. J. Owren, and C. S. Evans (Springer-Verlag, Berlin), pp. 129–161.

Owren, M. J., and Dieter, J. A. (**1989**). “Infant cross-fostering between Japanese (*Macaca fuscata*) and rhesus macaques (*M. mulatta*),” Amer. J. Primatol. **18**, 245 – 250.

Owren, M. J., Dieter, J. A., Seyfarth, R. M., and Cheney, D. L. (**1992a**). “Food calls produced by adult female rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques, their normally-raised offspring, and offspring cross-fostered between species,” Behav. **120**, 218 – 231.

Owren, M. J., Dieter, J. A., Seyfarth, R. M., and Cheney, D. L. (**1992b**). “Evidence of limited modification in the vocalizations of cross-fostered rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques,” In *Topics in Primatology, Vol. 1: Human Origins*, edited by T. Nishida, W. C. McGrew, P. Marler, M. Pickford, and F. de Waal (University of Tokyo Press, Tokyo), pp. 257–270.

Owren, M. J., Dieter, J. A., Seyfarth, R. M., and Cheney, D. L. (**1993**). “Vocalizations of rhesus (*Macaca mulatta*) and Japanese *(M. fuscata*) macaques cross-fostered between species show evidence of only limited modification,” Devel. Psychobiol. **26**, 389 – 406.

Owren, M. J., and Rendall, D. (**1997**). “An affect-conditioning model of nonhuman primate vocal signaling,” In *Perspectives in Ethology: Vol. 12. Communication* edited by D. H. Owings, M. D. Beecher, and N. S. Thompson (Plenum, New York), pp. 299–346.

Owren, M. J., and Rendall, D. (**2001**). “Sound on the rebound: Bringing form and function back to the forefront in understanding nonhuman primate vocal signaling,” Evol. Anthro. **10**, 58-71.

Recanzone, G. H., and Beckermann, N. S. (**2004**). “Effects of intensity and location on sound location discrimination in macaque monkeys,” Hear. Res. **198**, 116-124.

Rendall, D., Kollias, S., Ney, C., and Lloyd, P. (**2005**). “Pitch (F_0) and formant profiles of human vowels and vowel-like baboon grunts: The role of vocalizer body size and voice-acoustic allometry,” J. Acoust. Soc. Amer. **117**, 944-955.

Riede, T. R., Owren, M. J., and Clark Arcadi, A. (**2004**). “Nonlinear acoustics in the pant-hoot vocalizations of common chimpanzees (*Pan troglodytes*): Frequency jumps, subharmonics, biphonation, and deterministic chaos,” Amer. J. Primatol. **64**, 277 – 291.

Rowell, T. E. (**1962**). “Agonistic noises of the rhesus monkey (*Macaca mulatta*),” Sympos. Zoolog. Soc. London **8**, 91 – 96.

Rowell, T. E., and Hinde, R. A. (**1962**). “Vocal communication by the rhesus monkey (*Macaca mulatta*),” Proc. Royal Soc. London **138**, 279 – 294.

Saez, S. J., and Martin, P. M. (**1976**). “Androgen receptors in human pharyngo-laryngeal mucosa and pharyngo-laryngeal epithelium,” J. Steroid Biochem. **7**, 919 – 921.

Seyfarth, R. M., and Cheney, D. L. (**1986**). “Vocal development in vervet monkeys,” Anim. Behav. **34**, 1640 – 1658.

Simpson, M. J. A., Simpson, A. E., and Howe, S. (**1986**). “Changes in the rhesus mother-infant relationship through the first four months of life,” Anim. Behav. **34**, 1528 – 1539.

Snowdon, C. T., Elowson, A. M., and Roush, R. S. (**1997**). “Social influences on vocal development in New World primates,” In *Social Influences on Vocal Development*, edited by C. T. Snowdon and M. Hausberger (Cambridge University Press, New York), pp. 234–248.

Soltis, J. (**2004**). “The signal functions of early infant crying,” Behav. Brain Sci. **27**, 443-490.

Stamps, J., Clark, A., Arrowood, P., and Kus, B. (**1989**). “Begging behavior in budgerigars,” Ethology **81**, 177 – 192.

Tabachnik, B. G., and Fidell, L. S. (**2001**). *Using Multivariate Statistics*, 4th ed. (Allyn and Bacon, New York).

Todt, D. (**1988**). “Serial calling as a mediator of interaction processes: Crying in primates,” In *Primate Vocal Communication*, edited by D. Todt, P. Goedeking, and D. Symmes (Springer-Verlag, Berlin), pp. 88–107.

Tokuda, I., Riede, T., Neubauer, J., Owren, M. J., and Herzel, H. (**2002**). Nonlinear prediction of irregular animal vocalizations. J. Acoust. Soc. Amer. **111**, 2908 – 2919.

Tomaszycki, M. L., Davis, J. E., Gouzoules, H., and Wallen, K. (**2001**). “Sex differences in infant rhesus macaque separation-rejection vocalizations and effects of prenatal androgens,” Horm. Behav. **39**, 267 – 276.

Wallen, K. (**2005**). “Hormonal influences on sexually differentiated behavior in nonhuman primates,” Front. Neuroendocrin. **26**, 7 – 26.

Wilden, I., Herzel, H., Peters, G., and Tembrock, G. (**1998**). “Subharmonics, biphonation, and deterministic chaos in mammal vocalization,” Bioacoustics **9**, 171 – 196.

Wood, R. M. and Gustafson, G. E. (**2001**). “Infant crying and adults' anticipated caregiving responses: Acoustic and contextual influences,” Child Devel. **72**, 1287 – 1300.

CHAPTER 3

Acoustic and behavioral analyses of silky sifaka (*Propithecus candidus*) "zzuss" vocalizations: Effects of context, sex, and individuality

Erik R. Patel[1,2] and Michael J. Owren[3]

ABSTRACT

"Zzuss" calls are among the most common and loudest vocalizations produced by Madagascar's rainforest silky sifakas (*Propithecus candidus*). They have been hypothesized to be anti-predator calls, raising the issue of possible word-like reference, but are also associated with group cohesion and other functions. Zzuss acoustics were examined in relation to context, vocalizer sex, and individual identity. Analysis included 160 zzuss vocalizations recorded from nine adults (four females and five males). Acoustically, the calls combined separate turbulent noise and tonal components, often including frequency jumps and rapid, highly frequency-modulated components. Call rate did not vary seasonally, but was highest in the early morning. Six call contexts were identified, with most vocalizations being produced during terrestrial disturbances, spontaneously while resting, and in response to separated group members. Little evidence of context-specificity was found, arguing against referential function. Although silky sifakas are sexually monomorphic, males and

---

[1] Author to whom correspondence should be addressed. Electronic mail: patel.erik@gmail.com
[2] Department of Psychology, 211 Uris Hall, Cornell University, Ithaca, New York, 14853
[3] Michael J. Owren is now at the Department of Psychology, Georgia State University, PO Box 5010, Atlanta, Georgia 30302-5010.
[4]Reprinted with permission from Patel, E.R. and Owren, M.J. (In Review). Acoustics and behavioral analyses of silky sifaka (*Propithecus candidus*) "zzuss" vocalizations: Effects of context, sex, and individuality. Journal of the Acoustical Society of America. Copyright 2011, American Institute of Physics.

female zzuss calls were acoustically different, most importantly in F_0- and amplitude-related features. All acoustic measures differed between individuals, with F_0-related variables again playing the largest role. Overall, zzuss calls are multi-function vocalizations used both for terrestrial disturbance and group coordination. They are shaped for salience, localizability, and caller identification rather than to have word-like meaning.

INTRODUCTION

Silky sifakas and the "zzuss" vocalization

The silky sifaka (*Propithecus candidus*) is a large white sifaka found only in northeastern Madagascar. It is one of the most critically endangered of all lemurs, with a global population estimated between 300 and 2,000 individuals (Patel, 2009; *Mittermeier* et al., 2010). While this species' common English name comes from its long, silky-white pelage, local residents refer to these sifakas as "simpona," an onomatopoetic label referring to its loud, frequency-modulated "zzuss" call (illustrated in Figure 3.1). Neither the zzuss nor any other alarm calls of the genus *Propithecus* have as yet received detailed acoustic analysis, making this commonly produced call a good starting point in examining the vocal repertoires of eastern sifakas.

Qualitative descriptions suggest that zzuss vocalizations may be generalized alarm calls. They are emitted primarily in response to disturbances and potential danger, such as during terrestrial predation, intrusion of human observers, when animals are suddenly startled, after receiving aggression, and in inter-group encounters (Macedonia and Stanger, 1994; Petter and Charles-Dominique, 1979; Wright, 1998). However, zzuss calls may also facilitate group coordination. Group members often produce zzuss calls antiphonally when hearing tonal, "howl" vocalizations emitted by a distant or "lost" group member. Zzuss calls are also emitted spontaneously without apparent cause (Irwin, 2006; Petter and Charles-Dominique, 1979). As the first quantitative study of silky sifaka vocalization, the current work examines the acoustics and usage of zzuss calls, and contrasts possible accounts of this signal based on predator-related, group-coordination, and other functions.

Primate “loud” calls

Six major functions have been proposed for primate “loud” calls, a category that includes the zzuss vocalization. These functions include mate attraction and mate defense (Buesching *et al.*, 1998; Craul *et al.*, 2004; Semple *et al.*, 2002; Wich and Nunn, 2002), territory defense (MacKinnon and MacKinnon, 1984; Mitani, 1985a,b; Pollack, 1986), food advertisement (Clark and Wrangham, 1993, 1994; Elowson *et al.*, 1991; Wrangham, 1977), auditory impact (Owren and Rendall, 2001; Rendall *et al.*, 2009), predator alarm (Cheney and Seyfarth, 1990; Macedonia and Evans, 1993), and group coordination (Boinski and Garber, 2000;Trillmich et al., 2004; Rasoloharijaona *et al.*, 2006). The mate attraction and defense hypotheses are typically applied to copulation calls or song-like vocalizations in pair-living primates such as indri or gibbons, and can be ruled out for rainforest sifakas. The latter do not have copulation calls or song-like vocalizations, and exhibit variable social structures that include, but are not limited to living in pairs (Patel, 2009). Food-advertisement calling is generally associated with anthropoid primates with diets of high-quality, clumped foods like fruit or gum, and is seldom applied to folivorous prosimians such as silky sifakas.

Auditory impact, predator alarm, and group coordination functions are likely the most relevant for zzuss vocalizations. Auditory impact refers to having acoustic features that are inherently arousing and attention-getting to perceivers, including abrupt onsets and dramatic frequency modulation (Owren and Rendall, 1997, 2001). Nonlinear phenomena, such as biphonation, subharmonics, frequency jumps, and deterministic chaos, are also hypothesized to induce these kinds of direct effects on listeners (Blumstein *et al.*, 2010; Blumstein and Recapet, 2009; Owren and Rendall, 2001; Reby and Charleton, 2011; Riede *et al.*, 2004). If so, auditory impact may be secondary to other functions in zzuss calls, with existing descriptions of usage suggesting predator alarm or group coordination as primary uses (Macedonia and Stanger, 1994; Petter and Charles-Dominique, 1979; Wright, 1998).

Predator-related calling

Specificity and "functional reference"

A question that naturally arises for any predator-related primate call is whether it is specific to a particular kind of threat. In some cases, such alarms are used broadly, as in most nocturnal primates (Evans, 1997; Petter and Charles-Dominique, 1979; Scheumann *et al.*, 2007; Zimmermann, 1995). Diurnal primates can also exhibit non-specific alarm calls, for example with white-faced capuchin (*Cebus capucinus*) "alerting" vocalizations emitted to many different mammals and snakes, including both predators and non-predators (Digweed *et al.*, 2005). Chacma baboons (*Papio cynocephalus ursinus*) emit tonal "barks" as contact calls, which grade into harsher variants of the same call in the presence of large predators (Fischer *et al.*, 2001). The researchers suggest that barks may all reflect the same general affective state, varying according to "response urgency" (Owings and Hennessy, 1984) and vocalizer arousal.

It is also common to observe more specific call usage against aerial than terrestrial threats, resulting in a "mixed alarm call system" (Fichtel and Kappeler, 2002). In semi-free-ranging ring-tailed lemurs (*Lemur catta*), for example, "shriek" vocalizations occur only to raptors, either when seen overhead or during attack. In contrast, "click" calls are used not only against mammalian predators, but also when approached by humans, when moving through the trees, and by mothers to infants (reviewed in Macedonia, 1993). Similarly, in other lemurs, alarm calls emitted to terrestrial predators often show low context specificity. A number of other “terrestrial alarms” in lemurs are notably non-specific, including black-and-white ruffed lemur (*Varecia variegata*) “pulsed squawks,” redfronted brown lemur (*Eulemur rufus*) “croaks” and “woofs,” and Verreaux’s sifaka (*Propithecus verreauxi*) “growls” and “faks.” In each case, the calls occur not only to predators, but also to nonpredators, in a variety of high-arousal social contexts, and spontaneously (Digweed *et al.*, 2005; Fichtel and Kappeler, 2002; Macedonia and Evans, 1993).

Finally, in a few cases, alarm calls of both types are used quite specifically. The clearest example comes from vervet monkeys (*Chlorocebus pygerythrus*), who exhibit distinctive alarms calls not only to raptors and terrestrial mammalian predators, but also snakes (Seyfarth *et al.*, 1980; Cheney and Seyfarth, 1990). In these cases, as well as for ring-tailed lemur click calls (Macedonia, 1990; Macedonia and Polak, 1989), the animals produce each vocalization almost exclusively in “appropriate,” predator-specific contexts. “Production specificity” is thus high for these calls (Macedonia and Evans, 1993). Responses of listeners also show strong “perceptual specificity,” meaning that they exhibit, distinct, predator-specific escape responses when hearing the various calls.

Acoustically differentiated vocalizations that show both production and perceptual specificity are argued to function much like human words (reviewed in Evans, 1997; Macedonia and Evans, 1993; Cheney and Seyfarth, 2010). As underlying production and perception mechanisms are not known, however, such sounds are typically described as showing language-like, “functional reference” rather than having linguistic meaning per se. Nonetheless, one persistent problem in claiming functional reference is that it is difficult to demonstrate strict production specificity. While researchers may observe usage to be quite specific, for example, it is difficult to rule out the possibility that the call can also occur in other contexts. Claims of specificity should therefore include systematic long-term data on a species' entire vocal repertoire and across all possible contexts (Crockford and Boesch, 2003; Owren *et al.*, 2003; Owren and Patel, 2008).

Predation on silky sifakas

If silky sifaka zzuss calls have a specialized, anti-predator function, the specific predator in question is the fossa (*Cryptoprocta ferox*). This carnivore is Madagascar's largest, a solitary species with both cat- and civet-like characteristics, both terrestrial and arboreal habits, and active both at night and during the day (Hawkins and Racey, 2005; Macedonia and Stanger, 1994; Wright, 1998; Wright *et al.*, 1997). The fossa is furthermore the only documented predator of eastern sifakas other than human beings (Goodman, 2003; Irwin *et al.*, 2009; Karpanty and Wright, 2007; Patel, 2005; but see Day *et al.*, 2009). Although these sifakas do exhibit marked anti-predator behavior and "roars" to several raptors, these animals are among the largest lemurs in Madgascar and are not known to be consumed by any extant, predatory bird (Goodman and Pidgeon, 1991; Karpanty, 2006; Karpanty and Goodman, 1999; Thorstrom and La Marca, 2000).

Group-cohesion functions

In addition to anti-predator usage, zzuss calling may facilitate "individuals of a group dispersed in space to gather" and to "coordinate group movement" (Rasoloharijaona *et al.*, 2006, p. 8). In a classic review of prosimian vocal communication, Petter and Charles-Dominique (1979) argue that zzuss vocalizations may have dual functions—acting both as an anti-predator alarm and as a group-cohesion call. As noted above, several species of rainforest sifakas are known to emit zzuss calls immediately following howl vocalizations from a distant or lost group member (Irwin, 2006; Petter and Charles-Dominique, 1979). Given a group-cohesion function, these sounds can be expected to include reliable cues to caller sex and identity, helping identify separated group members to one another while also advertising group size and composition to neighboring groups.

Lemurs are different from many other primates in that males and females are often generally equivalent in body size (Kappeler, 1990, 1991; Wright, 1999). Sex differences in vocal acoustics occur nonetheless including in crowned lemur (*Eulemur coronatus*) “clicks,” “hoots,” and “tonal” alerting and contact sounds (Gamba and Giacoma, 2007). Individual variation in vocal acoustics has also been reported, including in crowned (Gamba and Giacoma, 2007), ring-tailed (Macedonia, 1986), and red-bellied lemurs (*E. rubriventer*; Gamba *et al.*, 2011). Four vocalizations have shown notable individual variability in gray mouse lemurs (*Microcebus murinus*), although with consistently larger differences found in harmonically structured and frequency modulated “trills” and “short whistles” than in broadband, noisy “grunts” (Leliveld *et al.*, 2011). Finally, both sex- and individual-related variation is evident in the acoustic structure of Milne-Edwards’ sportive lemur (*Lepilemur edwardsi*) loud calls, which may also have a group-cohesion function (Rasoloharijaona *et al.*, 2006). Given this overall evidence, as well as the fact that harmonic structure and frequency modulation are visible in many zzuss vocalizations (see Figure 3.1), there is reason to also expect both sex- and individual-variation in this silky sifaka loud call as well.

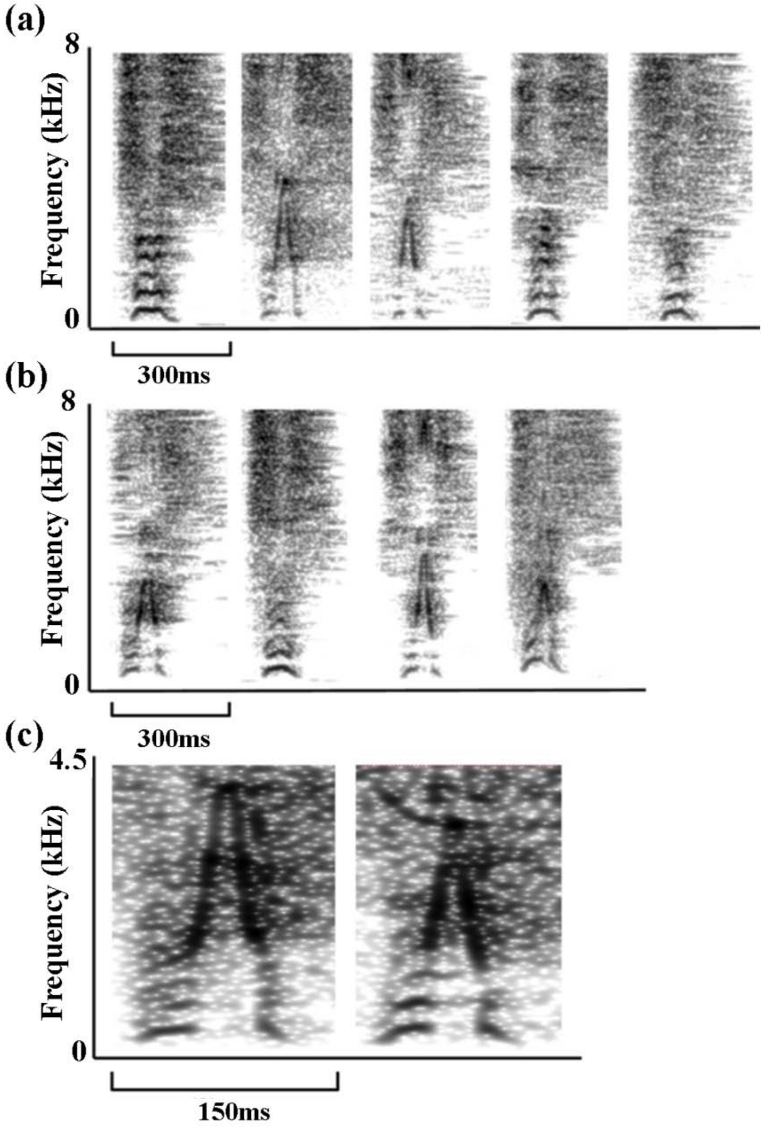


Figure 3.1 Representative narrowband FFT spectrograms (20-ms Hanning analysis window, 16-kHz sampling rate) of (a) one zzuss call from each of five adult males (left to right: AS-2, BB, BC, Camp 3-1, PF); (b) each of four adult females (left to right: AF, AS-1, BP, Camp 3-2); and (c) examples from one adult male (left: BB) and one adult female (right: BP) enlarged to clearly reveal the frequency jumps occurring between the lower F0 contour and the rapid, frequency-modulated component.

The current work

The goal of this investigation was to characterize the acoustics, usage, and behavior associated with zzuss calls, and thereby also determining the function or functions of this vocalization. Several outcomes were expected if the zzuss is a specialized, anti-predator call. First, its acoustic structure and usage were predicted to be specific to predation contexts, in this case involving fossa. Associated anti-predator behavior was also expected, which for the arboreal silky sifaka should include movement upward in the trees with downward staring (Fichtel and Kappeler, 2002; Karpanty and Wright, 2007; Macedonia and Evans, 1993; Sauther, 1989). Finally, rates of occurrence were predicted to show both seasonal and circadian peaks congruent with fossa hunting patterns. Seasonal variation was expected because fossa are known to kill more sifakas during the dry than the wet season (Dollar *et al.*, 2007; Irwin *et al.*, 2009; Wright, 1998). Circadian variation was expected because fossa are suspected to hunt sifaka in the predawn hours when the lemurs are asleep (Dollar *et al.*, 2007; Hawkins and Racey, 2005; Wright, 1998).

Alternatively, if the zzuss call is primarily a group-coordination vocalization, most instances would be expected in response to the howl vocalizations of spatially separated or lost group members. In this case, usage should be evenly distributed across seasons and times of day. Those outcomes have been observed for the roar and shriek choruses of ruffed lemurs (*Varecia spp.*), which function both as general alarm and group-coordination vocalizations (Geissman and Mutchler, 2006; Pereira *et al.*, 1988; Vasey, 2003). Finally, as described above, sex differences and individual variation in zzuss acoustics were specifically expected given a group-coordination function.

METHODS

Subjects and study site

Silky sifakas are large (approximately 6 kg), diurnal, arboreal, and highly social. They inhabit mid-elevation, montane rainforests (generally 700 to 1900 m above sea level) within a few protected areas in northeastern Madagascar (Patel, 2009) and do not survive in captivity (Mittermeier *et al.*, 2010). Silky sifakas live in small cohesive groups with a mean of 4.3 individuals (± 1.8; range 2 to 9). Social structure is either polygynous or pair-bonded, but occasionally multiple adult males are found in the same group. These animals are territorial and maintain exclusive home ranges. The 95% kernel home range size is 41.4 hectares, with a daily path length averaging 528 m ± 162. The species is a folivorous seed predator that consumes more than 100 different plants (Patel, 2009, 201l).

The study was conducted at two mountainous reserves in northeastern Madagascar: Camps 2 and 3 of Marojejy National Park, and Site 1a of Anjanaharibe-Sud Special Reserve. At the time of this work, the group at Marojejy Camp 2 was comprised of three adult males, two adult females, a juvenile male, and two infants. The Marojejy Camp 3 group contained a single adult male, an adult female, and one infant. The Anjanaharibe-Sud group contained one adult male and one adult female (see Table 3.1). Despite some selective logging of precious wood (e.g., rosewood; Patel, 2007), the large elevation ranges of both reserves contribute to making their rainforests among the most pristine and biologically diverse in Madagascar. Marojejy National Park has recently been inaugurated as part of a World Heritage Site cluster (Garreau and Manantsara, 2003; Goodman, 1998, 2000; IUCN, 2007), and may contain more species of forest-dwelling birds (Goodman *et al.*, 2000), reptiles and amphibians (Raselimanana *et al.*. 2000), and ferns (Rakotondrainibe 2000) than any other reserve on the island. With 11 species of lemurs, its primate diversity is also extensive (Duckworth *et al.*, 1995; Sterling and McFadden, 2000).

Table 3.1 Subject demographics and representation in the zzuss sample.

Subject	Sex	Site	Bouts	Calls
AS-2	Male	Anjanaharibe-Sud Site 1a	4	8
BB	Male	Marojejy Camp 2	10	13
BC	Male	Marojejy Camp 2	11	21
PF	Male	Marojejy Camp 2	13	30
Camp 3-1	Male	Marojejy Camp 3	4	8
AS-1	Female	Anjanaharibe-Sud Site 1a	4	12
AF	Female	Marojejy Camp 2	14	26
BP	Female	Marojejy Camp 2	15	35
Camp 3-2	Female	Marojejy Camp 3	4	7
		Total	79	160
		M/s.d.	8.8/4.8	17.8/10.5

Apparatus and procedure

Audio-recording and behavioral observation

Vocalizations were recorded using equipment and procedures recommended by Budney and Grotke (1997), including a Sony TC-D5 PRO IIR stereo cassette recorder (Sony Corporation of America, New York), directional Sennheiser MKH-70 microphone (Sennheiser Electronic Corporation, Old Lyme, CT), MZA-14-P48U 48v phantom power supply, MZW 60-1 blimp windscreens, and MZS 20-1 pistol grip shockmount. RF condenser microphones, such as the Sennheiser MKH70, are resistant to rainforest humidity and static discharge that can produce audible crackling and popping. Recordings were made on one side of Maxell Professional MS Studio 60-minute, audio-cassette tapes (IEC Type II; Maxell Corporation of America, Woodland Park, NJ) with noise reduction and automatic gain control turned off. The microphone signal was recorded on both channels simultaneously, with offset input levels that helped ensure good recording quality across a range of signal amplitudes.

Vocalizations were recorded using all-occurrence sampling (Altmann, 1974; Lehner, 1996) from July 15, 2001 to November 26, 2001, and from January 10, 2003 to May 31, 2003. Continuous audio recording of all vocalizations was initiated whenever weather conditions permitted and subjects were within 15 meters. Data recorded for zzuss calls included Date and Time, Caller Identity, Anti-Predator Behavior, and Context. Anti-predator Behavior was defined as caller movement of one meter or more, or staring for more than 3 s that began within 3 s of vocalizing. Movement codes included mutually exclusive categories of “Movement Up,” “Movement Down,” and “Movement Horizontally” (versus “No Movement”). Staring codes included mutually exclusive categories of “Staring Up” and “Staring Down” (versus “No Directed Gaze”). Context included six mutually exclusive categories: “Aerial Disturbance,” “Agonism,” “Howl Vocalization” (by a conspecific), “Other

Lemur Species" (within 20 m), "Spontaneously During Rest," and "Terrestrial Disturbance."

Estimating calling rate

Zzuss call rate was estimated for the Marojejy Camp 2 group using all-occurrence counts during known time periods. Zzuss calls are emitted with a closed mouth and it is sometimes difficult for observers to determine individual callers when multiple animals are vocalizing. However, all-occurrence counting was deemed to include scoring of virtually every zzuss. When the group was not traveling and remained in the same location for more than five min., all vocalizations heard were tabulated and classified into one of the ten main call types that comprise the silky sifaka vocal repertoire (Patel, 2009). The total durations of these rest periods were also recorded. The call rate of the group was then determined by dividing the numbers of calls by the durations of the respective sampling periods involved. While labor intensive, this method has successfully been used to estimate call rates in other primates, such as gorillas (Stewart and Harcourt, 1994). Call-rate estimation was conducted over 15 months (July 15, 2001 to November 26, 2001 and July 21, 2002 to May 31, 2003).

Call selection

Vocalizations were digitized using a sampling rate of 44.1 kHz with 16-bit accuracy. To improve frequency resolution in Fourier analysis, calls were subsequently downsampled to 22.05 kHz. Analyses were conducted using the ESPS/waves+ 5.3 "xwaves" package (Entropic Research, Washington, DC) running on an SGI O2 workstation (Silicon Graphics Incorporated, Mountain View, CA). Waveforms and spectrograms were first inspected to identify zzuss bouts that did not coincide with noticeable background noise (e.g., river noise, bird song). A bout was defined as a series of one or more consecutive zzuss calls uttered by a single individual, preceded and followed by 30 s or more during which no zzuss vocalizations were emitted by that caller. Approximately seven bouts were excluded because of high background noise levels. Seventy-nine zzuss bouts comprised of 160 individual calls were selected for analysis, representing five adult males and four adult females from three different social groups (see Table 3.1). A similar number of bouts were analyzed for males (n = 42) and females (n = 37), with a total of 80 calls for each sex. Although the final sample of calls was not perfectly balanced across individuals, we chose not to risk losing statistical power by reducing the already moderate sample size any further. Therefore, at the risk of compromising independence, the entire final sample of calls was analyzed. All calls were preprocessed to remove DC offset, filter out 60-Hz energy, and rescale the sound to the full, 16-bit available amplitude range (Owren and Bachorowski, 2007).

Acoustic Analysis

Nineteen continuous acoustic measures were used, spanning temporal, amplitude, and frequency-spectrum features of the vocalizations (see Table 3.2 for definitions of all variables). Temporal aspects of zzuss calls were examined by determining the absolute duration of each call (Call-Dur), mean interval between calls within the same bout (Inter-Call), and the interval from the end of a call and the lip-smack that often followed (LS-Latency). The amplitude of each call was estimated as a signal-to-noise ratio (SNR) calculated as the root-mean-square (RMS) amplitude of the call in dB minus the RMS amplitude of a representative, adjacent segment of background noise. SNR was subject to influence by the vocalizer’s distance from and orientation to the microphone, as well as by variation in background noise. However, such effects were present across the entire sample of calls, with little reason to suspect systematic error due to either factor. Preliminary analyses suggested that many zzuss calls exhibit an initial and ending lower-frequency F_0 contour that jumps to and from a rapid, frequency-modulated middle component (see Figure 3.1c). This kind of frequency jump is an abrupt, discontinuous F_0 change and is considered a nonlinear phenomenon (Brown *et al.*, 2003; Riede *et al.*, 1997; Riede et al., 2004; Wilden *et al.*, 1998). All calls were scored in a one-zero fashion for the occurrence of this nonlinear event.

Frequency-spectrum measurements were made for each call by computing a single spectral slice midway through the sound. Each slice was characterized by superimposing a twelve-coefficient, autocorrelation-based linear predictive coding (LPC) function (0.023-s Hanning window) on a 512-point FFT spectrum (0.023-s Hanning window) over the same segment (Owren and Bernacki, 1998). Frequency and amplitude values were extracted from the LPC envelope through cursor-based measurement. Variables included first and second LPC peaks (Peak 1 and Peak 2), overall slope of the LPC spectrum (Spectral-Tilt), and mean, standard deviation, skewness, and kurtosis of the Fourier spectrum (Spectral-Mean, Spectral-StDev, Spectral-Skew, Spectral-Kurtosis). The latter were computed as the first four moments of the normalized power spectrum, examined as a statistical distribution (Forrest *et al.*, 1988). The number of harmonics present was determined through visual inspection of narrow-band, fast-Fourier-transform-based spectrograms (22.05-kHz sampling rate, 512-point Hanning window) of all calls. Number of harmonics was recorded as an integer value between zero and ten. Not all calls were harmonically structured, but those that were never exceeded ten evident harmonics.

Procedures used to determine F_0 closely resemble those described in Owren and Casale (1994) and Bachorowski *et al.* (2001). Calls were first downsampled to

Table 3.2 The 19 variables used in acoustic analysis.

Acoustic Measure	Definition
Amplitude	RMS amplitude (dB)
Call-Dur	Duration of a zzuss call (s)
F_0-Mean	Mean rate of vocal-fold vibration (Hz)
F_0-StDev	Standard deviation of the F_0 (Hz)
F_0-Min	Minimum value of the F_0 contour (Hz)
F_0-Max	Maximum value of the F_0 (Hz)
F_0-Range	Difference between F_0-Max and F_0-Min (Hz)
F_0-Rate	F_0-Range divided by duration of F_0 (Hz/s)
Harmonic-Num	Number of visible harmonics
Inter-Call	Mean interval between calls within a bout (s)
LS-Latency	Interval between a call and a subsequent lip-smack (s)
Peak 1	Frequency of the first LPC peak (Hz)
Peak 2	Frequency of the second LPC peak (Hz)
Signal-to-Noise Ratio (SNR)	Difference between the RMS amplitude of a call and adjacent background noise (dB)
Spectral-Mean	Mean of the normalized frequency spectrum (Hz)
Spectral-StDev	Standard deviation of the normalized spectrum
Spectral-Skew	Relative symmetry of the normalized spectrum
Spectral-Kurtosis	Relative peakedness of the normalized spectrum
Spectral-Tilt	Overall slope of the LPC function

11.025 kHz to improve frequency resolution and inspected in narrow-band spectrographic form. When possible, the ESPS/waves+ pitch-tracking routine was used to extract an F_0 contour for each sound, verifying algorithm performance by overlaying the contour on its corresponding spectrogram. However, this approach was frequently supplemented by manually enclosing the visible F_0 contour using a cursor-box. The contour was then extracted as a series of maximum-amplitude points falling within that box, with automatic calculation of the mean (F_0-Mean), standard deviation (F_0-StDev), maximum (F_0-Max), minimum (F_0-Min), range (F_0-Range), and rate of change (F_0-Rate) across the call.

Statistical analysis

Statistical analyses were conducted using NCSS 2004 (Jerry Hintze, Kaysville, UT) and SPSS 13.0 (SPSS Inc., Chicago, IL). Nonparametric statistics were used when dependent variables were not normally distributed according to Shapiro-Wilk and Anderson-Darling tests. Multinomial, discriminant-function analyses were used in call classification by context, sex, and individual caller (e.g., Fischer *et al.*, 2002; Gouzoules and Gouzoules, 2000; Macedonia, 1986; Patel and Owren, 2007). Here, principal components analysis was applied before discrimination function analysis order to reduce the original, inter-correlated variables to a smaller set of orthogonal factors robust to multicollinearity and singularity (Mitani and Gros-Louis, 1995; Mundry and Sommer, 2007; Notman and Rendall, 2005).

RESULTS

Zzuss acoustics

General description

Descriptive statistics for the acoustic features of zzuss vocalizations are shown in Table 3.3. On average, zzuss bouts contained two, 220-ms calls spaced 2.4 s apart. Individual calls were often accompanied by a rapid head jerk, and though emitted with the mouth closed, the vocalizations were often high in amplitude. The mean SNR value associated with these calls was almost 13 dB, even though recorded in a noisy environment. SNR values ranged up to a maximum of 66 dB. LPC analysis revealed two consistent frequency peaks, the first at 2670 Hz ± 860 appeared to be a formant, and was generally located near the upper frequency limit of the harmonic region. The second peak, found at 6130 Hz ± 1310, was more variable. The mean Spectral-Mean was just above 2400 Hz. As illustrated in Figure 3.1, the vocalizations include a broadband “noisy” component bracketing a middle, tonal section. These noisy regions contributed to an overall spectral slope that was virtually flat. The tonal region of the calls exhibited a mean F_0-Mean of 1229 Hz ± 620, a mean of 3.7 ± 1.7 harmonics, and a mean F_0-Range of 1927 Hz ± 1323. Frequency jumps associated with a strongly frequency-modulated middle section occurred in 51.3% of zzuss calls, with the frequency modulation exhibiting a high mean F_0-Rate of 8970 Hz/s ± 6532. In the remaining 49.7% of the calls, the original F_0-contour continued uninterrupted without dramatic frequency modulation. About 80% of zzuss bouts were followed within 1 s by an audible lip-smack.

Table 3.3 Descriptive acoustics of zzuss vocalizations, based on 79 bouts and 160 total calls.

Acoustic Measure	*M*	s.d.	Min	Max	Range	CV
Amplitude	73.6	2.57	64.7	79.3	14.9	0.04
Call-Dur	0.22	0.04	0.10	0.34	0.23	0.18
F_0-Mean	1229.1	619.5	327.8	2704.4	2376.6	0.50
F_0-StDev	44.7	36.6	2.84	211.7	208.8	0.82
F_0-Min	390.6	147.9	168.0	904.4	736.4	0.38
F_0-Max	2317.2	1359.5	390.6	8354.9	7964.3	0.59
F_0-Range	1926.6	1322.8	86.13	8053.4	7967.3	0.69
F_0-Rate	8970.0	6532.1	395.6	37031.5	36635.9	0.73
Harmonic-Num	3.71	1.69	0.0	10.0	10.0	0.46
Inter-Call	2.37	1.13	0.22	5.8	5.58	0.48
LS-Latency	0.54	0.14	0.23	0.97	0.74	0.25
Peak 1	2671.6	855.9	1580.2	6704.6	5124.4	0.32
Peak 2	6127.4	1306.4	3670	9400.3	5730.3	0.21
SNR	13.4	11.7	-7.77	65.77	73.53	0.87
Spectral-Mean	2432.8	850.1	581.54	4155.2	3573.7	0.35
Spectral-StDev	1754.8	425.3	898.5	3090.9	2192.5	0.24
Spectral-Kurtosis	10.8	9.34	-0.42	48.41	48.8	0.87
Spectral-Skew	2.33	0.99	0.56	6.15	5.59	0.42
Spectral-Tilt	.015	.076	-0.44	0.20	0.64	5.20

Influence of caller sex

Results of nonparametric, univariate testing for sex differences in zzuss acoustics are displayed in Table 3.4. Mann-Whitney *U* tests revealed sex differences in 11 of the 19 acoustic measures. Two-sample randomization tests, based on 100,000 Monte Carlo samples (Manly, 1997), were also significant for the same subset of measures (all *p*s < .015). Female zzuss calls exhibited higher F_0-Mean, F_0-Range, and SNR values, longer LS-Latency, and slightly more negative Spectral-Tilt than male versions. F_0-Mean, which showed the highest effect size (i.e., 1.1), averaged 1526 Hz ± 533 for females and 932 Hz ± 557 for males. A two-proportion test with continuity correction confirmed that many more female calls (72.5%) contained frequency jumps and a strongly modulated region than did male calls (30.0%), $\chi^2 = 27.2$, $p < .001$.

Principal-components analysis conducted prior to discriminant-function classification revealed four factors with eigenvalues greater than 1.0, which together explained 62.7% of the total variance in the original 19 acoustical measurements (see Table 3.5). Factor 1 accounted for the most variance (33.6%), and was most strongly associated with F_0-Mean, F_0-Max, F_0-Range, and F_0-Rate. Factor 2 accounted for 14.3% of the variance and was most strongly associated with Spectral-Tilt and Spectral-Mean. Factor 3 accounted for only 8.2% of the variance and was most strongly associated with Amplitude, LS-Latency, and Inter-Call. Factor 4 accounted for 6.6% of the variance and was most strongly associated with Peak 1 and Peak 2.

Discriminant-function classification of caller sex was based on principal-component scores, and was initially conducted using approximately 70% of calls, randomly selected from the total set of 160. The remaining 30% of calls were used as a validation sample. A final test was conducted on the whole sample, using the jackknife (“leave one out”) cross-validation technique to estimate percentage correct classification. The initial model classified 71.3% of the animals by sex, which was statistically above chance, and classification success was similar using the jackknife technique at 69.4% (Wilks' lambda = .738, $\chi^2 = 47.3$, d.f. = 4, $p < .001$). Calculating percentage error reduction helps clarify discriminant-function performance in taking chance rates into account (Bachorowski and Owren, 1999), which here was 50%. Percentage-correct in the final validation test thus corresponds to a 38.8% reduction in the expected error rate. The canonical structure coefficients showed correlations between principal-component factors and the discriminant function to be .80 for Factor 1, .41 for Factor 2, -.04 for Factor 3, and .01 for Factor 4. In other words, the F_0-related measures captured by Factor 1 were clearly the most influential in classifying the acoustical measures according to vocalizer sex.

Influence of individual caller

Results of nonparametric, univariate testing of individual differences in acoustic structure are displayed in Table 3.6. Kruskal-Wallis one-way, analysis of variance by ranks revealed significant individual variation in all acoustic measures (*p*s $< .05$). Dunn's test was used post-hoc in order to examine more precisely which acoustic features differed between particular individuals. This statistic is a distribution-free multiple-comparison test that conservatively adjusts alpha level using Bonferroni correction according to the number of comparisons (Glantz, 2002). All acoustic measures differed significantly between some pairs of individuals, with the

Table 3.4 Statistically significant Mann-Whitney U tests for sex differences in zzuss acoustics.

Acoustic Measure	Males (M/s.d.)	Females (M/s.d.)	Direction of Difference	Z	Effect Size (d)	$P <$
Amplitude	73.1/2.9	74.1/2.1	F > M	2.78	.39	.005
F_0-Mean	931.9/556.7	1526.2/532.6	F > M	5.74	1.1	.001
F_0-StDev	35.3/33.5	54.0/37.3	F > M	4.86	.53	.001
F_0-Min	360.8/136.5	420.4/153.7	F > M	3.61	.41	.001
F_0-Max	1745.0/981.6	2889.3/1446.8	F > M	5.49	.93	.001
F_0-Range	1384.2/958.1	2469.0/1417.0	F > M	5.47	.90	.001
F_0-Rate	6223.8/4314.2	11716.2/7210.5	F > M	5.28	.92	.001
LS-Latency	0.51/0.11	0.58/0.15	F > M	2.63	.53	.009
Peak 1	2629.8/530.8	2713.4/1090.5	F > M	2.59	.10	.01
SNR	10.6/4.9	16.2/15.4	F > M	3.11	.49	.002
Spectral-Tilt	0.024/0.082	0.005/0.067	M > F	2.90	.26	.004

Table 3.5 Critical acoustics of zzuss calls identified through principal components analysis.

Factor	Eigenvalue	% Variance Explained	Acoustic Dimension	Associated Acoustic Features (item weights)
1	6.38	33.6	F_0 contour	F_0-Mean (.85), F_0-Max (.94), F_0-Range (.96), F_0-Rate (.95)
2	2.71	14.3	Spectral moments	Spectral-Tilt (.66), Spectral-Mean (.68), Spectral-StDev (.89)
3	1.56	8.23	Duration-amplitude	Call-Dur (.03), SNR (.1), Amplitude (.5), F_0-StDev (.57), F_0-Min (.83), LS-Latency (.49), Inter-Call (.40)
4	1.26	6.64	LPC Peak	Peak 1 (.70), Peak 2 (.80)

exception of Call-Dur. F_0 measures and Spectral-Mean differed most between pairs of individuals. The occurrence of frequency jumps and associated, strong frequency modulation also varied significantly between individuals ($\chi^2 = 105.9$, df = 8, $p < .001$). The percentage of calls containing frequency jumps averaged 43.2% per individual, but ranged from 0% (for three individuals) to 92.3%.

Discriminant-function classification by individual caller was conducted based on the same statistical procedures described earlier. To ensure that these analyses did not confound sex and individual, separate sets of discriminant function analyses for individual were conducted for the five males and four females. For males, the initial model classified a statistically significant 76.3% of the calls, and classification success using the jackknife validation technique was similar at 72.5% (Wilks' lambda = .085, $\chi^2 = 183.475$, d.f. = 16, $p < .001$). Chance-level assignment was 20% for these five dependent variables, meaning the final validation test produced 65.6% error reduction. The canonical structure coefficients showed correlations between principal-component factors and the discriminant function to be .76 for Factor 1, .34 for Factor 2, .23 for

Table 3.6 Statistically significant Kruskal-Wallis tests for individual differences in zzuss acoustics.

Acoustic Measure	Chi-Square Value	Pairs of Individuals Different by Dunn's Test
Amplitude	26.2***	2
Call-Dur	19.6*	0
F_0-Mean	117.9***	17
F_0-StDev	84.5***	9
F_0-Min	66.4***	11
F_0-Max	117.9***	20
F_0-Range	114.3***	20
F_0-Rate	112.9***	18
Harmonic-Num	52.7***	10
Inter-Call	79.1***	11
LS-Latency	38.9***	4
Peak 1	66.3***	9
Peak 2	58.1***	11
SNR	50.1***	10
Spectral-Mean	80.1***	15
Spectral-StDev	24.5**	2
Spectral-Kurtosis	49.8***	7
Spectral-Skew	43.8***	8
Spectral-Tilt	34.2***	4

*$p < .05$, **$p < .01$, ***$p < .001$

Factor 3, and -.13 for Factor 4. Thus, the F_0-related measures captured by Factor 1 were clearly the most influential in classifying the acoustical measures according to individual males. For females, the initial model classified a statistically significant 63.8% of the calls, and classification success was similar using the jackknife validation technique at 58.8% (Wilks' lambda = .188, χ^2 = 125.37, d.f. = 12, $p < .001$). Chance assignment with four dependent variables is 25%, meaning an error reduction of 45.1% in the final validation test. The canonical structure coefficients showed correlations between principal-component factors and the discriminant function to be .54 for Factor 1, .28 for Factor 2, .28 for Factor 3, and -.69 for Factor 4. The spectral peaks captured by Factor 4 were therefore the most important in classifying the vocalizations by individual female caller, while the F_0-related measures captured by Factor 1 were influential as well.

Influence of context

Each of the 160 zzuss calls was assigned to one of the six contexts during recording. A Kruskal-Wallis one-way analysis of variance showed that SNR was the only acoustic measure that differed between these contexts (χ^2 =16.1, d.f. = 5, $p < .007$). The highest mean SNRs were associated with Terrestrial Disturbance (*M* = 19.2 dB) and Agonism (*M* = 19.1 dB). The lowest mean SNRs were associated with Spontaneously During Rest (*M* = 10.2 dB) and Other Lemur Species Within 20 m (*M* = 11.1 dB). To control for the influence of individual SNR differences on context, an additional Kruskal-Wallis test was run using only mean SNR values for each individual in each context. No effect of context was apparent after controlling for caller identity (χ^2 = 6.73, d.f. = 5, $p > .23$). A cross-validated, multinomial discriminant-function analysis was then conducted to determine the extent to which the principal component scores predicted call context. No overall effect was found for the first four discriminant functions (Wilks' lambda = .886, χ^2 = 18.6, d.f. = 20, $p >$ .55) and all eigenvalues were less than 0.1. The final model classified only 20.6% of cases correctly, against a chance rate of 16.7%

Zzuss usage and associated behavior

General occurrence

Zzuss calls occurred mainly in the Howl Vocalization (39.4%), Spontaneously During Rest (21.3%), and Terrestrial Disturbance (16.9%) contexts. To a lesser extent, zzuss calls were emitted in the Other Lemur Species (13.1%), Agonism (7.5%), and Aerial Disturbance (1.9%) contexts. A chi-square, goodness-of-fit test revealed that observed frequencies were not equivalent across the six contexts (χ^2 = 81.8, df = 5, $p < .001$). However, it is possible that some of the "spontaneously" emitted zzuss calls were actually responses to unobserved terrestrial disturbance. No difference was found in the relative proportions of zzuss emitted by males and females by context (χ^2 = 3.5, d.f. = 5, $p > .62$).

Overall, daily, and seasonal variation in call rate

Analyses confirmed zzuss calls as one of the most common silky sifaka sounds, making up 29.9% (14,952 of 50,036) of all vocalizations scored during all-occurrence counts. A total of 14,952 zzuss calls occurred during 1,676 resting and feeding periods over 1,530 total observation hours. On average, the group produced 10.5 ± 45.5 of these vocalizations per hour. The overall rate was extremely variable, however, likely due to the antiphonal nature of zzuss calls and their occurrence across multiple contexts. The highest rate noted was 481 zzuss calls during a 40-minute period, while these vocalizations did not occur at all in 54.9% (939 of 1709) of sampling periods.

Seasonal effects on calling were examined based on reproductive and weather cycles established for eastern sifakas living in northeastern Madagascar (Pochron *et al.*, 2005; Vasey, 2006). Zzuss rate was found not to vary significantly between gestation (February to April), birth (May to July), lactation (August to October), and mating (November to January) reproductive seasons (Kruskal-Wallis, $\chi^2 = 4.0$, d.f. = 3, $p > .20$). Rates also did not vary significantly between hot-rainy (January to March), transitional-cold (April to May), cold-rainy (June to August), and hot-dry (September to December) weather seasons (Kruskal-Wallis, $\chi^2 = 4.6$, d.f. = 3, $p > .20$). However, zzuss rate did vary on a circadian cycle (Kruskal-Wallis, $\chi^2 = 48.9$, d.f. = 3, $p < .001$). As displayed in Fig. 2.2, call rate was highest early in the morning soon after the animals awoke (5:00 to 7:59 AM). Rates were also high during late afternoon, around the time the group began traveling toward and settling into their sleeping trees (2:00 to 4:59 PM). The lowest zzuss rates occurred during late morning (8:00 to 10:59 AM) and early afternoon (11:00 AM to 1:59 PM), respectively.

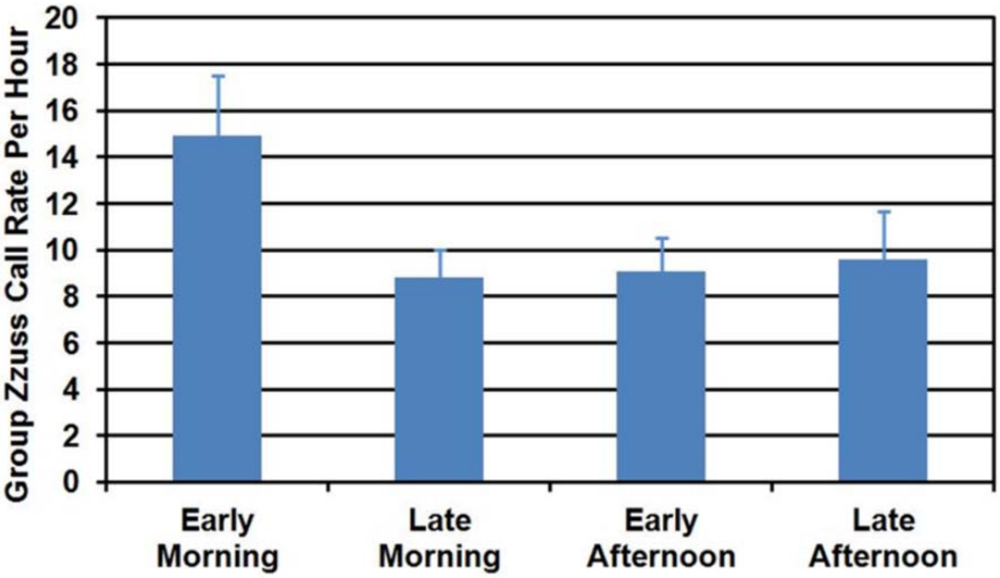


Figure 3.2 Zzuss call rates by time of day for the Camp 2 group.

Anti-predator behavior

Caller Movement could be coded for 92.5% (148 of 160) of the audio-recorded vocalizations, with the caller being partially out of view for the remaining instances. A chi-square goodness-of-fit test revealed that observed rates were not equivalent between the four Caller Movement categories ($\chi^2 = 108.4$, d.f. = 3, $p < .001$). In the majority of cases (56.9%), callers did not move either while or after vocalizing. Movement Upward (14.4%) and Horizontally (15.0%) occurred about equally, with Movement Downward (6.8%) occurring least. Caller gaze data were also available for these 148 calls, and observed rates were also significantly different between the three categories coded for this variable ($\chi^2 = 35.9$, d.f. = 2, $p < .001$). No Directed Gaze was the most common outcome (54.7%). However, a two-proportion test with continuity correction showed that Staring Downward (28.1%) during zzuss calling did occur significantly more often than Staring Upward (13.8%), $\chi^2 = 9.14$, $p < .003$.

DISCUSSION

Structure and function in zzuss acoustics

General features

Analyses revealed that zzuss calls are accompanied by a rapid head jerk, and most often emitted in bouts of two that are followed by an audible lipsmack. On average, a given group produced more than 10 zzuss vocalizations per hour, although not in simultaneous choruses which often characterize their “aerial disturbance” roars. However, group members could emit these calls for sustained periods in some cases, including one instance of hundreds of zzuss vocalizations occurring over a period of about 40 min. Overall, the calls were most often produced in the early morning hours.

Zzuss calls are somewhat unusual in routinely showing broadband noise at the beginning and end, with a prominent, tonal mid-section. Aside from zzuss variants in other, related sifakas, this overall structure has not been documented in other lemurs (Macedonia and Stanger, 1994), and is not common in mammalian vocalizations generally (cf. Beeman, 1998). Mammals do routinely produce calls in which "nonlinear" vocal-fold vibration can create a mix of chaotic noise and tonality (Wilden *et al.*, 1998; Fitch *et al.*, 2002; Tokuda *et al.*, 2002). However, the noise in zzuss calls is relatively uniform and appears to reflect turbulent airflow rather than vibration-based, deterministic chaos—although these two kinds of noise can be difficult to distinguish (e.g., Tokuda *et al.*, 2002). The origins of the noise component of zzuss calls are thus as yet unknown. In contrast, the tonal component clearly reflects regular, well-synchronized vocal-fold vibration. Given the high amplitude, elevated mean frequency, and frequent extreme frequency modulation involved, this segment almost certainly entails substantial subglottal air pressure and vocal-fold tension (Fitch *et al.*, 2002; Riede *et al.*, 2007), which in turn likely reveals a high level of caller arousal (reviewed by Zimmermann *et al.*, in press). The frequency jumps and rapid frequency modulation are particularly dramatic, with pitch changes of almost 4 kHz up and down occurring over a period of less than 100 ms.

Frequency jumps have not previously been identified in lemur vocalizations, while being found in just over half of the zzuss calls analyzed here—although mainly among females. Although possibly widespread in primate vocalizations, frequency jumps have thus far been pointed out only in chimpanzees (Riede *et al.*, 2004) and in infant macaques (Riede *et al.*, 1997). While this phenomenon represents a bifurcation in vibration regimes and is thus associated with some instability in vocal-fold action, there was no evidence of other nonlinear phenomena. Some primate species possess specializations such as vocal sacs (Hewitt *et al.*, 2002) and vocal membranes or vocal "lips" (Mergell *et al.*, 1999) that may contribute to such nonlinearities. It is unknown if *Propithecus* has such these specializations, although vocal membranes are found in ring-tailed lemurs (Schön Ybarra, 1995; Stark and Schneider, 1960) and could be implicated by the rapid and extreme degree of frequency modulation shown here.

Perception

Both the acoustic structure and behavioral circumstances of zzuss calling likely makes these sounds highly audible, salient, and localizable. For example, while audiograms are not available for *Propithecus spp.*, frequency sensitivity data are available for ring-tailed lemurs and some sifaka-sized monkeys. Overall body size is important in such comparisons, as region of greatest auditory sensitivity in mammals is roughly inversely related to head (and body) size in (Masterton *et al.*, 1969). Ring-tailed lemurs are smaller than sifakas, with maximal sensitivity at 8 kHz (Heffner, 2004) and strong sensitivity between 5.7 and 16 kHz (Ramsier and Dominy, 2010). Silky sifakas would thus be expected to show greatest sensitivity at lower frequencies, which is consistent with finding that the somewhat larger blue monkey (*Cercopithecus mitis*) whose region of highest sensitivity lies between 1 and 16 kHz (Brown and Waser, 1984). The 2.4 kHz spectral mean of zzuss vocalizations likely makes these calls readily perceptible to silky sifakas. Furthermore, while ambient noise is often highest between 2 and 4 kHz in African rainforests, levels are lowest early in the morning (Waser and Brown, 1986), when zzuss calls are most common. Zzuss vocalizations are also generally produced by animals 6 to 25 m above the ground (E. R. Patel, pers. obs.), which significantly improves transmission range relative to calling from locations closer to the ground (Waser and Brown, 1984; Mitani and Stuht, 1998).

The high amplitudes, frequency jumps, and extreme frequency modulation of many zzuss calls likely makes these sounds highly attention-getting, and are well designed for interrupting a conspecific listener’s ongoing behavior and triggering autonomic changes consistent with response readiness (Owren and Rendall, 2001; Rendall et al., 2009). Broadband noisiness and frequency modulation are also both major contributors to localizability in mammals, with high-frequency spectral cues being particularly important for the vertical plane (Brown *et al.*, 1980; Brown *et al.*, 1982; Recanzone and Beckermann, 2004). Auditory localization is further facilitated when salient visual events are also produced when vocalizing (Heffner, 2004), such as the head jerk that accompanies zzuss calls.

Acoustic variation by sex

Acoustics and classification

Sex differences were found in the majority of acoustic measures, with the highest effect sizes observed for F_0-related features, followed by aspects of call amplitude. For example, F_0-Mean values were approximately 60% higher in females than in males, and their calls were also much more likely to exhibit frequency jumps (72.5%) and extreme frequency modulation than were male versions (30.0%). Sex differences also included female zzuss calls having higher amplitudes and SNR values, long latencies to lipsmack, slightly higher first spectral peaks, and slightly less noisy calls (slightly lower Spectral-Tilt). There were no sex differences in call duration, which has also been the case for crowned lemur vocalizations (Gamba and Giacoma, 2007).

Discriminant-function classification was just over 71% correct by sex, statistically higher than expected by chance but only an intermediate degree of error reduction at less than 40%. Classification by sex was thus not as accurate as in a number of other primate studies (*Leontopithecus rosalia*: Benz *et al.*, 1990; *Eulemur coronatus*: Gamba and Giacoma, 2007; *Indri indri*: Giacoma *et al.*, 2010; *Pan troglodytes*: Mitani and Gros Louis, 1995; *Callithrix kuhlii*: Smith *et al.*, 2009). On the one hand, any evidence of sex differences is of interest given that silky sifakas are considered monomorphic (Kappeler, 1990, 1991; Lawler *et al.*, 2005). On the other hand, the overall similarity across sexes suggests that differences in vocal acoustics will likely not occur primarily based on anatomical features correlated with overall body size, such as vocal-tract length (although contrast recent reviews by Patterson *et al.*, 2008 and Rendall *et al.*, 2007). The frequency difference found in the first spectral peak of male versus female calls does hint at some divergence in body size, but the discrepancy was quite small.

The origin of sex differences

More pronounced differences are to be expected in call characteristics with greater "lability," such as call duration and F_0 features. For example, zzuss call duration is probably not importantly influenced by vocalizer body-size, but could reflect underlying neural "programming," vocal effort, or other factors. While no sex differences occurred in zzuss duration, other monomorphic species such as indri (Giacoma *et al.*, 2011) and sportive lemurs (Rasoloharijaona *et al.*, 2006) do show such differences. F_0 characteristics can also be considered labile, even in an evolutionary context. For example, larynx size is relatively unconstrained by body size, while overall larynx morphology is considered rather uniform among primates (Ankel-Simons, 2007), at least in the absence of additional specialization. F_0 characteristics are largely proportional to vocal-fold length and thickness in nonhuman primates and humans (Rendall *et al.*, 2005; Titze, 1989), meaning that selection pressure can act relatively freely in modifying larynx dimensions, vocal-fold size, and associated F_0 characteristics.

A reasonable conclusion is therefore that, while similar in overall size, silky sifaka males and females probably do differ in larynx and vocal-fold dimensions.

Some new world monkeys also exhibit little or no sexual dimorphism in weight, skeletal features, or pelage color/pattern, yet show sex differences in vocalization structure and laryngeal sac size (Hershkovitz, 1977). Examples include “trills” and “long calls” produced by monomorphic golden-lion tamarins (*Leontopithecus rosalia*: Benz *et al.*, 1990), as well as the “phee” calls of Wied’s black-tufted-ear marmosets (*Callithrix kuhlii*: Smith *et al.*, 2009) and common marmosets (*Callithrix jacchus*: Norcross and Newman, 1993). Developmentally, sex differences in laryngeal morphology have been traced to targeted gonadal steroid hormone effects occurring during reproductive maturation (e.g., Abitbol *et al*., 1999; Aufdemorte *et al*., 1983; Beckford *et al*., 1985). As call types within a primate’s vocal repertoire can vary in the extent to which they exhibit sex differences, other silky sifaka vocalizations may show greater or smaller effects.

Acoustic variation by individual

Acoustics and classification

Differences between individual callers were found in all acoustic measures. Call duration and amplitude contributed relatively little in either sex, while F_0-related measures were important in both cases. Spectral peaks also showed statistically significant variability, although more so in females than in males. Discriminant-function analysis successfully classified 73% of calls from the five males and 59% from the four females, with corresponding error-reduction rates of 66% and 45% respectively. Interpreting these outcomes is complicated by the small sample sizes involved, but taking them at face value implies that silky sifaka males may show more variation in body-size and vocal-production anatomy than females. The acoustics of sooty mangabey (*Cercocebus torquatus atys*) grunts have also been found to be more individually distinctive in males than in females—which is at least partially attributable to possibly greater male body-size variation (Range and Fischer, 2004).

The origin of individual differences

In general, vocal-tract filtering has been identified as an anatomically grounded feature that can be particularly well suited for creating individual distinctiveness in spectrally dense primate calls (Owren *et al.*, 1997; Rendall *et al.*, 1998). For instance, such effects have been observed in broadband, noisy lemur calls, including grunts in red-bellied lemurs (Gamba *et al.*, 2011) and snorts in crowned lemurs (Gamba and Giacoma, 2007). In other primates, examples include a variety of calls, incluing tonal "coos" and noisy grunts in macaques (Rendall *et al.*, 1998), tonal grunts in chacma baboons (Fischer *et al.*, 2002; Owren *et al.*, 1997; Rendall *et al.*, 2009), and noisy grunts in sooty mangabeys (Range and Fischer, 2004). The relative stability of vocal-tract filtering effects can be contrasted with the lability of features such as temporal measures and F_0-related acoustics, which may therefore be less likely to contribute significantly to individual distinctiveness (Gamba *et al.*, 2011).

Yet, it is not clear that such vocal-tract filtering is a critical factor in individual distinctiveness in zzuss calls. For example, the two frequency peaks measured here likely did not directly reflect vocal-tract filtering. They were also more important in females—who were less well classified by individual than were males. Instead, the current findings point specifically to F_0-related features as being the most important, an outcome that has also been reported for tonal, frequency-modulated calls in both gray mouse lemurs (Leliveld *et al.*, 2011) and sportive lemurs (Rasoloharijaona *et al.*, 2006). Further, both F_0 modulation and filtering-related spectral peaks contribute significantly to individual distinctiveness in ring-tailed lemur contact vocalizations (Macedonia, 1986).

Zzuss function

Contexts of zzuss calling

Overall, there was little evidence of context specificity for zzuss calls. Acoustically, only SNR appeared to differ among production contexts, but the statistical effect disappeared after controlling for individual variation. The highest values were evident during terrestrial disturbance and agonistic contexts, but this trend was more likely indicative of generally higher caller arousal in these circumstances (Zimmermann *et al.*, in press) rather than context-specific acoustic variation per se. Zzuss calls were also emitted in a variety of contexts, notably during terrestrial disturbance, spontaneously while resting, and in response to howls by distant group members. The calls were also sometimes, but less frequently emitted when other lemur species were present, during agonism within the group, and in some cases of aerial disturbance. Although it is possible that some of the "spontaneous" zzuss calls were emitted to terrestrial disturbances that the humans could not see, there would have been little effect on the overall heterogeneity of usage.

Zzuss calling also showed little seasonal variation, as might have been expected if the calls were not predominantly predator-related, in that fossa tend to hunt sifakas more during the dry season than at other times (Dollar *et al.*, 2007; Irwin *et al.*, 2009; Wright, 1998). The calls were produced at higher rates when sifakas were first waking up in the morning, which may be when fossa are hunting sifakas most actively (Wright, 1998). However, elevated rates at that time of day may also reflect increased predator-related vigilance rather than predator-specific usage. While callers did stare downward more than upward, they seldom moved upward. Furthermore, that most common outcome was that zzuss calls were not associated with any particular gaze direction.

Implications for zzuss function

The key criteria for functionally referential vocalizations are high production specificity and high perceptual specificity. Finding low production specificity for the zzuss call here is consistent with previous research in Verreaux's and Milne-Edwards' sifakas in which playbacks of fossa vocalizations to Milne-Edwards' and Verreaux's sifakas did not elicit significant change in general activity, vigilance, height in canopy, or escape behavior (Fichtel and Kappeler, 2002; Karpanty and Wright, 2007). Neither species uttered their hypothesized terrestrial predator vocalizations more after the playbacks than in a control period, although Verreaux's sifakas did look downward more than upward after hearing the sounds. As in the current study, the researchers found that the "alarm" vocalization was given across a number of contexts associated with high caller arousal (Fichtel and Kappeler, 2002). Perceptual specificity was not tested in the current work, but evidence from other sifaka species suggests it would also be low. For example, playing back "growl" calls that Verreaux sifakas calls emit to terrestrial predators has not been found to evoke clear escape responses—although subjects did look downward more than upward when producing the calls (Fichtel and Kappeler, 2002).

Overall, silky sifaka zzuss calls, cannot be considered functionally referential signals. Instead, like Verreaux's sifaka growl and fak calls, they are likely best interpreted as having both anti-predator and group-coordination functions. On the one hand, the calls do occur in the context of both terrestrial and (occasionally) aerial disturbance—including when human researchers first start to follow these animals from the ground (E. R. Patel, personal observation). On the other hand, every howl vocalization heard from a spatially separated or lost group member elicits immediate zzuss calls from group members (E. R. Patel, personal observation). This result strongly supports a group-coordination function.

The findings furthermore reinforce previous evidence that anti-predator calls used against terrestrial species are less likely to be narrowly used or to evoke specific escape responses than are aerial predator vocalizations. While there is no doubt that zzuss calls are triggered by the threat of predation, it may not be possible for listeners to respond effectively exclusively based on hearing the call by itself. As predators, fossa exhibit both terrestrial and arboreal habits, thereby decreasing the chances that a particular or "standardized" escape response will work across most predation attempts. One conclusion, therefore, is that there has been little selection pressure on silky sifakas for more differentiated calling, at least as far as terrestrial predation is concerned. A second, broader conclusion is that the lack of specificity shown by these zzuss calls underscores that even threat-related primate vocalizations need not be context-specific and word-like to be effective communication signals. In other words, rather than simply viewing such calls though the lens of language and symbolic meaning, they should be understood on the own terms. In this case, the calls may be best interpreted as multi-purpose sounds that have mainly been selected for high salience.

The role of acoustic variation by sex and individual

The multi-function nature of zzuss vocalizations may be consistent with the pattern of sex- and identity-related acoustic variation found. Specifically, classification results were stronger by individual than by sex, which must be considered at least somewhat surprising even in this generally monomorphic species. However, while listeners need not necessarily be able to distinguish either the sex or identity of a caller to effectively respond to alarm calls, effective group-cohesion function does require individual distinctiveness. For example, being separated from the group for even a few days can prove fatal, particularly in juvenile silky sifakas

(E.R. Patel, personal observation). Speculatively then, while there may not have been significant selection for individuality in zzuss calls stemming from their use as anti-predator vocalizations, such cuing is important in allowing a lost animal to recognize and home in on zzuss calls heard antiphonally from its own particular group (see also Gamba *et al.*, 2011; Macedonia, 1986; Rasoloharijaona *et al.*, 2006).

CONCLUSIONS

A 15-month study of the loud zzuss vocalization that characterizes the silky sifaka lemur—one of the world's rarest mammals—shows this call to typically include sections of turbulent noise, frequency jumps, and rapid, as well as rather extreme, frequency modulation. Long-term data further shows that the zzuss usage and acoustic variation were consistent with having a combined function as a terrestrial-disturbance and group-coordination call. These results are consistent with outcomes from a number of other lemur and monkey species, but inconsistent with at least two aspects of some current research on primate communication.

First, the lack of specificity in producing and responding to zzuss vocalizations underscores that signals need not have reference-like meanings in order to be functional. Rather, zzuss calls are perhaps most strongly marked by having relatively extreme acoustic features that make them well suited to a more general, attention-getting and alerting function that is useful across a variety of contexts. One can also surmise that this kind of generalized function likely represents an evolutionarily older and more common condition for primate vocalizations. Given the greater complexity involved, reference-like function probably emerges more rarely—for instance in circumstances of particularly well-differentiated threats and response strategies.

Second, sex- and identity-related variation in acoustic structure were found in spite of this species' generally monomorphic anatomy and lack of pronounced vocal-tract filtering effects. In other words, vocal dimorphism can evidently occur even in the absence of other, common sexually selected primate traits, and individual distinctiveness can be mediated by acoustic cues that some have argued to be too labile to provide stable identity cuing. Overall, selection on the zzuss call appears to have acted more strongly on its acoustic characteristics than the way it is used.

ACKNOWLEDGMENTS

We thank the government of the Democratic Republic of Madagascar for permission to conduct research in Marojejy National Park and Anjanaharibe-Sud Special Reserve. Particular thanks are due to Madagascar's Ad Hoc Committee for Fauna and Flora and Organizational Committee for Environmental Research (CAFF/CORE), Ministry of the Environment and Water and Forests, and National Association for the Management of Protected Areas (ANGAP) for granting permits. For logistical support, we thank P. Wright, B. Andriamihaja, ANGAP Andapa Director J. H. Bakarizafy, the Malagasy Institute for the Conservation of Tropical Environments (MICET), and the Institute for the Conservation of Tropical Environments (ICTE). For assistance in habituation and counting zzuss calls in the field, thanks are due to S. Benson-Amram, S. Rosenbaum, and C. Santorelli. Thanks to H. Parathian for data entry assistance and to J. Anderson for processing vocalizations. Numerous local residents, particularly Nestor Jean Randrianasy and Rabary Desire, provided invaluable assistance in tracking silky sifakas. We gratefully acknowledge that funding for this project was provided to Erik R. Patel by the Margot Marsh Biodiversity Foundation, a John Wallace Dallenbach Fellowship from Cornell University's Department of Psychology, Institute of African Studies, and Mario Einaudi Center for International Studies. Michael J. Owren was partly supported by NICHD P01 HD-060563 and the Research on Challenges in Acquisition of Language and Literacy Initiative at Georgia State University.

REFERENCES

Abitbol, J., Abitbol, P., and Abitbol, B. (**1999**). Sex hormones and the female voice. J. Voice **13**, 424-446.

Altmann, J. (**1974**). Observational study of behavior: Sampling methods. Behav. 49, 227-265.

Ankel-Simons, F. (**2007**). *Primate Anatomy: An Introduction*, 3nd ed. (Elsevier, San Diego).

Aufdemorte, T. B., Sheridan, P. J., and Holt, G. R. (**1983**). “Autoradiographic evidence of sex steroid receptors in laryngeal tissues of the baboon,” Laryngoscope **93**, 1607-1611.

Bachorowski, J. A., Smoski, M. J., and Owren, M. J. (**2001**). “The acoustic features of human laughter,” J. Acoust. Soc. Amer. **110**, 1581-1597.

Beckford, N. S., Rood, S. R., and Schaid, D. (**1985**). “Androgen stimulation and laryngeal development,” Annals Otol. Rhin. Laryng. **94**, 634-640.

Beeman, K. (**1998**). “Digital signal analysis, editing and synthesis,” In *Animal Acoustic Communication: Sound Analysis and Research,* edited by S. L. Hopp, M. J. Owren, and C. S. Evans (Springer-Verlag, Berlin), pp. 59-104.

Benz, J. J., French, J. A., and Leger, D. W. (**1990**). “Sex differences in vocal structure in a callitrichid primate, *Leontopithecus rosalia*,” Amer. J. Primatol. **21**, 257-264.

Blumstein, D. T., Davitian, R., and Kaye, P. D. (**2010**). “Do films contain nonlinear analogues to influence emotion?” Biol. Letters **6**, 251-254.

Blumstein, D. T., and Recapet, C. (**2009**). “The sound of arousal: The addition of novel non-linearities increases responsiveness in marmot alarm calls,” Ethology **115**, 1074–1081.

Boinski, S., and Garber, P. A. (eds.) (**2000**). *On the Move: How and Why Animals Travel in Groups* (University of Chicago Press, Chicago).

Brown, C. H., Beecher, M. D., Moody, D. B., and Stebbins, W. C. (**1980**). “Localization of noise bands by Old World monkeys,” J. Acoust. Soc. Amer. **68**, 127-132.

Brown, C. H., Schessler, T., Moody, D., and Stebbins, W. (**1982**). “Vertical and horizontal sound localization in primates,” J. Acoust. Soc. Amer. **72**, 1804-1811.

Brown, C. H., and Waser, P. M. (**1984**). “Hearing and communication in blue monkeys (*Cercopithecus mitis*),” Anim. Behav. **32**, 66-75.

Brown, C. H., Alipour, F., Berry, D. A., and Montequin, D. (**2003**). “Laryngeal biomechanics and vocal communication in the squirrel monkey (*Saimiri boliviensis*),” J. Acoust. Soc. Amer. **113**, 2114-2126.

Budney, G. F., and Grotke, R. W. (**1997**). “Techniques for audio recording vocalizations of tropical birds,” Ornithol. Monog. **48**, 1-25.

Buesching, C. D., Heistermann, M., Hodges, J. K., and Zimmermann, E. (**1998**). “Multimodal oestrus advertisement in a small nocturnal prosimian, *Microcebus murinus*,” Folia Primatol. **69**, 295-308.

Cheney, D. L. and Seyfarth, R. M. (**1990**). *How Monkeys See the World* (University of Chicago Press, Chicago).

Cheney, D. L., and Seyfarth, R. M. (**2010**). “Primate communication and human language: Continuities and discontinuities,” In P. M. Kappeler and J. Silk (Eds.), *Mind the Gap: Tracing the Origins of Human Universals* (pp. 283-298). Springer-Verlag, New York.

Clark, A., and Wrangham, R. (**1993)**. “Acoustic analysis of wild chimpanzee pant hoots: Do Kibale Forest chimpanzees have an acoustically distinct food arrival pant hoot?” Am. J. Primatol. **31**, 99-109.

Clark, A., and Wrangham, R. (**1994)**. “Chimpanzee arrival pant hoots: Do they signify food or status?” Int. J. Primatol. **15**, 185-206.

Craul, M., Zimmermann, E., and Radespiel, U. (**2004)**. “First experimental evidence for female mate choice in a nocturnal primate,” Primates **45**, 271-274.

Crockford, C., and Boesch, C. (**2003**). “Context-specific calls in wild chimpanzees, *Pan troglodytes verus*: Analysis of barks,” Anim. Behav. **66**, 115-125.

Day, S. D., Ramarokotol, R., Sitzmann, B. D., Randriamboahanginjatovo, R., Ramanankirija, H., Randriaanindrina, V., and Ravololonarivo, G. (**2009**). “Re-introduction of diademed sifakas (*Propithecus diadema*) and black and white ruffed lemurs (*Varecia variegata editorum*) at Analamazaotra Special Reserve, eastern Madagascar,” Lemur News **14**, 32-37.

Digweed, S. M., Fedigan, L. M., and Rendall, D. (**2005)**. “Variable specificity in the anti-predator vocalizations and behaviour of the white-faced capuchin, *Cebus capucinus*,” Behaviour **142**, 997-1021.

Dollar, L. J., Ganzhorn, J. U., and Goodman, S. M. (**2007**). “Primates and other prey in the seasonally variable diet of *Cryptoprocta ferox* in the dry deciduous forest of western Madagascar,” in *Primate Anti-Predator Strategies*, edited by S. L. Gursky and K. A. I. Neckaris (Springer, New York), pp. 63-76.

Duckworth, J. W., Evans, M. I., Hawkins, A. F. A., Stafford, R. J., and Wilkinson, R. J. (**1995**). “The lemurs of Marojejy Strict Reserve, Madagascar: A status overview with notes on ecology and threats,” Int. J. Primatol. **16**, 545-559.

Eaton, R. C. (Ed.), (**1984**). *Neural Mechanisms of Startle Behavior* (Plenum Press, New York).

Elowson, A. M., Tannenbaum, P. L., and Snowdon, C. T. (**1991)**. “Food-associated calls correlate with food preference in cotton-top tamarins,” Anim. Behav. **42**, 931-937.

Evans, C. S. (**1997**). “Referential signals,” in *Perspectives in Ethology, Vol. 12: Communication*, edited by D. H. Owings, M. D. Beecher, and N. S. Thompson. (Plenum Press, New York), pp. 99-143.

Fichtel, C., and Kappeler, P. M. (**2002)**. “Anti-predator behaviour of group-living Malagasy primates: Mixed evidence for a referential alarm call system,” Behav. Ecol. Sociobiol. **51**, 262-275.

Fischer, J., and Hammerschmidt, K. (**2001)**. “Functional referents and acoustic similarity revisited: The case of Barbary macaque alarm calls,” Anim. Cog. **4**, 29-35.

Fischer, J., Hammerschmidt, K., Cheney, D. L., and Seyfarth, R. M. (**2001**). “Acoustic features of female chacma baboon barks,” Ethol. **107**, 33-54.

Fischer, J., Hammerschmidt, K., Cheney, D. L., and Seyfarth, R. M. (**2002**). “Acoustic features of male baboon loud calls: Influences of context, age, and individuality,” J. Acoust. Soc. Am. **111**, 1465-1474.

Fitch, W. T. (**1997**). “Vocal tract length and format frequency dispersion correlate with body size in rhesus macaques,” J. Acoust. Soc. Am. **102**, 1213-1222.

Fitch, W. T., and Giedd, J. (**1999**). “Morphology and development of the human vocal tract: A study using magnetic resonance imaging,” J. Acoust. Soc. Am. **106**, 1511-1522.

Fitch, W. T., Neubauer, J., and Herzel, H. (**2002**). “Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production,” Anim. Behav. **63**, 407-418.

Forrest, K., Weismer, G., Milenkovic, P., and Dougall, R. N. (**1988**). “Statistical analysis of word-initial obstruents: Preliminary data,” J. Acoust. Soc. Am. **84**, 115-123.

Frey, R., and Riede, T. (**2003**). “Sexual dimorphism of the larynx of the Mongolian gazelle (*Procarpa gutturosa*). Zool. Anzeiger **242**, 33-62.

Gamba, M., and Giacoma, C. (**2007)**. “Quantitative acoustic analysis of the vocal repertoire of the crowned lemur,” Ethol. Ecol. Evol. **19**, 323-343.

Gamba, M., Colombo, C., and Giacoma, C. (**2011**). “Acoustic cues to caller identity in lemurs: A case study,” Ethology. http://dx.doi.org/10.1007/s10164-011-0291-z

Garreau, J. M., and Manantsara, A. (**2003**). “The protected-area complex of the Parc National de Marojejy and the Reserve Speciale d’Anjanaharibe-Sud,” in *The Natural History of Madagascar,* edited by S. M. Goodman and J. P. Benstead (University of Chicago Press, Chicago), pp. 1451-1458.

Geissmann, T., and Mutschler, T. (**2006**). “Diurnal distribution of loud calls in sympatric wild indris (*Indri indri*) and ruffed lemurs (*Varecia variegata*): implications for call functions,” Primates **47**, 393-369.

Giacoma, C., Sorrentino, V., Rabarivola, C., and Gamba, M. (**2010**). “Sex differences in the song of *Indri indri*,” Int. J. Primat. **31**, 539-551.

Glantz, S. A. (**2002**). *A Primer for Biostatistics* (McGraw Hill, New York).

Goodman, S. M. (**1998**). “Description of the 1994 biological inventory of the Reserve Speciale d’Anjanaharibe-Sud, Madagascar,” Field. Zool. **90**, 1-7.

Goodman, S. M. (**2000**). “Description of the Parc National de Marojejy, Madagascar, and the 1996 biological inventory of the reserve,” Fieldian. Zool. **97**, 1-18.

Goodman, S. M., Hawkins, A. F. A., and Razafimahaimodison, J. C. (**2000**). “Birds of the Parc National de Marojejy, Madagascar: With reference to elevational distribution,” Fieldian. Zool. **97**, 175-200.

Goodman, S. M. (**2003**). “Predation on lemurs,” in *The Natural History of Madagascar,* edited by S. M. Goodman and J. P. Benstead (University of Chicago Press, Chicago), pp. 1221-1228.

Goodman, S. M., and Pidgeon, M. (**1991**). "Madagascar harrier hawk, *Polyboroides radiates,* preying on flying fox *Pteropus rufus,*" Ostrich **62**, 215-216.

Gouzoules, H., and Gouzoules, S. (**2000**). "Agonistic screams differ among four species of macaques: The significance of motivation-structural rules." Anim. Behav. **59**, 501-512.

Harrison, D. F. N. (**1995**). *The Anatomy and Physiology of the Mammalian Larynx* (Cambridge University Press, Cambridge).

Hawkins, C. E. and Racey, P. A. (**2005**). "Low population density of a tropical forest carnivore, *Cryptoprocta ferox*: Implications for protected area management," Oryx **39**, 35-43.

Heffner, R. S. (**2004**). "Primate hearing from a mammalian perspective," Anat. Rec. Part A **281A**, 1111-1122.

Hershkovitz, P. (**1977**). *Living New World Monkeys (Platyrrhini) with an Introduction to Primates, Vol. 1* (University of Chicago Press, Chicago).

Hewitt, G., MacLarnon, A., and Jones, K. E. (**2002**). "The functions of laryngeal air sacs in primates: A new hypothesis," Folia Primat. **73**, 70-94.

Hirano, M., Kurita, S., and Nakashima, T. (**1983**). "Growth, development, and aging of human vocal folds," in *Vocal Fold Physiology: Contemporary Research and Clinical Issues*, edited by D. M. Bless and J. H. Abbs (College-Hill, San Diego), pp. 22-43.

Irwin, M.T. (2006). "Ecological Impacts of Forest Fragmentation on Diademed Sifakas (*Propithecus diadema*) at Tsinjoarivo, Eastern Madagascar: Implications for Conservation in Fragmented Landscapes," Ph.D. dissertation, New York: Stony Brook University, Stony Brook.

Irwin, M. T., Raharison, J. L. and Wright, P. C. (**2009**). "Spatial and temporal variability in predation on rainforest primates: Do forest fragmentation and predation act synergistically?" Anim. Conserv. **12**, 220-230.

IUCN (**2007**). "World heritage nomination. IUCN technical evaluation. Rainforests of the Atsinanana (Madagascar)," *IUCN Evaluation Report,* **ID No. 1257**, 1-9.

Kappeler, P.M. (**1990**). "The evolution of sexual size dimorphism in prosimian primates," Am. J. Primat. **21**, 201-214.

Kappeler, P. M. (**1991**). “Patterns of sexual dimorphism in body weight among prosimian primates,” Folia Primat. **57**, 132-146.

Karpanty, S.M. (**2006**). “Direct and indirect impacts of raptor predation on lemurs in southeastern Madagascar,” Int. J. Primatol. **27**, 239–261.

Karpanty, S.M., and Goodman S.M. (**1999**). “Diet of the Madagascar harrier-hawk, *Polyboroides radiatus*, in southeastern Madagascar,” J. Raptor Res. **33**, 313–316.

Karpanty, S. M., and Wright, P. C. (**2007**). “Predation on lemurs in the rainforest of Madagascar by multiple predator species: observations and experiments,” in *Primate Anti-Predator Strategies,* edited by S. L. Gursky and K. A. I. Neckaris (Springer: New York), pp. 77-99.

Lawler, R. R., Richard, A. F., and Riley, M. A. (**2005**). “Intrasexual selection in Verreaux's sifaka (*Propithecus verreauxi verreauxi*),” J. Human Evol. **48**, 259-277.

Lehner, P. N. (**1996**). *Handbook of Ethological Methods*. (Cambridge University Press, New York).

Leliveld, L., Scheumann, M., and Zimmermann, E. (**2011**). “Acoustic correlates of individuality in the vocal repertoire of a nocturnal primate (*Microcebus murinus*),” J. Acoust. Soc. Am. **129**, 2278-2288.

Macedonia, J. M. (**1986)**. “Individuality in a contact call of the ringtailed lemur *(Lemur catta)*,” Am. J. Primatol. **11**, 163-179.

Macedonia, J. M. and Polak, J. F. (**1989**). “Visual assessment of avian threat in semi-captive ringtailed lemurs (*Lemur catta*),” Behaviour **111**, 291-304.

Macedonia, J. M. (**1990**). “What is communicated in the antipredator calls of lemurs: Evidence from playback experiments with ringtailed and ruffed lemurs,” Ethology **86**, 177-190.

Macedonia, J. M. (**1993**). “Adaptation and phylogenetic constraints in the anti-predator behavior of ringtailed and ruffed lemurs,” in *Lemur Social Systems and Their Ecological Basis*, edited by P. M. Kappeler and J. U. Ganzhorn (Plenum Press, New York), pp. 67-83.

Macedonia, J. M., and Evans, C. S. (**1993)**. “Variation among mammalian alarm call systems and the problem of meaning in animal signals,” Ethology **93**, 177-197.

Macedonia, J. M. and Stanger, K. (**1994)**. "Phylogeny of the Lemuridae revisited: Evidence from communication signals," Folia Primat. **63**, 1-43.

MacKinnon, J. R., and MacKinnon, K. S. (**1984**). "Territoriality, monogamy and song in gibbons and tarsiers," in *the Lesser Apes: Evolutionary and Behavioral Biology*, edited by H. Preuschoft, D. J. Chivers, W. Y. Brockelmann, and N. Creel (Edinburgh University Press, Edinburgh), pp. 291-297.

Manly, B. F. (1997). *Randomization, Bootstrap and Monte Carlo Methods in Biology* (Chapman and Hall, London).

Masterton, B., Heffner H., and Ravizza, R. (1969). "The evolution of human hearing." J. Acoust. Soc. Am. **45,** 966–985.

Mergell, P., Fitch, W. T., and Herzel, H. (**1999**). "Modeling the role of non-human vocal membranes in phonation," J. Acoust. Soc. Am. **105**, 2020-2028.

Mitani, J. C. (**1985a)**. "Location-specific responses of gibbons (*Hylobates muelleri*) to male songs," Zeit. Tierpsychol. **70**, 219-224.

Mitani, J. C. (**1985b)**. "Responses of gibbons (*Hylobates muelleri*) to self, neighbor, and stranger song duets," Int. J. Primatol. **6**, 193-200.

Mitani, J. C., and Gros-Louis, J. (**1995**). "Species and sex differences in the screams of chimpanzees and bonobos," Int. J. Primat. **16**, 393-411.

Mitani, J. C., and Stuht, J. (**1998**). "The evolution of nonhuman primate loud calls: Acoustic adaptation for long-distance transmission," Primates **39**, 171-182.

Mittermeier, R. A., Louis, E. E., Richardson, M., Schwitzer, C., Langrand, O., Rylands, A. B., Hawkins, F., Rajaobelina, S., Ratsimbazafy, J., Rasoloarison, R., Roos, C., Kappeler, P. M., and MacKinnon, J. (**2010**). *Lemurs of Madagascar*, 3rd Ed. (Conservation International, Washington, DC).

Mundry, R., and Sommer, C. (**2007**). "Discriminant function analysis with nonindependent data: Consequences and an alternative," Anim. Behav. **74**, 965-976.

Norcross, J. L., and Newman, J. D. (**1993**). "Context and gender- specific differences in the acoustic structure of common marmoset (*Callithrix jacchus*) phee calls," Am J. Primatol. **30,** 37-54.

Notman, H., and Rendall, D. (**2005**). "Contextual variation in chimpanzee pant hoots and its implications for referential communication," J. Anim. Behav. **70**, 177-190.

Owings, D. H., and Hennessy, D. F. (**1984**). "The importance of variation in sciurid visual and vocal communication," in *The Biology of Ground-Dwelling Squirrels*, edited by J. O. Murie and G. R. Michener (University of Nebraska Press, Omaha), pp. 171-200.

Owren, M. J., and Bachorowski, J.A. (**2007**). "Measuring emotion related vocal acoustics," in *Handbook of emotion elicitation and assessment*, edited by J. A. Coan and J. J. B. Allen (Oxford University Press, New York), pp. 239-266.

Owren, M. J., and Bernacki, R. H. (**1998**). "Applying linear predictive coding (LPC) to frequency-spectrum analysis of animal acoustic signals," in *Animal Acoustic Communication: Sound Analysis and Research*, edited by S. L. Hopp, M. J. Owren, and C. S. Evans (Springer-Verlag, Berlin), pp. 129-161.

Owren, M. J., and Casale, T. M. (**1994**). "Variations in fundamental frequency peak position in Japanese macaque (*Macaca fuscata*) 'coo' calls," J. Comp. Psychol. **108**, 291-297.

Owren, M. J., and Patel, E. R. (**2008**). "A little of this, a lot of that: Specificity and variability in nonhuman primate vocal repertoires," Primate Eye **96**, 742.

Owren, M. J., and Rendall, D. (**1997**). "An affect-conditioning model of nonhuman primate vocal signaling," in *Perspectives in Ethology*, edited by D. H. Owings, M. D. Beecher, and N. S. Thompson (Plenum, New York),pp. 299–346.

Owren, M. J., and Rendall, D. (**2001**). "Sound on the rebound: Bring form and function back to the forefront in understanding nonhuman primate vocal signaling," Evol. Anthropol. **10**, 58-71.

Owren, M. J., Seyfarth, R. M., and Cheney, D. L. (**1997**). "The acoustic features of vowel-like grunt calls in chacma baboons (*Papio cynocephalus ursinus*): Implications for production processes and functions," J. Acoust. Soc. Am. **101**, 2951-2963.

Owren, M. J., Rendall, D., and Bachorowski, J.-A. (**2003**). "Nonverbal vocal communication," in *Primate Psychology*, edited by D. Maestripieri (Harvard University Press, Cambridge, MA), pp. 359-394.

Patel, E. R. (**2005)**. "Silky sifaka (*Propithecus candidus*) predation by a fossa (*Cryptoprocta ferox*)," Lemur News **10**, 25-27.

Patel, E. R. (**2007**). "Logging of rare rosewood and palisandre (*Dalbergia spp.*) within Marojejy National Park, Madagascar," Madagascar Conserv. Develop. **2**, 11-16.

Patel, E. R. (**2009**). “Silky Sifaka, *Propithecus candidus*, 1871,” in *Primates in Peril: The World's 25 Most Endangered Primates 2008-2010,* edited by R. A. Mittermeier, J. Wallis, A. B. Rylands, J. U. Ganzhorn, J. F. Oates, E. A. Williamson, E. Palacios, E. W. Heymann, M. C. M. Kierulff, L. Yongcheng, J. Supriatna, C. Roos, S. Walker, L. Cortés-Ortiz, and C. Schwitzer (Conservation International, Arlington, VA), pp. 23-26.

Patel, E. R. (**2011**). *Diet, Habitat, and Ranging of the Silky Sifaka (Propithecus candidus),* Unpublished report to Madagascar National Parks.

Patel, E. R., and Owren, M. J. (**2007**). “Acoustics and behavioral contexts of ‘gecker’ vocalizations in young rhesus macaques (*Macaca mulatta*),” J. Acoust. Soc. Am. **121**, 575-585.

Patterson, R. D., Smith, D. R. R., van Dinther, R., and Walters, T. C. (**2008**). “Size information in the production and perception of communication sounds,” Springer Handbk. Aud. Res. **29**, 43-76.

Pereira, M. E., Seeligson, M. L., and Macedonia, J. M. (**1988**). “The behavioral repertoire of the black-and-white ruffed lemur, *Varecia variegata variegata* (Primates: Lemuridae),” Folia Primat. **51**, 1-32.

Pereira M. E., and Macedonia, J. M. (**1991**). “Ringtailed lemur anti-predator calls denote predator class, not response urgency.” Anim. Behav. **41**, 543-544.

Petter, J. J., and Charles-Dominique, P. (**1979**). “Vocal communication in prosimians,” in *The Study of Prosimian Behavior,* edited by G. A. Doyle and R. D. Martin (Academic Press, New York), pp. 247-305.

Pochron, S. T., Morelli, T. L., Terranova, P., Scirbona, J., Cohen, J., Kunapareddy, G., Rakotonirina, G., Ratsimbazafy, R., Rakotosoa, R., and Wright, P. C. (**2005**). “Patterns of male scent-marking in Propithecus edwardsi of Ranomafana National Parc, Madagascar,” Am. J. Primatol. **65,** 103-115.

Pollack, J. I. (**1986)**. “The song of the indris (*Indri indri*; Primates: Lemuroidea) Natural history, form, and function,” Int. J. Primatol. **7**, 225-264.

Rakotondrainibe, F. (**2000**). “Pteridophyte diversity patterns along an elevational gradient in the Parc National de Marojejy,” Field. Zool. **97**, 19-28.

Ramsier, M. A., and Dominy, N. J. (**2010**). “Comparison of auditory brainstem responses and behavioral estimates of hearing sensitivity in *Lemur catta* and *Nycticebus coucang,*” Am. J. Primatol. **72**, 217-233.

Range, F., and Fischer, J. (2004). “Vocal repertoire of sooty mangabeys (*Cercocebus torquatus atys*) in the Taï National Park,” Ethology **110**, 301-321.

Raselimanana, A. P., Raxworthy, C. J., and Nussbaum, R. A. (**2000**). “Herpetofaunal species diversity and elevational distribution within the Parc National de Marojejy, Madagascar,” Fieldian. Zool. **97**, 157-174.

Rasoloharijaona, S., Randrianambinina, B., Braune, P., and Zimmermann, E. (**2006)**. “Loud calling, spacing, and cohesiveness in a nocturnal primate, the Milne Edwards' sportive lemur (*Lepilemur edwardsi*),” Am. J. Phys. Anthro. **129**, 591-600.

Reby, D. and Charleton, B. (**2011**). “Attention grabbing in red deer sexual calls,” Anim. Cogn. http://dx.doi.org/10.1007/s10071-011-0451-0.

Recanzone, G. H., and Beckermann, N. S. (**2004**). “Effects of intensity and location on sound location discrimination in macaque monkeys,” Hear. Res. **198**, 116-124.

Rendall, D., Kollias, S., Ney, C., and Lloyd, P. (**2005**). “Pitch (F_0) and formant profiles of human vowels and vowel-like baboon grunts: The role of vocalizer body size and voice-acoustic allometry,” J. Acoust. Soc. Am. **117**, 944-955.

Rendall, D., Owren, M. J., and Rodman, P. S. (**1998**). “The role of vocal tract filtering in identity cueing in rhesus monkey (*Macaca mulatta*) vocalizations,” J. Acoust. Soc. Am. **103**, 602-614.

Rendall, D., Owren, M. J., and Ryan, M. J. (**2009**). “What do animal signals mean?” Anim. Behav. **78**, 233-240.

Rendall, D., Vokey, J. R., and Nemeth, C. (**2007**). “Lifting the curtain on the wizard of Oz: Biased voice-based impressions of speaker size.” J. Exp. Psych. Hum. Perc. Perf. **33**, 1208-1219.

Riede, T., Wilden, I., and Tembrock, G. (**1997**). “Subharmonics, biphonations, and frequency jumps—common components of mammalian vocalization or indicators for disorders?” Z. Säugetierkunde **62 (Suppl. II**), 198-203.

Riede, T. R., Owren, M. J., and Arcadi, A. C. (**2004**). “Nonlinear acoustics in the pant-hoot vocalizations of common chimpanzees (*Pan troglodytes*): Frequency jumps, subharmonics, biphonation, and deterministic chaos,” Am. J. Primatol. **64**, 277-291.

Riede, T. R., Arcadi, A. C., and Owren, M. J. (**2007**). “Nonlinear acoustics in the pant-hoot vocalizations of common chimpanzees (Pan troglodytes), II: Vocalizing at the edge,” J. Acoust. Soc. Am. **121**, 1758-1767.

Sauther, M. L. (**1989**). “Antipredator behavior in troops of free-ranging Lemur catta at Beza Mahafaly Special Reserve, Madagascar,” Int. J. Primatol. **10,** 595-606.

Scherer, K. (**1986**). “Vocal affect expression: A review and a model for future research,” Psychol. Bull. **99**, 143-165.

Scheumann, M., Rabesandratana, A. and Zimmermann, E. (**2007**). “Predation, communication, and cognition in lemurs,” in *Primate Anti-Predator Strategies*, edited by S.L. Gursky and K.A.I. Nekaris (Springer, New York), pp. 100-126.

Schön Ybarra, M. (**1995**). “A comparative approach to the nonhuman primate vocal tract: Implications for sound production,” in *Current Topics in Primate Vocal Communication*, edited by E. Zimmerman and J. D. Newman (Plenum, New York), pp. 185-198.

Semple, S., McComb, K., Alberts, S., and Altmann, J. (**2002)**. “Information content of female copulation calls in yellow baboons,” Am. J. Primatol. **56**, 43-56.

Seyfarth, R. M. and Cheney, D. L. (**1980**). “The ontogeny of vervet monkey alarm calling behavior: A preliminary report,” Zeit. Tierpsy. **54**, 37-56.

Seyfarth, R. M., Cheney, D. L., and Marler, P. (**1980)**. “Vervet monkey alarm calls: Semantic communication in a free-ranging primate,” Anim. Behav. **28**, 1070-1094.

Smith, A. S., Birnie, A. K., Lane K. R., and French, J. A. (**2009**). “Production and perception of sex differences in vocalizations of Wied’s black-tufted-ear marmosets (*Callithrix kuhlii*),” Am. J. Primatol. **71,** 324-332.

Stark, D., and Schneider, R. (**1960**). “Respirationsorgane,” in *Primatologia III/2*, edited by H. Hofer, A. H. Schultz, and D. Starck (Karger, Basel).

Sterling, E., and McFadden, K. (**2000**). “Rapid census of lemur populations in Parc National de Marojejy, Madagascar,” Fieldian. Zool. **97**, 265-274.

Stewart, K. J., and Harcourt, A. H. (**1994**). “Gorillas' vocalizations during rest periods: Signals of impending departure?” Behaviour **130**, 29-40.

Thorstrom, R., and La Marca, G. (**2000**). “Nesting biology and behavior of the Madagascar Harrier-hawk (*Polyboroides radiatus*) in northeastern Madagascar,” J. Rapt. Res. **34**, 120-125.

Titze, I. R. (**1989**). “Physiologic and acoustic differences between male and female voices,” J. Acoust. Soc. Am. **85**, 1699-1707.

Tokuda, I., Riede, T., Neubauer, J., Owren, M. J., and Herzel, H. (**2002**). "Nonlinear prediction of irregular animal vocalizations," J. Acoust. Soc. Am. **111**, 2908-2919.

Trillmich, J., Fichtel, C., and Kappeler, P.M. (**2004**). "Coordination of group movements in wild Verreaux's sifakas (*Propithecus verreauxi*)," Behaviour **141**, 1103-1120.

Vasey, N. (**2003**). "*Varecia*, ruffed lemurs," in *The Natural History of Madagascar*, edited by S.M. Goodman and J. Benstead (U. Chicago Press, Chicago), pp. 1332–1336.

Vasey, N. (**2006**). "Impact of seasonality and reproduction on social structure, ranging patterns, and fission-fusion social organization in red ruffed lemurs," in *Lemurs: Ecology and Adaptation*, edited by L. Gould and M. L. Sauther (Springer, New York), pp. 275-304.

Waser, P. M., and Brown, C. H. (**1984**). "Is there a "sound window" for primate communication?" Behav. Ecol. Sociobiol. **15**, 73-76.

Waser, P. M., and Brown, C. H. (**1986**). "Habitat acoustics and primate communication," Am. J. Primatol. **10**, 135-154.

Wich, S. A., and Nunn, C. L. (**2002)**. "Do male "long-distance calls" function in mate defense? A comparative study of long-distance calls in primates," Behav. Ecol. Sociobiol. **52**, 474-484.

Wilden, I., Herzel, H., Peters, G., and Tembrock, G. (**1998**). "Subharmonics, biphonation, and deterministic chaos in mammal vocalization," Bioacoustics **9**, 171–196.

Wrangham, R. W. (**1977**). "Feeding behaviour of chimpanzees in Gombe National Park Tanzania," in *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys, and Apes*, edited by T. H. Clutton-Brock (Academic Press, London), pp. 504-538.

Wright, P. C., Heckscher, S. K., and Dunham, A. E. (**1997)**. "Predation on Milne-Edwards' sifaka (*Propithecus diadema edwardsi*) by the fossa (*Cryptoprocta ferox*) in the rainforest of southeastern Madagascar," Folia Primat. **68**, 34-43.

Wright, P. C. (**1998)**. "Impact of predation risk on the behaviour of *Propithecus diadema edwardsi* in the rainforest of Madagascar," Behaviour **135**, 1-30.

Wright, P. C. (**1999)**. "Lemur traits and Madagascar ecology: Coping with an island environment," Yrbk. Phys. Anthro. **42,** 31-72.

Zimmermann, E. (**1995**). “Acoustic communication in nocturnal prosimians,” in *Creatures of the Dark: The Nocturnal Prosimians*, edited by L. Alterman, G.A. Doyle, and M.K. Izard (Plenum Press, New York), pp. 311-330.

Zimmermann, E., Leliveld, L., and Schehka, S. **(in press, 2012). “**Toward the evolutionary roots of affective prosody in speech and music: universal affect cues in mammalian voices?” in *Evolution of Emotional Communication: From Sounds in Nonhuman Mammals to Speech and Music in Man*, edited by E. Altenmüller, S. Schmidt, and E. Zimmermann (Oxford University Press, Oxford).

CHAPTER 4

Non-nutritive tree gouging in wild silky sifakas (*Propithecus candidus*) and Milne-Edwards' sifakas (*P. edwardsi*)

Erik R. Patel[1,2]

ABSTRACT

Male sifakas routinely gouge trees just before chest scent marking, leaving long lasting visible marks. Eastern sifakas, such as silky sifakas (*Propithecus candidus*) and Milne-Edwards' sifakas (*P. edwardsi*), are believed to seldom consume bark or any tree exudates. Therefore, male gouging is generally considered unrelated to foraging but rather is communicative in function, although the form and function of this remarkable behavior has not previously been examined in detail. In this study, gouging behavior and the physical marks on trees were examined in wild silky sifakas and Milne-Edwards' sifakas in Madagascar. Species differences were found in gouge mark morphology. Dominant males gouged most frequently and tended to have longer gouge marks. Gouging was most frequent just before and during the mating season. The resource gouging hypothesis was supported which proposes that gouging and associated scentmarking of critical resources (such as food and sleeping trees) advertises ownership and may facilitate relocation. Most of the 102 gouged tree, vine, and epiphite species were food species (61.8%), and many were known species of sleeping trees (38.2%). Moreover, multiple regression analysis revealed that the number of gouges per tree species was predicted by the percentile rank of those

---

[1] Author to whom correspondence should be addressed. Electronic mail: patel.erik@gmail.com
[2] Department of Psychology, 211 Uris Hall, Cornell University, Ithaca, New York, 14853

species as food tree species and sleeping tree species. Gouging appears to be an honest species-specific signal of male status that may promote scent longevity, attract the visual attention of conspecifics, and possibly remove the scentmarks of conspecifics.

INTRODUCTION

Many mammals, particularly felids and ungulates, create visual anomalies in conjunction with scent mark deposition. For example, wild tigers (*Panthera tigris*) are known to urine mark in scrapes made on the ground (Smith, 1989). Rutting male roe deer (*Capreolus capreolus*) that mark with scent glands between their hooves and on their heads, paw the ground to leave scratch marks and rub their antlers and head against tree branches to create scars (Johannson and Liberg, 1996). In some cases tree death can result from extreme debarking produced by extensive body rubbing on tree trunks by moose (*Alces alces gigas*) and bison (*Bison bison*) (Bowyer et al., 1994; Bowyer et al., 1998), these phenomena were well known to 19th century American biologists:

> "…the satisfaction [Moose and Bison] take in rubbing themselves against whatever will oppose resistance, whether it be rocks, trees, bushes, or a clay-bluff; the telegraph-poles, however, erected along the railroads that cross their range, afforded them especial delight as scratching posts, and soon became as well smoothed and covered with tufts of hair and grease from their unctuous hides as are the posts about a farmer's cattle yard." Allen (1877), p. 468

In England, bark stripping followed by urination and scent marking by eastern gray squirrels *(Sciurus carolinensis)* was a widespread problem with 50% to 100% of the trees damaged in some locations (reviewed in Koprowski, 1991). Reward money was actually issued in the 1950's for killing squirrels to mitigate this behavioral pattern:

> "In 1953 the Forestry Commission launched a bounty scheme, whereby a shilling was paid for the tail of every grey squirrel killed anywhere in England, Scotland, or Wales. Between March 1953 and the end of September 1955 nearly £33,000 was paid out. At the beginning of 1956 the reward was doubled…" Shorten (1957), p. 151

Amongst primates, several exudativorous species scent mark while gouging trees with their teeth for food resources such as gum, sap, and nectar. Wild marmosets (*Callithrix spp.*) of both sexes often place circumgenital scent marks and urinate in newly opened exudate sources (Lacher et al., 1981), as well as gouging and scent marking dead wood that has no nutritional value (Coimbra-Filho and Mittermeier, 1976; Rylands, 1985). Captive male and female Asian slow lorises (*Nycticebus spp.*) facial scent mark and urinate in the majority of their gouges. Freshly gouged branches, likely to contain the most exudate, are scent marked most while gouging (Nekaris et al., 2010). The earliest observations come from gummivorous galago species (*Galago sp.*) that repeatedly bite branches, though often in non-foraging contexts, and rub their chest glands on the bite marks (Bearder and Doyle, 1974; reviewed in Schilling, 1979).

Remarkably, some lemur species gouge and scent mark trees exclusively in non-foraging contexts. Sifaka males, for example, routinely gouge trees by biting tree trunks removing bark, and then chest scent marking over the resulting depression created by the gouge (Lewis, 2005; Patel and Girard-Buttoz, 2008; Pochron et al., 2005). Such tree gouging and bark removal, for presumably non-nutritive reasons, has only been described in a few primate species, all of which are lemurs. Powyzk (1997, 2002) first considered the function of this behavior in diademed sifakas (*Propithecus diadema*) and proposed that males gouge just before over-marking in order to remove the scent marks of females, thereby preventing other males from retrieving olfactory cues to female estrus. Gouging has also been noted in male Alaotran bamboo lemurs (*Hapalemur alaotrensis*) that scratch papyrus reeds with their lower teeth and then rub the scratched spot with their well-developed brachial glands (Nievergelt et al., 1998). A similar behavioral pattern has been observed in captive greater bamboo lemurs (*Prolemur simus*) (pers. obs.). In the most recent gouging study to date, it has been discovered that nocturnal weasel sportive lemurs (*Lepilemur mustelinus*) also gouge trees for non-nutritive, communicative reasons, although it is not associated with scent marking behavior. Male and female sportive lemurs were found to gouge trees adjacent to their sleeping trees, but not sleeping trees per se, which suggests that gouging signals sleep site ownership and may be a form of saliva scent marking (Rasoloharijaona et al., 2010). In most of these species, individuals may gouge many times per day resulting in long-lasting, visible marks that are believed to have a communicative function.

The goal of this study was to conduct the first detailed examination of gouging in a *Propithecus* species in order to distinguish between several possible communicative functions. Because western dry-forest sifakas occasionally consume bark (Richard, 1985), the first goal of this study was to confirm that gouging is actually non-nutritive in silky sifakas and bark is not part of their diet. Therefore, the first long-term dietary study was undertaken of this critically endangered species (Patel, 2009).

There is only one breeding male in many sifaka groups, even though the group may contain several males (Kappeler and Schäffler, 2008; Morelli and Wright, 2006). Dominant male sifakas are known to scent mark at higher rates than subordinate males (Lewis, 2005; Pochron et al., 2005), have higher testosterone levels (Kraus et al., 1999; Lewis, 2009), and more darkly stained chests due to increased secretion and marking with the sternal gland (Lewis, 2009). It is therefore predicted that gouging is a male status signal and that one sifaka male will gouge most and likely have the largest gouges.

Some mammals scent mark critical resources such as food trees and sleeping sites in order to facilitate relocation and advertise ownership and willingness to defend these resources (honey badgers: Begg et al., 2003; sportive lemurs and bamboo lemurs: Irwin et al., 2004; otters: Kruuk, 1992; marmosets: Lazaro-Perea et al., 1999; golden lion tamarins: Miller et al., 2003), but this hypothesis has not been extensively tested in eastern sifakas. Such resources are also highly visited by other group members, leading to a potentially large audience for these gouges and the scent marks that accompany them. Sleep trees and food trees are often found along travel routes, and gouging these trees may produce a “bulletin board” effect (Johnston et al., 1994) that increases the likelihood of receivers detecting them (Gosling and Roberts, 2001). It is therefore predicted that silky sifakas gouge predominantly on tree species known to be food trees and sleeping trees. Finally, as gouge marks may be a species-specific trace of the critically endangered silky sifaka, they can serve as a census tool during population surveys if correctly identified. A final goal was therefore to identify key features of silky sifaka gouge marks, and to determine how they differ from gouges in a closely related sifaka species. Therefore, the gouge marks of Milne-Edwards’s sifaka (*Propithecus edwardsi*) were also studied. This work occurred at a field site where gouges were made rather low in height which permitted actual measurements and video recording of gouging behavior as well as photos.

Two specific predictions of the resource gouging hypothesis will be tested in this study. First that, the percentiles of tree species in the diet of silky sifakas (food tree percentile) is a significant predictor of the number of gouges on food tree species, and second that the percentiles of tree species among sleeping trees (sleep tree percentile) is a significant predictor of the number of gouges on sleep tree species.

METHODS

Study site and subjects

For silky sifakas, data were collected on a single group from July 12 2009 to July 3 2010 at Camp 2 (Marojejia) of Marojejy National Park in northeastern Madagascar (See Table 4.1). For Milne-Edwards' sifakas (*Propithecus edwardsi*), the data presented are measurements and photos of gouge marks by members of Group 4 (2 adult males, 3 adult females, 1 juvenile female) at Ialatsara Private Reserve in southeastern Madagascar from August and September 2007.

Table 4.1 Silky sifaka subjects in the Camp 2 group of Marojejy N.P.

Individual	Age-Sex Class	Age Estimate[1] (years)	Years in Group
AF	Adult Female	20 to 25	9+
BP	Adult Female	15 to 20	9+
LV	Adult Male	10 to 15	3+
CC[2]	Subadult Female	4	4+
FB	Juvenile Male	3	3+
TL[3]	Juvenile Male	2	2+
MB	Infant Male	1	1+

[1] Age estimates refer to the start of the study in July, 2009 are based on dental wear for AF and BP.
[2] Emigrated (natural dispersal) in September, 2010 and no longer in the group.
[3] Disappeared from the group in February, 2011 and presumed dead since too young to disperse.

Gouge behavior in silky sifakas

All occurrences of gouging by group members were recorded in Rite-in-the-Rain field data books (Altmann, 1974; Lehner, 1996). Focal sampling was not conducted here for two reasons. First, because gouging is a quick unpredictable behavior that often occurs while the group is traveling rapidly. Secondly, because each gouged tree species had to be identified by a local botanical expert (Mr. Jean Chrysostome Bevao), which often took 5 to 10 minutes and would have created too many interruptions in the focal data being collected for the dietary study (see below).

For each gouge, the following data were recorded: "Date/Time", "Tree species", "Height", and "Name of the gouging individual". Local names for trees were initially determined by consultation with the local botanical expert who worked daily with our team. Scientific names were subsequently confirmed when dried samples were identified by a professional botanist (Honoré Andriamiarinoro) at Missouri Botanical Garden in Antananarivo, Madagascar.

Sleeping trees in silky sifakas

Each afternoon, the silky sifaka group was followed to their sleeping trees. When eyes were closed and heads were down for more than 15 minutes, it was assumed that the current tree was their sleeping tree. Each sleeping tree was then flagged, numbered, and a GPS point was taken of the location. Species and local names were also identified for each sleeping tree. The height of each sleeping individual and each sleep tree was also estimated.

Diet composition in silky sifakas

Data on feeding behavior were collected using random two hour focal animal sampling of all seven group members (Altmann, 1974; Lehner, 1996). For each feeding bout, the following data were recorded: "Food species", "Plant part eaten", and "Feeding start and stop times to the nearest second". Activity height of the focal subject was determined using five minute instantaneous samples. Food species was initially recorded as a local/vernacular name (identified by Mr. Bevao) and later identified with scientific names at the Missouri Botanical Garden (identified by Mr. Andriamiarinoro) using botanical samples which were collected, pressed, and dried from every food species. Most of the samples were dried in the nearby city of Sambava using Cole Parmer drying ovens which were brought from the United States. These ovens are capable of maintaining a stable low temperature of approximately 40 degrees Celsius.

Gouge measurements, photos, and video of silky sifakas and Milne-Edwards' sifaka

Milne-Edwards' sifaka tree gouging behavior was recorded using a Sony Handycam DCR VX2100 Camcorder. Silky sifaka tree gouging behavior was recorded using a Sony Handycam HDR-CX 150 High Definition camcorder. Gouge marks were measured for Milne-Edwards' sifakas, but not for silky sifakas, as their gouge marks were too high to measure. When a Milne-Edwards' sifaka was observed gouging, the length, width, and height of each gouge was immediately measured whenever possible. Photos of newly gouged marks were taken for both species. Each photographed mark was later scored for specific aspects of gouge shape, including: 1) Number of discrete marks, 2) Overall shape, 3) Presence/Absence of the "bird footprint" pattern (see Figure 4.2).

RESULTS

Gouge size, shape, and substrates

1169 total silky sifaka gouges, made only by males, were documented on 102 species of trees, vines, and epiphytes (see Figures 4.1 and 4.2; Table 4.6). Almost all gouges occurred on the trunks and limbs of living trees (94.7%), although some vines (3.7%) and epiphytes (1.6%) were also gouged. In two rare instances, infant MB gouged the branches of a dead tree. The number of silky sifaka gouges per plant species ranged from 1 to 95 with a mean of 11.5 ± 18.8. Gouge height averaged 8.4 m ± 3.8.

One high-quality video was made of tree-gouging in silky sifakas and is available online: http://vimeo.com/30899285. Photos were taken of 30 newly gouged marks by silky sifaka adult male LV. Six of these photos were too low in quality (wrong angle, low resolution, or too dark) to be evaluated. In the 24 usable silky sifaka gouge photos, all gouges were found to be single irregular polygons (see Figure 4.2), including circular (83.3%), rectangular (12.5%), and one triangular mark (4.2%). None exhibited the "bird footprint" pattern (described below), which has never been observed in silky sifakas (pers. obs.). Most were circular (83.3%) in overall shape, though a few were rectangular (12.5%), and one was triangular (4.2%).

One high quality video was made of tree gouging in Milne-Edwards' sifakas and is available online: http://vimeo.com/30452561. Measurements were made of 38 Milne-Edwards' sifaka gouges from two adult males, BR (n = 34) and BO (n = 4). On average, each gouge was 2.84 cm ± .72 long, 1.99 cm ± .63 wide, and .30 cm ± .10 deep. Photos were taken of 42 Milne-Edwards' sifaka gouges. 66.7% of the gouges exhibited a distinctive morphology that will be labeled the "bird footprint" pattern (see Figure 4.2). Here, each gouge was comprised of a single larger oval region and several thinner "bullet" shapes with a small ungouged region in between. Field observations suggest that it is likely the larger oval region is made by upward movement of the toothcomb, while the several thinner "bullet" shapes are made by the downward gouging and dragging of the canines and incisors. The remaining 33.3% of gouges were single circular irregular polygons similar to silky sifaka gouges.

Photo: Eric Mathieu

Figure 4.1 Silky sifaka adult male LV gouging (Marojejy National Park).

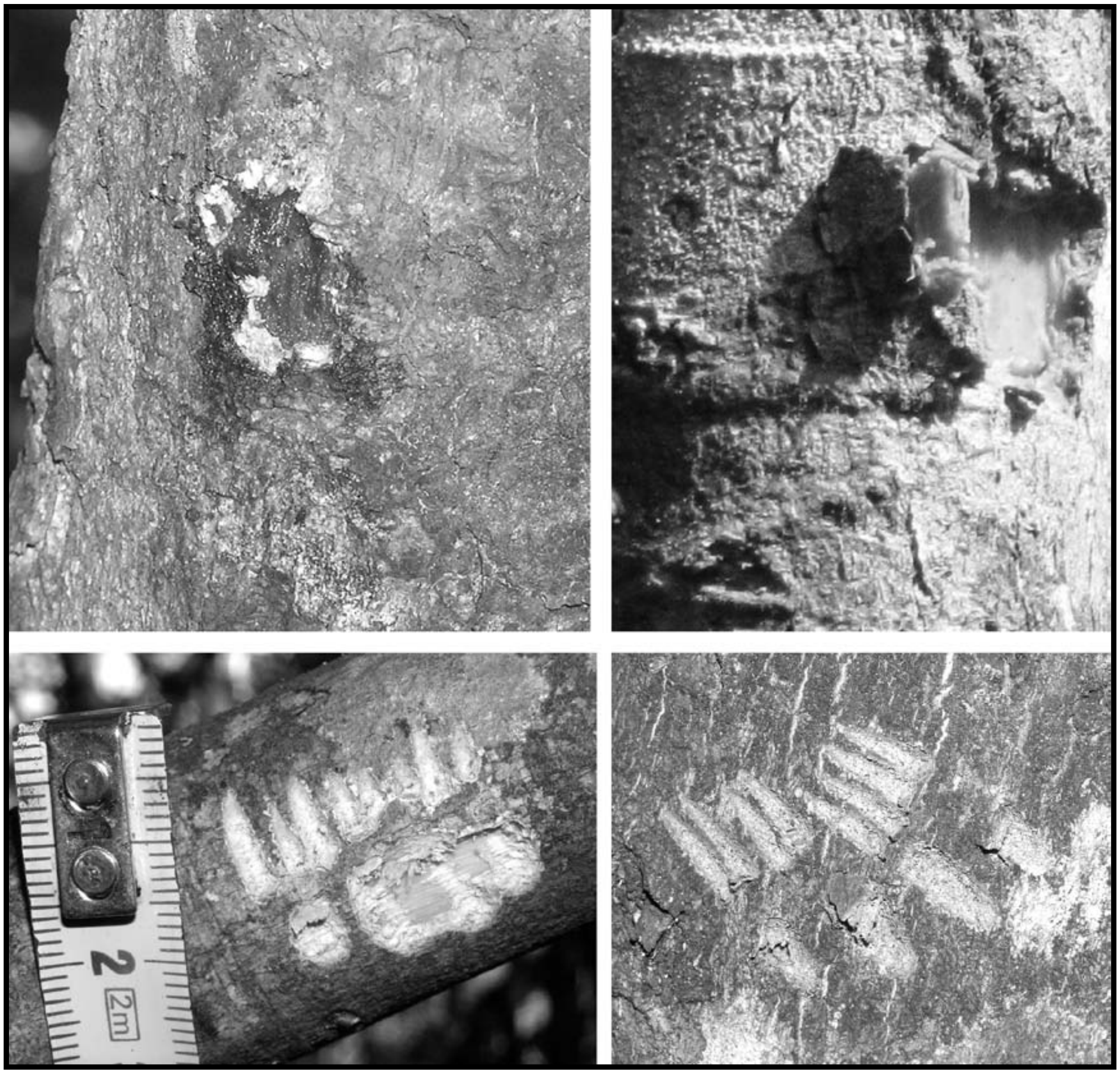


Figure 4.2 Representative gouge marks from silky sifakas (top two photos with a single round irregular polygon per gouge) and Milne-Edwards' sifakas (bottom two photos with the "bird footprint" pattern showing the scraping of individual canines and toothcomb). Total gouges per photo: upper left (1), upper right (1), bottom left (3), bottom right (4). Photos by Erik Patel (top left), Kristen Alldredge (top right), and Cedric Girard-Buttoz (bottom left and right).

Among the four silky sifaka males (see Table 4.2), significant differences were found in the number of total gouges per male ($\chi^2 = 1460.9$, df = 3, $p < .001$). Most gouges were made by adult male LV (73.3%) who is the dominant male (E.R. Patel, unpubl. data), although juveniles MB (10.8%), TL (9.8%), and FB (6.1%) also periodically gouged. It was surprising that the 1-2 year old infant gouged more than the older juveniles. Males also differed in the heights at which gouges were made (Kruskal-Wallis, $\chi^2 = 18.7$, d.f. = 3, $p >.001$), with the adult male and juvenile TL tending to gouge at lower heights than juvenile FB and the infant. Significant differences were furthermore found in the total number of gouges per month ($\chi^2 = 204.6$, df = 9, $p < .001$). For both the adult male and the younger males, the largest number of gouges was observed in November and December, just before and during the onset of the mating season (See Figure 4.3).

Measurements were made of 38 Milne-Edwards' sifaka gouges from two adult males, BR (n = 34) and BO (n = 4). BR is known to be the dominant male (J. Foltz, pers. comm.). Gouge mark length was significantly longer in the dominant male BR (2.93cm ± .67) than BO (2.13cm ± .81; Mann-Whitney U, z = 1.77, p < .04). The mean gouge width of BR was .52 cm higher than the mean width for BO, though this outcome was not significant (Mann-Whitney U, z = 1.41, p > .07). Gouge depth was not different between the two males (Mann-Whitney U, z = .546, p > .57).

Table 4.2 Gouging patterns for each male silky sifaka.

Male	**Age-Class**	**Total Gouges (%)**	**Mean Gouge Height (m)**	**Most Gouged Tree (%)**	**Rank (Percentile) of Most Gouged Food Tree**	**Rank (Percentile) of Most Gouged Sleep Tree**
LV	Adult	857 (73.3%)	8.2	Hazinina (9.0%)	1 (99.0)	6 (85.7)
FB	Sub-Adult	71 (6.1%)	9.5	Tavolo (9.9%)	26 (74.3)	3 (92.9)
TL	Juvenile	115 (9.8%)	7.9	Mankavia (8.7%)	15 (85.1)	40 (4.8)
MB	Infant	126 (10.8%)	9.4	Paka (8.7%)	35 (65.3)	2 (95.2)

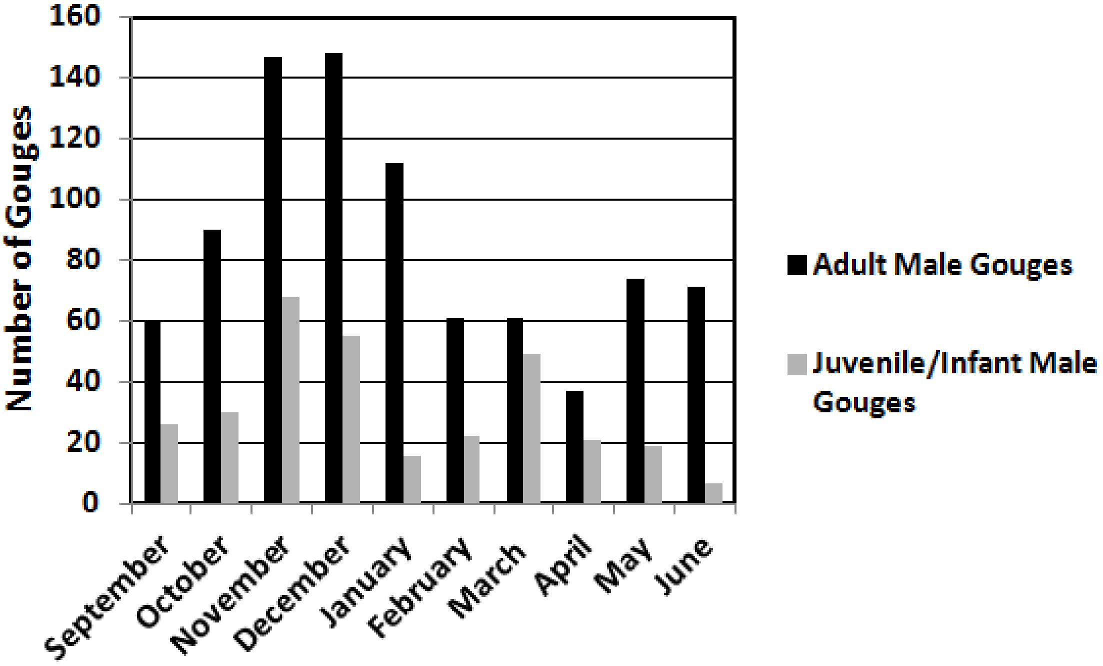


Figure 4.3 Number of silky sifaka gouges per month by the adult male and three juvenile males

Silky sifaka diet

3828 focal hours of feeding data were collected. Of the 101 food species consumed, most were trees (75.25%) and vines (15.84%). Epiphyte ferns (2.97%), epiphyte hemi-parasites (2.97%) and terrestrial parasitic plants (1.98%) were also eaten. One non-plant food, soil, was also sometimes eaten (.99%). The most commonly consumed plant part was leaves (48%). While predominantly folivorous, they consume considerable amounts of seeds (31%) as well. They are frequent seed predators, consuming more seeds than fruit, and often discarding fruit to access seeds. However, fruit alone (11%) was also periodically consumed, as well as flowers and flower buds (10%). Bark was never eaten, nor were any other exudates consumed (See Figure 4.4). The percentile rank of each of the 101 food species consumed was determined based upon the total feeding time on each food species. These percentile ranks were used in the multiple regression analysis described below. A full listing of all silky sifaka food species is presented in Patel (2011).

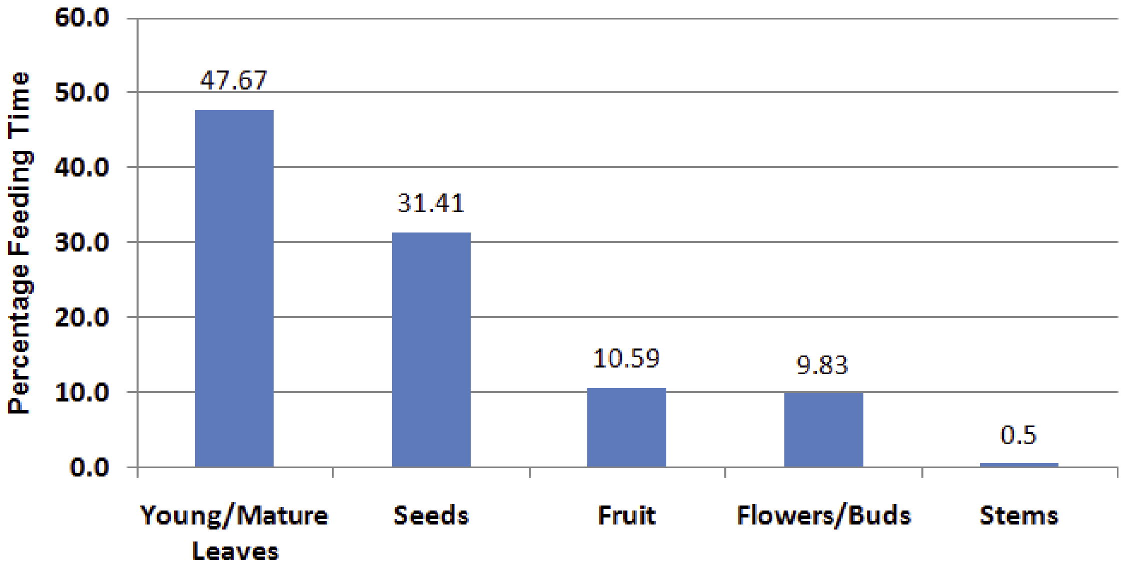


Figure 4.4 Percentage feeding time for plant parts in the silky sifaka diet.

Silky sifaka sleep trees

Sleeping tree data were obtained on 314 nights. Each night the individuals within the group slept in 1 to 6 different trees within 25 meters of one another. Individuals commonly slept alone or huddled in groups of two (particularly mother and infant). The largest sleeping huddles contained three group members. All individuals slept high in the canopy with mean sleeping heights of 15.5 m ± 4.09; mean sleeping tree height was 19.1 m ± 4.38. Mean activity height throughout the day (11.6 m ± 5.30) was lower than mean sleeping height (Mann Whitney U, Z = 26.9, p < .001).

339 sleeping trees were flagged, identified, numbered, and comprised of 44 species. 79.5% (35/44) of these sleeping tree species were food species. The seven most

used sleeping tree species (all of which are highly preferred food trees) accounted for 75.2% of all sleeping trees. The number of nights a given tree species was used by at least one silky sifaka ranged from 1 to 329 nights and averaged 28.4 ± 62.3. The number of nights a specific sleeping tree (n = 339) was slept in by at least one silky sifaka ranged from 1 to 47 nights and averaged 3.8 ± 5.4. Preferences were also apparent for individual sleeping trees. 30 sleeping trees (8.8% of sleeping trees) were slept in more than 10 times and accounted for 40.6% of all sleep trees. 93.3% of these highly preferred individual trees were food trees. The percentile rank of each of the 44 sleeping tree species was determined based upon the number of nights the species was used as sleeping tree. These percentile ranks (see Table 4.6) were used in the multiple regression analysis described below. A full listing of all silky sifaka sleeping trees species is presented in Patel (2011).

Gouging distribution on silky sifaka food and sleep tree species

63 (61.8%) of the 102 gouged tree, vine, and epiphyte species were known silky sifaka food species, and 39 (38.2%) of the gouged species were known sleeping tree species. Because silky sifakas sleep very high in the canopy it was seldom possible to count gouges on sleeping trees, particularly given the ever dimming light. However, gouging of a sleeping tree just before sleeping was observed on 16 occasions.

Table 4.6 displays the number of gouges for each gouged species and the percentile rank of each of these species as food trees and sleeping trees. Using the data in Table 4.3, a Spearman rank correlation matrix (with row-wise removal of missing values) was constructed to examine the monotonic pair-wise association between the numbers of gouges, food tree percentile, and sleep tree percentile. Number of gouges was moderately correlated with food tree percentile ($r = .44$, $p <$

.001, n = 62) and sleep tree percentile (r = .58, p < .001, n = 38). Food tree percentile was not significantly correlated with sleep tree percentile (r = .08, p > .69, n = 28).

A multiple-regression model was conducted to examine the extent to which the numbers of gouges made on particular trees were predicted by the extent to which those tree species are food trees and sleeping tress for this group of silky sifakas. With an adjusted R-square of .424, the model successfully accounted for 42.4% of the variance (see Table 4.3). Table 4.4 displays ANOVA results indicating that the linear relationship between the variables is significant ($F_{2,25} = 10.95$, p < .001). Table 4.5 shows the multiple linear regression equation estimates including the intercept. Both of the independent variables, food tree percentile (t = 2.788, p < .001) and sleep tree percentile (t = 3.807, p < .001) were significant positive predictors of the number of gouges. Examination of the standardized beta coefficients revealed that sleep tree percentile (beta = .556) was a better predictor of the number of gouges than food tree percentile (beta = .407). No evidence of collinearity was found, as seen in the low variance inflation factor (VIF = 1.00) for each independent variable. A scatterplot of the independent variables revealed no relationship. Cook's D was low for all rows, ranging from .000 to .365, which indicates that no single observation had a disproportionately large influence. A Sharpiro-Wilk normality test of the residuals (test value = .946, p > .15) and examination of the normal probability plot found that the residuals were approximately normally distributed. Finally, "residual versus predicted" and "residual versus predictor" plots did not reveal gross deviations from constant variance.

Table 4.3 Model Fit Summary

Model	R	R Square	Adjusted R Square	Std. Error
1	.683[a]	.467	.424	20.735

[a] Predictors: (Constant), Sleep Tree Percentile, Food Tree Percentile

Table 4.4 ANOVA Results of the Multiple Linear Regression Model

Model		Sum of Squares	df	Mean Square	F	P <
1	Regression	9412.225	2	4706.112	10.946	.001[a]
	Residual	10748.454	25	429.938		
	Total	20160.679	27			

[a]Predictors: (Constant), Sleep Tree Percentile, Food Tree Percentile
[b]Dependent Variable: Number of Gouges

Table 4.5 Coefficients of the Linear Regression Model

Model		Unstandardized Coefficients		Standardized Coefficients		
		B	Std. Error	Beta	t	P <
1	(Constant)	-33.800	15.069		-2.243	.034
	Food Tree Percentile	.471	.169	.407	2.788	.010
	Sleep Tree Percentile	.529	.139	.556	3.807	.001

[a]Dependent Variable: Number of Gouges

Table 4.6 Genera, local names, and characteristics for all trees, vines, and epiphytes gouged by silky sifakas (n = 1169 gouges).

Genus	**Local Name**	**Gouge Count (Percentage)**	**Food Tree Rank (Percentile)**	**Sleep Tree Rank (Percentile)**
Uapaca	Paka	95 (8.1)	35 (65.4)	2 (95.5)
Symphonia	Hazinina	89 (7.6)	1 (99.0)	6 (86.4)
Criptocarya	Tavolo	81 (6.9)	26 (74.2)	3 (93.2)
Eugenia	Rotro	67 (5.7)	6 (94.1)	7 (84.1)
Weinmannia	Lalona	56 (4.8)	2 (98.0)	1 (97.7)
Mammea	Vongo	55 (4.7)	11 (89.1)	15 (65.9)
Syzigium	Biando	51 (4.4)	14 (86.1)	25 (43.2)
Ficus	Mankavia	44 (3.8)	15 (85.2)	40 (9.1)
Mimusops	Nanto	38 (3.3)	10 (90.1)	4 (90.9)
Polyscias	Voantsilana	37 (3.2)	29 (71.3)	2 (95.5)
Unknown	Tsilomparimbarika	34 (2.91)	98 (3.0)	8 (81.8)
Calophyllum	Todinga	29 (2.48)	19 (81.2)	23 (47.7)
Albizia	Volomborona	24 (2.1)	4 (96.0)	13 (70.5)
Ficus	Fotsidity	21 (1.8)	9 (91.1)	24 (45.5)
Dichapetalium	Vahivy	19 (1.6)	7 (93.1)	N/A
Chrisophyllum	Famelona	18 (1.5)	33 (67.3)	N/A
Albizia	Sambalahy	18 (1.5)	18 (82.2)	32 (27.3)
Diospyros	Maintimpototra	17 (1.5)	25 (75.3)	N/A
Schefflera	Aviavilahy	16 (1.4)	30 (70.3)	N/A
Plagioscyphus	Soretry	16 (1.4)	5 (95.1)	N/A
Homalium	Hazombato	15 (1.28)	34 (66.3)	17 (61.4)
Erithroxylum	Tapiky	14 (1.2)	16 (84.2)	33 (25.0)
Unknown	Tsimialarano	13 (1.1)	73 (27.7)	N/A
Unknown	Vintanona	13 (1.1)	41 (59.4)	N/A
Ficus	Voara	13 (1.1)	21 (79.2)	N/A
Canarium	Haramy	12 (1.0)	57 (43.6)	5 (88.6)
Grewia	Sely	12 (1.0)	68 (32.7)	N/A
Schizoleana	Tsiarinkarina	12 (1.0)	23 (77.2)	12 (72.7)
Mascarenhasia	Barabanja	11 (.94)	17 (83.2)	37 (15.9)
Unknown	Lalombary	11 (.94)	N/A	14 (68.2)
Potameia	Antaivaratra	10 (.86)	74 (26.7)	21 (52.3)
Ampelocysios	Vahinkiribina	10 (.86)	12 (88.1)	N/A
Vernonia	Biaty	9 (.77)	80 (20.8)	N/A
Pittosporum	Maimbovitsika	9 (.77)	31 (69.3)	39 (11.4)
Bathiorhamnis	Telotritry	9 (.77)	45 (55.5)	20 (54.5)
Tinopsis	Fandifihana	8 (.68)	47 (53.5)	N/A
Homallum	Mankaranana	8 (.68)	28 (72.3)	N/A

Table 4.6 (Continued)

Genus	Local Name	Gouge Count (Percentage)	Food Tree Rank (Percentile)	Sleep Tree Rank (Percentile)
Dombeya	Hafomena	7 (.60)	83 (17.8)	N/A
Unknown	Mongy	7 (.60)	N/A	N/A
Ficus	Nonosay	7 (.60)	13 (87.1)	N/A
Unknown	Mantalany	6 (.51)	N/A	19 (56.8)
Tambourissa	Ambora	5 (.43)	65 (35.6)	26 (40.9)
Abrahamia	Haramy tangongona	5 (.43)	39 (61.4)	17 (61.4)
Ocotea	Tafonana	5 (.43)	50 (50.5)	11 (75)
Garcinia	Vongomena	5 (.43)	53 (47.5)	N/A
Oiospyros	Hazonankodavitra	4 (.34)	84 (16.8)	N/A
Unknown	Piro	4 (.34)	N/A	9 (79.5)
Abrahamia	Rotro fotsy	4 (.34)	37 (63.4)	N/A
Bakerella	Taintsitsihy	4 (.34)	8 (92.1)	N/A
Gouania	Vahintsivory	4 (.34)	22 (78.2)	N/A
Unknown	Ombavy	4 (.34)	76 (24.8)	N/A
Treculla	Sitindry	4 (.34)	40 (60.4)	N/A
Homalium	Hazambato	4 (.34)	34 (66.3)	N/A
Ampalis	Ampaly	4 (.34)	41 (59.4)	N/A
Unknown	Hazomafana	3 (.26)	N/A	29 (34.1)
Apodytes	Lengo	3 (.26)	58 (42.6)	N/A
Aphloia	Ravimbafotsy	3 (.26)	32 (68.3)	N/A
Abrahamia	Tarantana	3 (.26)	59 (41.6)	30 (31.8)
Ficus	Trotroboara	3 (.26)	27 (73.3)	N/A
Landolphia	Vahindrobanga	3 (.26)	3 (97.0)	N/A
Unknown	Andravokona	2 (.17)	N/A	N/A
Unknown	Fanjavasarotra	2 (.17)	N/A	N/A
Ficus	Hamontana	2 (.17)	24 (76.2)	38 (13.6)
Oncostemum	Hasintoho	2 (.17)	43 (57.4)	N/A
Unknown	Hazomena	2 (.17)	N/A	N/A
Polyscias	Loha	2 (.17)	62 (38.6)	N/A
Oncostemum	Maimboloha	2 (.17)	56 (44.6)	N/A
Unknown	Menahihy	2 (.17)	N/A	N/A
Unknown	Sarimanga	2 (.17)	N/A	N/A
Unknown	Tomenja	2 (.17)	N/A	N/A
Unknown	Tsivahibahitra	2 (.17)	N/A	N/A
Unknown	Dead Stick	2 (.17)	N/A	N/A
Unknown	Baroabe	1 (.09)	N/A	N/A
Unknown	Baromaitso	1 (.09)	N/A	28 (36.4)
Abrahamia	Fanonahona	1 (.09)	48 (52.5)	N/A

Table 4.6 (Continued)

Genus	Local Name	Gouge Count (Percentage)	Food Tree Rank (Percentile)	Sleep Tree Rank (Percentile)
Streblus	Hampaly	1 (.09)	38 (60.40)	N/A
Harungana	Harongana	1 (.09)	43 (57.4)	N/A
Unknown	Hasina	1 (.09)	N/A	N/A
Unknown	Kabob'ala	1 (.09)	N/A	N/A
Unknown	Lalombary	1 (.09)	N/A	14 (68.2)
Unknown	Mena voajofo	1 (.09)	N/A	N/A
Unknown	Somitrorana	1 (.09)	N/A	N/A
Unknown	Somotraorana BR	1 (.09)	N/A	N/A
Unknown	Tafomena	1 (.09)	N/A	N/A
Unknown	Tofonambory	1 (.09)	N/A	N/A
Unknown	Trotroka	1 (.09)	N/A	42 (4.5)
Unknown	Trotrokoala	1 (.09)	N/A	35 (20.5)
Unknown	Tsaramanga	1 (.09)	N/A	N/A
Unknown	Tsetseala	1 (.09)	N/A	N/A
Unknown	Tsialaramy	1 (.09)	N/A	N/A
Unknown	Tsifontso	1 (.09)	N/A	N/A
Unknown	Tsirangadranga	1 (.09)	N/A	N/A
Unknown	Vahileho	1 (.09)	N/A	N/A
Unknown	Vahimivotro	1 (.09)	N/A	N/A
Unknown	Vahimpanafana	1 (.09)	N/A	N/A
Landolphia	Vahimpingitra	1 (.09)	19 (81.2)	N/A
Unknown	Vahinamalona	1 (.09)	N/A	N/A
Unknown	Valangariky	1 (.09)	N/A	N/A
Unknown	Valotra	1 (.09)	N/A	27 (38.6)
Unknown	Vamivohotro	1 (.09)	N/A	N/A
Unknown	Voalombona	1 (.09)	N/A	N/A
Unknown	Voantsilankazaha	1 (.09)	N/A	44 (.01)

DISCUSSION

Silky sifaka diet

The intensive dietary study described in this report identified more than 100 silky sifaka foods (Patel, 2011) and confirms that silky sifakas are folivorous seed predators. Although more than 3800 hours of feeding data were collected, bark was never eaten, nor were tree exudates consumed.

However, silky sifakas at the Andaparaty field site in the Makira Natural Park, have been observed very rarely to consume the bark of Harungana trees (pers. obs.). Other eastern sifakas, such as diademed sifakas (*P. diadema*), also very occasionally consume bark and exudates, for example, feeding on bark accounted for .005% and exudates .006% of overall feeding time (Irwin, 2008). Virtually all tree gouging in eastern sifakas is therefore probably non-nutritive and does not serve as a means of exudativory (Burrows and Nash, 2010). However, western sifakas such as *P. verreauxi*, are reported to use their tooth comb to scrape and consume bark more frequently (Richard, 1978).

Gouging functions

Several functions of primate non-nutritive gouging have been proposed. Gouging may be a visual signal attracting conspecifics to scentmarks accompanying the gouge (Epple, 1970). By removing bark, gouging may promote scent longevity by creating a more absorptive substrate (Rylands, 1985). Gouging may remove female scentmarks and allow gouging males exclusive access to olfactory cues of female reproductive state (Powzyk, 1997, 2002). Like scentmarking, gouging may be performed competitively between males and function as a male status signal (Kappeler, 1998). Also like scentmarking, gouging may be a form of resource marking that advertises ownership of critical resources and facilitates relocation (Lazaro-Perea et al., 1999; Miller et al., 2003; Rasoloharijaona et al., 2010).

Male status function

The results of this study support the idea that gouging, like scent marking, functions as a male status signal. 73.3% of all silky sifaka gouges observed in this study were made by the dominant male who was the only adult male in this group. In slightly less than one year he gouged 857 times. Between the onset of adulthood at 5 years of age and an estimated maximum life expectancy of 27 years (King et al., 2005), he may gouge nearly 20,000 times in his lifetime. Gouging is likely to be energetically costly and may be an honest signal of male quality.

Although data were only obtained on two adult male Milne-Edwards' sifaka, the gouge marks of the dominant male were actually longer in size than the subordinate male. Seasonal patterns in silky sifakas also support a male status function. For both the adult and three younger males, the largest number of gouges was observed just before and during the mating season, in November and December. These results are consistent with previous research on sifakas which has found that rates of male chest scent marking are influenced by male dominance status and season (Lewis, 2005; Pochron et al., 2005; Patel, 2006). Dominant male silky sifakas and Milne-Edwards’ sifakas may gouge and scent mark more than subordinates because they are engaging in more overmarking (Patel, 2006; Patel and Girard-Buttoz, 2008). Given the size of the gouge marks (measured for the first time in this study), it is possible that males may be gouging out the scent marks of females in order to obtain exclusive access to odor cues of female estrus (Powzyk, 1997, 2002). Consistent with this, occurrences of males overmarking females accounts for the highest proportion of overmarks in silky sifakas and Milne-Edwards' sifaka. However, males do frequently overmark other males which may be more consistent with a competitive male status function (Patel, 2006).

Male-male competition is substantial in sifakas, resulting in extreme male reproductive skew (i.e., one male siring most offspring). This level of competition may not be expected, for example given the lack of sexual dimorphism in body size and canine size, a female dominant social system, and a tendency for even sex ratios (Kappeler and Schaffler, 2008). The most reproductively successful sifaka males have been found to have longer legs and greater thigh circumference than males siring fewer offspring. Male-male competition in this genus seems "…more dependent on traits related to locomotor performance rather than on traits related to fighting ability" (Lawler et al., 2005, p. 273). Gouging and scent marking, do in fact, require considerable locomotor ability, considering how often gouging and marking occurs and how rapidly males overmark the scent marks of females and other males. In silky sifakas it is not unusual for the adult male to lag behind, out of view. However, once a female scent marks, particularly during the mating season, the male seemingly "comes out of nowhere" leaping explosively between multiple trees to overmark her scentmark generally in less than 2 minutes. Such episodes like this happen dozens of times each day in the mating season (Patel, 2006). Intrasexual selection for longer and stronger legs may allow some males to be more effective at gouging, scentmarking, and overmarking.

Critical resource function

The hypothesis that gouge marks function to signal critical resources, such as food trees and sleeping sites, was supported. 61.8% of the 102 gouged tree, vine, and epiphyte species are known silky sifaka food species, and 38.2% of the gouged species are known sleeping tree species. The multiple regression analysis tested this hypothesis more precisely. Food tree percentile and sleeping tree percentile were significant predictors of the number of tree gouges accounting for 42.4% of the variance. Males within a group may vary in the extent to which they gouge critical resources (see Table 4.2). It is indeed telling that the dominant male gouged hazinina trees (*Symphonia spp.*) most, which is the most favored silky sifaka food (for the Marojejy Camp 2 group), as well as the sixth most preferred sleeping tree.

Gouging of food trees may improve foraging efficiency and advertise willingness to defend these resources. In eastern sifakas, gouging and scent marking occur continuously throughout the day, throughout the home range, often as the group is traveling. Given the large home ranges (95% kernel = 41.4 ha), daily path lengths (528 ± 162m), and considerable dietary diversity (>100 food species) of silky sifakas (Patel, 2011), gouging may also facilitate relocation of foods. In contrast to current results, Verreaux’s sifakas have not been found to preferentially scent mark food trees (Lewis, 2006). This discrepancy may be attributable to differences between species or study methodology. In the Verreaux's sifaka study, a "food tree" was defined as a tree an individual fed in just before or just after it was scent marked. In the current study, a "food tree" is a tree species determined to be part of the silky sifaka diet during the course of a one year dietary study.

In the current study, sleeping tree percentile better predicted the number of gouges by silky sifakas than food tree percentile. In retrospect, this difference is not surprising given the sleeping tree species preferences identified. The seven most slept in tree species (all of which are highly preferred food trees) accounted for 75.2% of all sleeping trees. Sleeping trees are likely to be a high priority resource since they are predominantly food trees and afford protection against predation by the fossa. The latter is Madagascar’s largest carnivore and the only known predator of eastern sifakas, other than humans (Karpany and Wright, 2007; Patel, 2005). Milne-Edwards’ sifaka may utilize several strategies against fossa predation, such as sleeping higher in the trees than when resting during the day, and almost never sleeping in the same area on consecutive nights (Wright, 1998). Similarly, silky sifakas in this study slept at higher heights when resting and group members never slept in the same trees on consecutive nights, even though some specific sleep trees were reused many times over time.

Non-nutritive gouging in sportive lemurs

Results thus suggest that male silky sifakas routinely gouge and scent mark their sleeping trees in order to advertise status, resource ownership, and food locations. Weasel sportive lemurs (*Lepilemur mustelinus*) also gouge trees near sleeping sites exclusively in non-foraging contexts. In this species, however, both sexes gouge with equal frequency and no scentmarking has been observed. Moreover, weasel sportive lemurs (*L. mustelinus*) have never been seen to gouge their actual sleeping trees, which could lead to predation. Gouging only occurs in proximity to, rather than on, sleeping trees. Unlike sifakas, sportive lemurs are cavity-nesting primates that sleep in tree holes. In other words, gouging trees adjacent to their sleeping trees may signal use and ownership of these very limited resources without compromising the ability to evade predation. Because eastern sifakas have a much larger home range and never sleep in the same region on consecutive nights, they may need to gouge sleeping trees to facilitate relocation. Any increased likelihood of predation may be offset by sleeping very high in the trees. Male golden lion tamarins (*Leontopithecus rosalia*) increase scentmarking rates soon before entering their sleeping tree cavities, despite high predation at these sites. Like silky sifakas, they may do so because these scent marks both facilitate their search for preferred tree cavities and are likely to be encountered by conspecifics (Franklin et al., 2007).

Despite different patterns of gouging, eastern sifakas and weasel sportive lemurs both seem to gouge locations that are often visited by conspecifics. These locations have a large “audience” and thereby serve as olfactory “bulletin boards” (Johnston, 1994; Rylands, 1985). Trees at Ialatsara Private Reserve, for example, have been found to have more than 100 gouge marks made by Milne-Edward’s sifakas (*P. edwardsi*) (Patel and Girard-Buttoz, 2008). Gouge marks in both sportive lemurs and sifakas may function as visual signals attracting conspecifics to chemical cues deposited by the gouger, and reduce the inefficiency of transmitting chemical signals so indirectly by scent marks (Gosling and Roberts, 2001). Milne-Edwards sifaka gouge marks that were revisited 5 months after they were made were still quite visible (pers. obs.). Saliva contained within the gouge marks may contain chemical cues utilized by females in the selection of sociosexual partners (meadow voles: Ferkin and Johnston, 1995; Mongolian gerbils: Smith and Block, 1991). Saliva may also contain androgen hormones that can influence female estrus (boars: Groschl, 2010).

Promoting scent longevity

Gouging may also be a technique to promote scent longevity and prevent scent contamination. Estimated scent mark persistence durations are generally quite brief. Scent marks may persist for ten days in dwarf mongooses (*Helogale parvula*; Rasa, 1973), a week in klipspringer antelope (*Oreotragus oreotragus*; Roberts, 1998), and up to 100 days in laboratory living golden hamsters (*Mesocricetus auratus*; Johnson and Schmidt, 1979). The high amount of rainfall in the humid forest habitats of silky sifakas and Milne-Edwards' sifaka likely considerably reduce scent mark persistence times (Regnier and Goodwin, 1977). By removing tree bark, gouging may create a smooth unadulterated or uncontaminated surface upon which scents can be deposited. Tree bark is much more chemically complex than the wood beneath it and can contain a variety of living organisms such as insects, mosses, fungi, and other plants (Harkin and Rowe, 1971). Scent marking the bark may well alter the chemical composition of the scent mark in unpredictable ways. For sifakas, gouging out a clean substrate beneath the bark may permit the oily secretions of their sebaceous chest glands to fix or preserve the volatile components in their anogenital secretions (Powzyk, 1997, 2002; Scordato et al., 2007). Gouging in sifakas is almost always followed by chest scent marking over the gouge mark which is immediately followed by ano-genital rubbing. The order of these behaviors (gouge, chest mark, ano-genital mark) is remarkably consistent and likely to be functional.

Potential gouging dental specializations

The silky sifaka adult male in this investigation is estimated to gouge 20,000 times in his lifetime. A final question is whether the morphology of the sifaka toothcomb can be considered an adaptation for tree gouging. A variety of cranial (Vinyard et al., 2003) and dental features (Eaglan, 1986) have been identified as potential specializations for exudativory in primates. For example, the “short tusked” anterior dentition of marmosets and the large tooth combs of fork-marked lemurs are generally considered adaptations for gummivory (reviewed in Nash and Burrows, 2010). Anatomists have remarked that amongst folivorous lemurs, sifakas have an unusually robust four-tooth comb. It is characterized by a “marmoset-like” morphology with high crowned teeth in the comb, which is narrow mesiodistally (Eaglen, 1986; Rosenberger, 2010). However, since no sex differences have been reported in toothcomb structure or wear to date, it seems unlikely that silky sifaka toothcombs are specialized for tree gouging. Lemur dentition does correlate with diet to some extent (reviewed in Cuozzo and Yamashita, 2006), and their robust tooth combs may therefore have evolved to facilitate periodic bark extraction and consumption by both sexes, which is seen more often in western sifakas (Richard, 1985). Sifaka tooth combs may be an example of a preadaptation where the dental morphology shared by both sexes, evolved for dietary reasons, yet permits one sex to gouge trees on a daily basis as a communication signal.

CONCLUSIONS

Non-nutritive tree gouging by male eastern sifakas likely serves multiple functions. This study has found evidence that gouging, like scent marking, functions as a male status signal as well as signalling critical resources. Because gouging is generally accompanied by chest (and maybe saliva) scent marking, it is difficult to separate the unique functions of gouging per se. However, preliminary data suggests that comparing responsiveness to male scentmarks with and without gouges may permit several gouging-specific hypotheses to be tested (Patel and Girard-Buttoz, 2008). Unique functions of gouging may include attracting the visual attention of conspecifics, promoting scent longevity by removing bark and scent marking the more absorptive wood beneath, and gouging out the scent marks of conspecifics (Powzyk, 1997, 2002; Rylands, 1985).

ACKNOWLEDGMENTS

I thank the government of the Democratic Republic of Madagascar for permission to conduct research in Marojejy National Park and Ialatsara Private Reserve. Particular thanks are due to Madagascar’s Ad Hoc Committee for Fauna and Flora and Organizational Committee for Environmental Research (CAFF/CORE), Ministry of the Environment and Water and Forests, and National Association for the Management of Protected Areas (ANGAP) for granting permits. For logistical support, I thank Dr. Benjamin Andriamihaja, ANGAP Andapa Director J. H. Bakarizafy, the Malagasy Institute for the Conservation of Tropical Environments (MICET), and the Institute for the Conservation of Tropical Environments (ICTE). Thanks are also due to Daniel and Berenice Rajaona for their permission and encouragement to study Milne-Edwards’ sifakas at Ialatsara Forest Station. For assistance in identifying tree species, thanks are due to Honoré Andriamiarinoro, Jean Chrysostome Bevao, and Desire Rabary. For assistance in collecting dietary, sleeping tree, and gouging data, thanks are due to Guy Irenel Raoliniaina, Lanto Andrianandrasana, Dez Kely, Kristen Alldredge, Daniela Herzog, and Cedric Girard-Buttoz. Finally, Jean Nestor Randrianasy and Janvier Rabe assisted in tracking silky sifakas each day. It is gratefully acknowledged that funding for this project was provided by the Silicon Valley Community Foundation, Seneca Park Zoo, Cheyenne Mountain Zoo, and the British Broadcasting Corporation.

REFERENCES

Allen, J.A. (**1877**). "History of the American bison, *Bison americanus*," Annual Rep. U.S. Geolog. Geograph. Surv. Territor. **9**, 443-587.

Altmann, J. (**1974**). "Observational study of behavior: Sampling methods," Behav. **49**, 227-265.

Bearder, S.K. and Doyle, G.A. (**1974**). "Field and laboratory studies of social organization in bushbabies (*Galago senegalensis*)," J. Hum. Evol. **3**, 37-50.

Bowyer, T.R., Manteca, X., and Hoymork, A. (**1998**). "Scent marking in American bison: Morphological and spatial characteristics of wallows and rubbed trees," In *International Symposium on Bison Ecology and Management in North America* edited by L.R. Irby and J.E. Knight (Montana State University: Bozeman, Montana), pp. 81-91.

Bowyer, T.R., Van Ballenberghe, V., and Rock, K.R. (**1994**). "Scent marking by Alaskan moose: characteristics and spatial distribution of rubbed trees," Canad. J. Zool. **72**, 2186-2192.

Burrows, A.M and Nash, L.T. (**2010**). *The Evolution of Exudativory in Primates*. Springer. Pp. 303.

Cuozzo, F.P. and Yamashita, N. (**2006**). Impact of ecology on the teeth of extant lemurs: a review of dental, adaptations, function, and life history. In Lemurs: Ecology and Adaptation edited by L. Gould and M.L. Sauther. Springer: New York. pp. 67-96.

Eaglen RH. (**1986**) "Morphometrics of the anterior dentition in strepsirhine primates," Amer. J. Phys. Anthrop. **71**, 185–202.

Franklin, S.P., Miller, K.E., Baker, A.J., Dietz, J.M. (**2007**). "Do cavity-nesting primates reduce scent marking before retirement to avoid attracting predators to sleeping sites?" Amer. J. of Primatol. **69**, 255-266.

Gosling, L.M. and Roberts, S.C. (**2001**). "Scent marking by male mammals: Cheat-proof signals to competitors and mates," Advan. Study Behav. **30**, 169-217.

Harkin, J.M. and Rowe, J.W. (**1971**). "Bark and its possible uses," USDA Research Note. FPL **091**, 1-56.

Irwin, M.T., Samonds, K.E., Raharison, J.L., and Wright, P.C. (**2004**). "Lemur latrines: Observations of latrine behavior in wild primates and possible ecological significance," J. Mammal. **85**, 420-427.

Irwin, M.T., Raharison, F.J.L., Rakotoarimanana, H., Razanadrakoto, E., Ranaivoson, E., Rakotofanala, J., and Randrianarimanana, C. (**2007**). "Diademed sifakas (*Propithecus diadema*) use olfaction to forage for the inflorescences of subterranean parasitic plants (Balanophoraceae: Langsdorffia sp., and Cytinaceae: Cytinus sp.)," Amer. J. Primatol. **69**, 471-476.

Johansson, A., and Liberg, O. (**1996**). "Functional aspects of marking behaviour by male roe deer *(Capreolus capreolus),*" J. Mammal. **77**, 558-567.

Johnston, R.E., Chiang, G. and Tung, C. (**1994**). "The information in scent over-marks of golden hamsters," Anim. Behav. **48**, 323-330.

Johnston, R. E., and Schmidt, T. (**1979**). "Responses of hamsters to scent marks of different ages," Behav. Neural Biol. **26**, 64-75.

Kappeler, P.M. and Schaeffler, L. (**2008**). "The lemur syndrome unresolved: extreme male reproductive skew in sifakas (*Propithecus verreauxi*), a sexually monomorphic primate with female dominance," Behav. Ecol. Sociobiol. **62**, 1007-1015.

Karpanty, S. M., and Wright, P. C. (2007). "Predation on lemurs in the rainforest of Madagascar by multiple predator species: observations and experiments," In *Primate Anti-Predator Strategies*, edited by S. L. Gursky and K. A. I. Neckaris (Springer: New York), pp. 77-99.

King, S.J., Arrigo-Nelson, S.J., Pochron, S.T., Semprebon, G.M, Godfrey, L.R., Wright, P.C., and Jernvall, J. (**2005**). "Dental senescence in a long-lived primate links infant survival to rainfall," Proc. Natl. Acad. Sci. USA **102**, 16579-16583.

Koprowski, J.L. (**1991**). "Damage due to scent marking by eastern gray and fox squirrels," Proc. Great Plains Wildlife Dam. Conf. **10**, 101-105.

Kraus C, Heistermann M, Kappeler PM. (**1999**). Physiological suppression of sexual function of subordinate males: a subtle form of intrasexual competition among male sifakas (*Propithecus verreauxi*)? *Physiology and Behavior* 66:855–861.

Kruuk H. (**1992**). "Scent marking by otters (*Lutra lutra*): signaling the use of resources," Behav. Ecol. **3**, 133–140.

Lacher, T.E., Da Fonseca, G.A.B., Alves, C., and Magalhaes-Castro, B. (**1981**). "Exudate-eating, scent-marking, and territoriality in wild populations of marmosets," Anim. Behav. **29**, 306-307.

Lazaro-Perea, C., Snowdon, C. T. & Fatima Arruda, M. (**1999**). "Scent marking behavior in wild groups of common marmosets (*Callithrix jacchus*)," Behav. Ecol. Sociobiol. **46**, 313–324.

Lehner, P.N. (**1996**). *Handbook of Ethological Methods*, 2nd Edition. Cambridge University Press: New York.

Lewis, R.J. (**2005**). "Sex differences in scent marking in sifaka: Mating conflict or male services?" Amer. J. Phys. Anthro. **128**, 389-398.

Lewis, R.J. (**2006**). "Scent marking in sifaka: no one function explains it all," Amer. J. Primatol. **68**, 622-636.

Lewis, R.J. (**2009**). "Chest staining variation as a signal of testosterone levels in male Verreaux's sifaka," Phys. Behav. **96**, 586-592.

Miller, K.E., Laszlo, K., and Dietz, J.M. (**2003**). "The role of scent marking in the social communication of wild golden lion tamarins, *Leontopithecus rosalia*," Anim. Behav. **65**, 795-803.

Morelli, T.L. and Wright, P.C. (**2006**). "Expect the unexpected: mating monogamy in a purportedly polygamous prosimian," Int. J. Primatol. **27**, Abstr. #497.

Nekaris, K.I., Starr, C.R., Collins, R.L., and Wilson, A. (**2010**). Comparative ecology of exudate feeding by lorises (*Nycticebus*, *Loris*) and Pottos (*Perodicticus*, *Arctocebus*). In *The Evolution of Exudativory in Primates* edited by Burrows, A.M and Nash, L.T. Springer. Pp. 155-168.

Nievergelt, C.M., Mutschler, T., and Feistner, A.T.C. (**1998**). "Group encounters and territoriality in wild Alaotran gentle lemurs (*Hapalemur griseus alaotrensis*)," Amer. J. Primatol. **46**, 251-258.

Patel, E. R. (**2005**). "Silky sifaka (*Propithecus candidus*) predation by a fossa (*Cryptoprocta ferox*)," Lemur News **10**, 25-27.

Patel, E.R. (**2006**). "Scent marking in wild silky sifakas (*Propithecus candidus*) in Madagascar: Sex differences and seasonal effects in usage and response across multiple scent mark types," Int. J. Primatol. **27**, Abstr. #496.

Patel, E. R. (**2011**). "Diet, habitat, and ranging of the silky sifaka (*Propithecus candidus*)," Unpublished report to Madagascar National Parks. Pp. 1-23.

Patel, E.R. and Girard-Buttoz, C. (**2008**). "Non-nutritive tree gouging in wild Milne-Edwards' sifakas (*Propithecus edwardsi*): Description and potential communicative functions," Primate Eye **96**: Abstr. #283.

Pochron, S.T., Morelli, T.L., Terranova, P., Scirbona, J., Cohen J., Kunaperredy G., Rakotonirina G, Ratsimbazafy, R., Rakotosoa, R., Wright, P.C. (**2005**). "Patterns of male scent-marking in *Propithecus edwardsi* of Ranomafana National Park, Madagascar," Amer. J. Primatol. **65**,103–115.

Powzyk, J.A. (**1997**). "The socio-ecology of two sympatric indriids: *Propithecus diadema diadema* and *Indri indri*, a comparison of feeding strategies and their possible repercussions on species- specific behaviors," Ph.D. dissertation, Duke University, Durham, NC.

Powzyk, J.A. (**2002**). "Scent wars," Nat. Hist. **111**: 82-85.

Rasa, O. A. E. (**1973**). "Marking behaviour and its social significance in the African dwarf mongoose, *Helogale undulata rufula*," Zeitschr. Tierpsych. **32**, 293-318.

Rasoloharijaona, S. Randrianambinina, B., and Joly-Radko, M. (**2010**). "Does nonnutritive tree gouging in a rainforest-dwelling lemur convey resource ownership as does loud calling in a dry forest-dwelling lemur?" Amer. J. Primatol. **72**, 1062-1072.

Regnier, F. E., and Goodwin, M. (**1977**). "On the chemical and environmental modulation of pheromone release from vertebrate scent marks," In *Chemical Signals in Vertebrates* edited by D. Miller-Schwarze and M. M. Mozell. New York: Plenum. pp. 115-133.

Richard, A.F. (**1978**). "Variability in the feeding behavior of a Malagasy prosimian, *Propithecus verreauxi*: Lemuriformes," In *The Ecology of Arboreal Folivores* edited by G.G. Montgomery. Smithsonian Institution Press: Washington, D.C. pp. 519-533.

Richard, A.F. (**1985**). *Primates in Nature* (Freeman and Company: New York).

Roberts, S.C. (**1998**). "Behavioural responses to scent marks of increasing age in klipspringer *Oreotagus oreotragu," Ethology* **104**, 585-592.

Rosenberger, A.L. (**2010**). "Adaptive profile versus adaptive specialization: Fossils and gummivory in early primate evolution," In *The Evolution of Exudativory in Primates* edited by A.M. Burrows and L.T. Nash. Springer. pp. 273-295.

Rylands, A. B. (**1985**). “Tree-gouging and scent-marking by marmosets,” Anim. Behav. **33**, 1365–1367.

Schilling, A. (**1979**). “Olfactory communication in prosimians,” In *The Study of Prosimian Behavior* edited by G.A. Doyle and R.D. Martin. (Academic Press: New York). pp. 461-542.

Scordato, E.S., Dubay, G., and Drea, C.M. (**2007**). “Chemical composition of scent marks in the ringtailed lemur (*Lemur catta*): glandular differences, seasonal variation, and individual signatures,” Chem. Sens. **32**, 493-504.

Shorten, M. (**1957**). “Damage caused by squirrels in Forestry Commission areas 1954-6,” Forestry **30**, 151-172.

Smith, J. L. D., McDougal, C., and Miquelle, D. (**1989**). “Scent marking in free-ranging tigers *Panthera tigris*,” Anim. Behav. **37**, 1-10.

Vinyard, C.J., Wall, C.E., Williams, S.H., and Hylander, W.L. (**2003**). “Comparative functional analysis of skull morphology of tree-gouging primates,” Amer. J. Phys. Anthro. **120**, 153-170.

CHAPTER 5

Dissertation Conclusion

This dissertation examined a number of issues that are of current interest to the fields of primate vocal and olfactory communication. The results of the first long-term study of the silky sifaka (*Propithecus candidus*) are also presented. The goals of the three studies within this dissertation were reviewed in Chapter 1. This final chapter reviews the results and discusses the broader implications of the findings.

The twenty-four month longitudinal study described in Chapter 2 identified several infant characterstics and acoustic features which influenced the likelihood of mothers responding to their infants' "gecker" vocalizations. Mothers were most responsive to tonal high frequency geckers with high harmonic-to-noise ratio (HNR) values and high values for the first spectral peak (see Figure 2.1.a.). High frequency variants of a distress call have often been correlated with increased arousal and pain as well as being perceived as aversive by receivers (human infants: LaGasse et al., 2005; redfronted lemurs: Fichtel and Hammerschmidt, 2002; pig-tailed macaque: Gouzoules and Gouzoules, 1989; piglets: Weary et al., 1998). Contrary to the results presented in Chapter 2, low HNR values (increased noisiness) are more often associated with high arousal contexts likely to induce receiver response (chacma baboons: Fischer et al., 2001, Rendall, 2003; infant elephants: Stoeger et al., 2011; bonnet macaques: Coss et al., 2007). However few studies have assessed receiver responses to variation in HNR.

Why might rhesus mothers be more responsive to gecker bouts containing more tonal gecker pulses? Tonal geckers may have higher mean frequencies and thereby lead to greater maternal response. Tonal geckers are also generally found within heterogenous bouts which also contain more typical noisy geckers (see Figure 2.1.a.). Heterogenous bouts, due to their novelty and variation, may be more salient to mothers (Todt, 1988; Jovanovic and Gouzoules, 2001). A third possibility is that this result is an artifact of mothers in general being more responsive to the geckers of males who have higher HNR's than the geckers of females.

Even after controlling for body weight, the geckers of males were found to be less noisy, louder, shorter, and have lower spectral peaks than female geckers. These results importantly show that sex differences in the acoustic structure of infant vocalizations are evident within the first two years of age. These acoustic cues to infant sex are possibly utilized by mothers since maternal responsiveness was higher for male geckers (47.2%) than female geckers (17.4%).

Acoustic cues to infant age were also found, although they were restricted to a few temporal measures. Younger infants emitted fewer pulses per bout, shorter pulses, and shorter bouts. These slight changes can be assumed to be maturational change, as seen in other nonhuman primates (Hammerschmidt et al., 2001; Winter et al., 1973). Mothers may have utilized these cues since they were most responsive to young infants. Although infants as old as 17 months emitted geckers, more than 75% of the geckers to which mothers responded were emitted by infants 4 months old or younger. Overall, mothers showed immediate response only to 38% of gecker bouts which is similar to stump-tailed macaques (Maestripieri, 1995). That most geckers were not responded to, particularly for older infants, suggests that geckers of older infants may not be an honest reflection of need (Maestripieri, 2002).

Acoustic variation did not differ appreciably between contexts which suggests that geckers are not differentiated signals of specific need. Geckers were produced in nine major behavioral contexts. Most geckers occurred while the infant was following its mother (25%), after receiving maternal aggression (22%), and when the distance to the mother changed such as when mothers moved away (19%). Spontaneous geckers (22%) were also common, which is consistent with the idea that some geckers are artifacts of basic nervous system development rather than having signaling functions per se (Newman, 1995).

In sum, geckers are likely to be highly salient and localizable to receivers. The overall acoustic structure of geckers consists of multiple pulses of broadband noise with occasional periodic components. With just one reliable frequency peak just below 3000Hz, geckers can be considered “spectrally structured noise” (Beeman, 1998). Their abrupt, high-amplitude pulses and broadband atonal spectra likely make geckers particularly difficult to ignore as an auditory event (Owren and Rendall, 1997, 2001). These same features also suggest that geckers should be easy to localize in both vertical and horizontal dimensions (Brown et al., 1982; Heffner, 2004; Recanzone and Beckermann, 2004). Moreover, auditory localization is facilitated when sounds are produced in conjunction with salient visual events (e.g., Heffner, 2004), such as the dramatic, spasmodic wholebody jerking that can accompany geckering. Geckers are thus well designed to serve as signals of distress, and communicative significance likely adds additional salience for species-specific listeners.

Chapter 3 discusses a 15 month study of zzuss vocalization structure and function in wild silky sifakas inhabiting the mountainous rainforests of northeastern Madagascar. These calls are one of the loudest and most commonly produced silky sifaka vocalizations. However, neither the zzuss nor any other alarm calls of the genus *Propithecus* have as yet received detailed acoustic analysis.

Acoustic analyses revealed that zzuss bouts, on average, are comprised of two, 220-ms calls spaced 2.4 s apart. While vocalizing, callers rapidly jerk their heads as if sneezing, and for unknown reasons most calls are followed by an audible lipsmack within 1 s. Though emitted with the mouth closed, signal-to-noise ratio was quite high confirming that these are “loud” calls. An average of 10.5 zzuss calls were produced by the group per hour, but up to several hundred calls have been documented within one hour. The acoustic structure of zzuss calls is somewhat unique in routinely showing broadband noise at the beginning and end, with a prominent, tonal mid-section. This overall structural pattern has not been documented in other lemur genera (Macedonia and Stanger, 1994), and is not common in mammalian vocalizations generally (cf. Beeman, 1998). The rapid frequency modulation and frequency jumps are particularly dramatic, with fundamental frequency changes of almost 4 kHz up and down occurring in less than 100 ms. 51.3% of zzuss calls contained frequency jumps which have not previously been identified in lemur vocalizations. Frequency jumps have thus far only been found in chimpanzees (Riede *et al.*, 2004) and in infant macaques (Riede *et al.*, 1997), though they are probably more widespread.

Zzuss vocalizations have most often been hypothesized to function as group coordination calls or anti-predator calls against predation by the civet-like fossa, Madagascar’s largest carnivore. Some of the predictions of the anti-predator hypothesis were partially supported. 16.9% of zzuss calls were emitted during obvious terrestrial disturbances. 21.3% of zzuss calls were emitted spontaneously while resting which may include some terrestrial disturbances which were not readily observable to us as researchers but were noticed by the animals. Callers also stared downwards (28.1%) more than they stared upwards (13.8%). Zzuss were also produced at higher rates when sifakas were first waking up in the morning, which may be when fossa are hunting sifakas most actively (Wright, 1998). However, several predictions were not well supported. Acoustic variation showed little evidence of context specificity. In other words, there was no zzuss variant or call subtype which was emitted during terrestrial disturbances or any of the other five major contexts. Callers seldom moved upwards, in most cases (56.9%) there was no movement.

Finally, although fossa tend to hunt sifakas more during the dry season (Dollar *et al.*, 2007; Irwin *et al.*, 2009; Wright, 1998), call rate did not vary seasonally.

The predictions of the group coordination hypothesis were more strongly supported. 39.4% of zzuss calls were emitted in response to the "howl" lost calls of distant group members; which is higher than any of the other five contexts. Seasonal peaks in call rate were not predicted and not observed. Callers were not predicted to move, and seldom did so. Sex and individual differences were found in zzuss acoustic structure which is characteristic of other lemur group cohesion calls (Milne-edwards' sportive lemur: Rasoloharijaona et al., 2006; gray mouse lemurs: Leliveld et al., 2011; ring-tailed lemurs: Macedonia, 1986). Thus, zzuss usage and acoustic variation are consistent with having a combined function as a terrestrial-disturbance and group-coordination call. They cannot be considered functionally referential calls due to the low production specificity documented in this study.

Individual differences in zzuss acoustic structure were slightly more robust than the sex differences. 59% of the calls from the four females and 73% of calls from the five males were successfully classified according to discriminant function analysis. Calculating percentage error reduction helps clarify discriminant-function performance by taking chance rates into account. Error reduction for classification by individual would be 66% for males and 45% for females. Classification success was just over 71% correct by sex, statistically higher than expected by chance but only an intermediate degree of error reduction at less than 40%. Classification by sex was thus not as accurate as in a number of other primate studies (*Leontopithecus rosalia*: Benz *et al.*, 1990; *Eulemur coronatus*: Gamba and Giacoma, 2007; *Indri indri*: Giacoma *et al.*, 2010; *Pan troglodytes*: Mitani and Gros Louis, 1995; *Callithrix kuhlii*: Smith *et al.*, 2009). However, since silky sifakas are considered monomorphic (Kappeler, 1990, 1991; Lawler *et al.*, 2005), any evidence of sex differences is of interest.

Finally, Chapter 3 also examined which acoustic features most distinguished individuals and the sexes. This is a topic of some debate. On the one hand, broadband noisy calls (e.g. "grunts") and tonal calls with low fundamental frequencies (e.g. "coos") have often been found to differ between individuals and the sexes in acoustic measures related to vocal tract filtering; namely, spectral peaks or formants which are proportional to the caller's vocal tract length and possibly body size (e.g., red-bellied lemurs: Gamba, 2011; chacma baboons: Owren et al., 1997; rhesus macaques: Rendall et al., 1998). Fundamental frequency measures, by contrast, are not proportional to body size, though they are proportional to vocal fold size and shape. Such observations have motivated some researchers to claim that fundamental frequency is "…a weak parameter for providing individual cues" (Gamba, 2011, p. 5). Recent work in small bodied nocturnal lemurs paints a different picture. High frequency tonal calls with considerable frequency modulation differ between individuals and the sexes in fundamental frequency measures (gray mouse lemurs: Leliveld et al., 2011; Milne-edwards' sportive lemurs: Rasoloharijaona et al., 2006).

Silky sifaka zzzus calls were found in this study to differ between individuals and the sexes in both fundamental frequency measures and spectral peaks; although the fundamental frequency measures were particularly effective at distinguishing males from females. For example, F_0-Mean values were approximately 60% higher in females than in males, and their calls were also much more likely to exhibit frequency jumps (72.5%) than were male versions (30.0%). Call duration was the only acoustic measure that did not differ between individuals, nor did it distinguish males and females. Sex differences also included female zzuss calls having higher amplitudes and SNR values, longer latencies to lipsmack, slightly higher first spectral peaks, and slightly less noisy calls.

Chapter 4 examined the form and function of male tree gouging behavior in two species of eastern sifakas. Eastern sifakas may be the only group of primates that routinely gouge trees for non-nutritive communicative reasons. The goal of this study was to conduct the first detailed examination of gouging in a *Propithecus* species in order to distinguish between several possible communicative functions. A one year study was conducted of silky sifaka (*Propithecus candidus*) gouging in relation to their dietary and sleeping tree preferences. During a one month study of Milne-edwards' sifakas (*P. edwardsi*), gouge marks were actually measured.

More than 3800 hours of feeding data were collected and confirms that male gouging in silky sifakas is non-nutritive. Though more than 100 plant foods were identified, bark was never eaten, nor were tree exudates consumed. These results resemble other eastern sifakas but differ from western dry forest sifakas, such as *P. verreauxi*, where up to 15% of their feeding time can be spent on bark during certain seasons (Richard, 1978, 1985).

The results of this study support the hypothesis that gouging functions as a male status signal. During one year, the dominant male silky sifaka gouged 857 times which accounted for 73.3% of all gouges observed. Gouging was most frequent just before and during the mating season. In Milne-edwards' sifakas, the more dominant of two males actually had longer measured gouge marks. Given the obvious energetic costs and the high frequency, it is reasonable to consider gouging an honest signal of male quality.

Gouging may also facilitate species recognition. Species differences were found in gouge mark morphology. 66.7% of Milne-edwards' sifaka gouge marks were examples of the highly distinctive "bird footprint" pattern which was never observed in silky sifaka gouge marks. All silky sifaka gouge marks were single irregular polygons, generally roundish.

The resource gouging hypothesis was tested and supported in silky sifakas. 61.8% of the 102 gouged tree, vine, and epiphyte species were known food species, and 38.2% of the gouged species were known sleeping tree species. Moreover, a multiple regression analysis revealed that the number of gouges per tree species was predicted by the percentile rank of those species as food tree species and sleep tree species. Sleep tree percentile better predicted the number of gouges by silky sifakas than food tree percentile which is not surprising given the strong sleeping tree species preferences identified in this study. The seven most slept in tree species (all of which are highly preferred food trees) accounted for 75.2% of all sleeping trees. Critical resources such as food trees and sleeping sites may be preferentially gouged in order to facilitate relocation and advertise ownership and willingness to defend these resources. These locations are likely to be highly visited and scent marked by conspecifics, thereby having a large "audience" and serving as olfactory "bulletin boards" (Johnston et al., 1994; Rylands, 1985). Gouging may deposit olfactory cues in saliva which may contain androgen hormones influencing female estrus and be utilized by females in the selection of sociosexual partners (Ferkin and Johnston, 1995; Groschl, 2010).

Gouge marks may also be visual signals that attract conspecifics to scent marks. Similarly, the scratch marks with urination in felids and the tree-rubs of moose and bison may function as "scent mark flags". Sifaka gouge marks may be visible for 5 months or longer (Patel and Girard-Buttoz, 2008) long after the scent mark has faded.

Finally, gouging may prevent scent contamination, a hypothesis that has not been proposed previously. By removing tree bark, gouging may create a smooth unadulterated or uncontaminated surface upon which scents can be deposited. Tree bark is much more chemically complex than the wood beneath it and may contain a variety of living organisms such as insects, mosses, fungi, and other plants (Harkin and Rowe, 1971). Scent marking the bark may well alter the chemical composition of the scent mark in unpredictable ways. For sifakas, gouging out a clean substrate beneath the bark may also permit the oily secretions of their sebaceous chest glands to fix or preserve the volatile components in their anogenital secretions (Powzyk, 1997, 2002; Scordato et al., 2007).

Non-nutritive tree gouging by male eastern sifakas likely serves multiple functions. This study has found evidence that gouging, like scent marking, functions as a male status signal as well as signalling critical resources. Because gouging is generally accompanied by chest (and maybe saliva) scent marking, it is difficult to separate the unique functions of gouging per se. However, preliminary data suggests that comparing responsiveness to male scentmarks with and without gouges may permit several gouging-specific hypotheses to be tested (Patel and Girard-Buttoz, 2008). Unique functions of gouging may include attracting the visual attention of conspecifics, promoting scent longevity by removing bark and scent marking the more absorptive wood beneath, and gouging out the scent marks of conspecifics (Powzyk, 1997, 2002; Rylands, 1985).

REFERENCES

Beeman, K. (**1998**). “Digital signal analysis, editing and synthesis,” In *Animal Acoustic Communication: Sound Analysis and Research*, edited by S. L. Hopp, M. J. Owren, and C. S. Evans (Springer-Verlag, Berlin), pp. 59-104.

Benz, J. J., French, J. A., and Leger, D. W. (**1990**). “Sex differences in vocal structure in a callitrichid primate, *Leontopithecus rosalia*,” Amer. J. Primat. **21**, 257-264.

Brown, C. H., Schessler, T., Moody, D., and Stebbins, W. (**1982**). “Vertical and horizontal sound localization in primates,” J. Acoust. Soc. Amer. **72**, 1804-1811.

Coss, R.G., McCowan, B., and Ramakrishnan, U. (**2007**). “Threat-related acoustical differences in alarm calls by wild bonnet macaques (*Macaca radiata*) elicited by python and leopard models,” Ethol. **113**, 352-367.

Dollar, L. J., Ganzhorn, J. U., and Goodman, S. M. (**2007**). “Primates and other prey in the seasonally variable diet of *Cryptoprocta ferox* in the dry deciduous forest of western Madagascar,” In *Primate Anti-Predator Strategies*, edited by S. L. Gursky and K. A. I. Neckaris (Springer, New York), pp. 63-76.

Epple, G. (**1970**). "Quantitative studies on scent marking in the marmoset (Callithrix jacchus)," Folia Primat. **13**, 48-62.

Fichtel, C. and Hammerschmidt, K. (**2002**). “Responses of redfronted lemurs to experimentally modified alarm calls: Evidence for urgency-based changes in call structure,” Ethol. **108**, 763-777.

Fischer, J., Hammerschmidt, K., Cheney, D.L., and Seyfarth, R.M. (**2001**). “Acoustic features of female chacma baboon barks,” Ethol. **107**, 33-54.

Gamba, M., and Giacoma, C. (**2007)**. “Quantitative acoustic analysis of the vocal repertoire of the crowned lemur,” Ethol. Ecol. Evol. **19**, 323-343.

Gamba, M., Colombo, C., and Giacoma, C. (**2011**). “Acoustic cues to caller identity in lemurs: A case study,” Ethol. http://dx.doi.org/10.1007/s10164-011-0291-z

Giacoma, C., Sorrentino, V., Rabarivola, C., and Gamba, M. (**2010**). “Sex differences in the song of *Indri indri*,” Int. J. Primat. **31**, 539-551.

Gouzoules, H. and Gouzoules, S. (**1989**). “Design features and developmental modification of pigtail macaque, *Macaca nemestrina*, agonistic screams,” Anim. Behav. **37**, 383-401.

Hammerschmidt, K., Freudenstein, T. and Jürgens, U. (**2001**). “Vocal development in squirrel monkeys,” Behaviour **138**, 1179-1204.

Harkin, J.M. and Rowe, J.W. (**1971**). “Bark and its possible uses,” USDA Research Note. FPL **091**, 1-56.

Heffner, R. S. (**2004**). “Primate hearing from a mammalian perspective,” Anat. Rec. Part A **281A**, 1111-1122.

Irwin, M. T., Raharison, J. L. and Wright, P. C. (**2009**). “Spatial and temporal variability in predation on rainforest primates: Do forest fragmentation and predation act synergistically?” Anim. Conserv. **12**, 220-230.

Johnston, R.E., Chiang, G. and Tung, C. (**1994**). “The information in scent over-marks of golden hamsters,” Anim. Behav. **48**, 323-330.

Jovanovic, T., and Gouzoules, H. (**2001**). “Effects of maternal restraint on the vocalizations of infant rhesus monkeys (*Macaca mulatta*),” Amer. J. Primat. **53**, 33 -45.

Kappeler, P.M. (**1990**). “The evolution of sexual size dimorphism in prosimian primates,” Am. J. Primat. **21**, 201-214.

Kappeler, P. M. (**1991**). “Patterns of sexual dimorphism in body weight among prosimian primates,” Folia Primat. **57**, 132-146.

LaGasse, L. L., Neal, A. R., and Lester, B. M. (**2005**). “Assessment of infant cry: Acoustic cry analysis and parental perception," Mental Retard. Develop. Disabil. Res. Rev. **11**, 83–93.

Lawler, R. R., Richard, A. F., and Riley, M. A. (**2005**). “Intrasexual selection in Verreaux's sifaka (*Propithecus verreauxi verreauxi*),” J. Human Evol. **48**, 259-277.

Leliveld, L., Scheumann, M., and Zimmermann, E. (**2011**). “Acoustic correlates of individuality in the vocal repertoire of a nocturnal primate (*Microcebus murinus*),” J. Acoust. Soc. Am. **129**, 2278-2288.

Macedonia, J. M. (**1986)**. “Individuality in a contact call of the ringtailed lemur *(Lemur catta)*,” Am. J. Primatol. **11**, 163-179.

Macedonia, J. M. and Stanger, K. (**1994)**. “Phylogeny of the Lemuridae revisited: Evidence from communication signals,” Folia Primat. **63**, 1-43.

Maestripieri, D. (**1995**). “Maternal responsiveness to infant distress calls in the stumptail macaque,” Folia Primatol. **64**, 201-206.

Maestripieri, D. (**2002**). “Parent-offspring conflict in primates,” Int. J. Primatol. **23**, 923-951.

Mitani, J. C., and Gros-Louis, J. (**1995**). “Species and sex differences in the screams of chimpanzees and bonobos,” Int. J. Primat. **16**, 393-411.

Newman, J. D. (**1995**). Vocal ontogeny in macaques and marmosets: Convergent and divergent lines of development. In Current Topics in Primate Vocal Communication, edited by E. Zimmermann, U. Jürgens, and D. Symmes (Plenum, New York), pp. 73–97.

Owren, M. J., Seyfarth, R. M., and Cheney, D. L. (**1997**). “The acoustic features of vowel-like grunt calls in chacma baboons (*Papio cynocephalus ursinus*): Implications for production processes and functions,” J. Acoust. Soc. Am. **101**, 2951-2963.

Owren, M. J., and Rendall, D. (**2001**). “Sound on the rebound: Bring form and function back to the forefront in understanding nonhuman primate vocal signaling,” Evol. Anthropol. **10**, 58-71.

Patel, E.R. and Girard-Buttoz, C. (**2008**). “Non-nutritive tree gouging in wild Milne-Edwards’ sifakas (*Propithecus edwardsi*): Description and potential communicative functions,” Primate Eye **96**: Abstr. #283.

Powzyk, J.A. (**1997**). “The socio-ecology of two sympatric indriids: *Propithecus diadema diadema* and *Indri indri*, a comparison of feeding strategies and their possible repercussions on species- specific behaviors,” Ph.D. dissertation, Duke University, Durham, NC.

Rasoloharijaona, S., Randrianambinina, B., Braune, P., and Zimmermann, E. (**2006)**. “Loud calling, spacing, and cohesiveness in a nocturnal primate, the Milne Edwards' sportive lemur (*Lepilemur edwardsi*),” Am. J. Phys. Anthro. **129**, 591-600.

Recanzone, G. H., and Beckermann, N. S. (**2004**). “Effects of intensity and location on sound location discrimination in macaque monkeys,” Hear. Res. **198**, 116-124.

Rendall, D., Owren, M. J., and Rodman, P. S. (**1998**). “The role of vocal tract filtering in identity cueing in rhesus monkey (*Macaca mulatta*) vocalizations,” J. Acoust. Soc. Am. **103**, 602-614.

Rendall, D. (**2003**). “Acoustic correlates of caller identity and affect intensity in the vowel-like grunt vocalizations of baboons,” J. Acous. Soc. Am **113**, 3390-3402.

Richard, A.F. (**1978**). “Variability in the feeding behavior of a Malagasy prosimian, *Propithecus verreauxi*: Lemuriformes,” In *The Ecology of Arboreal Folivores* edited by G.G. Montgomery. Smithsonian Institution Press: Washington, D.C. pp. 519-533.

Richard, A.F. (**1985**). *Primates in Nature* (Freeman and Company: New York).

Riede, T., Wilden, I., and Tembrock, G. (**1997**). “Subharmonics, biphonations, and frequency jumps—common components of mammalian vocalization or indicators for disorders?” Z. Säugetierkunde **62 (Suppl. II**), 198-203.

Riede, T. R., Owren, M. J., and Arcadi, A. C. (**2004**). “Nonlinear acoustics in the pant-hoot vocalizations of common chimpanzees (*Pan troglodytes*): Frequency jumps, subharmonics, biphonation, and deterministic chaos,” Am. J. Primatol. **64**, 277-291.

Rylands, A. B. (**1985**) “Tree-gouging and scent-marking by marmosets,” Anim. Behav. **33**, 1365–1367.

Scordato, E.S., Dubay, G., and Drea, C.M. (**2007**). “Chemical composition of scent marks in the ringtailed lemur (*Lemur catta*): glandular differences, seasonal variation, and individual signatures,” Chem. Sens. **32**, 493-504.

Smith, A. S., Birnie, A. K., Lane K. R., and French, J. A. (**2009**). “Production and perception of sex differences in vocalizations of Wied’s black-tufted-ear marmosets (*Callithrix kuhlii*),” Am. J. Primatol. **71,** 324-332.

Stoeger, A., Charlton, B.D., Kratochvil, H., and Fitch, W.T. (**2011**). “Vocal cues indicate level of arousal in infant African elephant roars,” J. Acous. Am. **130**, 1700-1710.

Todt, D. (**1988**). “Serial calling as a mediator of interaction processes: Crying in primates,” In *Primate Vocal Communication*, edited by D. Todt, P. Goedeking, and D. Symmes (Springer-Verlag, Berlin), pp. 88–107.

Weary, D.M. (**1998**). “Vocal response to pain in piglets,” Appl. Anim. Behav. Sci. **56**, 161-172.

Winter, P., Handley, P., Ploog, D., and Schott, D. (**1973**). "Ontogeny of squirrel monkey calls under normal conditions and under acoustic isolation," Behav. **47**, 230 – 239.

Wright, P. C. (**1998)**. "Impact of predation risk on the behaviour of *Propithecus diadema edwardsi* in the rainforest of Madagascar," Behav. **135**, 1-30.