Male-male competition and loud calls in one-male groups of simakobu (*Simias concolor*)

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Abstract of the Dissertation

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Sexual selection arises when individuals compete for access to mates, resulting in differences in reproductive success. In mammals, where females invest much more in offspring through gestation and lactation, sexual selection is usually stronger in males, whose fitness is limited by access to receptive females and who compete to monopolize them. Males can maintain exclusive access to a group of females by avoiding other groups, aggressively excluding rival males, or by herding females or defending an area in which they range. In polygynous species, male weapons, ornaments, and displays are often well developed for intrasexual competition, and males may use vocal displays in particular to resolve conflicts without costly fights. These signals may provide information about the caller, such as his body size, age, rank, or physical condition; however, the honesty of these calls can only be maintained by costs or constraints on callers that prevent cheating.

This suite of behavioral traits is exemplified by the Asian colobines, which typically live in one-male social groups inhabiting small home ranges. Male territorial behavior and loud calls are common, and have been proposed to function in male-male competition. As female dispersal occurs in most species, these behaviors also have the potential to play a role in female mate choice. One Asian colobine, however, has been described as an exception. Simakobu (*Simias concolor*) are reported to form adult male-female pairs, giving the appearance of a monogamous mating system, though their pronounced sexual dimorphism makes monogamy seem unlikely. Since information on simakobu is based on very few studies, most of which involved brief observations of unhabituated groups, often at disturbed sites, it is possible that their unusual groups are a result of human disturbance. In fact, early researchers suggested that the social organization of simakobu may be influenced by hunting either by increasing mortality or selecting for cryptic behavior. Thus, a long-term study of habituated groups at an undisturbed site was needed to clarify the status of simakobu.

This dissertation investigated male-male competition in one-male groups of simakobu and the role of loud calls as honest signals of male competitive ability at a protected forest in northeastern Siberut, Indonesia, with five main objectives. The first three objectives provided the social, temporal and spatial context of within- and between-group relationships and established the potential for male-male competition and female choice. 1) To establish the social setting for male-male competition, I described the social organization and dispersal patterns for groups, with the secondary goal of explaining the frequent occurrence of small socially monogamous groups often reported in the past. 2) To understand the seasonal patterns of ecology and reproduction, I documented the annual distribution of births and conceptions in relation to climate, phenology, feeding behavior, and female physical condition. 3) I investigated the spatial relationships among groups by establishing the size and exclusivity of home ranges and describing the nature and frequency of intergroup encounters. The final two objectives evaluated the use of loud calls in male-male competition. 4) To assess whether loud calls are honest signals of male energy status, I examined how calling rate and call duration vary in relation to long-term and short-term changes in energy availability. 5) To determine which acoustic features differentiate callers and contexts, I used acoustic analysis to assess which call characteristics may signal male stamina and fighting ability. To address these objectives, I studied simakobu during July-August 2005 and November 2006-December 2008 at Pungut, Siberut Island, Indonesia. Behavioral, demographic and acoustic data were collected from 11 groups (nine one-male and two all-male) of simakobu as well as phenological data from 404 trees and lianas.

As part of the first objective, I addressed the apparent paradox that simakobu represent as pair-living Asian colobines with signs of strong sexual selection, including marked sexual dimorphism. I documented the social organization and demographic changes of 10 simakobu groups throughout the two-year study. I hypothesized that the small groups documented in previous reports were the result of human disturbance due to hunting and habitat disturbance. To test this, I compiled data on hunting rates, habitat disturbance and demography (group size, adult sex ratio, number of immatures, immature-to-adult female ratio) for seven additional populations from the literature. I found that simakobu at this site reside in one-male groups that comprise three adult females and immatures and in all-male groups with males of all age classes in addition to juvenile females. Both male and female dispersal occurred, and juveniles seemed to disperse more frequently than adults. The results of the inter-population comparison revealed that the adult male-female pairs reported for this species appear to be a result of hunting pressure reducing group size.

For the second objective, I examined the timing of simakobu reproduction in relation to patterns of environmental seasonality. Southeast Asian primates in general show moderate birth seasonality due to either low environmental seasonality or unpredictable fluctuations of mast-fruiting food resources. Simakobu, however, have been reported to be strict seasonal breeders with births occurring in June and July only. It is unclear whether these observations are characteristic of the species or resulted from a sampling bias. To address this question, I documented the annual distribution of 11 births and conceptions in eight groups of simakobu over two consecutive years, and assessed annual variation in ecology and reproduction via rainfall, temperature, food availability, feeding time, and female physical condition. I hypothesized that, like other Southeast Asian species, simakobu would not exhibit strict birth seasonality, and if they were capital breeders, conceptions would occur immediately after food peaks when female physical condition should be best. I found that simakobu foods were abundant throughout the year, but fruit feeding showed seasonal peaks in June and September. Breeding was not strictly seasonal, as births occurred in seven months, with a peak in the wettest month of the year (October) at the end of the period of highest fruit availability. Females seemed to conceive following a peak in unripe fruit, and when physical condition was best, suggesting a capital breeding strategy.

To address the third objective, I established the spatial distribution of groups as well as the nature of intergroup relationships. I hypothesized that males would attempt to maintain exclusive access to females via aggressive intergroup encounters and loud calls. I compiled ranging and intergroup encounter data from all-day follows of four groups over five consecutive months. Using GIS methods, I mapped and described the size and overlap of their home range areas. I compared behavior, ranging patterns and space use of one-male groups and all-male groups and evaluate the hypothesis that males attempt to monopolize females by defending the areas in which they range. I found that simakobu home ranges were very small, 6-7 ha on average, and are used almost exclusively (*ca*. 10% overlap). Most encounters involved aggressive behavior from adult males and occurred in the peripheral areas of OMG home ranges, and in core areas for AMGs only. Overall, the exclusive use and aggressive defense of areas by males in OMGs suggested that males are indirectly defending females through the defense of the areas in which they range.

For the fourth objective, I investigated whether loud calls are honest advertisements of male energy status, testing the hypothesis that loud calls are energetically costly handicap signals. I combined behavioral and ecological data with acoustic analysis to determine the influence of energy status on calling effort, measured as calling rates and call duration. Using data from all-day follows of three adult males and loud call recordings from an additional three, I examined the relationship between short-term (time of day, temperature, amount of rain, and travel distance) and long-term (fruit availability, physical condition) measures of energy availability. I found that the duration of simakobu loud calls was negatively affected by short-term changes in energy status, with shorter calls produced during wet periods and at higher post-dawn temperatures, supporting the hypothesis that calls may be energetically costly. A peak of early morning calls of long duration suggested this might be the best time for males to advertise their quality. Contrary to predictions, daily calling rate increased with decreasing fruit availability and did not appear to reflect male energy status. I hypothesize that calling rate may instead be linked to strategies involving feeding and/or mate competition and signal the motivation, rather than fighting ability, of the caller.

To address the fifth objective, I examined the structure and usage of loud calls to determine which acoustic features vary within and between individuals. Using four acoustic parameters, call duration, inter-unit interval (IUI), fundamental frequency (F0) and peak frequency (pf), I tested hypotheses about call variation related to the size, arousal, and exhaustion of the callers. I analyzed 170 recordings made from 10 adult males and described acoustic differences among contexts, individuals, and callers of different ages, as well as changes that occur during a single call bout. I found that individuals, were well discriminated by the acoustic features of their loud calls, including F0, IUI and duration. Contexts were not well discriminated, spontaneous calls had higher pf, suggesting a higher level of arousal. The loud calls of older males had shorter IUI and lower F0. These differences likely reflect the caller's size, stamina and fighting ability, and could thus be a way for males and females to assess competitors and mates from long distances.

Overall, results from this research revealed that, rather than being an exceptional primate, simakobu appear to fit the Asian colobine pattern with respect to group size and composition, dispersal, reproduction, ranging, and male competition. Simakobu show morphological and behavioral signs of strong male-male competition. Adult males attempt to monopolize females and appear to aggressively defend at least part of the area in which they range. They produce loud calls several times daily, and despite very small home range areas, meet other groups only once or twice per week. Results suggest that males use loud calls to signal their presence and fighting ability to defend females and/or the resources within their home ranges. Loud calls may function as honest signals of male condition, age, and strength, which are likely used by males and females alike to assess rivals and mates. Future research is needed to fully investigate the role of loud calls as part of a strategy by males to defend females, food resources, and/or infants.

“What makes simakobu happy?
Not their daintiness, or graces,
nor arresting beauty –
they’ve such wistful, homely faces.

Under those silly noses
with their tilted, snubby tips,
are they happy when they’re avidly
dispatching leaves through lips,
into their bloated bellies which
obscure their chests and hips?

What do female simakobu see
in the noisy, nasal males?
Are they happy with their pungency
(so tricky to inhale)
and absurdly, piggy thingies
that they dare to call their tails?

What makes simakobu happy
is actually easy to presume,
when you hear their squeals
of rapture meeting, greeting
friends to groom.”

- Liz Brownlee
(http://poetlizbrownlee.co.uk)

For the males in my life, who never had to compete for my love and affection: my father, my brother, and my husband.

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At the age of twelve, I received a defining piece of life advice from my father: "Do what you love." As a child who filled my days catching snakes and lizards in the forest, caring for the countless creatures in our family's menagerie, and memorizing animal encyclopedias, my future career as a zoologist was decided in an instant. During my graduate studies, my girlhood dreams came true as I spent two years in a pristine jungle living among and learning about one of the most fascinating animals on the planet. Thanks, Dad, for setting me on this amazing life path!

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CHAPTER ONE:

Introduction

Sexual selection arises when individuals compete for access to mates, resulting in differences in reproductive success (Darwin 1871). The strength of this selection depends, in part, on sex differences in parental investment as well as the ratio of fertilizable females to sexually active males or operational sex ratio (Williams 1966, Trivers 1972, Emlen & Oring 1977, Andersson 1994). In most mammals, where females exclusively bear the costs of early investment in offspring (i.e., gestation and lactation), sexual selection is usually stronger in males, who compete to monopolize access to females or to mate more often and/or at the right time (Trivers 1972, Kappeler 1999, Kappeler & van Schaik 2004). The potential for males to monopolize females is not only influenced by the spatial distribution of females but also by the timing of their receptive periods (Emlen & Oring 1977, Nunn 1999).

In species where females can be monopolized, males often engage in contest competition to exclude rivals, which can result in the formation of one-male polygynous groups (Emlen & Oring 1977). Males can maintain exclusive access to a group of females by preventing their interaction with other males through avoidance of other groups, aggressive exclusion of rival males, and/or forceful herding of females (Pereira et al. 2000, Kappeler & van Schaik 2004). In some cases, males indirectly defend females by defending an area in which they range. This can be achieved via aggressive interactions during intergroup encounters or long-distance signals, such as loud vocalizations (Cheney 1987, Clutton-Brock 1989). In species characterized by such polygynous mating systems, male weapons, ornaments and displays are typically well developed for intrasexual competition (Andersson 1994.

This suite of social, behavioral and morphological traits is exemplified by the Asian colobines. These monkeys typically live in one-male social groups that inhabit relatively small home ranges (Kirkpatrick 2011, but see, e.g., Kirkpatrick & Grueter 2010). Intergroup encounters occur frequently in many species, where males are often the most active participants (van Schaik et al. 1992, Yeager & Kool 2000). Male loud calls are also common in several langur species, and have been proposed to function in intrasexual competition (e.g., Steenbeek et al. 1999, Wich & Nunn 2002, Delgado 2006). The energetic constraints imposed by their folivorous diets (McNab 1978) make it likely that these calls are costly and honest signals. Therefore, loud calls are liable to be used as part of an assessment strategy to reduce the costs of energetically expensive chases and fights.

This dissertation investigates the strategies that male pig-tailed langurs (simakobu: *Simias concolor*) residing in one-male social groups employ to maintain access to females and the signals they use to advertise and assess the competitive abilities of one other. In particular, I examine the use of loud calls as honest signals of strength, stamina and fighting ability to deter rival males and attract female mates.

The Asian Colobines

The Asian colobines are a diverse group of Old World monkeys that exhibit broad variation in demography, ecology, behavior and reproduction. Compared to their cercopithecine cousins, the Asian colobines tend to live in smaller groups of about 15 individuals, typically with one male, five adult females and their offspring (Kirkpatrick 2011). In addition to these one-male groups (OMGs), multi-male (multi-female) groups and all-male groups (AMGs: groups comprising males of different age classes and occasionally juvenile females) are also common (Yeager & Kool 2000, Kirkpatrick 2011, Grueter & van Schaik 2010).

Although male-biased dispersal is the norm for mammals in general and Old World monkeys in particular (Greenwood 1980, Pusey & Packer 1987), female dispersal is common among Asian colobines (Sterck, 1998). The possible benefits of female dispersal include incest avoidance, access to better quality habitat and food resources, reduced aggression, access to a higher quality male, and protection against infanticide (Moore 1984, Sterck et al. 2005). The combination of one-male groups and female transfer in most Asian colobines highlights the potential for both male-male competition and female choice.

Many Asian colobines show some degree of reproductive seasonality, where births are concentrated in periods of two to six months of the year (Kirkpatrick 2011). The degree of reproductive seasonality, however, is in part related to the extent of environmental seasonality. Among Hanuman langur populations, for example, the degree of birth seasonality increases with increasing latitude, indicating that populations inhabiting more seasonal habitats exhibit more seasonally restricted reproduction (Newton & Dunbar 1994). Indeed, for primate species residing in the tropical and sub-tropical climates of Southeast Asia, there tends to be limited (predictable) environmental and reproductive seasonality (Brockman & van Schaik 2005). Seasonality of reproduction has implications for male-male competition, as those species with less birth seasonality exhibit more reproductive skew (Cowlishaw & Dunbar 1991, Nunn 1999, van Noordwijk & van Schaik 2004).

Home ranges of Asian colobines show wide variation, covering areas of less than 10 ha (e.g., purple-faced langurs, *Trachypithecus vetulus*: Rudran 1973) to those exceeding 1,000 ha (e.g., snub-nosed monkeys, *Rhinopithecus* spp.: Kirkpatrick & Grueter 2010). Home range overlap also varies greatly across species, with groups in some species maintaining exclusive use of areas (e.g., dusky leaf monkeys, *Trachypithecus obscurus* and Sumatran surili, *Presbytis melalophos*: Curtin 1980; Phayre's leaf monkeys, *Trachypithecus phayrei crepusculus* Gibson & Koenig 2012), and in others completely overlapping (e.g., capped langurs, *Trachypithecus pileatus*: Stanford 1991; proboscis monkeys, *Nasalis larvatus*: Boonratana 2000).

Among Southeast Asian langurs, encounter rates are not related to home range defensibility, the degree of home range overlap, or to the population density; they are, however, influenced by group composition, such that one-male groups meet with higher frequency than do multi-male groups (van Schaik et al. 1992). Aggression during intergroup encounters is typically restricted to adult males and males often respond more aggressively towards solitary males or those residing in AMGs than the males of neighboring mixed-sex groups (van Schaik et al. 1992, Wich et al. 2002a, 2004). Together, these observations led van Schaik and colleagues (1992) to conclude that male aggression during encounters was related to the defense of females. However, alternate hypotheses emphasize the importance of (food) resource defense and infant defense, particularly where infanticide is a major cause of infant mortality (Fashing 2001, Wich & Sterck 2007). For example, playback studies with Thomas langurs (*Presbytis thomasi*) revealed that males showed more aggressive responses to simulated intrusions in the center *versus* the edge of the home range, but there were no differences related to important feeding sites. This was interpreted as a form of infant defense, since encounters with infanticidal males often occur in the center of the home range (Wich et al. 2002b).

Loud calls are common among Asian colobine males and are thought to play a role in mediating group spacing and preventing encounters and fights between groups (Delgado 2006). Their role in between-group communication is supported by the fact that they are often contagious (i.e., the calling of one male stimulates a response from another), and are almost universally produced by males only (Wich & Nunn 2002). As agonistic displays, loud calls have also been hypothesized to function in mate, resource and infant defense (Wich & Nunn 2002) and may signal the motivation or fighting ability of the caller. On the other hand, calling throughout the day may simply be a statement that an area or group is currently occupied and defended (cf. Clutton-Brock & Albon 1979). Among Asian colobines, the loud calls of Thomas langurs are the best-studied. Behavioral observations, acoustic analyses, and playback studies have revealed that 1) calls produced by different individuals and in different contexts are acoustically distinct (Steenbeek & Assink 2000, Wich et al. 2003a, 2) males and females discriminate between familiar/unfamiliar and younger/older callers (Wich et al. 2002a, 2004), 3) participation in dawn call bouts is an honest signal of male strength (Steenbeek et al. 1999), and 4) call production and call acoustics of males in AMGs are distinct from males in mixed-sex groups (Steenbeek et al. 1999, Wich et al. 2003b). The loud calls of other Asian colobines species have not been well studied (but see Hohmann & Vogl 1991), and it is unknown whether the patterns found in Thomas langurs can be generalized to other species.

Simakobu: An Extreme Asian Colobine?

Simias concolor (simakobu or pig-tailed langur) is a critically endangered species of Asian colobine endemic to the Mentawai Islands of Indonesia (Whittaker & Mittermeier 2008). Simakobu belong to the odd-nosed monkey group, which includes *Nasalis*, *Pygathrix*, *Rhinopithecus* and *Simias* (Sterner et al. 2006, Whittaker et al. 2006). They have been described as extreme primates based on their unusual social grouping pattern. They are just one of two species of Asian colobines that are reported to frequently reside in adult male-female groups, providing the appearance of a monogamous mating system (Tilson 1977, Kirkpatrick 2011). Curiously, they are also the only Asian colobine with conspicuous sexual swellings (Tenaza 1989a, Kirkpatrick 2011 but see Murai 2006). However, information on this species is based on few studies, most of which were conducted in the 1970s's and 1980's and involved brief observations of unhabituated groups.

History of Research

The first account of the natural history of simakobu was published by Ronald Tilson in 1977. Tilson conducted his research at the Sirimuri study area in central Siberut between September 1972 and November 1974 (Tilson 1977). During his study, he accumulated approximately 80 hours of observations of five unhabituated groups, and spent 72 days surveying areas of northern and southern Siberut, documenting the composition of 10 additional groups. Kunio Watanabe studied simakobu in southeastern Siberut at the Sarabua study site, about 12 km east of Sirimuri. Between 1974 and 1976, he observed six groups during 36 contact hours (Watanabe 1981). In November 1976, he moved his study to the Grukna study site in northern Siberut, where monkey densities were considerably higher. At Grukna, Watanabe observed nine study groups and an additional 14 groups through roadside surveys, accumulating 312 contact hours between 1976 and 1978.

The first published accounts of simakobu outside of Siberut Island were provided by Syunzo Kawamura and Erri Megantara. They observed four species of Mentawai primates on

Sipora Island for 62 days in 1985 (Kawamura & Megantara 1986). During this period, they encountered individuals or groups of simakobu on 23 occasions. Richard Tenaza extended simakobu research further south to the Pagai Islands. During 20 weeks in 1986 and 1987, he observed 12 groups on the islets of Sinakak and Simalegu (Tenaza 1987, Tenaza 1989a, 1989b, Tenaza & Fuentes 1995). He made additional observations of three groups elsewhere in the Pagai Islands in 1986 and 1987 and on Siberut (at Sirimuri) in 1972.

In 1992, Agustin Fuentes observed seven groups of simakobu for seven months on North Pagai Island at the Betumonga study site (Fuentes 1995, Tenaza & Fuentes 1995). Although Fuentes' dissertation research focused on the behavior of the sympatric Mentawai langur (*Presbytis potenziani*), he was able to make several observations of the simakobu from hiding during this time. Lisa Paciulli continued research at Betumonga between July and October 1996, (Miller & Paciulli 2002). Paciulli was the first to habituate simakobu and was able to make observations of four animals in two groups.

Finally, Susilo Hadi and I began our dissertation studies around the same time at the Pungut study site in 2005. Hadi's thesis research is focused on niche divergence of the two sympatric colobines (*Presbytis potenziani* and *Simias concolor*). He began his observations of an all-male group of simakobu in 2006. This group eventually split into three as two of the males matured and established one-male groups nearby, leaving a single juvenile to range solitarily. Hadi made additional observations of a neighboring simakobu group.

Demography and Reproductive Seasonality

The first account of the social organization of simakobu documented mixed-sex groups that uniformly comprised an adult male-female pair, ranging in size from 2-5 individuals (Table

1.1; Tilson 1977). Tilson additionally documented the presence of bachelor males, one of which resided with a juvenile after the adult female had disappeared (presumably shot by hunters). Throughout his two-year study period, the adults at Sirimuri remained in stable groups. At Sarabua, Watanabe confirmed Tilson's observations, finding that groups were never larger than adult male-female pairs with juveniles and infants (Table 1.1; Watanabe 1981). There, too, groups remained stable during the study period.

In Grukna, however, Watanabe observed groups that contained an adult male accompanied by one to four adult females, two of which comprised at least 15 individuals (Table 1.1), the largest groups of simakobu documented to date (though, interestingly, the largest group split into three during his study). Like Tilson, he documented the occurrence of several solitary subadult and adult males. Watanabe noted that there appeared to be an incline in group size from the small monogamous groups along the roadside to larger polygynous groups inhabiting the interior forest, and suggested that monogamous groups were the result of human disturbance, and most likely excessive hunting. Although simakobu at Grukna had been hunted to extinction by 1990 (Tenaza & Fuentes 1995), Hadi and colleagues documented three groups at the nearby site of Loh Bajou (~12 km north of Grukna) in December 2006 (Hadi et al. 2009). They recorded the composition of groups killed during a ceremonial hunt, and found groups comprising 3-4 adult females (Table 1.1).

The occurrence of adult male-female pairs, OMUs, and solitary males were confirmed in other regions of the Mentawai Islands. On Sipora Island, Kawamura and Megantara encountered simakobu on 23 occasions, 17 of which involved solitary males (Kawamura & Megantara 1986). On the remaining six occasions, groups comprised 2-5 individuals with one adult male and one or two females (Table 1.1). In the Pagai Islands, Tenaza and Fuentes observed one-male groups with 1-5 adult females and offspring, the largest of which comprised nine individuals (Table 1.1; Tenaza 1987, Tenaza & Fuentes 1995). They also observed eight bachelor males, two of which appeared to range together. This study was the first to document the occurrence of two-male groups (one mixed-sex and one same-sex). Taken together, these studies indicate that, although OMGs do occur in some populations, adult male-female pairs represent the most common grouping pattern. Despite the prevalence of adult pairs, approximately one in five males resides outside mixed-sex groups (Table 1.1), only rarely forming AMGs. To date, there have been no reports of dispersal events in this species.

In the few cases births have been described, simakobu appear to be seasonally restricted to a two- or three-month period. However, different studies have documented different birth seasons which together span six months of the year. Tilson (1977) observed a single birth in one study group in 1972 and five newly-born infants during surveys throughout Siberut in 1973-1974. An additional five births were reported by Mentawai hunters, all of which occurred in the months of June and July (Table 1.1). At Grukna, four infants were born into Watanabe's study groups between December 1977 and February 1978 (Watanabe 1981). He observed an additional six newly-born infants in the area during these months, and none at other times of the year. He suggested that the simakobu birth season was concentrated at the end of the wet season (Table 1.1). Lastly, Hadi and colleagues documented the presence of six infants in three groups at Loh Bajou (Hadi et al. 2009). The local hunters estimated the age of five of these infants as less than one month, indicating they were born in November and/or December (Table 1.1). Thus, the extent of birth seasonality within and among sites remains unclear as are the underlying factors influencing the timing of reproduction in this species.

Ranging Patterns and Intergroup Encounters

Home ranges of simakobu tend to be small, with groups occupying areas of approximately 15-20 ha at most sites (Table 1.1). The largest home ranges were observed at Sirimuri, where Tilson (1977) reported that groups inhabited 25-30 ha areas (Table 1.1). At Sarabua, Watanabe (1981) estimated that home ranges were approximately 6.5-20 ha, but there was a large area not occupied by any groups (Table 1.1). At Grukna, the smallest home ranges were observed, about 3.5 ha per group (Table 1.1: Watanabe 1981). Unlike at Sarabua, few areas were unused by the simakobu at Grukna. Despite the 10-fold variation in home range size, group ranges are used almost exclusively. At Sarabua, and Sirimuri, where home ranges were relatively large, adjacent groups appeared to show little or no overlap (Tilson 1977, Watanabe 1981). At Grukna, despite home ranges being much smaller, overlap was minimal (about 8%) between adjacent groups (Watanabe 1981).

Three studies have described intergroup encounters in simakobu, all of which appeared to involve adult males only. Tilson (1977) observed several encounters at Sirimuri, noting that when males detected one another at the periphery of their ranges, they would both approach and give a single loud vocalization. Following this, both males would retreat to the center of their ranges without chasing or fighting. Similarly, at Sarabua, Watanabe (1981) observed males rapidly approaching one another when two groups were within 50 m, exchanging a single loud call and moving away quickly. In contrast, Grukna groups tended to ignore each other at 50 m distance. When an aggressive encounter began, however, it often lasted more than 30 minutes. The adult males would display with jumps and exchanges of loud nasal barks repeated several times. After these lengthy displays, groups would gradually move away from each other. In Pagai, Tenaza and Fuentes (1995) documented a single intergroup encounter. Males leapt and moved violently in canopy, while producing loud nasal meowing sounds. They then descended to the ground and fought, during which time one of them uttered a 2-bark loud call. After a few minutes they returned to the canopy and one male left while the other stayed and whimpered for 20 minutes. Although there are a number of possible explanations for this variation, it is interesting to note that at sites characterized by low sex ratios (i.e., reduced male-male competition), encounters were brief and non-aggressive, while those at sites with OMGs appear to involve aggressive physical combats between adult males. It is important to note, however, that all of these observations were made of unhabituated groups, and it is unknown whether and how the presence of human observers may have influenced their behaviors.

Signs of Sexual Selection – Loud Calls and Sexual Dimorphism

Several researchers have noted that adult male simakobu produce loud, distinct vocalizations throughout their range. Like intergroup encounters, loud calling behavior appears to be highly variable across sites. At some sites, loud calls were only rarely heard (Sirimuri: Tilson 1977, Sarabua: Watanabe 1981, Sipora: Kawamura & Megantara 1986). At Sirimuri, for example, Tilson (1977) observed loud calls just 32 times during 348 days in the field. Eighteen of these calls were produced within a one-week period, during which one male called 2-3 times/day while mating with a female, after which he abruptly stopped calling.

While one study reported a complete absence of predawn calling (Tilson 1977), others described variability in the frequency and timing of early morning calls. At Grukna, for example, simakobu produced loud predawn calls at 6 am (Watanabe 1981), while on Sipora, Kawamura and Megantara (1986) documented the occurrence of pre-dawn calls between 3 and 5 am. In Pagai, Tenaza reported that loud calling exhibited a distinct bimodal distribution with a peak in the early morning (5-7am) and another in late afternoon (5-7 pm). In contrast, in a study of the acoustic niches of primates at Pungut, Schneider and colleagues (2008) noted that the distribution of loud calls showed no clear peak and that most calls were produced between 6-10 am. In all studies, loud calls were recorded ad libitum, often outside the context of group contact and the sampling efforts were often not systematic (but see Schneider et al. 2008: sampling occurred between 6 am-12 pm and 1pm-6pm). Thus, the full circadian distribution of simakobu loud calling remains unknown.

Tenaza (1989b) conducted a more thorough analysis of simakobu loud calls at Simalegu and Sinakak. He tape-recorded 15 loud calls, which consisted of about 15 barks and lasted 12 seconds on average. Calls elicited replies from other males, typically within 30 seconds. Tenaza noted that calls were produced spontaneously and following the loud call of another male, a tree fall or thunder, and on one occasion, single-bark loud calls were produced during a fight between two males. He conducted playback experiments by broadcasting a loud call and repeating the broadcast after five minutes. Six of seven trials elicited a response to the first call, while none elicited a response from the second call. Based on his observations, Tenaza concluded that calls were used in communication among males, and served to maintain or increase inter-group distance. The absence of a response to the second playback suggests that calls might be costly or difficult to produce, and that males need a period of "recovery" before they can call again.

Estimates of simakobu sexual dimorphism have been documented in two studies. Tenaza and Fuentes compiled data from museum specimens and published accounts to describe dimorphism in head-body length, canine length, and body mass. Adult males were 12% longer, 29% heavier, and their canines were 95% longer than females. Hadi and colleagues (2009) collected data from two males and six females that were killed during a hunt. In their study, males were 13% longer and 24% heavier. Taken together, these behavioral and morphological traits indicate strong sexual selection in this species (Plavcan & van Schaik 1992). Male-male competition and/or female mate choice has likely selected for the larger bodies, longer canines, and conspicuous calls of adult males.

Overview of Study Methods

Research was conducted at the Siberut Conservation Programme’s Pungut study site in the Peleonan forest in northern Siberut, Indonesia (Fig. 1.1). The hilly study area covers 1100 ha of primary mixed evergreen rainforest (altitude: ca. 25 – 190 m), and is part of the 45000 ha Peleonan forest (0°56’ – 1°03’S, 98°48’ – 98°51’E, 1 – 165 m a.s.l.). Although this area is officially designated as production forest, it has been protected from hunting and logging through agreements with the local community and Indonesian officials since 2002.Data were collected in July-August 2005 and November 2006-December 2008. During the pilot study in 2005, I familiarized myself with the study area and a few groups, made preliminary behavioral observations, and recorded several loud calls. In November 2006, I targeted groups for habituation and in January-February 2007, together with local assistants, I began following two groups (OMG-H and AMG-D). All individuals were recognized and most were habituated by May 2007. We began habituating a neighboring group (OMG-S) in March 2007. Although this group was never fully habituated, all group members were recognized from April 2007 onward. In order to increase the sample size for male behavior, I observed two additional OMGs (A and E) in 2008 for the final six months of the study. These groups were formed when males matured and left the all-male group that resided near the camp, and had been observed by Hadi since 2006 (see *History of Research* above). Five other OMGs (C, F, J, P and Z) and one AMG (G) were unhabituated neighbors of these focal groups. Unhabituated groups were identified by distinctive features of the adult males and other easily-recognized group members.

Overview of Thesis Chapters

Chapter two addresses the apparent paradox that simakobu represent as pair-living Asian colobines with signs of strong sexual selection, including marked sexual dimorphism. In this chapter, I describe the social organization of 10 simakobu groups and document demographic changes due to births, disappearances and dispersals throughout the two-year study. I hypothesize that the small groups documented in previous reports were the result of human disturbance in the form of hunting and habitat disturbance. To test this hypothesis, I compile data on hunting rates, habitat disturbance and demography (group size, adult sex ratio, number of immatures, immature-to-adult female ratio) for seven additional populations from the literature.

In Chapter three, I examine the timing of simakobu reproduction in relation to patterns of environmental seasonality. I document the annual distribution of births and conceptions, and assess ecological variation by examining annual patterns of rainfall, temperature, phenology of simakobu foods, feeding times, and female physical condition. I hypothesize that, like other Southeast Asian species, simakobu do not exhibit strict birth seasonality, and if they are capital breeders, conceptions occur immediately after food peaks when female physical condition is best.

Chapter four establishes the spatial distribution of groups as well as the nature of intergroup relationships. I compile ranging and intergroup encounter data from all-day follows of four groups over five consecutive months. Using GIS methods, I map and describe the size and overlap of their home range areas. I compare behavior, ranging patterns and space use of one-male groups and all-male groups and evaluate the hypothesis that males attempt to monopolize females by defending the areas in which they range.

In Chapter five, I investigate whether loud calls are honest advertisements of male energy status, testing the hypothesis that loud calls are energetically costly handicap signals. I combine behavioral and ecological data with acoustic analysis to determine the influence of energy status on calling effort, measured as calling rates and call duration. Using data from all-day follows of three adult males and loud call recordings from an additional three, I examine the relationship between short-term (time of day, temperature, amount of rain, and travel distance) and long-term (fruit availability, physical condition) measures of energy availability.

Chapter six examines the structure and usage of loud calls to determine which acoustic features vary within and between individuals. Using four acoustic parameters, call duration, inter-unit interval, fundamental frequency and peak frequency, I test hypotheses about call variation related to the size, arousal, and exhaustion of the callers. I present an analysis of 170 recordings made from 10 adult males and describe acoustic differences among contexts, individuals, and callers of different ages, as well as changes that occur during a single call bout.

In the final chapter, I provide a summary and synthesis of the major results from this research. I present my results in the context of previous research on simakobu and suggest some modifications regarding the current view of this species. I discuss some limitations of the present study, and point to questions that remain open, with suggestions for future research directions.

Tables and Figures

Table 1.1. Size and composition of mixed-sex groups, proportion of extra-group males, birth season and home range size of simakobu populations.

Islands	Pagai				Siberut					Sipora	All
Site	Betumonga^1	Sinakak^1	Simalegu^1	Other Pagai^1	Sarabua^2	Grukna^2	Sirimuri^3	Loh Bajou^4	Other Siberut^3	Sipora^5*	Total
N	6	4	7	3	9	23	4	3	10	6	75
Mean GS	5.5	5.0	3.1	2.0	3.0	6.2	3.8	8.7	3.6	n/a	4.8
Range GS	2-7	3-9	2-5	2	2-5	2-20	2-5	8-10	2-5	2-5	2-20
Mean AF	2.5	2.8	1.3	1.0	1.0	1.9	1.0	3.3	1.0	1.3*	1.6
Range AF	1-3	2-5	1-2	1	1	1-4	1	3-4	1	1-2*	1-5
% pair	16.7	0	71.4	100	100	39.1	100	0	100	66.7*	60.0
% EM	30.0	33.3	12.5	0.0	0.0	28.1	33.3	n/a	9.1	n/a	20.5
Births	n/a	n/a	n/a	n/a	n/a	Dec-Feb	Jun- Jul	Nov- Dec	n/a	n/a	
HR (ha)	7-20	20	15-19	n/a	6.5-20	2.5-5	25-30	n/a	n/a	n/a	2.5-30

N = number of groups, GS = group size, AF = adult females, % pair = % of mixed-sex groups comprising an adult male-female pair, % EM = % of adult extra-group males (i.e., residing outside of mixed-sex groups), Births = months of observed births, HR = home range size, n/a = data not available (table adapted from Tenaza & Fuentes 1995). *The authors reported encountering 6 groups ranging in size from 2-5 individuals. They noted that two of these groups had two females each, and it was assumed that the remaining four groups were adult male-female pairs for these calculations. References: 1 = Tenaza & Fuentes 1995, 2 = Watanabe 1981, 3= Tilson 1977, 4 = Hadi et al. 2009, 5 = Kawamura & Megantara 1986.

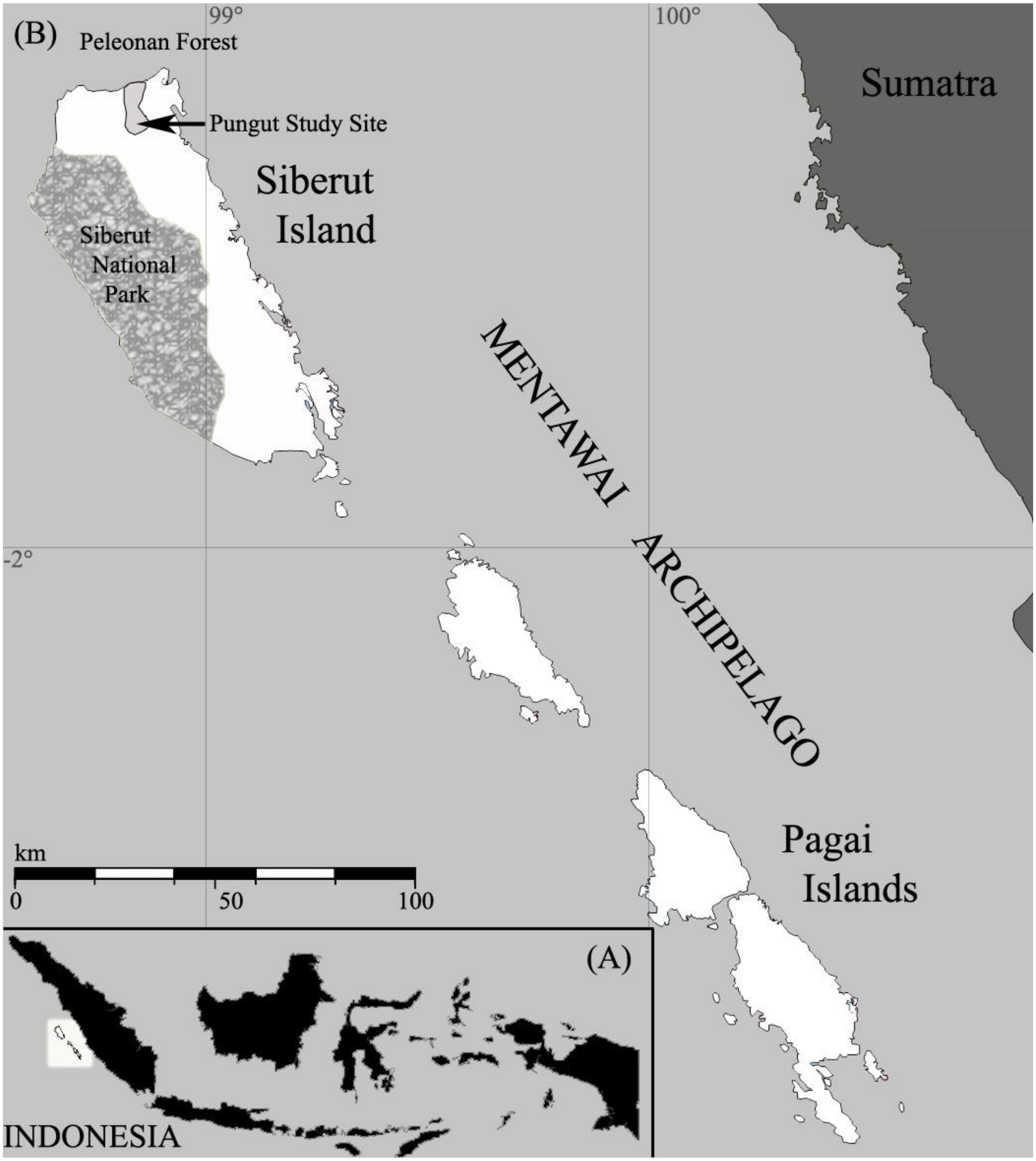


Fig. 1.1. Location of (a) Mentawai Islands in Indonesia and (b) the Pungut study site in the Peleonan Forest, Siberut Island. (Map adapted from Michael J. Lowe©2007).

References

Andersson MB (1994) Sexual selection. Princeton University Press, Princeton, New Jersey

Boonratana R (2000) Ranging behavior of proboscis monkeys (*Nasalis larvatus*) in the Lower Kinabatangan, Northern Borneo. Int J Primatol 21:497-518

Brockman DK, van Schaik CP (2005) Seasonality and reproductive function. In: Brockman DK, van Schaik CP (eds) Seasonality in primates: Studies of living and extinct human and non-human primates. Cambridge University Press, Cambridge, pp 269-305

Cheney DL (1987) Interactions and relationships between groups. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 267-281

Clutton-Brock TH (1989) Review lecture: mammalian mating systems. Proc R Soc Lond B 236:339-372

Clutton-Brock TH, Albon SD (1979) The roaring of red deer and the evolution of honest advertisement. Behaviour 69:145-170

Cowlishaw G, Dunbar RIM (1991) Dominance rank and mating success in male primates. Anim Behav 41:1045-1056

Curtin SH (1980) Dusky and banded leaf monkeys. In: Chivers DJ (ed) Malayan forest primates: ten years' study in tropical rain forest. Plenum Press, New York, pp 107-145

Darwin C (1871) The descent of man and selection in relation to sex. John Murray, London

Delgado RA (2006) Sexual selection in the loud calls of male primates: signal content and function. Int J Primatol 27:5-25

Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223

Fashing PJ (2001) Male and female strategies during intergroup encounters in guerezas (*Colobus guereza*): evidence for resource defense mediated through males and a comparison with other primates. Behav Ecol Sociobiol 50:219-230

Gibson L, Koenig A (2012) Neighboring groups and habitat edges modulate range use in Phayre’s leaf monkeys (*Trachypithecus phayrei crepusculus*). Behav Ecol Sociobiol 66:633-643

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140-1162

Grueter CC, van Schaik CP (2010) Evolutionary determinants of modular societies in colobines. Behav Ecol 21:63-71

Hadi S, Ziegler T, Hodges JK (2009) Group structure and physical characteristics of Simakobu monkeys (*Simias concolor*) on the Mentawai Island of Siberut, Indonesia. Folia Primatol 80:74-82

Hohmann G, Vogl L (1991) Loud calls of male Nilgiri langurs (*Presbytis johnii*): age-, individual-, and population-specific differences. Int J Primatol 12:503-524

Kappeler PM, van Schaik CP (2004) Sexual selection in primates: review and selective preview. In: Kappeler PM, van Schaik CP (eds) Sexual selection in primates: new and comparative perspectives. Cambridge University Press, New York, pp 3-20

Kawamura S, Megantara EN (1986) Observation of primates in logged forest on Sipora Island, Mentawai. Kyoto University Research Report of Studies on Asian Non-Human Primates 5:1-12

Kirkpatrick RC (2011) The Asian colobines: diversity among leaf-eating monkeys. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf R (eds) Primates in perspective. Oxford University Press, New York, pp 189-202

Kirkpatrick RC, Grueter CC (2010) Snub-nosed monkeys: multilevel societies across varied environments. Evol Anthropol 19:98-113

McNab BK (1978) Energetics of arboreal folivores: physiological problems and ecological consequences of feeding on an ubiquitous food supply. In: Montgomery GG (ed) The ecology of arboreal folivores. Smithsonian Institution Press, Washington, DC, pp 153-162

Miller CT, Paciulli LM (2002) Patterns of lateralized hand use in an arboreal primate, *Simias concolor*. Am J Primatol 56:231-236

Moore J (1984) Female transfer in primates. Int J Primatol 5:537-589

Murai T (2006) Mating behaviors of the proboscis monkey (*Nasalis larvatus*). Am J Primatol 68:832-837

Newton PN, Dunbar RIM (1994) Colobine monkey society. In: Davies AG, Oates JF (eds) Colobine monkeys: their ecology, behaviour and evolution. Cambridge University Press, Cambridge, pp 311-346

Nunn CL (1999) The number of males in primate social groups: a comparative test of the socioecological model. Behav Ecol Sociobiol 46:1-13

Pereira ME, Clutton-Brock TH, Kappeler PM (2000) Understanding male primates. In: Kappeler PM (ed) Primate males: causes and consequences of variation in group composition. Cambridge University Press, New York, pp 271-277

Plavcan JM, van Schaik CP (1992) Intrasexual competition and canine dimorphism in anthropoid primates. Yearb Phys Anthropol 87:461-477

Pusey AE, Packer C (1987) Dispersal and philopatry. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. The University of Chicago Press, Chicago, pp 250-266

Rudran R (1973) Adult male replacement in one-male troops of purple-faced langurs (*Presbytis senex senex*) and its effect on population structure. Folia Primatol 19:166-192

Schneider C, Hodges JK, Fischer J, Hammerschmidt K (2008) Acoustic niches of Siberut primates. Int J Primatol 29:601-613

Stanford CB (1991) Social dynamics of intergroup encounters in the capped langur (*Presbytis pileata*). Am J Primatol 25:35-47

Steenbeek R, Assink P (2000) Individual differences in long-distance calls of male wild Thomas langurs (*Presbytis thomasi*). Folia Primatol 69:77-80

Steenbeek R, Assink P, Wich SA (1999) Tenure related changes in wild Thomas's langurs II: loud calls. Behaviour 136:627-650

Sterck EHM (1998) Female dispersal, social organization, and infanticide in langurs: are they linked to human disturbance? Am J Primatol 44:235-254

Sterck EHM, Willems EP, van Hooff JARAM, Wich SA (2005) Female dispersal, inbreeding avoidance and mate choice in Thomas langurs (*Presbytis thomasi*). Behaviour 142:845-868

Sterner KN, Raaum RL, Zhang YP, Stewart CB, Disotell TR (2006) Mitochondrial data support an odd-nosed colobine clade. Mol Phylogenet Evol 40:1-7

Tenaza RR (1987) The status of primates and their habitats in the Pagai Islands, Indonesia. Primate Conserv 8:104-110

Tenaza RR (1989a) Female sexual swellings in the Asian colobine *Simias concolor.* Am J Primatol 17:81-86

Tenaza RR (1989b) Intergroup calls of male pig-tailed langurs (*Simias concolor*). Primates 30:199-206

Tenaza RR, Fuentes A (1995) Monandrous social organization of pigtailed langurs (*Simias concolor*) in the Pagai Islands, Indonesia. Int J Primatol 16:295-310

Tilson RL (1977) Social organization of simakobu monkeys (*Nasalis concolor*) in Siberut Island, Indonesia. J Mammal 58:202-212

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man, 1871-1971. Aldine-Atherton, Chicago, pp 136-179 van Noordwijk MA, van Schaik CP (2004) Sexual selection and the careers of primate males: paternity concentration, dominance-acquisition tactics and transfer decisions. In: Kappeler PM, van Schaik CP (eds) Sexual selection in primates: new and comparative perspectives. Cambridge University Press, New York, pp 208-229

van Schaik CP, Assink PR, Salafsky N (1992) Territorial behavior in Southeast Asian langurs: resource defense or mate defense. Am J Primatol 26:233-242

Watanabe K (1981) Variations in group composition and population density of the two sympatric Mentawaian leaf-monkeys. Primates 22:145-160

Whittaker DJ, Ting N, Melnick DJ (2006) Molecular phylogenetic affinities of the simakobu monkey (*Simias concolor*). Mol Phylogenet Evol 39:887-892

Wich SA, Assink PR, Becher F, Sterck EHM (2002a) Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): the effect of familiarity. Behaviour 139:79-87

Wich SA, Assink PR, Becher F, Sterck EHM (2002b) Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): the effect of location. Behaviour 139:65-78

Wich SA, Assink PR, Sterck EHM (2004) Thomas langurs (*Presbytis thomasi*) discriminate between calls of young solitary versus older group-living males: a factor in avoiding infanticide? Behaviour 141:41-51

Wich SA, Koski S, de Vries H, van Schaik CP (2003) Individual and contextual variation in Thomas langur male loud calls. Ethology 109:1-13

Wich SA, Nunn CL (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

Wich SA, Sterck EHM (2007) Familiarity and threat of opponents determine variation in Thomas langur (*Presbytis thomasi*) male behaviour during between-group encounters. Behaviour 144:1583-1598

Wich SA, van der Post DJ, Heistermann M, Möhle U, van Hooff JARAM, Sterck EHM (2003) Life-phase related changes in male loud call characteristics and testosterone levels in wild Thomas langurs. Int J Primatol 24:1251-1265

Williams GC (1966) Adaptation and natural selection. Princeton University Press, Princeton

Yeager CP, Kool K (2000) The behavioral ecology of Asian colobines. In: Whitehead PF, Jolly CJ (eds) Old World monkeys. Cambridge University Press, Cambridge, pp 496-521

CHAPTER TWO:

Demography of Simakobu (*Simias concolor*) and the Impact of Human Disturbance

(With Carola Borries, Nurul S Lestari, Thomas Ziegler: *American Journal of Primatology,* 74:580-590)

Abstract

Asian colobines typically live in small one-male groups (OMGs) averaging 5 adult females but *Simias concolor* (simakobu or pig-tailed langur) is considered an exception because mostly adult male-female pairs have been reported. However, based on their phylogenetic position and marked sexual dimorphism, simakobu are also expected to form OMGs with multiple females. The preponderance of small groups could be the result of human disturbance (hunting or habitat disturbance) reducing group size in the recent past. To investigate this possibility, we documented the demography of 10 wild simakobu groups from January 2007 until December 2008 at an undisturbed site, the Peleonan Forest, Siberut Island, Indonesia. We assessed the population-specific size and composition of groups and documented demographic changes due to births, disappearances, and dispersals throughout our 2-year study. We found OMGs with 3.0 adult females on average in addition to all-male groups, but no adult male-female pairs. The ratio of 0.5 infants per adult female (and 0.64 births per female-year in focal groups) suggested that birth rates were similar to those of other Asian colobines. In 5.1 group-years, we observed 6 dispersal events and 6 temporary presences (i.e., less than 3 months residency). Both males and females dispersed, and juveniles seemed to disperse more frequently than adults. To assess the impact of human disturbance on simakobu demography, we compiled data for 7 additional populations from the literature and compared them using general linear models. Adult sex ratio was influenced negatively by hunting while the number of immatures and reproductive rates were not significantly affected by either variable. These findings suggest that adult male-female pairs may result from hunting pressure reducing group size, and that conservation action to reduce hunting in the Mentawai Islands is needed to ensure the survival of this critically endangered species.

Keywords: all-male group · dispersal · group size · habitat disturbance · hunting, one-male group · pig-tailed langurs

Introduction

Asian colobines are a diverse group of Old World monkeys, exhibiting broad variation in social organization and demography. Individuals are typically organized into one-male (multi-female) groups (OMGs), though multi-male (multi-female) groups, and all-male groups (AMGs: groups consisting of males of different ages and occasionally juvenile females) also occur [Yeager & Kool, 2000; Kirkpatrick, 2007; Grueter & van Schaik, 2010]. Group sizes of Asian colobines tend to be small, typically about 15 individuals and 5 adult females [Kirkpatrick, 2007]. At one extreme, however, some odd-nosed colobines form large multi-level or modular societies, which can exceed 400 individuals [*Rhinopithecus* species, Kirkpatrick & Grueter, 2010; Grueter & van Schaik, 2010]. Another odd-nosed colobine, *Simias concolor,* seems to represent the other extreme, in which adult males and females typically reside in pairs [Tilson, 1977; Kirkpatrick, 2007].

Simias concolor (simakobu or pig-tailed langur) is a critically endangered species [Whittaker & Mittermeier, 2008], restricted to the Mentawai Islands of Indonesia. Most knowledge of this species is based on data collected in the 1970s and 1980s [Tilson, 1977; Watanabe, 1981; Tenaza & Fuentes, 1995; but see Hadi et al., 2009a]. Although a few larger groups were observed, most groups contained only adult male-female pairs and immatures [mean group size 4.6, across sites; Tenaza & Fuentes, 1995: 304]. These findings seem to be at odds with the degree of sexual dimorphism in simakobu, as adult males are 23%-29% heavier [Tenaza & Fuentes, 1995; Hadi et al., 2009a] and their maxillary canines 95% longer than those of adult females [Tenaza & Fuentes, 1995]. Pair-living in simakobu would represent a deviation from a broadly consistent pattern in anthropoid primates, as pair-living species are characterized by very little canine dimorphism [Plavcan & van Schaik, 1992; but see Leutenegger & Lubach, 1987].

The disparity between dimorphism and group composition in simakobu suggests pair-living to be a recent phenomenon perhaps in response to human disturbance. Early researchers suggested that the social organization of simakobu may be influenced by hunting [Tilson, 1977; Watanabe, 1981], which could reduce group size by increasing mortality and/or selecting for cryptic behavior, favoring smaller less conspicuous groups [Cowlishaw & Dunbar, 2000]. Such effects occurred among several Brazilian primates, in which group size was smaller when hunting pressure was high [Pinto et al., 1993], and in red colobus monkeys, whose groups were significantly smaller where hunting by chimpanzees was frequent [Stanford, 1998]. Habitat disturbance could also lead to smaller group size via resource scarcity, which could force animals to emigrate from affected areas and/or increase mortality through starvation [Cowlishaw

& Dunbar, 2000]. Habitat degradation led to reduced group size in both red colobus and howler monkeys [Struhsaker, 2008; Arroyo- Rodríguez & Dias, 2010]. It is thus possible that the small single-female groups reported for simakobu could be due to hunting and/or habitat disturbance.

Here we present demographic data across 2 consecutive years for individually-known groups of wild simakobu in an undisturbed habitat. Thus far, information about this species comes primarily from surveys, which can provide only limited information about group membership and dispersal patterns. We report group size and composition and document changes in groups due to births, disappearances, and dispersals. To determine the influence of human disturbance on simakobu demography, we then compare different simakobu populations varying in hunting pressure and habitat disturbance. Because small groups could arise through different demographic processes, we examine the composition of groups using 3 variables: adult female-to-adult male ratio, the number of immatures, and immature-to-adult female ratio [as a measure of reproductive rate, cf. Zucker & Clarke, 2003; Mbora & Meikle, 2004; Marshall, 2010]. We predict lower adult sex ratios, fewer immatures as well as lower immature-to-adult female ratios in areas with high hunting pressure and/or habitat disturbance [Cowlishaw & Dunbar, 2000]. Simakobu are one of the world's 25 most endangered primate species [Mittermeier et al., 2009], and an understanding of their survival and mortality in response to different threats is critical for effective conservation measures.

Methods

Study Site

We conducted this research at the Siberut Conservation Programme's Pungut study site in the Peleonan Forest in northern Siberut, Indonesia (0°56' – 1°03'S, 98°48' – 98°51'E, site number 8 in Fig. 2.1). This area has been protected from hunting and logging through agreements with the local community and Indonesian officials since 2002. The climate is equatorial with mean minimum and maximum monthly temperatures of 21.5 and 31.7°C and mean annual precipitation of 3,601 mm [Chapter 3]. The study site lies within a 10.7 km^2 area of hilly (altitude: *ca.* 25 – 190 m) primary mixed evergreen rainforest [Hadi et al., 2009b].

Siberut Island harbors 4 endemic primate species (simakobu: *Simias concolor*, Kloss' gibbon: *Hylobates klossii*, Mentawai langur: *Presbytis potenziani*, and Siberut macaque: *Macaca siberu*). While all 4 species inhabit the study area, *Simias* is the most abundant [Waltert et al., 2008]. Mammalian predators are historically absent from the Mentawai Islands, but serpent eagles (*Spilornis cheela sipora*) and reticulated pythons (*Python reticulatus*) are potential predators [Whitten & Whitten, 1982]. Humans do hunt and eat primates, but hunting pressure in northern Siberut is thought to be relatively low [Watanabe, 1981; Hadi et al., 2009a].

Study Subjects and Period

Simakobu are medium-sized Asian colobines [males 7.7-8.9 kg, females 5.2-7.1 kg, Tenaza & Fuentes, 1995; Hadi et al., 2009a]. Subjects were 10 wild groups: 8 OMGs and 2 AMGs. Of these, we contacted 3 groups throughout the study period and they were the focal groups for this study. We followed 2 of these focal groups (OMG-H and AMG-D) beginning in January and February 2007, respectively, and most group members were habituated by May 2007. Habituation efforts for the third focal group (OMG-S) began in March 2007. Although this group was never fully habituated, we recognized all individuals from April 2007 onward. We observed an additional 2 habituated OMGs (A and E) for the final 6 months of the study (June – December 2008). We included these 2 groups only in the dispersal calculations and the population-specific assessment of group size and composition. Four other OMGs (F, J, P and Z) and 1 AMG (G) were unhabituated neighbors of the focal groups. We censused these groups from January 2007 until December 2008 at irregular intervals, whenever the schedule (designed to collect data on the behavior of adult males) would allow. Data from non-focal groups were used only for the assessment of population-specific group size and composition.

Data Collection

We collected demographic data on 487 contact days during the 24-month study period (January 2007 – December 2008; WME, NSL and local assistants). We typically searched for groups in the evening, followed them to their sleep sites, and relocated them the next morning before dawn. The central group for this study, OMG-H, was contacted in each month of this study; however, because of difficult observation conditions in the very dense forest, occasional staffing shortages, and additional research activities (e.g., botanical assessments not described here), we could not observe all groups each month. We followed each focal group on average 4.8 days each month (range 0 – 21) and non-focal groups on average 1.2 days each month (range 0 – 6). We identified unhabituated groups by the adult males' distinctive features and other easily-recognized group members.

During contact with a group, we recorded the presence or absence of known individuals and performed group counts, indicating the age/sex classes of all group members. We identified individuals by tail shape and hair pattern, crest size and shape, and facial hair coloration and pattern. Males and females were easily distinguished by differences in body size (adults only) ischial callosities (touching in males, separated in females) and sexual characteristics (penis and scrotum in males, pink sex skin and/or swellings in females). Age classes were modified after

National Research Council [1981] as: 1. *adult* = full head-body length (assessed via comparison to known adults as well as the cessation of growth) or at first parturition (i.e., first infant born) in females, whichever occurred first; 2. *subadult male* = male whose head-body length matched adult females but was smaller than adult males (note: there is no subadult category for females); 3. *juvenile* = weaned immature, never observed in nipple contact, smaller than an adult female; 4. *older infant* = unweaned immature that travels independently (note: we know from focal groups that independent travel begins to occur regularly at 9 months of age: Erb, unpublished data.); 5. *younger infant* = unweaned immature that is carried during travel. We could not apply the distinction between infant 1 and infant 2 used for other Asian colobines [e.g., Winkler et al., 1984] because simakobu have no distinct natal coat.

Research permits were issued by the Indonesian Institute of Sciences (LIPI) in accordance with the legal requirements of conducting research in Indonesia. Methods were approved by the Institutional Animal Care and Use Committee (IACUC) at Stony Brook University and are in accordance with the ASP's principles for the ethical treatment of nonhuman primates.

Data Analysis

To determine the population-specific group size and composition, we compiled the best count (i.e., for which most age-sex classes could be determined) for each focal and non-focal group closest to the end of the study when individuals were best known and most easily identified (see Table 2.1). Furthermore, for focal groups, we scored the size and composition each month by compiling all presence/absence records for known individuals. In 15 of 53 group months (AMG-D = 4 / 20, OMG-H = 5 / 23, OMG-S = 6 / 10 months), counts were incomplete (i.e., known individuals were not observed), and we reconstructed group composition based on the previous and following month to minimize assumptions about group membership changes (i.e., an individual seen before and after but not during a month with incomplete counts was not rated as absent). We did not reconstruct group compositions when counts for more than 2 consecutive months were incomplete (N = 8).

We classified changes in group compositions as: *disappearance* (never observed again), *emigration* (observed again later outside of the group), *temporary presence* (residing only 1 or 2 months), *immigration* (residing 3 or more months), *birth*, or *maturation*. We calculated birth rate as N infants born / adult female-year. We calculated rates of dispersal and temporary presence in the 3 focal and the 2 additional habituated groups by dividing the number of events by the number of individual-years within each age-sex class.

For comparison, we compiled published data for simakobu. At 1 site, censuses were conducted twice [Watanabe, 1981]. Although the author stated it was possible that 2 of the surveyed groups were counted twice (once in each census), because censuses took place 2 years apart we treated them as different groups. Because age classifications were not standardized across studies, we used only 2 categories: adult and immature (includes subadults, juveniles, and infants). For mixed-sex groups, we further calculated mean group size, adult sex ratio, number of immatures, and immature-to-adult female ratio.

We then compared group size and composition across 8 sites, including ours. For each site, we compiled all information available on hunting activities and habitat disturbance, including logging, gardening, and collection of trees by local people around the time of data collection. In studies where the authors reported the number of animals hunted, we estimated hunting rates by dividing the number of animals killed by the study period (in months). For both hunting and habitat disturbance, we used a ranking of 1 to 4, with 4 representing the highest human impact [cf. Oates, 1996]. With respect to hunting, sites were ranked as follows (monthly hunting rates in parentheses): *1 = Pungut* [no hunting observed, Erb, unpublished data], *2 = Betumonga*, *Simalegu*, *Sirimuri* [<1/month, Fuentes & Ray, 1996; Tilson, 1977], *3 = Grukna* [1 – 2/month, Watanabe, 1981], *4 = Sarabua* [2 – 3/month, Watanabe, 1981]. For habitat disturbance, sites were ranked as: *1 = Simalegu* and *Sirimuri* [pristine, undisturbed, Tilson, 1977; Tenaza, 1989], *2 = Pungut* and *Sarabua* [occasionally local people fell trees for canoes, Erb, pers. obs.; Watanabe, 1981], *3 = Betumonga* [19% secondary forest, 9% disturbed, Fuentes, 1994], *4 = Grukna* [commercial logging 1970-1976, Watanabe, 1981]. Note that for 2 sites comparable details on hunting and/or habitat disturbance were not available [i.e., Sinakak and Loh Bajou].

We used 1-way ANOVA to test for group size differences among sites. We used general linear mixed models (GLMM) to assess the influence of hunting and habitat disturbance on adult sex ratio, the number of immatures, as well as the immature-to-adult female ratio per group; study site was treated as a random effect in each analysis. Model assumptions were checked (collinearity of predictor variables, leverage, residuals, and influence) following Quinn & Keough [2002]. Due to a skewed distribution of the residuals, we log-transformed ratio data prior to analysis to achieve normality [Quinn & Keough, 2002]. We performed statistical analyses with Statistica 9.1 (© StatSoft, Inc. 1984-2010) and JMP (© SAS Institute, Inc. 2012). One-tailed tests were used to evaluate each directed prediction with α set at 0.05.

Results

Group Size and Composition

Of the 10 groups at Pungut, 8 were mixed-sex. All mixed-sex groups were OMGs with more than 1 adult female; neither adult male-female pairs nor multi-male groups were encountered. Mean OMG size was 7.9 individuals (range 5-12, Table 2.1). OMGs comprised 1.0 adult male and 3.0 adult females (range 2-5, Table 2.1), 2.0 juvenile females (range 1-4) and 1.5 infants (range 0-3) on average. Neither subadult nor juvenile males were found in mixed-sex groups, although the sex of 2 juveniles in OMG-Z could not be determined. The immature-to-adult female ratio was 1.3 : 1.0 and the infant-to-adult female ratio was 0.5 : 1.0. AMGs, by contrast, comprised 4.5 individuals on average (range 2-7), with 2.0 adult males (range 1-3, Table 2.1), 0.5 subadult males (range 0-1), 1.5 juvenile males (range 1-3), and 0.5 juvenile females (range 0-1). AMG-D also had a second juvenile female and an adult female temporarily present during the study (Table 2.2).

Over nearly 2 years, focal groups ranged in size from 5-12 individuals in OMG-H, 7-9 individuals in OMG-S, and 6-8 individuals in AMG-D (Table 2.2). OMG-H nearly doubled in size during the course of the study, due to immigration of adult and juvenile females as well as 3 births. In contrast, the average-sized OMG-S was more stable with 1 birth and the loss of an adult female and an infant.

Births

Over the course of this study, 5 infants were born into focal groups (Table 2.2), of which 2 disappeared. One was only 2 months old and we assume it died. The second was an older infant (estimated at 12-15 months of age), and we do not know whether her disappearance was due to death or dispersal. Based on the 2 focal groups OMG-H and OMG-S and 2 other habituated groups OMG-A and OMG-E, the birth rate was 0.64 infants per female-year (7.8 adult female-years).

Dispersal

In 5.1 group-years, 6 dispersal events were documented (Table 2.2), of which 5 were immigrations: 1 adult and 2 juvenile females into OMG-H; and 1 juvenile male and 1 juvenile female into AMG-D. One juvenile female emigrated from AMG-D (Table 2.2) into an adjacent group. This represents a rate of 1.2 dispersal events per group-year. Six temporary presences were also documented. These included an adult female and a juvenile female in AMG-D, an adult female in OMG-H, an adult female and a juvenile female in OMG-E, and an adult female in OMG-A, for a total of 1.2 temporary presences per group-year.

In 7.8 adult female-years, we observed 1 dispersal (0.1 / year) and 4 temporary presences (0.5 / year), totaling 5 between-group movements (0.6 / year). In 7.25 adult male-years, we did not observe any instances of dispersal or temporary presences. In 11.5 juvenile female-years, we observed 4 dispersals (0.3 / year) and 2 temporary presences (0.2 / year), totaling 6 between-group movements (0.5 / year). In 3.8 juvenile male-years, we observed 1 dispersal (0.3 / year).

Inter-Population Comparison

Across the 8 study sites (Fig. 2.1, Table 2.3), adult sex ratio showed significant variation (ANOVA: $F_{7,54} = 10.90$, $P < 0.01$). A post-hoc Tukey HSD test (with $\alpha = 0.05$) revealed that the sex ratios at Pungut were higher than at 4 other sites, but similar to those at nearby Loh Bajou as well as Betumonga and Sinakak. In the GLMM, hunting had a significant negative impact on adult sex ratio, while habitat disturbance had no effect (full model explained 51.9% of the variance, Table 2.4, Fig. 2.2a, 2.3a).

The number of immatures and immature-to-adult female ratio varied significantly across the 8 sites (ANOVA – N immatures: $F_{7,54} = 5.31$, $P < 0.01$; immature-to-adult female ratio: $F_{7,54} = 2.85$, $P = 0.01$). A Tukey test showed that the number of immatures was higher at Pungut and nearby Loh Bajou than at Simalegu and Sarabua. For immature-to-adult female ratio, only Grukna and Sinakak differed significantly from each other. In the GLMM, there was a trend for the number of immatures in groups to be negatively influenced by hunting (full model accounted for 32.6% of the variance, Table 2.4, Fig. 2.2b, 2.3b). For immature-to-adult female ratio, however, there was no significant relationship with hunting or habitat disturbance (full model accounted for 15.0% of the variance, Table 2.4, Fig. 2.2c, 2.3c).

Discussion

Simias *Past and Present*

To date, there have been 4 published studies of simakobu social organization. The first was conducted by Tilson [1977] between 1972 and 1974. He observed 5 mixed-sex groups at 1 site, and documented 10 additional groups during censuses throughout Siberut. All 15 groups comprised 1 adult male, 1 adult female, and immatures, leading Tilson to conclude that simakobu were pair-living and to speculate that their unique social organization was an adaptation to avoid hunting. Shortly afterwards, Watanabe [1981] observed 29 mixed-sex simakobu groups at 2 sites on Siberut between 1974 and 1978. While at 1 site he found only adult male-female pairs, at the other site he observed pairs as well as OMGs with 2-4 adult females (61% multi-female groups). Based on the observation that pairs were most common along the roadside where hunting was most frequent, Watanabe assumed that the small groups resulted from human disturbance. Between 1986 and 1992, Tenaza and Fuentes [1995] observed 20 mixed-sex groups on the Pagai islands. Like Watanabe, they found both adult male-female pairs and OMGs with multiple adult females (55% multi-female groups), suggesting a flexible monandrous social organization. The most recent study by Hadi and colleagues [2009a] documented the composition of 3 OMGs killed during a hunt in 2006. However, because a population-wide census was not conducted and details of the sampling effort were not provided, we do not discuss this study below. In addition, all studies reported solitary adult and subadult males. Only 2 encountered small AMGs, 1 consisting of 2 adult males [Tenaza & Fuentes, 1995], and the other an adult male and an unsexed juvenile [Tilson, 1977]. None of the studies documented dispersal events.

Our study provides the first data on group membership and dispersal for simakobu based on follows of habituated groups at an undisturbed site covering 2 consecutive years. Nevertheless, our sample size is small, and thus only limited conclusions can be drawn. In contrast to previous studies, we did not find adult male-female pairs in our study population at Pungut. All mixed-sex groups had a single adult male and multiple adult females. In addition, we documented 2 AMGs. One was as small as the AMGs reported previously, but the other had 7 individuals, including juvenile females. At Pungut, both male and female juveniles dispersed and it is likely that juveniles disperse more frequently than adults. Juvenile females dispersed into OMGs as well as AMGs, while juvenile males dispersed only into AMGs, and adult females only into OMGs. Since we did not observe dispersal of adult males, this aspect of group formation remains unknown.

The results of our inter-population comparison highlight the influence of human disturbance on simakobu social organization, and confirm the previously-hypothesized negative impact of hunting [Tilson, 1977; Watanabe, 1981]. As hunting reduces population size, the remaining groups likely become smaller through dispersal of adult females and juveniles into previously-occupied areas [cf. ideal free distribution, Fretwell & Lucas, 1969]. This idea is supported by juvenile and adult female dispersal documented for Pungut. Furthermore, variation in population-wide adult sex ratios across populations is lower (range = 0.7 – 2.0: data not shown) than variation in within-group sex ratios (range = 1.0 – 3.3: Table 2.3). Overall, these findings suggest that the adult male-female pairs observed in previous studies resulted when hunting reduced the numbers of adult females and immatures and increased the proportion of adult males residing in mixed-sex groups.

We found a birth rate of 0.64 infants per female-year in our focal groups. Compared to the only other population for which data are available [we calculated a birth rate of 0.14 based on Tilson, 1977: 206], birth rates at Pungut were high. In addition, we estimated reproductive rates as the number of immatures per adult female as these data were available for most sites. We observed 1.29 immatures per adult female at Pungut, and it is likely that this rate represents a sustainable population [Zucker & Clarke, 2003]. For the other sites, the immature-to-adult female ratio varied between 0.40 and 1.75 and was lower than Pungut at 5 of the 7 sites. Across populations, hunting and habitat disturbance had no effect on reproductive rates (Table 2.4). However, immature-to-adult female ratios in mixed-sex groups should be interpreted cautiously because immatures can also reside in AMGs. Juveniles and subadults were documented outside of mixed-sex groups at 2 Siberut sites (Sirimuri and Pungut), and thus reproductive rates were underestimated in these populations.

Is* Simias *an Unusual Asian Colobine?

Like many Asian colobines, simakobu mixed-sex groups at Pungut consisted of a single adult male, multiple adult females, and immature individuals. With a mean of 8 individuals per group in this population, *Simias concolor* groups were smaller than the mean group size of 15 for Asian colobines [calculated from Kirkpatrick, 2007]. Nonetheless, of 36 populations reviewed, mixed-sex groups averaged fewer than 10 individuals in 33% of the cases and fewer than 8 in 14% of cases [Kirkpatrick, 2007]. Thus, while at the small end of the spectrum, simakobu groups are within the normal group size range for wild Asian colobines.

In addition to OMGs, we documented AMGs at Pungut. Among Asian colobines, AMGs are reported regularly, occurring in 17 – 18 of 24 species considered [Yeager & Kool, 2000]. The presence of juvenile females in AMGs has also been observed in several species [e.g., *Nasalis larvatus*, Boonratana, 1993; *Presbytis thomasi*, Steenbeek et al., 2000; *Trachypithecus leucocephalus*, Jin et al., 2009]. Rather than being unusual, *Simias concolor* exhibits the typical grouping pattern for an Asian colobine.

Within 8 mixed-sex groups, we observed 0.5 infants for each adult female, which provides an indirect measure of birth rate [cf. Struhsaker et al., 2004]. This value is very close to the mean value for 12 populations of Asian colobines of comparable body mass [mean = 0.47, range = 0.30 – 0.71, Kirkpatrick, 2007; for species with female body mass within 1 kg of that reported for simakobu, Smith & Jungers, 1997], suggesting that simakobu at Pungut are reproducing at an expected rate.

With respect to female dispersal, simakobu seem to fit the general pattern for Asian colobines [Sterck, 1998]. The causes of female dispersal in simakobu are unknown; however, the temporary visits we observed may have been attempts to assess opportunities prior to making a dispersal decision. These observations highlight the potential for female choice and male-male competition for mates in this species.

The lack of juvenile males in OMGs at Pungut suggests that natal males disperse early, which is supported by the presence of very young juvenile males in AMGs and the immigration of a juvenile male into an AMG that we observed. In the closely related proboscis monkey, while there were no subadult males in OMGs, juvenile males were present [Yeager, 1990]. This suggests that simakobu males may disperse at a younger age than proboscis monkey males. Furthermore, AMGs existed throughout our 2-year study period and were thus stable for extended periods, similar to the AMGs in some Hanuman langur populations [Rajpurohit et al., 1995].

Overall, and contrary to previous assessments, simakobu fit the Asian colobine pattern with respect to social organization and group size. Our results demonstrate that *Simias concolor* is not a pair-living primate but, when undisturbed, lives in small OMGs including several adult females as well as AMGs. The regular occurrence of adult and juvenile dispersal by both males and females is another common colobine trait.

Threats and Conservation

Habitat disturbance and hunting are the 2 greatest threats to wild primate populations [Mittermeier, 1987]. Identifying the relative impact of these threats on endangered species is critical for conservation management [Cowlishaw & Dunbar, 2000]. Several studies have demonstrated that hunting has a greater negative impact on primate populations than moderate habitat disturbance [e.g., Oates, 1996; Tutin & Fernandez, 1984; reviewed in Cowlishaw &

Dunbar, 2000]. While many of these studies have examined the impact of human disturbance on population densities, few have considered its effects on group composition [reviewed in Schwitzer et al., 2011]. Red colobus (*Procolobus gordonorum*) and black-and-white colobus (*Colobus angolensis*) had smaller groups in areas with human disturbance, but the relative impacts of hunting and habitat disturbance could not be determined [Marshall et al., 2005]. Both red colobus (*Procolobus gordonorum*) and bearded saki (*Chiropotes satanas*) groups were smaller in disturbed (i.e., fragmented and/or degraded) habitats [Struhsaker, 2008; Boyle & Smith, 2010]. In howler monkeys, the number of males per group decreased while the proportion of OMGs in the population increased in more disturbed habitats [*Alouatta palliata, A. pigra, A. seniculus*, reviewed in Arroyo-Rodríguez & Dias, 2010]. Finally, group sizes of 5 Brazilian primates were smaller where hunting occurred, but habitat differences might have contributed to these group differences [Pinto et al., 1993].

In our analysis of hunting and habitat disturbance, we found that moderate habitat disturbance, in the form of felling large trees or creating small gardens, had nosignificant impact on simakobu groupsHowever, we should note that we did not assess the long-term effects of logging and habitat loss in this study, and we do not know how they could affect simakobu demography [see Paciulli, 2004 for other impacts of logging]. In contrast, hunting pressure had a significant negative impact on adult sex ratios and a weak negative impact on immature numbers indicating that, to ensure the long-term survival of this critically endangered species, hunting should be reduced as much as possible. Of the 5 primate species endemic to the Mentawai Islands, *Simias concolor* is the most hunted, because it is the best-tasting and easiest to hunt [Mitchell & Tilson, 1986]. While local tradition and taboos once kept hunting rates low, acculturation has relaxed these restrictions. The occurrence of logging throughout the region threatens to intensify the problem, as such operations make forests more accessible [Cowlishaw & Dunbar, 2000].

The Siberut National Park (established in 1993, Fig. 2.1) comprises nearly half of Siberut Island and is the largest protected area in the Mentawai Islands. Although logging and hunting are largely prohibited within the park [PHPA, 1995], the laws are not enforced and hunting continues throughout the island, including protected areas [Whittaker, 2006]. The results of our study underscore the importance of the conservation action plan proposed by Whittaker [2006] in its recommendations for improving protection of the Siberut National Park via increased enforcement of hunting laws and for establishing a conservation education campaign throughout the Mentawai Islands, especially in regards to hunting.

Our study further emphasizes the importance of northern Siberut for the long-term survival of this species as larger groups, greater reproductive rates and higher densities [Waltert et al., 2008; Quinten et al., 2010; present study] occur in this region. If adjacent areas, including the Siberut National Park, can remain connected via corridors, northern Siberut could maintain an important source population for *S. concolor*.

Tables and Figures

Table 2.1. Composition and size of OMGs and AMGs at the Pungut study site.

OMGs	Month	AM	AF	SM	JM	JF	J ?	IO	IY	Unk	GS
A*	Oct 08	1	3			1		1			6
E*	Oct 08	1	2			2					5
F	Dec 08	1	3			3		2			9
H*	Dec 08	1	3			4		1	2		11
J	Jun 08	1	2			2		2			7
P	Dec 08	1	3			1			1		6
S*	Jun 08	1	3			2		1			7
Z	May 08	1	5			1	2	1	1	1	12
Mean		1.0	3.0	0.0	0.0	2.0	0.3	1.0	0.5	0.1	7.9

AMGs	Month	AM	AF	SM	JM	JF	J ?	IO	IY	Unk	GS
D*	Dec 08	3		1	2	1					7
G	Jun 08	1			1						2
Mean		2.0	0.0	0.5	1.5	0.5	0.0	0.0	0.0	0.0	4.5

OMGs/AMGs = group name; Month = sample month, for selection criteria see methods; AM = adult male; AF = adult female; SM = subadult male; JM = juvenile male; JF = juvenile female; J? = unsexed juvenile; IO = older infant; IY = younger infant; Unk = unknown age/sex class; GS = group size; * = all group members individually recognized. For selection criteria of survey month see methods.

Table 2.2. Group composition and membership changes in focal groups.

	OMG-H								OMG-S								AMG-D							
Month	AM	AF	SM	JM	JF	IO	IY	GS	AM	AF	SM	JM	JF	IO	IY	GS	AM	AF	SM	JM	JF	IO	IY	GS
Feb-07	1	1			3	1		6																
Mar-07	1	1			3	1		6									1		2	2	1			6
Apr-07	1	1			3	1		6	1	4			2			7	1		2	2	1			6
May-07	1	1			3	1		6	1	4			2		1°	8	1		2	2	1			6
Jun-07	1	1			3	0'		5	1	4			2		1	8	1		2	2	1			6
Jul-07	1	1			3			5	1	4			2		1	8	1		2	2	1			6
Aug-07	1	1			3			5	1	4			2		1	8	1		2	2	1			6
Sep-07	1	1			3			5									1		2	2	1			6
Oct-07	1	1			3			5									3		0	2	1			6
Nov-07	1	1			3			5																
Dec-07	1	1			3			5									3			3♦	1			7
Jan-08	1	1			5♦♦		1°	7									3			3	1			7
Feb-08	1	2♦			5		1	9	1	4			2	1	0	8	3			3	1			7
Mar-08	1	2			5		1	9	1	4			2	1		8	3			3	1			7
Apr-08	1	2			5		1	9	1	4			2	1	1°	9	3			3	1			7
May-08	1	2			5		1	9	1	4			2	1	1	9	3			3	1			7
Jun-08	1	2			5		1	9	1	3'			2	1	0'	7								
Jul-08	1	2			5		1	9									3		1	2	1			7
Aug-08	1	2			5		1	9									3		1	2	1			7
Sep-08	1	4*			4		2°	11									3	1*	1	2	0◊			7
Oct-08	1	4			4	1	2°	12									3		1	2	1♦			7
Nov-08	1	3			4	1	2	11									3		1	2	2*			8
Dec-08	1	3			4	1	2	11									3		1	2	1			7
Mean	1.0	1.7	0.0	0.0	3.9	0.3	0.7	7.6	1.0	3.9	0.0	0.0	2.0	0.5	0.6	8.0	2.3	0.1	1.0	2.3	1.0	0.0	0.0	6.7

A = adult; S = subadult; J = juvenile; IO = older infant; IY = younger infant; M = male; F = female; GS = group size; gray highlight = maturation (old and new age class highlighted); ° = birth; ′ = disappearance; * = temporary presence; ♦ = immigration; ◊ = emigration (each symbol indicates 1 individual).

Table 2.3. Composition of mixed-sex simakobu groups at various sites on the Mentawai Islands.

Site	Hunting Rank	Habitat Disturbance Rank	N Groups	GS Mean	GS Range	AF / AM	N Imm	Imm / AF	Ref
1. Betumonga	2	3	6	5.5	3-9	2.25	1.83	0.75	a
2. Sinakak	--	--	4	5.0	3-9	2.75	1.25	0.40	a
3. Simalegu	2	1	7	3.1	2-5	1.29	0.86	0.71	a
4. Sirimuri	2	1	4	3.8	2-5	1.00	1.75	1.75	b
5. Sarabua	4	2	9	3.0	2-5	1.00	1.00	1.00	c
6. Grukna	3	4	23*	6.2	3-20	1.67	2.48	1.48	c
7. Loh Bajou	--	--	3	8.7	8-10	3.33	4.33	0.58	d
8. Pungut	1	2	8	7.9	5-12	3.00	3.75	1.29	e

GS = group size; AF = adult female; AM = adult male; Imm = immature. Ref: a = Tenaza & Fuentes 1995; b = Tilson 1977; c = Watanabe 1981 (*2 group counts estimated (reported as "15-20" and "~20"), used for group size (entered as 15 and 20) but not for ratios); d = Hadi et al. 2009a; e = present study (unidentified individual not used for ratios). Site numbers refer to study locations in Fig. 2.1. For hunting and human disturbance ratings see methods.

Table 2.4. Results of general linear mixed models comparing demographic structure of mixed-sex groups across study sites (treated as a random effect) as a function of both hunting and habitat disturbance.

	Hunting			Habitat Disturbance			Full Model
Variable	F	*P*	β	F	*P*	β	Adjusted r^2
Log AF/AM	8.810	0.033	-0.217	4.190	0.928	0.133	0.519
N Imm	4.040	0.074	-0.755	2.446	0.884	0.524	0.326
Log Imm/AF	0.111	0.383	-0.030	0.448	0.716	0.054	0.151

AF = adult female; AM = adult male; Imm = immature.

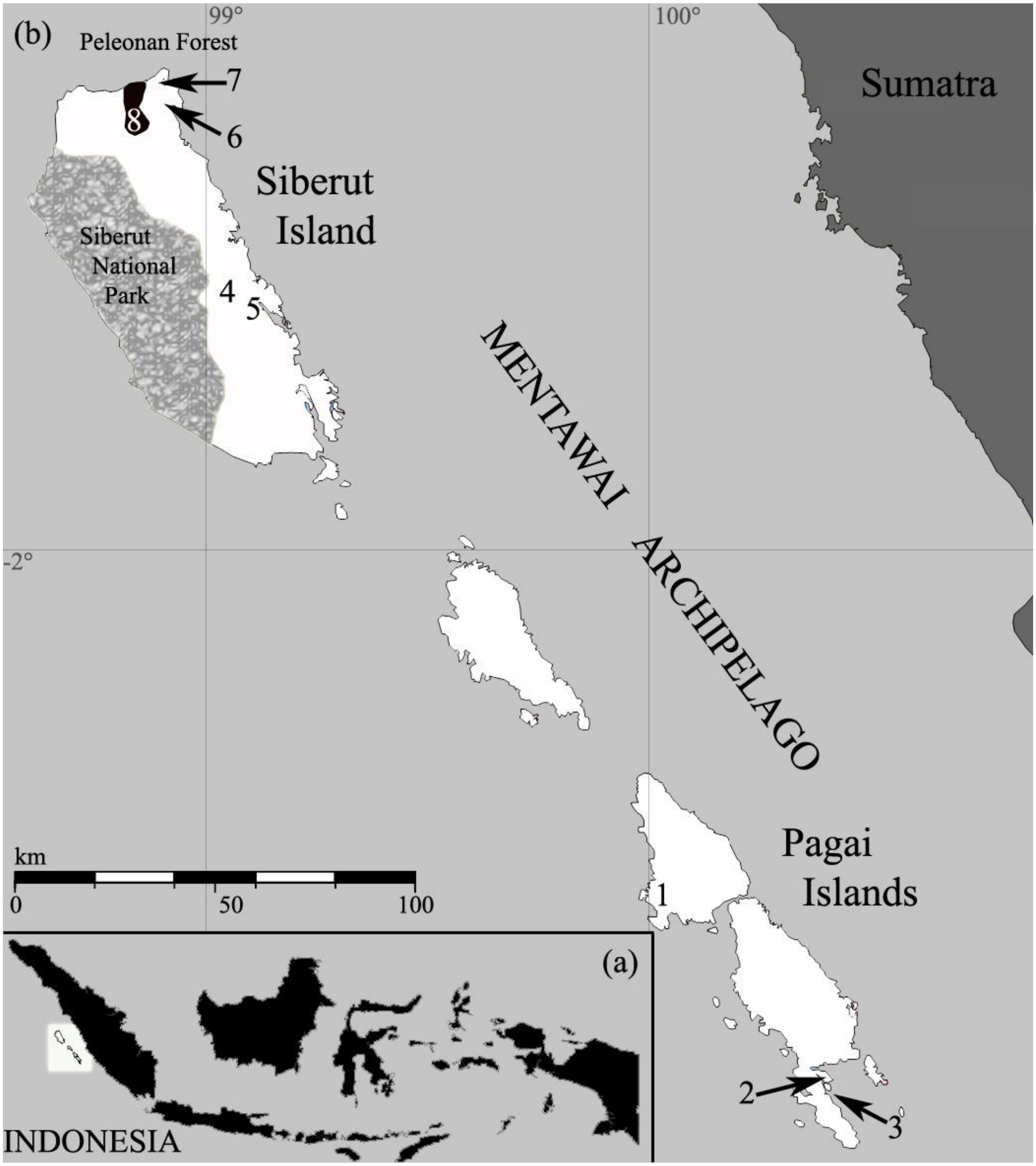


Fig. 2.1. Location of (a) Mentawai Islands in Indonesia and (b) simakobu study locations. Numbers correspond to study sites in Table 2.3: 1 = Betumonga, 2 = Sinakak, 3 = Simalegu, 4 = Sirimuri, 5 = Sarabua, 6 = Grukna, 7 = Loh Bajou, 8 = Pungut (present study). [Map adapted from Michael J. Lowe©2007].

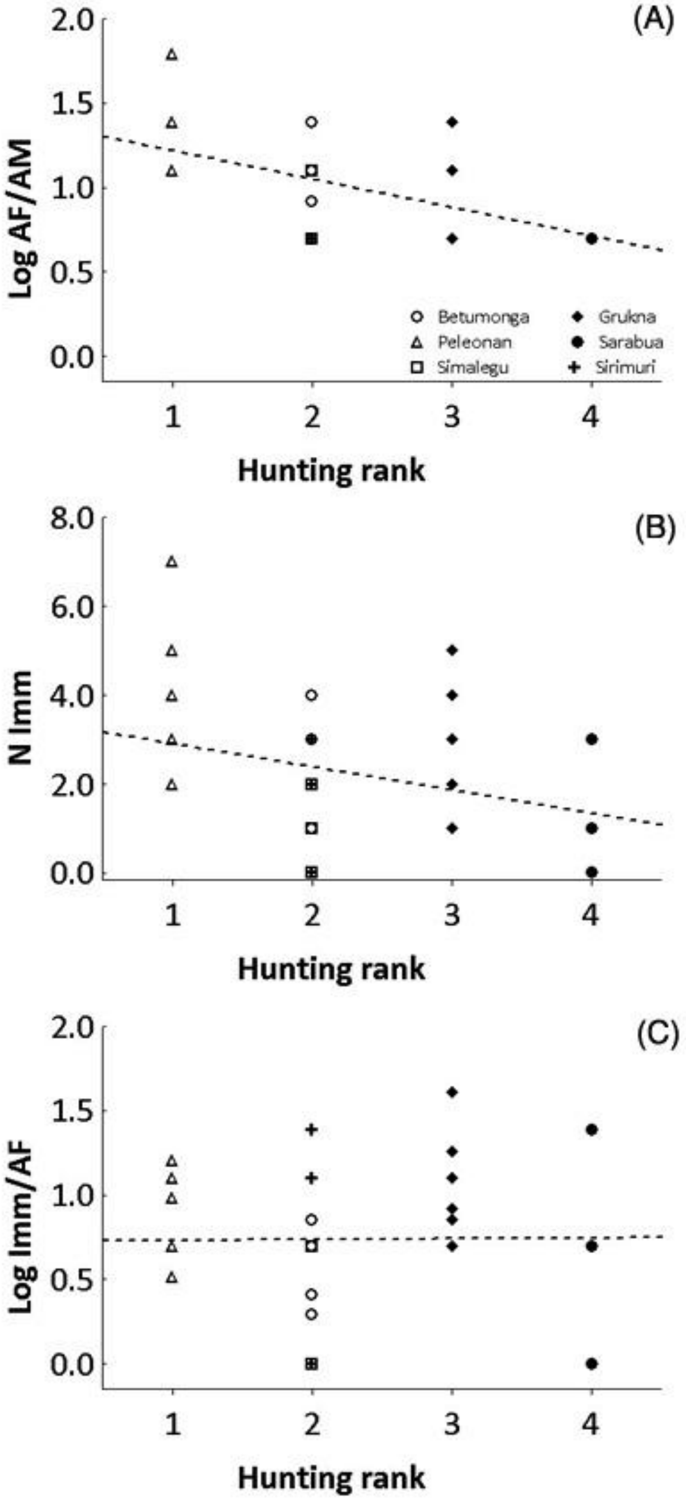


Fig. 2.2. Adult sex ratio (Log AF/AM) (a), number of immatures (N Imm) (b), and immature-to-adult female ratio (Log Imm/AF) (c) in relation to hunting. Hunting ranks increase from 1-4. Each point is a simakobu group. Best fit-lines added for demonstration purposes only.

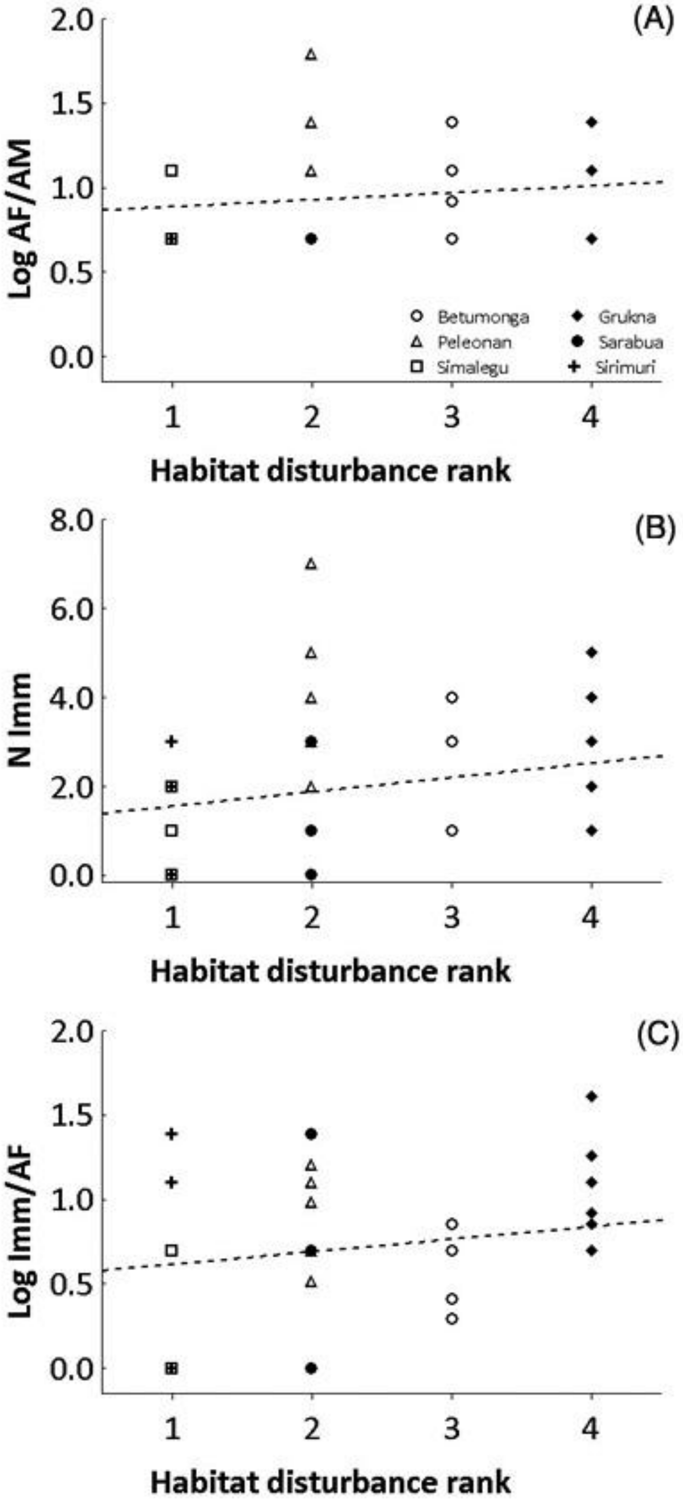


Fig. 2.3. Adult sex ratio (Log AF/AM) (a), number of immatures (N Imm) (b), and immature-to-adult female ratio (Log Imm/AF) (c) in relation to habitat disturbance. Habitat disturbance ranks increase from 1-4. Each point is a simakobu group. Best-fit lines added for demonstration purposes only.

References

Arroyo-Rodríguez V, Dias PAD. 2010. Effects of habitat fragmentation and disturbance on howler monkeys: a review. American Journal of Primatology 72:1-16.

Boonratana R. 1993.The ecology and behaviour of the proboscis monkey (*Nasalis larvatus*) in the Lower Kinabatangan, Sabah [dissertation]. Bangkok: Mahidol University, Bangkok. 165 p.

Boyle SA, Smith AT. 2010. Behavioral modifications in northern bearded saki monkeys (*Chiropotes satanas chiropotes*) in forest fragments of central Amazonia. Primates 51:43-51.

Cowlishaw G, Dunbar RIM. 2000. Primate conservation biology. Chicago: University of Chicago Press. 498 p.

Fretwell SD, Lucas HL. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16-36.

Fuentes A. 1994. The socioecology of the Mentawai Island langur (*Presbytis potenziani*) [dissertation]. Berkley (CA): University of California at Berkeley. 161 p.

Fuentes A, Ray E. 1996. Humans, habitat loss and hunting: the status of the Mentawai Islands primates on Sipora and Pagai Islands. Asian Primates 5:5-9.

Grueter CC, van Schaik CP. 2010. Evolutionary determinants of modular societies in colobines. Behavioral Ecology 21:63-71.

Hadi S, Ziegler T, Hodges JK. 2009a. Group structure and physical characteristics of simakobu monkeys (*Simias concolor*) on the Mentawai Island of Siberut, Indonesia. Folia Primatologica 80:74-82.

Hadi S, Ziegler T, Waltert M, Hodges JK. 2009b. Tree diversity and forest structure in northern Siberut, Mentawai Islands, Indonesia. Tropical Ecology 50:315-327.

Jin T, Wang D, Zhao Q, Yin L, Qin D, Ran W, Pan W. 2009. Social organization of white-headed langurs (*Trachypithecus leucocephalus*) in the Nongguan Karst Hills, Guangxi, China. American Journal of Primatology 71:206-213.

Kirkpatrick RC. 2007. The Asian colobines: diversity among leaf-eating monkeys. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK, editors. Primates in perspective. Oxford: Oxford University Press. p 186-200.

Kirkpatrick RC, Grueter CC. 2010. Snub-nosed monkeys: multilevel societies across varied environments. Evolutionary Anthropology 19:98-113.

Leutenegger W, Lubach G. 1987. Sexual dimorphism, mating system, and effect of phylogeny in de Brazza's monkey (*Cercopithecus neglectus*). American Journal of Primatology 13:171-179.

Lowe, MJ. 2007. Downloaded on March 3, 2011 from http://commons.wikimedia.org/wiki/File:Mentawai_Islands_Map.png

Marshall AJ. 2010. Effect of habitat quality on primate populations in Kalimantan: gibbons and leaf monkeys as case studies. In: Gursky-Doyen S, Supriatna J, editors. Indonesian primates. New York: Springer. p 157-177.

Marshall AR, Topp-Jørgensen JE, Brink H, Fanning E. 2005. Monkey abundance and social structure in two high-elevation forest reserves in the Udzungwa Mountains of Tanzania. International Journal of Primatology 26:127-145.

Mbora DNM, Meikle DB. 2004. The value of unprotected habitat in conserving the critically endangered Tana River red colobus (*Procolobus rufomitratus*). Biological Conservation 120:91-99.

Mitchell AH, Tilson RL. 1986. Restoring the balance: Traditional hunting and primate conservation in the Mentawai Islands, Indonesia. In: Else JG, Lee PC, editors. Primate ecology and conservation. Cambridge: Cambridge University Press. p 249-260.

Mittermeier RA. 1987. Effect of hunting on rain forest primates. In: Marsh CW, Mittermeier RA, editors. Primate conservation in the tropical rain forest. New York: Alan R. Liss. p 109-146.

Mittermeier RA, Wallis J, Rylands AB, Ganzhorn JU, Oates JF, Williamson EA, Palacios E, Heyman EW, Kierulff MCM, Yongcheng L, Supriatna J, Roos C, Walker S, Cortes-Ortiz L, Schwitzer C. 2009. Primates in peril: The world's 25 most endangered primates 2008-2010. Arlington, VA: IUCN/SSC Primate Specialist Group, International Primatological Society, and Conservation International. 84 p.

National Research Council, US. 1981. Techniques for the study of primate population ecology. Washington, D.C.: National Academy Press. 233 p.

Oates JF. 1996. Habitat alteration, hunting and the conservation of folivorous primates in African forests. Australian Journal of Ecology 21:1-9.

Paciulli LM. 2004. The effects of logging, hunting, and vegetation on the densities of the Pagai, Mentawai Island primates [dissertation]. Stony Brook (NY): State University of New York at Stony Brook. 428 p.

PHPA. 1995. Siberut National Park integrated conservation and development plan (1995-2020). Jakarta : Biodiversity Conservation Project. 568 p.

Pinto LP, Costa CM, Strier KB, da Fonseca GA. 1993. Habitat, density and group size of primates in a Brazilian tropical forest. Folia Primatologica 61:135-143.

Plavcan JM, van Schaik CP. 1992. Intrasexual competition and canine dimorphism in anthropoid primates. American Journal of Physical Anthropology 87:461-477.

Quinn GP, Keough MJ. 2002. Experimental design and data analysis for biologists. Cambridge: Cambridge University Press. 537 p.

Quinten MC, Waltert M, Syamsuri F, Hodges JK. 2010. Peat swamp forest supports high primate densities on Siberut Island, Sumatra, Indonesia. Oryx 44:147-151.

Rajpurohit, LS, Sommer V, Mohnot SM. 1995. Wanderers between harems and bachelor bands: Male Hanuman langurs (*Presbytis entellus*) at Jodhpur in Rajasthan. Behaviour 132:255-299.

Schwitzer C, Glatt L, Nekaris KA, Ganzhorn JU. 2011. Responses of animals to habitat alteration: an overview focussing on primates. Endangered Species Research 14: 31-38.

Smith R, Jungers WL. 1997. Body mass in comparative primatology. Journal of Human Evolution 32:523-559.

Stanford CB. 1998. Chimpanzee and red colobus: the ecology of predator and prey. Cambridge MA: Harvard University Press. 305 p.

Steenbeek R, Sterck EHM, de Vries H, van Hooff JARAM. 2000. Costs and benefits of the one-male, age-graded, and all-male phases in wild Thomas's langur groups. In: Kappeler PM, editor. Primate males: causes and consequences of variation in group composition. Cambridge: Cambridge University Press. p 130-145.

Sterck EHM. 1998. Female dispersal, social organization, and infanticide in langurs: are they linked to human disturbance? American Journal of Primatology 44:235-254.

Struhsaker TT. 2008. Demographic variability in monkeys: implications for theory and conservation. International Journal of Primatology 29:19-34.

Struhsaker TT, Marshall AR, Detwiler K, Siex K, Ehardt C, Lisbjerg DD, Butynski TM. 2004. Demographic variation among Udzungwa red colobus in relation to gross ecological and sociological parameters. International Journal of Primatology 25:615-658.

Tenaza RR. 1989. Intergroup calls of male pig-tailed langurs (*Simias concolor*). Primates 30:199-206.

Tenaza RR, Fuentes A. 1995. Monandrous social organization of pigtailed langurs (*Simias concolor*) in the Pagai Islands, Indonesia. International Journal of Primatology 16:295-310.

Tilson RL. 1977. Social organization of simakobu monkeys (*Nasalis concolor*) in Siberut Island, Indonesia. Journal of Mammalogy 58:202-212.

Tutin CEG, Fernandez M. 1984. Nationwide census of gorilla (*Gorilla g. gorilla*) and chimpanzee (*Pan t. troglodytes*) populations in Gabon. American Journal of Primatology 6:313-336.

Waltert M, Abegg C, Ziegler T, Hadi S, Priata D, Hodges JK. 2008. Abundance and community structure of Mentawai primates in the Peleonan Forest, North Siberut, Indonesia. Oryx 42:375-379.

Watanabe K. 1981. Variations in group composition and population density of the two sympatric Mentawaian leaf-monkeys. Primates 22:145-160.

Whittaker DJ. 2006. A conservation action plan for the Mentawai primates. Primate Conservation 20: 95-105.

Whittaker DJ, Mittermeier RA. 2008. *Simias concolor*. In: IUCN 2011. IUCN Red List of Threatened Species. Version 2011.1. Downloaded on September 25, 2011 from http://www.iucnredlist.org.

Whitten AJ, Whitten JEJ. 1982. Preliminary observations of the Mentawai macaque on Siberut Island, Indonesia. International Journal of Primatology 3:445-459.

Winkler P, Loch H, Vogel C. 1984. Life history of Hanuman langurs (*Presbytis entellus*): Reproductive parameters, infant mortality, and troop development. Folia Primatologica 43:1-23.

WorldClim. 2000. "WorldClim." Downloaded on November 16, 2010 from http://www.worldclim.org/tiles.php.

Yeager CP. 1990. Proboscis monkey (*Nasalis larvatus*) social organization: group structure. American Journal of Primatology 20: 95-106.

Yeager CP, Kool K. 2000. The behavioral ecology of Asian colobines. In: Whitehead PF, Jolly CJ, editors. Old World monkeys. Cambridge: Cambridge University Press. p 496-521.

Zucker EL, Clarke MR. 2003. Longitudinal assessment of immature-to-adult ratios in two groups of Costa Rican *Alouatta palliata*. International Journal of Primatology 24:87-101.

CHAPTER THREE:

Annual Variation in Ecology and Reproduction of Wild Simakobu (*Simias concolor*)

(With Carola Borries, Nurul S Lestari, J Keith Hodges: *International Journal of Primatology*, in press)

Abstract

Seasonal breeding in primates is related to the degree of environmental seasonality, particularly the availability and predictability of food. Southeast Asian species in general show moderate birth seasonality due to either low environmental seasonality or unpredictable fluctuations of mast-fruiting food resources. One Southeast Asian primate, however, the simakobu (*Simias concolor*), has been reported to be a strict seasonal breeder with births occurring in June and July only. It is unclear whether these observations are characteristic of the species or result from a sampling bias. To address this question, we documented the annual distribution of 11 births in eight groups of simakobu over two consecutive years at Pungut, an undisturbed site on Siberut Island, Indonesia. We assessed annual variation in ecology and reproduction via rainfall, temperature, food availability, feeding time, physical condition, conceptions, and births. Mean monthly temperature was nearly constant (26.3 – 27.1°C), and monthly precipitation always high (219 – 432 mm). Although simakobu foods were abundant year-round, there were two fruit-feeding peaks in June and September. In contrast to previous reports, we documented births in seven months. Most births occurred in October (45%), the wettest month of the year, and most conceptions in March and April, following a peak in unripe fruit availability. Although sample sizes are very small, females seemed to conceive when their physical condition was best, suggesting that simakobu time conceptions flexibly to the recovery of energy reserves. Across study sites, births occurred in 10 calendar months indicating that simakobu reproduction is not strictly seasonal.

Keywords: birth distribution • capital breeding • conception • food availability • seasonal breeding • Southeast Asian colobines

Introduction

The timing of reproduction is often related to the availability of foods, resulting in breeding seasons in populations where plant productivity is seasonally restricted (reviewed in Janson and Verdolin 2005). Breeding seasonality is typically indicated via measures of the evenness of the distribution of births across months. One quantitative measure that has often been used is the percentage of births observed during the three-month period with the most births (i.e., three-month birth peak), where 25% indicates an even distribution, and 100% indicates that births are restricted to three (or fewer) months of the year (cf. van Noordwijk and van Schaik 2004). More recently, another measure, mean vector length (*r*), has been employed to indicate the degree of concentration of births in a circular distribution, where $r = 0$ when births are evenly distributed across all intervals and $r = 1$ when all births occur within the same interval (cf. Di Bitetti and Janson 2000, Janson and Verdolin 2005).

Among primates, most populations show at least some degree of seasonality in the timing of births (reviewed in Janson and Verdolin 2005). Three general patterns in the annual distribution of births can be identified: 1) strict seasonality (cf. Lancaster and Lee 1965), where births occur at around the same time every year and there are multiple consecutive months with no births (e.g., Hanuman langurs, *Semnopithecus entellus*: Koenig et al. 1997, Verreaux's sifakas, *Propithecus verreauxi*: Lewis and Kappeler 2005); 2) moderate seasonality, where births occur in all or most months of the year, but with a clear peak that may or may not occur in the same months across years (e.g., long-tailed macaques, *Macaca fascicularis*: van Schaik and van Noordwijk 1985); and 3) no seasonality, where births occur throughout the year with no peak in the distribution (e.g., mountain gorillas, *Gorilla beringei*: Watts 1998).

Birth seasonality in primates is related, in particular, to the length and predictability of the period of food abundance and is lowest for species that rely on non-seasonal resources and live in relatively aseasonal environments, such as those with folivorous diets living at low latitudes (Lindburg 1987, Di Bitetti and Janson 2000). Conversely, frugivores residing at high latitudes are among the most seasonal breeders (Di Bitetti and Janson 2000). Building on previous work (i.e., Drent and Daan 1980; Jönsson 1997; Stearns 1989), Brockman and van Schaik (2005) described two patterns of reproductive seasonality in primates in relation to environmental seasonality and predictability of seasonal food peaks, namely "income" and "capital" breeding (cf. Stearns 1992). Income breeders use current *energy intake* to offset the costs of reproduction, while capital breeders build up *energy reserves* prior to reproduction. Consequently, for income breeders, birth peaks coincide with or directly follow food peaks such that the most costly aspect of reproduction, i.e., *early lactation* (Lee et al. 1991) occurs when food is abundant, whereas for capital breeders, *conception* occurs when food is abundant, after females have built up their energy reserves, resulting in birth peaks and lactation occurring at less favorable times. While the income breeding tactic is expected in habitats with predictable food peaks, the capital breeding tactic is expected when food peaks are unpredictable or when environmental seasonality is moderate or absent (van Schaik and van Noordwijk 1985). Thus, income breeders should respond to predictable environmental cues (e.g., photoperiod) to resume cycling, whereas capital breeders should respond to internal cues about their physical and energetic condition (Brockman and van Schaik 2005).

Most Southeast Asian primates have been characterized as capital breeders, often showing moderate birth seasonality (Brockman and van Schaik 2005). For example, long-tailed macaques in northern Sumatra gave birth year-round, with a peak between July and November, during or after the peak in fruit availability (van Noordwijk and van Schaik 1999). This pattern has been interpreted as being a consequence of highly unpredictable resources in habitats characterized by mast-fruiting events leading to reduced seasonality across years (Brockman and van Schaik 2005, Janson and Verdolin 2005). While Brockman and van Schaik's (2005) capital breeding generalization was made about macaques and orangutans, it is likely that the pattern also holds for the less frugivorous Southeast Asian colobines (e.g., red-shanked doucs, *Pygathrix nemaeus*: Phiapalath et al. 2011).

In light of these observations it is surprising that one Southeast Asian colobine, the simakobu (*Simias concolor*) on Siberut Island, is reported to be a strict seasonal breeder with births occurring in just two months of the year, June and July (Tilson 1977). This pattern suggests that lactation coincides with high food availability (as predicted for income breeders) since fruiting in the area was reported to peak in July (Whitten 1980). Although Tilson's study covered a 21-month period, due to very small group sizes, just five births were documented. A single birth occurred in one study group, while the others were recorded during surveys throughout Siberut. An additional five births were reported by hunters, all during June and July. It is unclear, however, whether the surveys and hunts were distributed evenly across months, and if a potential bias in data collection could explain the reported bias in births. Two other studies suggested that simakobu births may be concentrated between November and February, following the wet season (Hadi et al. 2009; Watanabe 1981). As with the Tilson study, the data in these studies were limited to five or fewer infants and covered less than two years each. Thus, it remains unclear whether and when a peak in births occurs for simakobu.

Here we present data on births recorded during systematic censuses of known wild simakobu groups over 25 consecutive months at an undisturbed site in northern Siberut, Indonesia. Our objective is to assess annual variation in simakobu ecology and reproduction by documenting year-round changes in rainfall, temperature, food availability, feeding time, physical condition, conceptions, and births in this population. Given the common Southeast Asian primate pattern, we do not expect to find strict birth seasonality. If, like other Southeast Asian primates, simakobu are capital breeders, we predict that conceptions occur during or immediately following food peaks when female physical condition is best. We further aim to compare the distribution of births in simakobu to those for other Southeast Asian colobines. Since simakobu reside at low latitudes, where periods of food abundance are generally longer and more predictable (di Bitteti and Janson 2000), we predict their three-month birth peak to be lower than the other species'.

Methods

Study Site and Species

We conducted research at the Siberut Conservation Programme’s Pungut study site in northern Siberut, Indonesia. The study area comprises 1,100 ha of primary mixed evergreen rainforest (altitude: ca. 25 – 190 m), which lies within the 4,500 ha area known as the Peleonan forest (0°56’ – 1°03’S, 98°48’ – 98°51’E). Although designated as production forest, it is currently protected from hunting and logging through agreements with the local community and Indonesian officials. Additional information about the study site is provided in Erb et al. (2012) and Waltert et al. (2008).

Simakobu are medium-sized Asian colobines (adult males 7.7 – 8.9 kg, adult females 5.2 – 7.1 kg: Hadi et al. 2009; Tenaza and Fuentes 1995). One-male, multi-female groups average 7.9 individuals with a mean of three adult females, two juvenile females and one or two infants. All-male groups average 4.5 individuals and comprise males of all non-infant age classes and occasionally juvenile females (Erb et al. 2012). Because to our knowledge the gestation length of simakobu has not yet been determined, we extrapolated a value of 201 days (6.6 months) from the fitted function between body mass and gestation length in wild Asian colobines (Figure 3 in Borries et al. 2011), assuming an average adult female body mass of 6.3 – 6.8 kg (Hadi et al. 2009, Smith and Jungers 1997, Tenaza and Fuentes 1995).

Phenology and Climate

To describe annual patterns of food availability, we collected phenological data monthly for 13 months (December 2007 – December 2008) on 404 trees and lianas. The sample included up to 10 adult specimens of the most common species from 9 botanical plots (0.9 ha total) established at the start of the study, plus feeding trees for species eaten by the monkeys but not present in the plots. For this study, we selected data from 152 tree and liana specimens representing the 21 top food species (accounting for 76% of feeding time). We estimated each phytophase (e.g., leaf bud, flower, ripe fruit) on a 4-point scale (from 0 = nothing, 1 = items in 1/3 of the crown area, 2 = in 2/3 of the crown area, and 3 = crown area full). We calculated the availability of young leaves, leaf buds, flowers, and unripe and ripe fruits using an adaptation of Marsh's index (Koenig et al. 1997; Marsh 1981), which weighs the mean phenological score of a given species by its importance percentage (includes density, area at breast height, and frequency – data collected from 15 botanical plots, which included the original 9 plots plus 6 plots established later in the study, covering 1.5 ha representing about 25% of the focal groups' ranges). Mature leaves were not considered as they were always abundant.

Due to equipment failure, weather data at the site were not available for the study period. We therefore obtained climate data from WorldClim (Hijmans et al. 2005). The WorldClim database compiles measurements recorded from weather stations between 1950 and 2000, which are interpolated for interlaying areas. We downloaded the following 30 arc-seconds data files: 1) Mean Temperature = average monthly mean temperature; 2) Precipitation = average monthly precipitation; 3) Altitude = elevation above sea level; and 4) Bioclim = annual mean temperature, mean diurnal temperature range, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation. Values from four point locations representing the boundaries of the Pungut study area were extracted from raster files using ESRI® ArcMapTM 9.3 and averaged. Based on these data, we constructed a climate diagram following the procedures established by Walter (1994).

Demography and Behavior

We contacted and made counts of eight wild one-male, multi-female simakobu groups on 373 group-census days from December 2006 through December 2008. Adult male membership in all groups remained stable over the study period. Two of these groups, H and S, were focal groups and were contacted during most months (H = 25, S = 20 months) for an average of 5.2 days per group per month (*N* = 262, range 0 – 21 days). A total of seven infants were born into these two groups during the study period. The remaining six groups were contacted at irregular intervals whenever the schedule (designed to collect data on the behavior of adult males) would allow (*N* = 54 days, mean 0.74 contact days per group per month, range 0 – 8). Although infants were born into five of the six groups, the month of birth could only be estimated for four infants in three of these groups (J, P and Z). Thus, the sample includes 11 births in five one-male groups.

Two of the 11 infants were found alone (alive, but later died) within the home range of one of the focal groups (S) in 2007. These infants had not been observed in the group beforehand and therefore the mothers were unknown. Based on known group ranging patterns (Erb, unpublished data), these infants were assigned to group S. Both infants were estimated to be two weeks of age when found.

Birth months were known for five infants (i.e., mother observed without infant on previous observation day in focal group). For the remaining six infants, we estimated their ages based on size, motor skills (begin moving away from mother at 6 – 7 weeks: Erb, unpubl. data), and/or skin coloration (melanin appears on hands/feet at 6 – 7 weeks, on faces at 2 – 3 months: Erb, unpubl. data). Of these, we estimated three to be less than one month old, and the other three to be less than two months old. We did not estimate birth dates for infants older than two months of age. Conception months were determined by subtracting 201 days from the estimated date of birth for each infant.

To calculate monthly feeding time, we used focal animal data from December 2007 until November 2008 for six adult males from three one-male, multi-female groups and one all-male group. We recorded instantaneous data on feeding at five-minute intervals during all-day follows of the adult males. Local names of food species were recorded and food item and age were reported in broad categories (e.g., young leaf, ripe fruit, etc.). We compiled a total of 1,787 feeding points, averaging 149 per month (range 64 – 281), and could identify the food item in 94.4% of the cases (range 81.8 – 98.4%). From these values, we calculated the amount of time spent feeding on leaves, flowers, fruits, and other foods (e.g., fungus, insects) in each month as a percentage of the total feeding points. Although feeding data for reproductive females would have been a more direct measure in this context, our main study focused on adult males and consequently these data are of much better quality (i.e., cover a longer period, were collected using instantaneous versus scan sampling, include more identified foods) and sample more individuals compared to those for females. In addition, adult males and females spent a similar amount of time feeding overall (Erb 2008). Furthermore, instantaneous focal (male only) and group scan (all group members) datasets for monthly fruit feeding times yielded comparable results which did not differ significantly (Wilcoxon signed-ranks test: $T = 32.00$, $P > 0.10$, $N = 12$ months).

In addition to feeding data, the physical condition of adult and juvenile females was assessed once per month by visual inspection of the back and limbs (following Koenig et al. 1997) and recorded on a 3-point scale (poor = lean, average = neither lean nor fat, good = fat). Female physical condition data were available for six females, five juveniles and one adult, who were sampled in at least six of the 13 months for which these data were collected. Although physical condition data were also collected for the other adult females in focal groups, these females could not be assessed regularly and thus data were not continuous enough to document changes throughout the reproductive cycle. The data for juvenile females were included to document seasonal changes in physical condition unrelated to reproduction.

To describe the annual distribution of births, we calculated the average percentage of births during the three consecutive months with the most births as well as the circular statistic mean vector length (*r*). We tested the value of r against a null hypothesis of no clustering via the Rayleigh test (Batschelet 1981) in the CircStats package 0.2-4 in R 2.12.0. We used Statistica 9.1 to conduct nonparametric analyses to test for the relationship between sampling effort and the number of births observed each month, and for that between latitude and three-month birth peaks among Southeast Asian colobine populations.

Research permits were issued by LIPI (Indonesian Institute of Sciences) in accordance with the legal requirements of conducting research in Indonesia. All research methods were approved by the Institutional Animal Care and Use Committee at Stony Brook University.

Results

Ecology

The climate at the Pungut study site was characterized by warm and wet conditions throughout the year (Fig. 3.1). Temperature showed almost no variation, with mean monthly temperatures varying between 26.3 and 27.1°C. Rainfall, however, did vary throughout the year. The wettest period occurred between September and December with a peak in rainfall in October

(432 mm). Even in the driest month, however, mean precipitation was more than 200 mm (219 mm in May) and the climate remained perhumid throughout the year.

Similarly, the phenology of simakobu food species lacked distinct annual variation (Fig. 3.2). Young leaves and leaf buds were abundant throughout the year (Fig. 3.2a). Flowers, while less abundant, were also available during most months of the year (Fig. 3.2b). They were least abundant in December 2008, but most abundant in December 2007, suggesting considerable inter-annual differences in phytophase availability. This high abundance of flowers was followed by a rise in the availability of unripe fruits two months later, but this was not the largest fruit peak of the year (Fig. 3.2b). Either unripe or ripe fruits were available in most months; with the exception of May, June, and December 2008. Unripe fruits were most abundant between June and September, and were also elevated between February and March, while ripe fruits were most abundant in April October, and November. Taken together, fruits were abundant during nine months of the year.

In spite of limited annual variation in food abundance, simakobu feeding time showed high variation across months (Fig. 3.3). Fruits accounted for an average of 17.1+SD 11.80% (CV = 68.9) of feeding time throughout the year, with monthly values ranging from 4.5% – 42.2%. Ripe fruits contributed to 25.4% (range 0 – 66.7%) and unripe fruits 70.5% (range 11.1 – 100%) of monthly fruit feeding time. Two distinct peaks of fruit feeding occurred in June (42.2%) and September (39.5%) at the start and end of the peak in unripe fruit availability. Flower feeding time was slightly less variable throughout the year (CV = 58.5), with flowers accounting for 25.5+SD 14.9% of the average monthly feeding time. Flower feeding peaked in August (59.7%) and was lowest in June (0%). Leaves contributed to 50.5+SD 12.0% of average monthly feeding time (range 25.4 – 67.7%; CV = 23.7), with young leaves and leaf buds accounting for 79.0%

(range 62.2 – 97.9%) and mature leaves 11.0% (range 0 – 32.4%) of monthly leaf feeding time. Leaves were the most commonly eaten foods throughout the year, except in January and August, when flowers contributed most to feeding time. Other foods, such as insects, fungus, and moss accounted for 1.1+SD 1.3% (range 0 – 3.2%; CV = 124.7) of monthly feeding time, and were highest in February (3.1%) and November to December (3.2%).

Reproduction

Births occurred in seven calendar months, with births in the two focal groups – for which data were collected most systematically – covering six of these months (Fig. 4). There was a peak of six births (55%) during September and October, which represents the three-month birth peak, since there were no births in August or November. This result cannot be explained by a sampling bias, as these two months accounted for 15% of our observation days (where 16.7% represents an even distribution) and there was no relationship between the number of days groups were censused and births observed each month (Fig. 4, *Kendall's Tau* = 0.06, $P = 0.79$, $N = 12$). Five of these births (45%) were in the month of October alone, which is the wettest month of the year (Fig. 3.1). The circular statistics, however, indicate that the distribution of births did not significantly deviate from a uniform distribution (mean vector length $r = 0.276$, Rayleigh test of uniformity: $P = 0.44$).

Other Southeast Asian colobines for which data are available show similar three-month birth peaks, ranging from 33 to 63% of births, 45.5% on average (silvered leaf monkeys, *Trachypithecus cristatus* = 33% [3°21', N = 76]: Wolf 1984; Thomas' langurs, *Presbytis thomasi* = 38% [3°30', N = 13]: Gurmaya 1986; Javan surili, *Presbytis comata* = 50% [7°11', N = 12]: Ruhiyat 1983; red-shanked doucs = 63% [17°15', N = 19]: Phiapalath et al. 2011). Even within this small dataset, we found a positive correlation between latitude and the extent of the birth peak (*Kendall's Tau* = 1.00, *P* = 0.04, *N* = 4), similar to that reported across Hanuman langur populations (Newton and Dunbar 1994). Although simakobu at Pungut reside at a lower latitude (1°3'S) than the other species, their three-month birth peak is of greater magnitude than all but the northernmost species (red-shanked doucs at 17°15'N), and when simakobu were added to the dataset above, the correlation disappeared (*Kendall's Tau* = 0.40, *P* = 0.33, *N* = 5).

The three-month period with the most conceptions was between February and April, when six (55%) conceptions occurred (Fig. 3.4). An additional three (27%) conceptions occurred between July and September. Both periods coincided with or immediately followed a peak in unripe fruit availability.

Juvenile female physical condition was good from April to June and in November 2008, following the two peaks in ripe fruit availability; and poor in March and July (Fig. 3.5). The adult female conceived after her physical condition had been good for at least two months. It dropped to average for most of her gestation and declined further after parturition, when juvenile females reached their best physical condition of the year.

Discussion

Siberut has been described as having four indistinct seasons: "two wet, one very wet, and one incredibly wet" (Whitten 1982a:76). We confirmed this characterization by constructing a climate diagram for our study site, which showed consistently warm temperatures and abundant rainfall throughout the year. Most rain fell between September and December, but there was never a month averaging less than 200mm of rain. Food was abundant throughout the year.

While there were periods when fruits were more abundant, these peaks were relatively shallow, and even when fruits were scarce, flowers and young leaves were available.

In light of this limited environmental variation, the variation in simakobu feeding behavior, particularly on fruits, is surprising. While the monthly feeding time on fruits was low during most months (between 10-20%), there were two months when fruits accounted for more than 39% of feeding time (June and September). The second of these peaks coincided with an increase in ripe fruits as well as the three-month birth peak. Although both fruit-feeding peaks coincided with the period of high fruit availability, it is unclear why fruit feeding was low in the two months between peaks. Because one group fed heavily on a rare species of *Ficus* in June, this peak could be a sampling artifact, and the fruit-feeding peak in September might be a better representation of the population on the whole.

As expected, simakobu breeding was not strictly seasonal. Despite an early report that births were restricted to June and July (Tilson 1977: Table 3.1), we documented just one of 11 births in these two months. This difference can likely be attributed to the smaller sample size in the Tilson study (i.e., one birth in one focal group observed year-round). The remaining births were based on surveys throughout Siberut and on information from hunters, so there may have been a sampling bias.

It is also possible, however, that ecological differences exist between the study locations that could affect reproduction. Birth rates at Sirimuri in southern Siberut (Tilson 1977), for example, were much lower than those at our site in northern Siberut (Erb et al. 2012). Though the two sites are only about 45 km apart, the compositions of the forests are different. Sirimuri is dominated by trees of the family Dipterocarpaceae (Whitten 1982b), which do not produce fleshy fruits and probably do not provide much energy for simakobu (but flowers may be an important fallback food during severe drought, Paciulli 2010). In contrast, Pungut lies within a mixed forest with a higher proportion of fruit trees, and presumably higher food availability (Whittaker 2005). Furthermore, phenology may differ between sites. Data collected at a site about 6 km from Sirimuri showed nearly identical patterns in young leaf production to Pungut, but very different patterns in fruit production, with peaks occurring between April and July (Whitten 1980).

The possibility of inter-site differences is further supported by the fact that two other studies in northern Siberut reported that births were concentrated between November and February (Hadi et al. 2009; Watanabe 1981: Table 3.1). At Pungut, conversely, only two of 11 births occurred during these months, despite being situated only about 10 km from the other northern Siberut sites. Alternatively, the differences between studies could indicate differences on a temporal, rather than spatial scale. Significant inter-annual variation, as occurs in habitats characterized by mast-fruiting, could further explain shifts in reproduction across years. We were unable to confirm the occurrence of mast-fruiting events in our study area, as we only documented a single year of phenology and masting cycles are irregular, occurring every two to 10 years (Ashton et al. 1988). The fact that availability of flowers varied greatly between December 2007 and December 2008, however, suggests that there could be considerable variation across years.

Taken together, these studies suggest that simakobu are capable of giving birth in almost every month of the year (Table 3.1). The variation across sites and over time, however, indicates that the timing of birth is most likely influenced by local fluctuations in food availability. Thus, while the population at Pungut and the species collectively lack distinct seasonality of reproduction, individual populations may still display moderate seasonality in the form of seasonal birth peaks whose timing is determined by factors operating at a local level which may vary from year to year.

In the current study, births occurred throughout the year, in most months and were not significantly clustered. However, our sample size was very small and as such this result should be viewed as preliminary. With a sample size of 11 births, an r value >0.50 would have been needed to reach statistical significance. At the same time, the r we observed (0.28), would require a sample size of $N \approx 40$ for this result to have been significant. Nonetheless, there was a three-month birth peak during the wettest period of the year, when 55% of births occurred. The fact that at least one birth occurred within the month of October in each year of our study suggests that this may be an important time for reproduction. October was characterized by a decrease in the availability of fruits and an increase in leaves, and occurred about six months after the first fruit peak of the year (Fig. 3.2). These observations suggest that simakobu may be capital breeders with conceptions flexibly timed to the recovery of energy reserves of individual females, an idea supported by the data on female physical condition. While the adult female in this study was in good physical condition before and at conception, and average through most of gestation, she quickly declined to poor condition following birth, which indicates that she was not able to compensate for the increased energetic demands of lactation by increasing energy intake (income breeding). More data covering multiple years are required to confirm this hypothesis.

Although simakobu at Pungut reside at lower latitude than the other Asian colobine species we examined, their three-month birth peak was unexpectedly higher. While this result is perhaps an artifact of small sample sizes, we cannot rule out the possibility that some ecological factors could be responsible for a more seasonal restriction of births in simakobu compared to most other Southeast Asian colobines. The Mentawai Islands differ from other parts of Southeast Asia in having very high rainfall and less fertile soils as well as fewer legumes (Whitten 1980). Thus, while the environment appears to exhibit little seasonality and relatively abundant food year-round, it is possible that low-quality food on Siberut constrains simakobu reproduction. This idea is supported by the observations that leaf quality decreases with increasing rainfall, and that primate population growth is more strongly limited by food quality during the lush season than by food quantity during the lean season (Ganzhorn et al. 2003). Future studies of the intra- and inter-annual patterns of both food quantity and quality are needed to address this hypothesis.

Tables and Figures

Table 3.1. Known birth months for simakobu.

Month	Tilson 1977	Watanabe 1982	Hadi et al. 2009	present study
January		x		x
February		x		x
March				
April				x
May				x
June	x			x
July	x			
August				
September				x
October				x
November			x	
December		x	x	

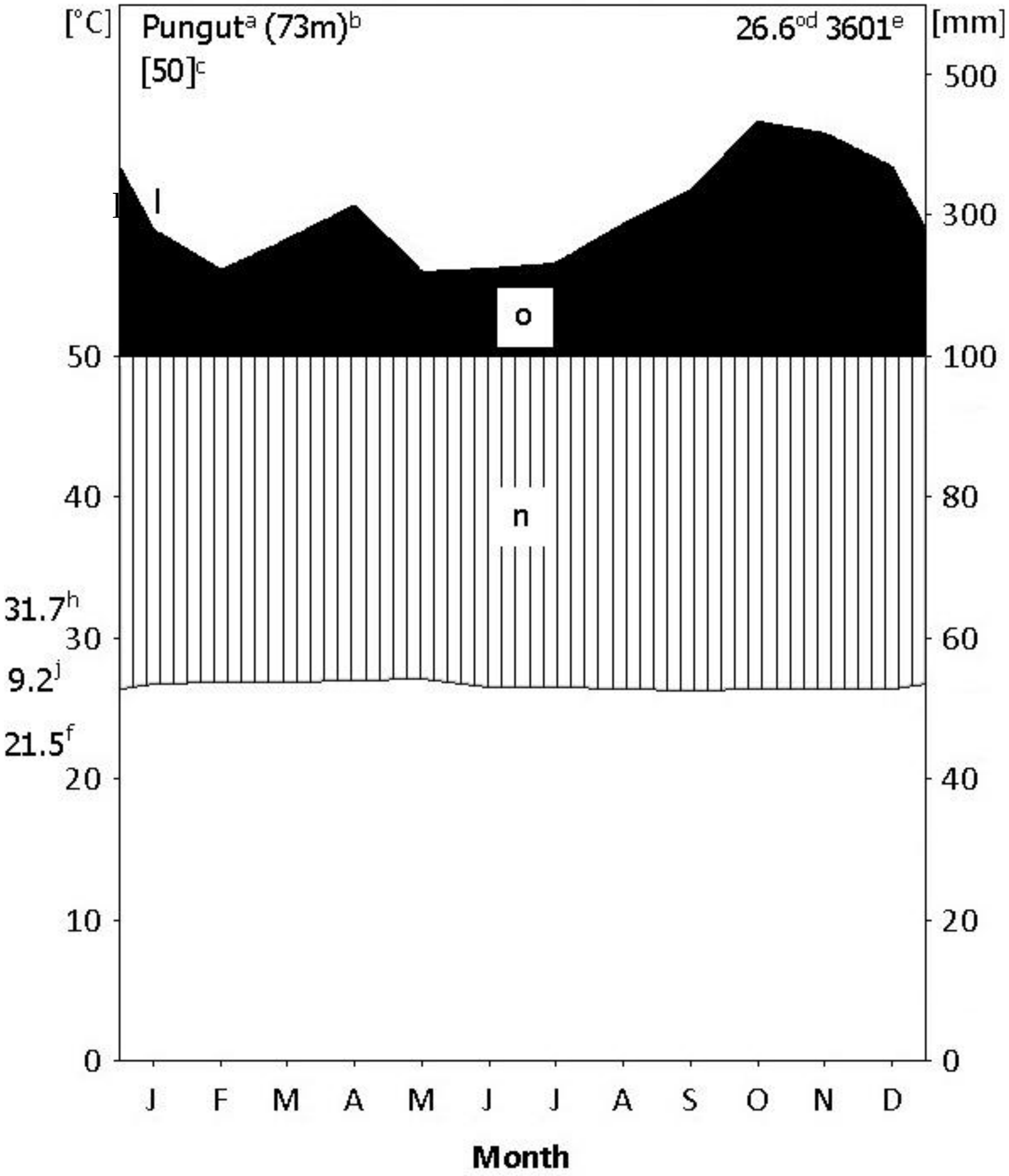


Fig. 3.1. Climate at Pungut between 1950-2000 (data obtained from WorldClim), plotted following Walter (1994): a = station, b = elevation above sea level, c = number of observation years, d = mean annual temperature; e = mean annual precipitation, f = mean daily minimum of the coldest month, h = mean daily maximum of the warmest month, j = mean daily temperature fluctuation, k = plot of mean monthly temperature, l = plot of mean monthly precipitation, n = humid period, o = perhumid period.

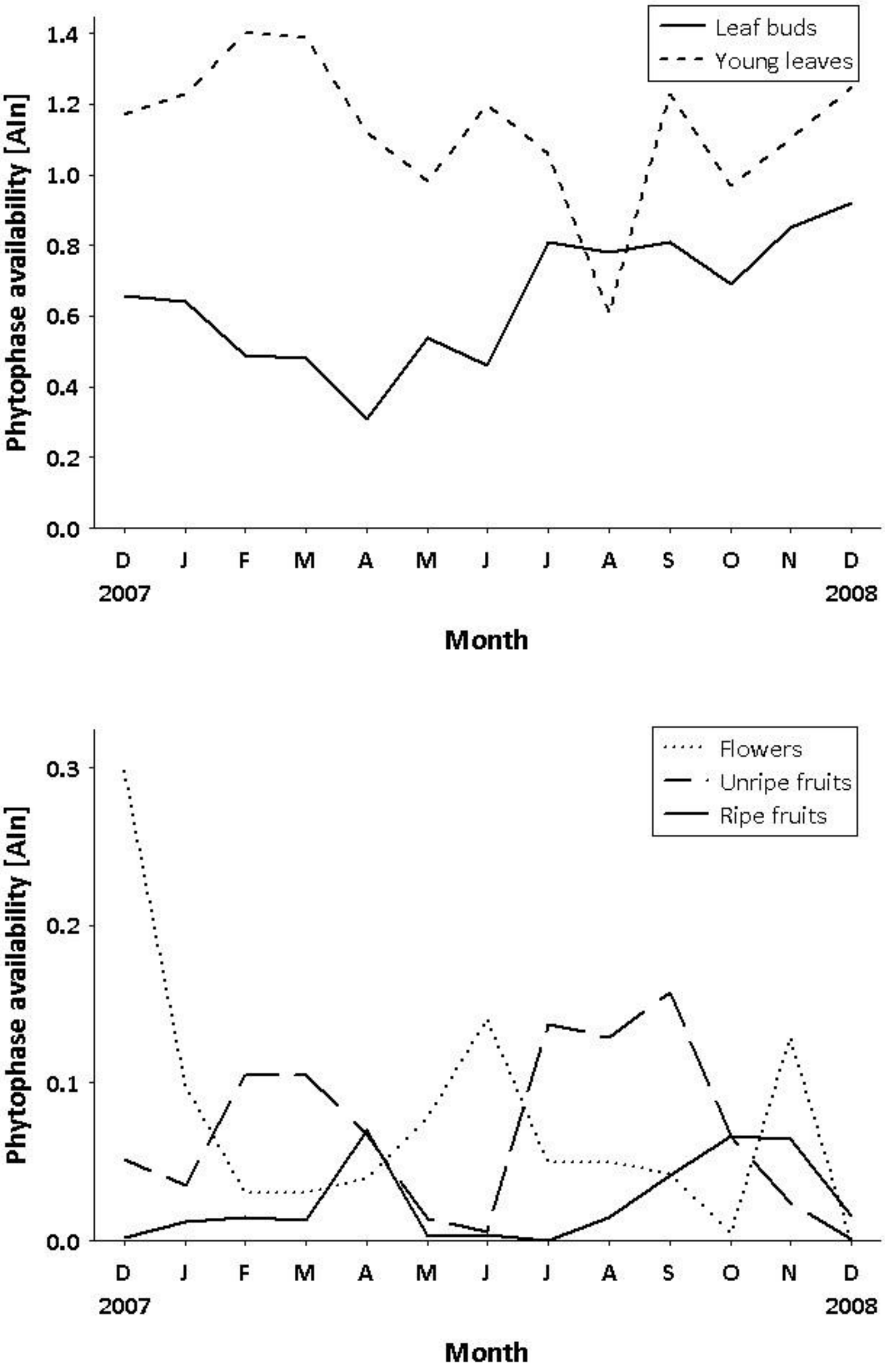


Fig. 3.2. Phytophase availability (Marsh's index) for December 2007 – December 2008 of the top 21 food species. (a) young leaves and leaf buds, (b) flowers, unripe fruits and ripe fruits.

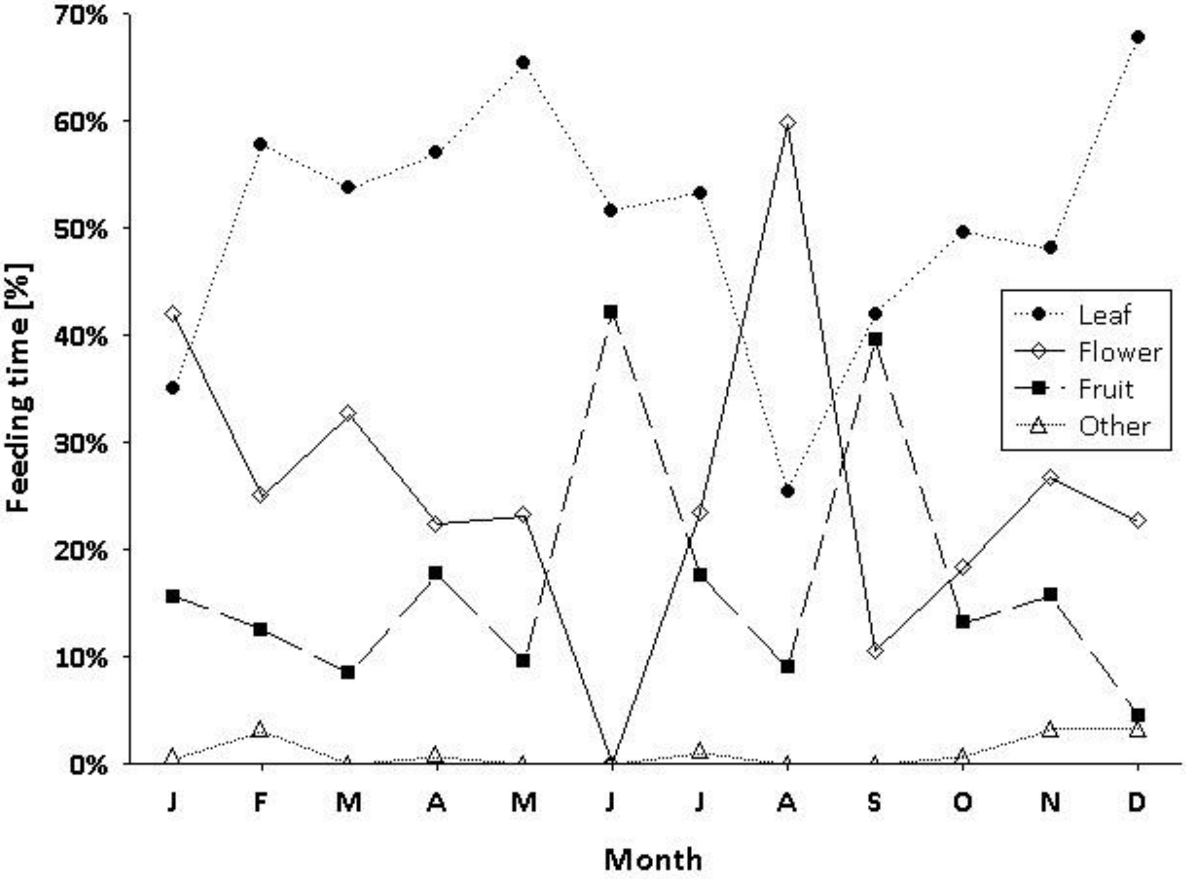


Fig. 3.3. Percent of feeding time devoted to leaves, flowers, fruits, and other items. Feeding data for December 2007 – November 2008.

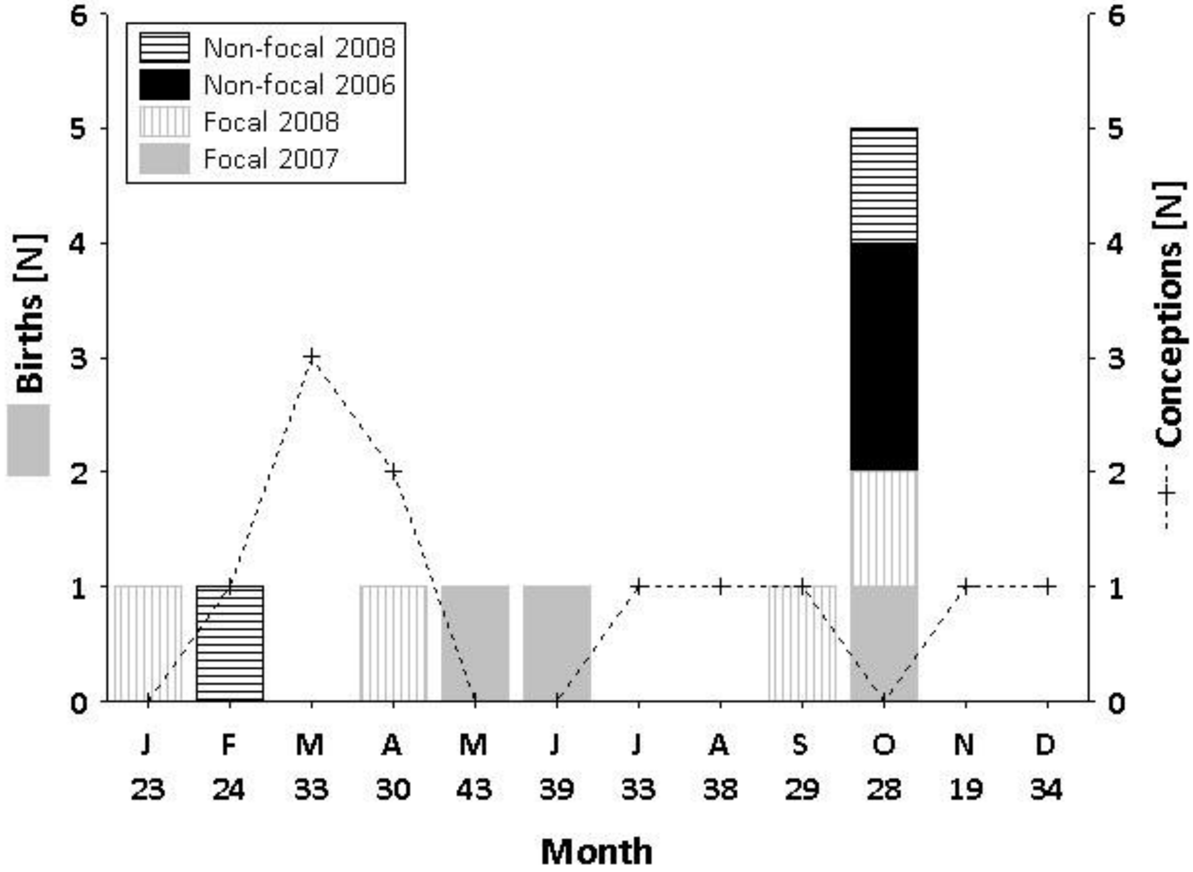


Fig. 3.4. Annual distribution of births and conceptions in focal and non-focal groups. Number of group census days indicated below each calendar month.

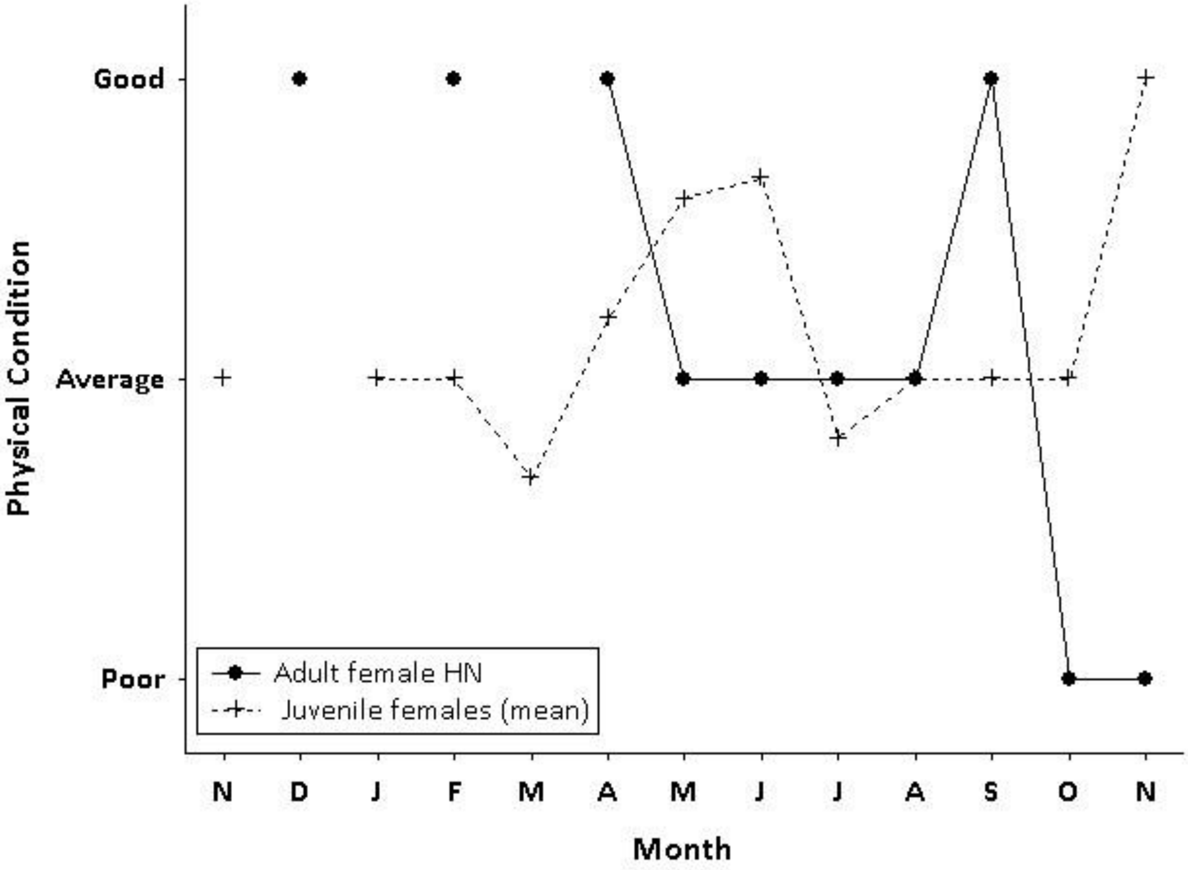


Fig. 3.5. Monthly average physical condition for juvenile females compared to that of an adult reproductive female. Adult female's conception and birth months indicated.

References

Ashton, P. S., Givnish, T. J., & Appanah, S. (1988). Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *American Naturalist*, *132*, 44-66.

Batschelet, E. (1981). *Circular statistics in biology.* New York: Academic Press.

Borries, C., Lu, A., Ossi-Lupo, K., Larney, E., & Koenig, A. (2011). Primate life histories and dietary adaptations: a comparison of Asian colobines and macaques. *American Journal of Physical Anthropology*, *144*, 286-299.

Brockman, D. K. & van Schaik, C. P. (2005). Seasonality and reproductive function. In D. K. Brockman & C. P. van Schaik (Eds.), *Seasonality in primates: Studies of living and extinct human and non-human primates.* (pp. 269-305). Cambridge: Cambridge University Press.

Di Bitetti, M. S. & Janson, C. H. (2000). When will the stork arrive? Patterns of birth seasonality in neotropical primates. *American Journal of Primatology*, *50*, 109-130.

Drent, R. H. & Daan, S. (1980). The prudent parent: Energetic adjustments in avian breeding. In H. Klomp & J.W. Woldendrop (Eds.), *The integrated study of bird populations*. (pp. 225-252). New York: North Holland.

Erb, W. M., Borries, C., Lestari, N. S., Ziegler, T. (2012). Demography of simakobu (*Simias concolor*) and the impact of human disturbance. *American Journal of Primatology*, *74*, 580-590.

Ganzhorn, J. U., Klaus, S., Ortmann, S., & Schmid, J. (2003). Adaptations to seasonality: Some primate and nonprimate examples. In P. M. Kappeler & M. E. Pereira (Eds.), *Primate life histories and socioecology.* (pp. 132-148). Chicago and London: The University of Chicago Press.

Gurmaya, K. J. (1986). Ecology and behavior of *Presbytis thomasi* in Northern Sumatra. *Primates*, *27*, 151-172.

Hadi, S., Ziegler, T., & Hodges, J. K. (2009). Group structure and physical characteristics of simakobu monkeys (*Simias concolor*) on the Mentawai Island of Siberut, Indonesia. *Folia Primatologica*, *80*, 74-82.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965-1978.

Janson, C. H. & Verdolin, J. (2005). Seasonality of primate births in relation to climate. In D. K. Brockman & C. P. van Schaik (Eds.) *Seasonality in primates: Studies of living and* *extinct human and non-human primates.* (pp. 307-349). Cambridge: Cambridge University Press.

Jönsson, K. I. (1997). Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*, *78*, 57-66.

Koenig, A., Borries, C., Chalise, M. K., & Winkler, P. (1997). Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). *Journal of Zoology*, *243*, 215-235.

Lancaster, J. B. & Lee, R. B. (1965). The annual reproductive cycle in monkeys and apes. In: I. DeVore (Ed.) *Primate behavior: Field studies of monkeys and apes*. (pp. 486-513). New York: Holt, Rinehart and Winston.

Lee, P. C., Majluf, P., & Gordon, I. J. (1991). Growth, weaning and maternal investment from a comparative perspective. *Journal of Zoology*, *225*, 99-114.

Lewis, R. J. & Kappeler, P. M. (2005). Seasonality, body condition, and timing of reproduction in *Propithecus verreauxi verreauxi* in the Kirindy Forest. *American Journal of Primatology*, *67*, 347-364.

Lindburg, D. G. (1987). Seasonality of reproduction in primates. In E. J. Mitchell (Ed.), *Comparative primate biology Vol. 2B.* (pp. 167-218). New York: Alan R. Liss.

Marsh, C. W. (1981). Diet choice among red colobus (*Colobus badius rufomitratus*) on the Tana river, Kenya. *Folia Primatologica*, *35*, 147-178.

Newton, P. N. & Dunbar, R. I. M. (1994). Colobine monkey society. In A. G. Davies & J. F. Oates (Eds.), *Colobine monkeys: Their ecology, behaviour and evolution*. (pp. 311-346). Cambridge: Cambridge University Press.

Paciulli, L. M. (2010). The relationship between nonhuman primate densities and vegetation on the Pagai, Mentawai Islands, Indonesia. In S. Gursky-Doyen & J. Supriatna (Eds.), *Indonesian primates*. (pp. 199-215). New York: Springer.

Phiapalath, P., Borries, C., & Suwanwaree, P. (2011). Seasonality of group size, feeding, and breeding in wild red-shanked douc langurs (Lao PDR). *American Journal of Primatology*, *73*, 1134-1144.

Ruhiyat, Y. (1983). Socio-ecological study of *Presbytis aygula* in West Java. *Primates*, *24*, 344-359.

Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology*, *3*, 259-268.

Stearns, S.C. (1992). *The evolution of life histories*. New York: Oxford University Press.

Tenaza, R. R. & Fuentes, A. (1995). Monandrous social organization of pigtailed langurs (*Simias concolor*) in the Pagai Islands, Indonesia. *International Journal of Primatology, 16*, 295-310.

Tilson, R. L. (1977). Social organization of simakobu monkeys (*Nasalis concolor*) in Siberut Island, Indonesia. *Journal of Mammalogy, 58*, 202-212.

van Noordwijk, M. A. & van Schaik, C. P. (1999). The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, *Macaca fascicularis. Primates, 40,* 105-130.

van Noordwijk, M. A. & van Schaik, C. P. (2004). Sexual selection and the careers of primate males: Paternity concentration, dominance-acquisition tactics and transfer decisions. In P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates: New and comparative perspectives*. (pp. 208-229). Cambridge: Cambridge University Press.

van Schaik, C. P. & van Noordwijk, M. A. (1985). Interannual variability in fruit abundance and the reproductive seasonality in Sumatran Long-tailed macaques (*Macaca fascicularis*). *Journal of Zoology, 206*, 533-549.

Walter, H. (1994). *Vegetation of the earth and ecological systems of the geo-biosphere.* Berlin: Springer.

Waltert, M., Abegg, C., Ziegler, T., Hadi, S., Priata, D., & Hodges, J. K. (2008). Abundance and community structure of Mentawai primates in the Peleonan Forest, North Siberut, Indonesia. *Oryx, 42*, 375-379.

Watanabe, K. (1981). Variations in group composition and population density of the two sympatric Mentawaian leaf-monkeys. *Primates, 22,* 145-160.

Watts, D. P. (1998). Seasonality in the ecology and life histories of mountain gorillas (*Gorilla gorilla beringei*). *International Journal of Primatology, 19,* 929-948.

Whittaker, D. J. (2005). New population estimates for the endemic Kloss's gibbon *Hylobates klossii* on the Mentawai Islands, Indonesia. *Oryx, 39*, 458-461.

Whitten, A. J. (1980). *The Kloss gibbon in Siberut rain forest.* Ph.D. thesis, King's College, Cambridge.

Whitten, A. J. (1982a). *The gibbons of Siberut*. London: J. M. Dent & Sons Ltd..

Whitten, A. J. (1982b). A numerical analysis of tropical rain forest, using floristic and structural data, and its application to an analysis of gibbon ranging behaviour. *Journal of Ecology, 70,* 249-271.

Wolf, K. E. (1984). *Reproductive competition among co-resident male silvered leaf monkeys (*Presbytis cristata*).* Ph.D. thesis, Yale University, New Haven.

CHAPTER FOUR:

Ranging and Intergroup Interactions in One-Male and All-Male Simakobu Groups (*Simias concolor*)

Abstract

In species where females can be monopolized, males engage in contest competition to exclude rivals. Males may attempt to defend a group of females by defending an area in which they range, often exhibiting territorial behavior such as aggressive encounters and displays. I studied home range use and territoriality in one-male (OMG) and all-male (AMG) groups of simakobu (*Simias concolor*) at Pungut, Siberut Island, Indonesia. I hypothesized that males attempt to maintain exclusive access to females via aggressive intergroup encounters and loud calls. I conducted all-day follows of adult males in three OMGs and one AMG over five months, during which I collected data on ranging and intergroup encounters (two groups within 50 m of each other). GPS data points were used to estimate each group's home range area using minimum convex polygon (MCP) and fixed Kernel estimates in ArcGIS. I found that both OMG and AMG home ranges were small using both MCP (6.56 and 7.24 ha, respectively) and Kernel methods (7.55 and 6.10 ha, respectively). Both OMGs and AMGs appeared to maintain exclusive access to most of their home range areas (0-13% overlap) and all of their core areas. Despite small home ranges, intergroup encounters were infrequent, occurring at a rate of 0.25 encounters/day, or one encounter every 4.0 days. Most encounters involved aggressive behavior from adult males and occurred in the peripheral areas of OMG home ranges. Intergroup encounters in core areas were observed for AMGs only. Overall, the exclusive use and aggressive defense of areas by males in OMGs suggests that males are indirectly defending females through the defense of the areas in which they range.

Keywords: home range · male-male competition · mate defense · territoriality

Introduction

In polygynous species, males engage in contest competition, often using weapons and displays to exclude rivals (Emlen & Oring 1977, Andersson 1994). Males may attempt to monopolize a group of females by preventing their interaction with other males through avoidance of other groups, aggressive exclusion of rival males, and/or herding of females (Pereira et al. 2000, Kappeler & van Schaik 2004). They may also indirectly defend females by defending an area (or territory) in which they range (Emlen & Oring 1977). In such species, males exhibit territorial behavior, which can involve aggressive fights during intergroup encounters or territorial displays, such as scent-marking or loud calling (Cheney 1987, Clutton-Brock 1989).

Territorial behavior is common among Asian colobines (van Schaik et al. 1992), which commonly form one-male groups and inhabit relatively small home range areas (Kirkpatrick 2011). Rates of intergroup aggression are variable, but are more frequent in one-male than in multi-male groups (van Schaik et al. 1992). Males frequently produce loud calls that can be heard from long distances and may also be used to mediate group spacing and prevent encounters (Delgado 2006). This function may be particularly important for colobines, who experience energetic constraints imposed by their folivorous diets (McNab 1978). When groups do meet, adult males are commonly the most active participants, and responses are more aggressive to solitary or all-male groups than to neighboring mixed-sex groups (van Schaik et al. 1992, Yeager & Kool 2000, Wich et al. 2002, 2004). All-male groups are typically smaller than mixed-sex groups, but range over much larger areas which are not defended (e.g., Hanuman langurs, *Semnopithecus* sp.: Rajpurohit et al. 1995; Thomas langurs, *Presbytis thomasi*: Steenbeek et al. 2000; white-headed langurs, *Trachypithecus leucocephalus*: Qing Zhao pers. com.).

Male territorial behavior in Asian colobines has thus been hypothesized to be related to the defense of females (Dunbar 1988, van Schaik et al. 1992). Mate defense might be especially important, as female dispersal is common and females may transfer to groups with better-quality males (Sterck 1998, Sterck et al. 2005). Other hypotheses, however, emphasize the role of male aggression in the defense of food resources and/or infants (Fashing 2001, Wich & Sterck 2007).

I studied home range use and territorial behavior in one-male and all-male groups of an Asian colobine, *Simias concolor* or simakobu. Previous reports suggested that home ranges are small and that groups maintain exclusive access to these areas (Tilson 1977, Watanabe 1981, Hadi et al. 2012). Males appear to be the most active participants in intergroup encounters, but their behavior is variable across sites. In some populations, for example, groups appeared to avoid each other (Tilson 1977, Watanabe 1981), while at others, males aggressively displayed and fought (Watanabe 1981, Tenaza & Fuentes 1995). At the Pungut site where this research was conducted, both one-male groups and all-male groups are common, and females frequently disperse to or visit other groups (Chapter 2). Based on these observations and the general patterns observed among Asian colobines, I hypothesize that males attempt to maintain exclusive access to females via aggression and loud calls. I predict that males in one-male groups will exhibit territorial behavior and maintain exclusive access to at least some parts of their range, while all-male groups will exhibit little or no territorial behavior and will not defend their home range.

Methods

Study Site

Research was conducted at the Siberut Conservation Programme’s Pungut study site in the Peleonan Forest in northern Siberut, Indonesia (0°56’ – 1°03’S, 98°48’ – 98°51’E). Although it lies within a logging concession, the Peleonan Forest is protected from hunting and logging through agreements with the local community and Indonesian officials. The study area comprises a 10.7 km^2 area of hilly (altitude: *ca*. 25 – 190 m) primary mixed evergreen rainforest (Hadi et al. 2009a). The climate is equatorial with mean minimum and maximum monthly temperatures of 21.5 and 31.7°C. Precipitation is always high, (219 – 432 mm per month) and mean annual rainfall is 3601 mm (Chapter 3).

Study Species and Subjects

Simakobu are medium-sized Asian colobines (males 7.7 – 8.9 kg, females 5.2 – 7.1 kg, Tenaza & Fuentes 1995, Hadi et al. 2009b). At this site, they reside in one-male groups (OMGs) with 7.9 individuals, and3.0 adult females on average as well as all-male groups averaging 4.5 individuals (Chapter 2). Adults and juveniles of both sexes disperse, and females frequently visit other mixed-sex and all-male groups (Chapter 2).

Subjects were four habituated groups: three OMGs (A, E, and H) and one AMG (D). For the present study, I included data from the five-month period (July – November 2008) during which I collected ranging behavior from all four groups on several consecutive days each month.

Data Collection

WME and research assistants (see Acknowledgments) conducted all-day focal follows of adult males (from sleeping tree to sleeping tree). Groups were followed on 93 days (range = 19 – 29 days/group) for an average of 4.7 days per group per month. We conducted follows of each of the three adult males in AMG-D, and include data from all three for the estimate of this group's home range area. During follows, we recorded a new GPS location using a handheld Garmin® GPSMap 60CSX (Garmin, Olathe, KS) each time the focal animal traveled >10 m distance. As such, data points do not represent periods of time spent in each location, but rather the frequency with which locations were visited.

Intergroup encounters were defined as any time two or more groups were within 50 m of one another (cf. Stanford 1991). Once an encounter began, we recorded the GPS location of the groups. During encounters, we continuously recorded data on vocalizations, threats, displays, chases and attacks from both groups (Altmann 1974). Intergroup encounters were scored as high aggression (chasing and/or physical fighting involved), low aggression (threat displays and/or vocalizations only), or neutral (cf. Harris 2006).

Data Analysis

I collected a total of 2030 GPS data points, which were used to estimate each group's home range area. I used ArcMap 9.3 (ESRI, Redlands, CA) to map GPS points. I calculated minimum convex polygons (MCP) with Hawth's tools (Beyer 2004) and 95% fixed kernels with home-range tools (HRT: Rodgers et al. 2007) to estimate the home range area for each group. Core areas were defined as 50% fixed kernel areas. For kernel calculations, data were rescaled to unit variance and the default h_{ref} method was used to establish the smoothing parameter, which determines the spread of the kernel for each observation. Once home range areas were mapped, encounter locations were added and described as occurring in edge areas (<25 m from the edge of the 95% Kernel area), core areas (inside the 50% Kernel area), or interior areas (within the 95% Kernel area, but outside core or edge areas).

Results

Ranging Patterns

MCP and Kernel estimates of OMG home range size yielded average areas of 6.56 (range 5.19 – 7.73) and 7.55 (range 5.09 – 9.75) ha, respectively (Table 4.1). AMG home range area estimates were similar, 7.24 and 6.10 ha for MCP and Kernel methods, respectively. Home range areas did not increase uniformly with group size; although the smallest group had the smallest home range, the largest group did not have the largest area. Core areas for OMGs were 2.20 ha on average, ranging from 1.27 – 2.98 ha per group. While there did not appear to be an effect of group size on core area size, the all-male group and the smaller OMG-E had the smallest core areas of the four groups.

The MCP ranges of groups AMG-D and OMG-H overlapped by 0.90 ha, representing 12.4% and 13.3% of their respective home range areas (Fig 4.1). The slightly larger 95% Kernel areas overlapped for all four groups, even if only slightly, indicating that home ranges bordered each other very closely. Although the 95% Kernel area of AMG-D overlapped a small fraction of

OMG-H’s core area and vice versa (Fig. 4.2), a closer inspection of the ranging locations reveals that individuals from AMG-D did not range in the area of OMG-H.. OMU-A and OMU-E showed no overlap in MCP home ranges, but there was a small area of their Kernel home ranges shared by both.

Intergroup Encounters

I observed a total of 23 group encounters involving at least one of the focal groups during 93 group-days. This represents a rate of 0.25 encounters/day, or one encounter every 4.0 days. Two groups (AMG-D, and OMG-H) had similar encounter rates (0.42 and 0.52/day, respectively), meeting about once every two days. OMG-E met other groups once every 5.3 days (0.19 encounters/day), and OMG-A encountered other groups least often, having just 0.11 encounters/day (or one encounter every 9.5 days). Of the 23 encounters, 19 (82.6%) were aggressive while the remaining four were neutral (Table 4.2). Of the aggressive encounters, 13 (68.4%) involved high-level aggression. For OMGs, 81.0% of encounters were aggressive, 57.1% involving high-level aggression. 90.0% of AMG encounters were aggressive (70.0% high-level), which reflects the fact that this group was often aggressively targeted by other OMG males. All types of encounters occurred in edge, interior and core areas of home ranges, but overall encounters were most common near the edge (Fig. 4.3). All OMG encounters occurred in edge or interior areas but never in the core. AMG encounters, on the other hand, were equally common in edge and interior areas, but were most frequent in core areas.

Discussion

Simakobu home ranges were small, covering fewer than 10 ha even for the largest groups. These results resemble those of previous simakobu studies, even though the latter were based on much smaller and less systematic sampling efforts. At two sites (Betumonga and Sarabua), for example, home ranges were as small as 6.5 – 7 ha (Watanabe 1981, Tenaza & Fuentes 1995). Even smaller ranges are reported for Grukna, where groups occupied areas of just 2.5 – 5 ha each. Similar to most Asian colobines, there was no apparent relationship between group size and home range size in the present simakobu study (Yeager & Kirkpatrick 1998). The very high population density at Grukna (220 animals/km^2) probably accounts, in part, for the small home ranges there, as a negative relationship between home range size and population density exists among Asian colobine species (Yeager & Kirkpatrick 1998).

The present study confirms previous reports (Tilson 1977, Watanabe 1981, Hadi et al. 2012) that the home range areas of OMGs were nearly exclusively used. However, overlap estimates reported here possibly underestimate the total area shared by adjacent groups, since there were at least eight other neighboring groups to the focal groups, which were not habituated. Thus, it is possible that at least some of these neighbors use a portion of the focal groups' home range areas. It is also possible, however, that home range overlap was actually *overestimated* in the current study. Home range areas were calculated from all-day follows of adult males and do not necessarily represent the area used by the rest of the group. Female home ranges are likely much smaller, since adult males frequently make incursions into neighboring groups' ranges, sometimes making stealthy attacks on other groups (details below), and especially on AMGs (Erb, pers. obs.). Additional observations of habituated neighboring groups are needed to more accurately estimate the extent of home range overlap for this species.

Nonetheless, the exclusive use of at least part of their home ranges suggests that males are indirectly defending females through the defense of their ranging and/or important feeding areas (Emlen & Oring 1977, van Schaik et al. 1992, Harris 2006). Aggressive intergroup encounters are a likely mechanism for males to monopolize females (Cheney 1987, Clutton-Brock 1989). Other hypotheses, however, emphasize the role of male aggression in the defense of food resources or infants in addition to mates (e.g., Fashing 2001, Wich & Sterck 2007). Detailed analyses of home range use and aggression in relation to important feeding sites as well as the presence of receptive females and vulnerable infants are needed to evaluate male defense strategies.

Despite their relatively small home range areas, however, simakobu groups met infrequently, only once or twice a week. This low encounter rate suggests that the frequency of encounters may be affected by behaviors other than ranging. Males produce loud calls on most mornings and several times throughout the day (Chapter 5), and these calls likely play a role in mediating intergroup interactions (cf. Curtin & Chivers 1978 for *Trachypithecus obscurus*). Although observers attempted to remain quiet and inconspicuous during group follows so as to avoid affecting natural encounter rates with unhabituated groups, it is possible that our presence was detected and caused other groups to avoid our location. However, encounter rates between a focal group and an unhabituated group were more common than those between two focal groups (N=15 and 8 encounters respectively); and for OMG-H, those with unhabituated neighbor OMG-S were nearly as frequent as those with AMG-D (N=6 and 8 respectively).

The idea that male territorial behavior is related to the monopolization of females receives some indirect support from the observations of AMG-D. Unlike the OMGs, AMG-D did not appear to defend or maintain exclusive access to an area, indicated, in part, by the frequent occurrence of encounters in their core area. Although not quantified, the area occupied by this group appeared to be irregular in shape and suggests that they might range in the “gaps” between neighboring OMGs (Fig. 4.2). As reported for other species, AMGs appeared to be targeted by adjacent OMG males, who frequently initiated high-aggression encounters within their core area (van Schaik et al. 1992, Wich et al. 2004). Indeed, on three occasions I observed the adult male from OMG-H descend to the ground and quietly stalk AMG-D before making an attack. Similar behavior was never observed in AMG males. These observations suggest that the home range overlap between OMG-H and AMG-D is due to the incursions by male H into the home range of AMG-D and not the reverse. Furthermore, unlike OMGs, males in AMGs only very rarely produce loud calls and nearly always flee when they are chased by other males (Erb, unpublished data). Additionally, OMG-A and OMG-E were both members of another AMG at the start of this study, and while their home ranges did not overlap with each other, both continued to share parts of their home range with a solitary male that remained in their former home range area. Overall, the fact that AMGs do not defend areas with aggressive encounters or loud calls provides further support for the role of these behaviors in mate defense.

Unlike the AMGs of other Asian colobines (see Introduction), simakobu AMGs do not range within large and flexible home ranges. Although I did not find evidence of territorial defense of an area by AMGs, they do appear to occupy small home ranges that remain stable over periods of at least two years (Erb, unpublished data). I am not aware of any other species of Asian colobine with similar ranging behavior, and thus simakobu appear to be unique in this regard. Future studies of simakobu AMGs are needed to investigate the significance of this unusual pattern.

Tables and Figures

Table 4.1. Group sizes and home range areas for four focal groups.

		Home range area (ha)		
Group	Size	MCP	Kernel (95%)	Kernel (50%)
OMG-A	5.2 (5-6)	7.73	9.75	2.98
OMG-E	3.6 (3-5)	5.19	5.09	1.27
OMG-H	10.4 (9-12)	6.77	7.81	2.34
AMG-D	7.2 (7-8)	7.24	6.10	1.31

Size = mean monthly group size (range), MCP = minimum convex polygon, Kernel (95) = 95% Kernel (home range) area, Kernel (50) = 50% Kernel (core) area.

Table 4.2. Locations and aggression levels of intergroup encounters for four focal groups.

		Location			Aggression		
Group	N	Edge	Interior	Core	High	Low	None
OMG-A	2	1	1	0	2	0	0
OMG-E	4	2	2	0	1	3	0
OMG-H	15	12	3	0	9	2	4
AMG-D	10	3	3	4	7	2	1

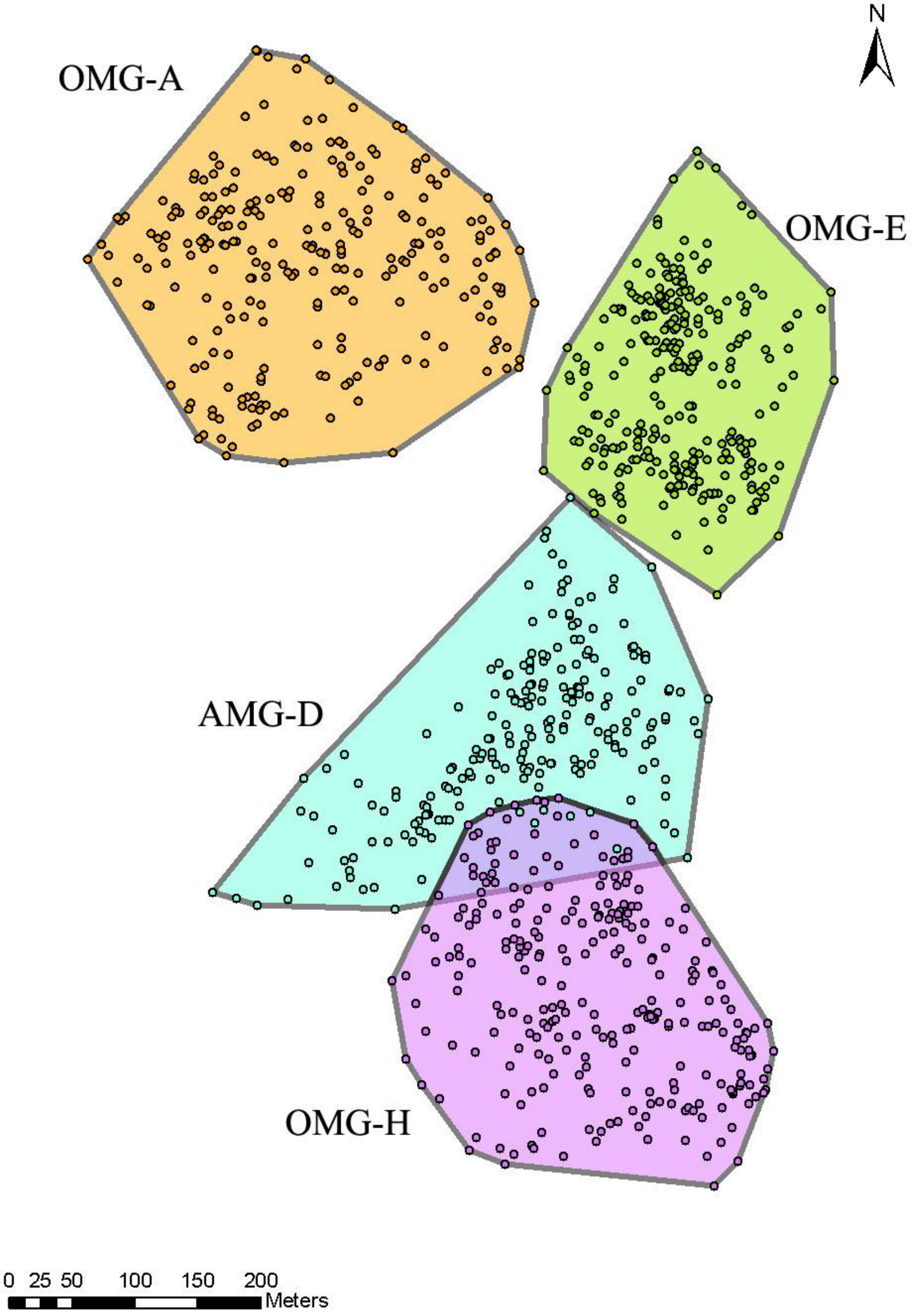


Fig. 4.1. Focal groups' MCP home range areas. Colored points represent GPS locations for focal males; colored polygons represent the minimum convex polygons.

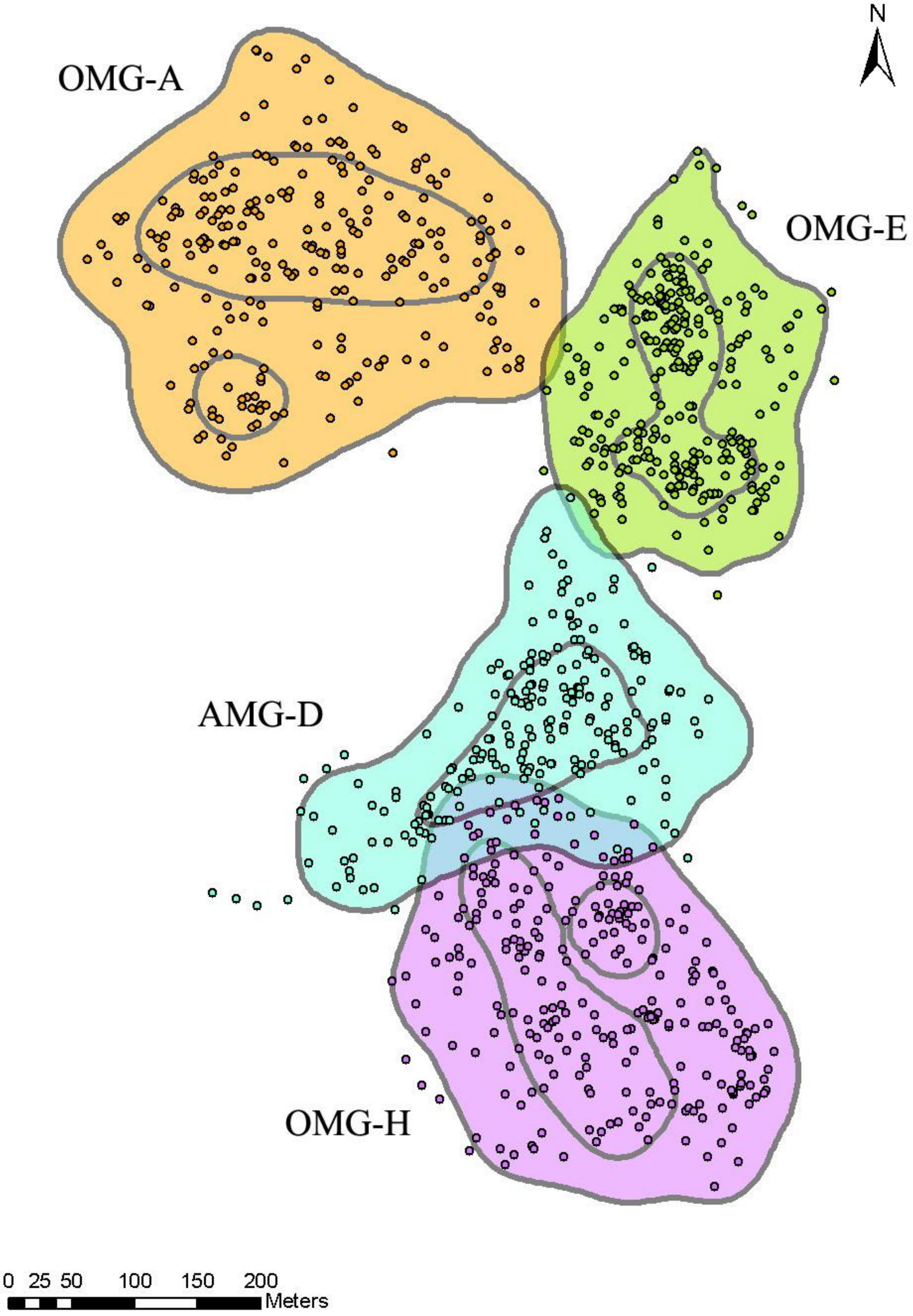


Fig. 4.2. Focal groups' Kernel home range areas. Colored points represent GPS locations for focal males; colored contours represent the 95% fixed kernel areas; inner contours represent 50% fixed kernel "core" areas.

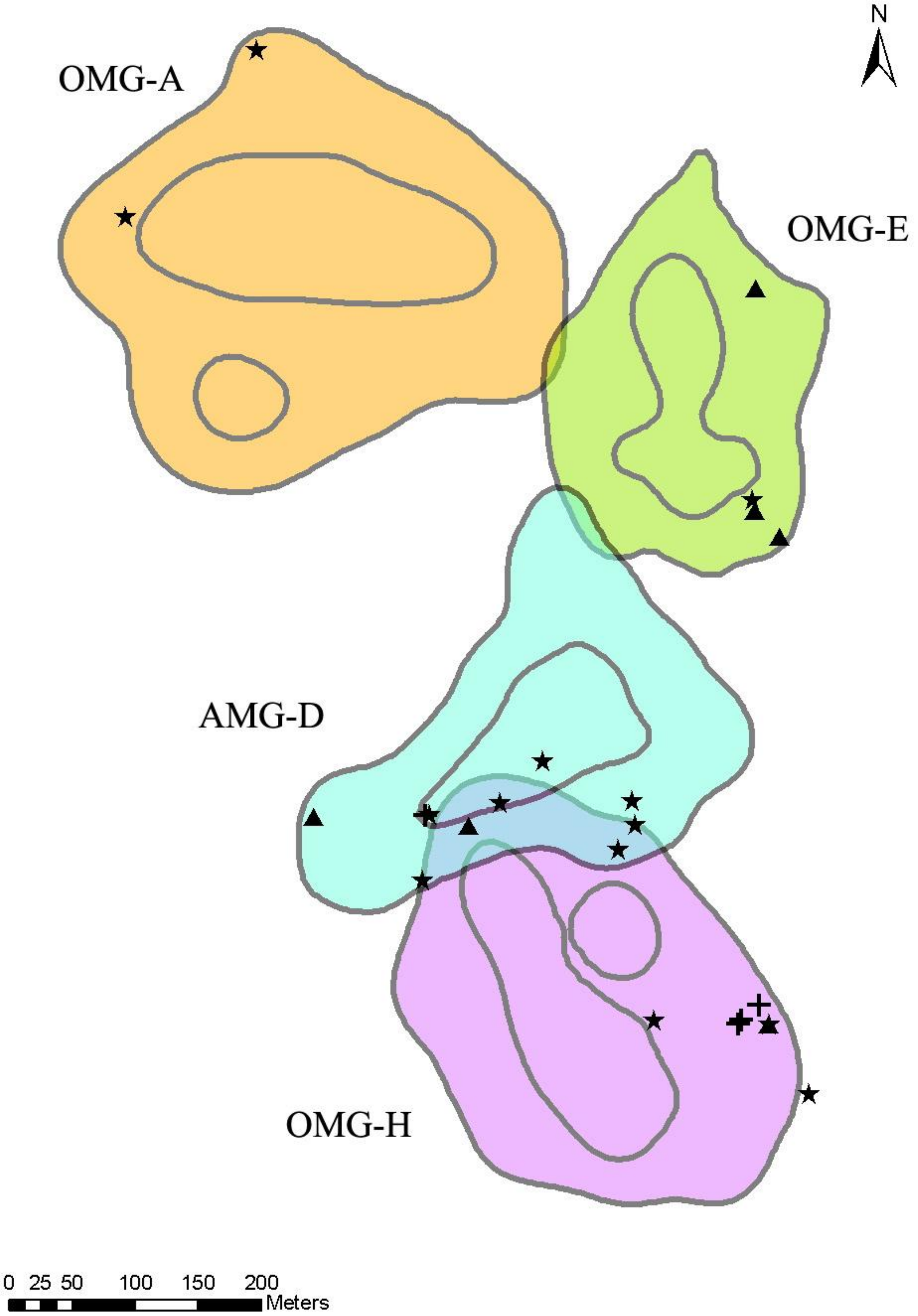


Fig. 4.3. Intergroup encounter locations. Crosses indicate tolerant encounters, triangles low-aggression encounters, and stars high-aggression encounters. Colored contours represent the 95% fixed kernel areas; inner contours represent 50% fixed kernel "core" areas.

References

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227-267

Andersson MB (1994) Sexual selection. Princeton University Press, Princeton, New Jersey

Beyer HL (2004) Hawth's analysis tools for ArcGIS . Available at http://www.spatialecology.com/htools

Cheney DL (1987) Interactions and relationships between groups. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 267-281

Clutton-Brock TH (1989) Review lecture: mammalian mating systems. Proc R Soc Lond B 236:339-372

Curtin SH, Chivers DJ. (1978) Leaf-eating primates of peninsular Malaysia: the siamang and the dusky leaf-monkey. In: Montgomery GG (ed) The ecology of arboreal folivores. Smithsonian Institution Press, Washington, DC, pp 441-464

Delgado RA (2006) Sexual selection in the loud calls of male primates: signal content and function. Int J Primatol 27:5-25

Dunbar RIM (1988) Primate social systems. Cornell University Press, Ithaca, New York

Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223

Fashing PJ (2001) Male and female strategies during intergroup encounters in guerezas (*Colobus guereza*): evidence for resource defense mediated through males and a comparison with other primates. Behav Ecol Sociobiol 50:219-230

Hadi S, Ziegler T, Hodges JK (2009) Group structure and physical characteristics of Simakobu monkeys (*Simias concolor*) on the Mentawai Island of Siberut, Indonesia. Folia Primatol 80:74-82

Hadi S, Ziegler T, Waltert M, Hodges JK (2009) Tree diversity and forest structure in northern Siberut, Mentawai Islands, Indonesia. Trop Ecol 50:315-327

Hadi S, Ziegler T, Waltert M, Syamsuri F, Mühlenberg M, Hodges JK (2012) Habitat use and trophic niche overlap of two sympatric colobines, *Presbytis potenziani* and *Simias concolor,* on Siberut Island, Indonesia. Int J Primatol 33:218-232

Harris TR (2006) Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). Behav Ecol Sociobiol 61:317-329

Kappeler PM, van Schaik CP (2004) Sexual selection in primates: review and selective preview. In: Kappeler PM, van Schaik CP (eds) Sexual selection in primates: new and comparative perspectives. Cambridge University Press, New York, pp 3-20

Kirkpatrick C (2011) The Asian colobines: diversity among leaf-eating monkeys. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf R (eds) Primates in perspective. Oxford University Press, New York, pp 189-202

McNab BK (1978) Energetics of arboreal folivores: physiological problems and ecological consequences of feeding on an ubiquitous food supply. In: Montgomery GG (ed) The ecology of arboreal folivores. Smithsonian Institution Press, Washington, DC, pp 153-162

Pereira ME, Clutton-Brock TH, Kappeler PM (2000) Understanding male primates. In: Kappeler PM (ed) Primate males: causes and consequences of variation in group composition. Cambridge University Press, New York, pp 271-277

Rajpurohit LS, Sommer V, Mohnot SM (1995) Wanderers between harems and bachelor bands: male Hanuman langurs (*Presbytis entellus*) at Jodhpur in Rajasthan. Behaviour 132:255-299

Rodgers AR, Carr AP, Beyer HL, Smith L, Kie JG (2007) HRT: home range tools for ArcGIS. Version 1.1. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada

Stanford CB (1991) Social dynamics of intergroup encounters in the capped langur (*Presbytis pileata*). Am J Primatol 25:35-47

Steenbeek R, Sterck EHM, de Vries H, van Hooff JARAM (2000) Costs and benefits of the one-male, age-graded, and all-male phases in wild Thomas's langur groups. In Kappeler PM (ed) Primate males: causes and consequences of variation in group composition. Cambridge University Press, Cambridge, pp 130-145

Sterck EHM (1998) Female dispersal, social organization, and infanticide in langurs: are they linked to human disturbance? Am J Primatol 44:235-254

Sterck EHM, Willems EP, van Hooff JARAM, Wich SA (2005) Female dispersal, inbreeding avoidance and mate choice in Thomas langurs (*Presbytis thomasi*). Behaviour 142:845-868

Tenaza RR, Fuentes A (1995) Monandrous social organization of pigtailed langurs (*Simias concolor*) in the Pagai Islands, Indonesia. Int J Primatol 16:295-310

Tilson RL (1977) Social organization of simakobu monkeys (*Nasalis concolor*) in Siberut Island, Indonesia. J Mammal 58:202-212

van Schaik CP, Assink PR, Salafsky N (1992) Territorial behavior in Southeast Asian langurs: resource defense or mate defense. Am J Primatol 26:233-242

Watanabe K (1981) Variations in group composition and population density of the two sympatric Mentawaian leaf-monkeys. Primates 22:145-160

Wich SA, Assink PR, Becher F, Sterck EHM (2002) Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): the effect of familiarity. Behaviour 139:79-87

Wich SA, Assink PR, Sterck EHM (2004) Thomas langurs (*Presbytis thomasi*) discriminate between calls of young solitary versus older group-living males: a factor in avoiding infanticide? Behaviour 141:41-51

Wich SA, Sterck EHM (2007) Familiarity and threat of opponents determine variation in Thomas langur (*Presbytis thomasi*) male behaviour during between-group encounters. Behaviour 144:1583-1598

Yeager CP, Kirkpatrick RC (1998) Asian colobine social structure: ecological and evolutionary constraints. Primates 39:147-155

Yeager CP, Kool K (2000) The behavioral ecology of Asian colobines. In: Whitehead PF, Jolly CJ (eds) Old World monkeys. Cambridge University Press, Cambridge, pp 496-521

CHAPTER FIVE:

Are Loud Calls Honest Signals of Male Energy Status in Simakobu (*Simias concolor*)?

(With Thomas Ziegler, Kurt Hammerschmidt)

Abstract

Male vocal displays play an important role in sexual selection in many species. If there are costs or constraints involved, calls may convey honest information about the caller. We studied the loud calls of adult male simakobu (*Simias concolor*), a sexually dimorphic primate that resides in one-male groups, at Pungut, Siberut Island, Indonesia to test the hypothesis that loud calls are energetically costly handicap signals. We combined behavioral and ecological data with acoustic analysis to determine the influence of energy status on calling effort. Based on all-day follows (N=107) and loud call recordings (N=186), we determined how calling rate and call duration varied in relation to short-term (time of day, temperature, amount of rain, and travel distance) and long-term (fruit availability, physical condition) measures of energy availability. We found that males avoided calling at times of the day with high temperatures. Call duration was negatively affected by short-term changes in energy status, with shorter calls produced during wet periods and at higher post-dawn temperatures, supporting the hypothesis that calls may be energetically costly. A peak of calls just before sunrise with longer durations further suggests that this might be the best time for simakobu males to advertise their quality. Contrary to predictions, daily calling rate increased with decreasing fruit availability and did not appear to reflect male energy status. We hypothesize that calling rate may instead be linked to strategies involving feeding and/or mate competition and signal the motivation, rather than fighting ability, of the caller.

Keywords: advertisement · dawn chorus · handicap signal · male-male competition · territoriality · thermoregulation

Introduction

In many species, males use vocal displays to signal their quality and competitive ability in order to resolve conflicts without costly fights or to attract potential mates. Because signaler and receiver have conflicting interests, the reliability of these signals can only be maintained by a cost or constraint on signalers that prevents cheating. Vehrencamp (2000) identified three signal types, according to their costs: 1) "Index" signals are physically or physiologically constrained, and therefore may provide honest information, e.g., on the size, strength or age of a caller. The formant frequencies of male red deer (*Cervus elaphus*) roars, for example, convey information about body size, with heaver stags producing calls with lower frequency dispersion (Reby & McComb 2003). 2) "Conventional" signals are maintained by high retaliation costs, whereby cheaters are punished for inaccurate signaling, such as in banded wrens (*Thryothorus pleurostictus*). In this species, song-matching behavior signals aggression and provokes aggressive attacks from neighboring males (Molles & Vehrencamp 2001). 3) "Handicap" signals are honest because they incur production costs, and thus provide listeners with accurate information about the caller, e.g., health, stamina, condition, and overall fighting ability (Zahavi

1975; Zahavi 1977; Grafen 1990). The wahoos of male chacma baboons (*Papio ursinus*), for example, are limited by the strength and stamina of the caller such that high-ranking males with the best competitive ability produce wahoo calls with higher formant dispersion at a higher rate and for longer duration (Kitchen et al. 2003, Fischer et al. 2004).

Whatever the costs, listeners should try to assess callers via signal traits that correlate with present competitive ability (Clutton-Brock & Albon 1979). In many species, the rate and duration (i.e., energy content) of vocal signaling can reflect even small day-to-day changes in fighting ability, and therefore may provide more reliable assessment criteria than stable body size cues (Clutton-Brock & Albon 1979). Call production costs include investment in signaling organs, risk of being detected and attacked by predators, time lost in displaying, and energetic expenditure during display (Prestwich 1994; Vehrencamp 2000).

There is ample evidence that energetic costs in particular are important for vocal displays (reviewed in Ryan 1988; Prestwich 1994). Studies of bird song, for example, have demonstrated that individuals reduce calling rates when body reserves are low (Reid 1987; Godfrey & Bryant 2000, Thomas 2002), when foraging success is low (Cucco & Malacarne 1997; Kacelnik 1979; Mace 1989), and when overnight temperatures are cold (Gottlander 1987; Reid 1987; Thomas 1999). Reduced calling rates for individuals in poor physical condition has also been observed in a number of mammals, including red deer (*Cervus elaphus*: Clutton-Brock & Albon 1979), Galapagos sea lions (*Zalophus wollebaeki*: Kunc & Wolf 2008), and European fallow deer (*Dama dama*: Vannoni & McElligott 2009). These studies provide evidence of the negative impact of low energy reserves and poor physical condition on vocal signaling.

Males in many nonhuman primates produce loud conspicuous vocalizations, or loud calls, that show specializations for transmission over long distances (Waser & Waser 1977, Mitani &

Stuht 1998). These calls have long been thought to function in intergroup spacing and intragroup cohesion (e.g., Waser 1977, Whitehead 1987, da Cunha & Jalles-Filho 2007). Calling throughout the day could simply be a statement that an area or group is currently occupied and defended (cf. Clutton-Brock & Albon 1979). Alternatively, loud calls have been demonstrated to indicate a caller's willingness or motivation to defend important resources and/or mates in a number of studies (e.g., Whitehead 1989, Cowlishaw 1992, Harris 2006). However, recent studies have also highlighted their potential role in mate attraction and male-male competition as advertisements of fighting ability (e.g., Cowlishaw 1996, Wich & Nunn 2002, Fischer et al. 2004, Delgado 2006).

Despite abundant evidence of call costs in numerous vertebrate taxa, there is less evidence that the loud calls of primates are energetically costly. In gibbons (*Hylobates* spp.), for example, male calling rates were lower at higher latitudes (i.e., lower temperatures, Cowlishaw 1996) and following rainy nights (Whitten 1982), indicating that the energetic costs of thermoregulation negatively affected calling behavior. The rates and duration of male gibbon calls were also reduced when high-energy food was less abundant (Cowlishaw 1996). Interestingly, these patterns were not observed for female singing, suggesting that male songs are sexually-selected honest signals. Other primate studies found reduced calling rates and/or durations with decreasing rank (chacma baboons: Kitchen et al. 2003, Fischer et al. 2004; chimpanzees, *Pan troglodytes*: Mitani & Nishida 1993; macaques, *Macaca nigra*: Neumann et al. 2010; guerezas, *Colobus guereza*: Harris 2006; ursine colobus monkeys, *Colobus vellerosus*: Teichroeb & Sicotte 2010) and increasing age/tenure (Thomas' langurs, *Presbytis thomasi*: Steenbeek et al. 1999), which suggest there is a relationship between competitive ability and vocal displays in these species. In a phylogenetic study of primate loud calls, Wich & Nunn 2002 found that loud calls were often secondarily lost in large-bodied species with large home ranges. They suggested that it may be too energetically costly to produce a call that covers the diameter of a large home range. Thus, there is relatively limited and mainly indirect support for the hypothesis that primate loud calls are energetically costly assessment signals.

We studied the vocal behavior of a wild primate (simakobu: *Simias concolor*) to test the hypothesis that loud calls are energetically costly handicap signals. In particular, we examined whether the energy invested in vocal displays varied in relation to several measures of energy availability. Loud calls are conspicuous vocalizations that are specialized for long-distance transmission (Waser & Waser 1977, Mitani & Stuht 1998). These calls are produced by males in 80% of diurnal primate species (Wich & Nunn 2002), and are proposed to function primarily in intergroup spacing and to play a role in intrasexual competition (Delgado 2006).

Simakobu live in one-male multi-female groups occupying small territories (Watanabe 1981, Erb unpublished data). Both males and females disperse (Chapter 2). This social setting suggests that males need to signal to potential rivals and mates from long distances. Furthermore, the degree of sexual dimorphism in body size and canine length (males are 29% heavier, their canines 95% longer: Tenaza and Fuentes 1995) indicate strong intrasexual competition in this species (cf. Plavcan 2001). Together, these observations indicate the potential for the use of loud calls as sexually-selected assessment signals in this species.

Simakobu loud calls are produced by males only and occur in a variety of contexts: 1. spontaneously, 2. in response to other male loud calls (often as a chorus), and 3. following loud environmental disturbances, e.g., tree falls (Tenaza 1989). These calls typically last 10-20 seconds, and are produced as a series of one- or two-syllable “huh-hoo” vocalizations, each consisting of a loud noisy bark “huh” syllable, sometimes accompanied by a quieter tonal “hoo” syllable (Fig. 5.1). Loud calls are the highest-amplitude vocalizations in this species (80 dB at 10m, Erb unpublished data), and can be heard from distances of more than 500m (Tenaza 1989). As there are no mammalian predators present in the Mentawai Islands (Whitten & Whitten 1982), other overall call costs may be reduced, emphasizing the potential to detect energy constraints in this system.

If simakobu loud calls are energetically costly signals, then aspects of calling related to energy should be influenced by the energy status of the caller. Although species inhabiting temperate climates are often inhibited by cold temperatures (see examples above), high temperatures are more likely to adversely affect equatorial species, where temperatures rarely drop below the thermoneutral zone. Other studies have shown that in warm climates primates are unable to actively prevent overheating, and therefore reduce their energy expenditure at high ambient temperatures (e.g., Sykes monkeys, *Cercopithecus mitis*, and guerezas: Mueller et al 1983, chacma baboons: Hill 2006). Even in regions with warm climates, rain has been shown to reduce the rate of calling (e.g., Kloss gibbons, *Hylobates klossii*: Whitten 1982), as animals experience heat and energy loss when they are wet and cold for long periods. The energy expended by animals during travel, and the energy they obtain through feeding should also impact their energy status. Further, energy reserves fluctuate during the day, and are most likely to be lowest at dawn due to overnight fasting and exposure to low temperatures (cf. Cowlishaw 1996).

We predict that the following factors will negatively impact the energy invested in calling (assessed here as rates and durations): in the short term - 1) *increased thermoregulation costs* due to high temperatures and/or high rainfall and 2) *increased energy expenditure* due to long travel distances; 3) *decreased energy reserves* at dawn due to overnight fasting; and the long term – 4) *decreased energy balance* due to poor physical condition, and 5) *decreased energy intake* due to low food availability.

Methods

Study Site

Research was conducted at the Siberut Conservation Programme's Pungut study site in northern Siberut, Indonesia. The study site lies within a 10.7 km^2 area of hilly (2 – 182 m a.s.l.) primary mixed evergreen rainforest (Hadi et al. 2009a) in the southern part of the Peleonan forest (0°58' – 1°03'S, 98°48' – 98°51'E). Although outside of the Siberut National Park, this area is protected from hunting and logging through agreements with local communities and Indonesian officials. The climate of the region is equatorial with mean minimum and maximum monthly temperatures of 21.5 and 31.7°C. Maximum temperatures are highest, exceeding 34°C, from December to February. Mean monthly precipitation ranges from 219 – 432 mm (3,601 mm annually), with the wettest period occurring between September and December, and a peak in rainfall in October (432 mm: Chapter 3).

Study Subjects and Period

Subjects for this research were adult male simakobu. Simakobu are medium-sized Asian colobines (males 7.7-8.9 kg, females 5.2-7.1 kg, Tenaza & Fuentes 1995; Hadi et al. 2009b). At the Pungut study site, simakobu reside in one-male groups with two to five adult females (mean group size = 7.9) and in all-male groups (mean group size = 4.5: Chapter 2). Study subjects were six adult males residing in one-male groups. Three of the study groups were habituated to observers in 2006/2007, and all individuals were identified. One of these groups (H) was followed beginning in February 2007, and most group members were habituated by April 2007. Two other habituated groups (A and E) were observed at the end of the study to increase the number of adult males in the sample. We attempted to habituate a fourth group (S) in March 2007, but had limited success, and discontinued habituation efforts in July 2008. The remaining groups (J and Z) were unhabituated neighboring groups, and were contacted from February 2007 – December 2008 at irregular intervals whenever the schedule (designed to collect data on the behavior of habituated adult males) would allow.

Data Collection

Data were collected on 320 contact days with the study groups during the 23-month study period (February 2007 – December 2008) by WME and local assistants (see acknowledgments). We typically searched for groups in the evening, followed them to the sleeping sites, and relocated them the next morning. During the study period, focal group H was contacted on a total of 130 days, while focal groups A and E were contacted on 19 and 21 days each. Non-focal groups J, S, and Z were each contacted on 14, 112, and 24 days, respectively. Unhabituated groups were identified by the adult males' distinctive features and other easily-recognized group members. Individuals were identified by the shape and hair patterns of the tail, by crest size and shape, and by patterns and coloration of facial hair.

While in contact with a group, we employed all-occurrence sampling (Altmann 1974) of loud calls. Every time a loud call was heard, the following was noted: time, location (GPS point), stimulus (preceded by another loud call, tree fall, thunder, airplane within five minutes), and identity of the caller(s). We further noted whether calls were produced as part of a chorus, operationally defined as bouts of calling by more than one male occurring within five minutes of each other (cf. Tenaza 1989). Most calls produced within a chorus, however, were no more than a few seconds apart, and often overlapped part of another call. Recordings of loud calls were made opportunistically (typically at distances < 100 m from the caller), using a Marantz PMD-660 solid state recorder (48 kHz sampling frequency, 16 bit: Kanagawa, Japan) and a Sennheiser directional microphone (K6 power module and ME66 recording head: Wedemark, Germany).

Additional behavioral data were collected from the three habituated study groups H (March 2007-November 2008), A, and E (July-November 2008). During all-day follows, we conducted focal animal sampling (Altmann 1974) of the adult male. All-day follows were defined as observation days when observers: 1) reached the sleeping site at least 20 minutes prior to sunrise, 2) remained in continuous contact with group members throughout the day, and 3) followed group members until they reached their sleeping site. Follows ranged from 12.4 and 13.6 hours (mean 13.1 hours), varying according to moderate seasonal shifts in day length at the site. Focal males were observed on 107 all-day follows (13-80 days per male). Movements of the adult male were tracked with a GPS unit (Garmin GPSMAP® 60CSx: Lenexa, KS), with a new location recorded each time the male traveled more than 10 meters. Travel distances were calculated by summing the straight-line distances between consecutive points. The physical condition of adults was assessed once per month by visual inspection of the back and limbs (following Koenig et al. 1997) and recorded on a 3-point scale (poor = lean, average = neither lean nor fat, good = fat). Two males (E and H) were observed in all three conditions, while male A was in either poor or average condition only.

Phenological data were collected monthly on 404 trees and lianas. The sample included 5-10 adult specimens of the 50 most common species from nine 10 x 100 m botanical plots and feeding trees for species known to be eaten by the monkeys but not present in the plots.

Phytophases were recorded each month on a 4-point scale (ranging from 0 = nothing to 3 = crown area full, cf. Koenig et al. 1997). Availability of unripe fruits for foods from the 21 most commonly eaten species (accounting for 76% of feeding time, 152 tree and liana specimens) were calculated using an adaptation of Marsh’s index (Marsh 1981, Koenig et al. 1997). This value provided our measure of monthly food availability, as fruits are likely the most energy-rich food for simakobu and unripe fruits in particular can account for more than 20% of feeding time per month (Erb unpublished data). Basic weather data were recorded continuously with a drip-through rain gauge and a temperature logger (30-min intervals) for most, but not all, of the study period (rain: 31%; temperature: 15% of months were sampled incompletely) due to apparatus failure. Daily sunrise and sunset times were downloaded from the GPS unit.

Acoustic Analysis

We recorded a total of 661 loud calls during the study period. Prior to analysis, we visually inspected calls at a sample frequency of 11,025 Hz using Cool Edit 2000 (Syntrillium, Phoenix, AZ), and selected those that were complete and not disturbed by background noise (e.g., birds, insects, other individuals calling). We used Avisoft SASLab Pro (Avisoft Bioacoustics, Berlin, Germany) to create the spectrograms (FFT length: 1024 points, window: Hamming, frame size: 100%, overlap: 93.75%), from which we measured the duration from start to finish for each call. Due to a high degree of variability at the tail end of calls (e.g., some males continued vocalizing for several minutes following a loud call), it was often difficult to determine the end point of a loud call. To address this problem, we generated a histogram of the time elapsed between successive syllables within all loud calls. We identified a change point in the distribution at 2 seconds, and used this to identify the end point of loud calls. In other words, once the duration between two successive syllables exceeded 2 seconds, we considered this to be the end of the call.

Data Analysis

We used three dependent datasets to assess male calling effort. The first two, circadian distribution and daily calling rate were based on all-day follows of the three habituated adult males. The circadian distribution was determined by creating a histogram of the number of calls occurring in 30-minute intervals throughout the day during all 107 all-day follows. Call times were standardized relative to dawn by subtracting the number of minutes elapsed since the time of sunrise on that day; calls made before dawn were assigned negative values. While there were a few ad lib observations of calls outside of observation hours (i.e., more than 30 minutes before or 12.5 hours after sunrise: N = 4), we were unable to collect systematic data on these early-morning and late-night calls, and excluded them from the analysis. Daily calling rates were determined by counting the number of times the adult male produced a loud call during all-day follows. Because additional data were not available for all 107 days, this sample included the 87 all-day follows for which the independent data were also available. The third variable, call duration, was based on acoustic analysis of individual call recordings. This dataset contained 127 calls recorded from 6 adult males, with 5-58 recordings per male.

As proxies for male energy status, we used several indirect measures as independent variables: temperature, amount of rain, fruit availability, physical condition and travel distance. In the daily calling rate dataset, we calculated maximum temperature, total rainfall, and daily path length. For call duration, we determined the temperature at the time of the call as well as the amount of rain and travel distance for the preceding 24 hours. We defined dawn calls as those made during the period 30 minutes before until 30 minutes after sunrise. To compare the durations of calls made around dawn from those later in the day, we excluded calls produced in the first hour after dawn calls (N = 13) to clearly separate dawn and post-dawn calls. We used measures of fruit availability and physical condition for the month in which the observation was made. Because the predictor variables were measured over different periods and were subject to various interruptions (e.g., equipment failure, lost animals, staffing issues), data were missing in both datasets (call duration: 82%, daily calling rate: 79% of cases with at least one missing variable). Therefore, we evaluated the effects of each variable independently. As such, sample sizes were different for each univariate test so that R^2 values could not be compared across tests. Caller identity was included as a variable in all tests.

In our analysis of the circadian distribution of calls, we aimed to describe the population-wide pattern of calling. As such, we compared the distributions of calling frequencies (N = 288 calls across 107 all-day follows) to mean temperatures (N = 29,347 points across 613 days) and total rainfall amounts (N = 24,288 points across 578 days) in each 30-minute interval standardized relative to dawn. Temperature and rainfall data were compiled across the entire study period, from which we used all data from days on which data were available for the entire 24-hour period. Due to a high correlation with temperature ($r=0.74$) in this dataset, however, amount of rain was not entered into the analysis.

We used general linear (GLM) and general linear mixed models (LMM) to test the influence of each independent variable on calling rate and call duration. Only variables that were not highly correlated ($r<0.7$) were used (Field 2009). Caller identity was incorporated as a random factor in the mixed models to control for repeated observations of the same subject

(Bolker et al. 2009). All statistical analyses were performed using Statistica 9 (StatSoft, Tulsa, OK). Two-tailed tests were used to evaluate each prediction with alpha set at 0.05.

Results

Circadian Distribution of Calling

In total, 288 loud calls were produced by the three focal males during all-day follows. The first call of the day typically occurred just before dawn, with calling beginning as early as ~20 minutes prior to sunrise. Dawn calls were produced on 67.1% of observation days (range: 57.7% - 78.9% per male) and occurred as part of a chorus 89.1% of the time. Calls were produced throughout the day until as late as 12.5 hours after dawn (i.e., around dusk). There was a clear peak of calling that occurred in the 30-minute period just before sunrise, with 19% (56/288) of all loud calls produced at this time (Fig. 5.2).

During the post-dawn hours, calls seemed to be distributed bimodally, with more calls produced in the early morning and late afternoon than in the mid-day hours (Fig. 5.2). We used a GLM analysis to examine the impact of average temperature in each 30-minute period. Calling rate was significantly affected by temperatures, as males called less during times of the day with higher average temperatures (Table 5.1). The model accounted for 15.4% of the variance in call frequencies. However, there were a disproportionately high number of calls produced immediately before sunrise. This pattern cannot be explained by temperature alone, however, since similarly high rates would be expected during the 60 minutes after dawn before temperatures began rising. Indeed, when these pre-dawn calls were removed from the analysis, the adjusted R^2 for the model increased to 0.41 (Table 5.1).

Daily Calling Rate

Calling rates ranged from 0-6 calls per day per male (mean = 2.85 $\pm$ 1.45 SD). Males called more on days with higher maximum temperatures and during months with lower fruit availability (Table 5.2). The remaining predictor variables (amount of rain, daily path length, and physical condition,) revealed no significant effect on males' calling rates. Male ID was a significant factor in two (and a trend in another) of the five models, suggesting small individual differences in this trait, though the number of individuals sampled was small (N = 3). When both significant predictor variables were included in a multivariate analysis, fruit availability was significant ($F_{1,63} = 7.18$, $P = 0.009$), whereas maximum temperatures was a statistical trend only ($F_{1,63} = 3.90$, $P = 0.052$; full model: multiple $R^2 = 0.26$, $P = 0<0.001$).

Call Duration

Loud calls ranged from 4.8 – 33.1 seconds in duration (mean 15.6 $\pm$ 4.25 SD). Time of day (dawn vs. post-dawn) affected call duration (Table 5.3), where calls produced at dawn were longer than those later in the day. To assess whether this result was due to an effect of dawn per se and not simply because they were the first calls of the day, we analyzed the relationship between call duration and call sequence. Our sample included 110 recordings from all-day follows of three adult males (range: 23-63 calls per male) that represented the first call to the seventh call of the day. We found that there was a significant negative relationship between call duration and call sequence ($F_{1,106} = 4.71$, $P = 0.03$). When we excluded dawn calls from the sample ($N = 36$ dawn calls), this relationship disappeared ($F_{1,70} = 0.68$, $P = 0.41$), indicating that call sequence did not have an independent effect on call duration. For post-dawn, but not dawn calls, temperature at the time of the call significantly influenced call duration, with longer calls occurring at cooler daytime temperatures (Table 5.3).

Call duration was also shorter following periods with more rain (Table 5.3). There was also a trend ($P<0.10$) for calls to be longer when males were in better physical condition. Fruit availability revealed no significant effect on the duration of calls. Male ID was a significant factor explaining variation in call duration in nearly all tests (and in all where $N>3$ individuals), indicating significant individual differences in call duration.

Discussion

Handicap Signals

Overall, results support the hypothesis that male simakobu loud calls are energetically costly handicap signals that likely advertise the caller's current competitive ability (Table 5.4)., We recognize, however that sample sizes were small, with only three to six males in each analysis so that only limited conclusions can be drawn. Call duration seemed to reflect short-term changes in the energy status of the caller. Males produced significantly shorter calls following periods of more rainfall, suggesting an influence of increased thermoregulation costs reducing callers' energy on rainy days. Another possibility is that calls are more costly to propagate on rainy days. A study of tawny owls (*Strix aluco*) found that their calls reached a 69-fold larger area in dry versus rainy conditions (Lengagne and Slater 2002). In both cases, shorter calls appear to indicate a lower energy status for the caller.

As predicted, the duration of post-dawn calls was negatively affected by increasing mid-day temperatures. This effect could not be explained by the relationship between time of day and previous calling effort, as there was no relationship between the call sequence within a day and its duration. This suggests that as animals become stressed by the high midday temperatures, they reduce their investment in calls. The circadian distribution of calls provides additional support for the negative impact of high temperatures. Although favorable acoustic transmission conditions in the early morning might help explain why there are more calls in the morning than later in the day (Waser & Waser 1977, they cannot explain the second calling peak in the evening. While background noise levels at this site are relatively constant throughout the day, there is a sharp increase in the late afternoon that coincides with these evening calls (Schneider et al. 2008). This indicates that animals prefer to call at the coolest times of the day, generally avoiding the peak temperatures of mid-day.

Dawn Calls

We found a very pronounced peak of calling in the 30 minutes before sunrise, however, that could not be explained by the low temperatures. This pre-dawn concentration of calls indicates that simakobu use this time of day to signal to their neighbors before leaving their sleeping trees. Dawn calls usually occurred as part of a chorus (i.e., the calling of one male stimulated that of other males), setting the stage for direct comparison among callers. Intense chorusing by males at dawn is also common in another vertebrate taxon, birds. A number of hypotheses exist to explain this pattern, generally falling into three classes: 1) calling at dawn is a nonfunctional consequence of the caller’s internal state, such as elevated testosterone levels, 2) dawn calling has a social function, such as mate attraction or territory defense, that is best served at dawn, and 3) environmental pressures, such as predation, acoustic transmission, or unpredictable conditions have selected for calling at dawn (reviewed in Staicer et al. 1996). Similarly, the early morning calls of red howlers (*Alouatta seniculus*) were thought to be due to:

1) sound transmission characteristics facilitating long-distance assessment, 2) low temperatures minimizing heat-related costs, and 3) announcement of location discouraging territorial intrusions (Sekulic 1982). Although we did not directly investigate these hypotheses here, our results suggest that dawn is likely the best time to assess competitors or attract females, as differences in call rates may signal differences among males in the amount of energy reserves they accumulated on the previous day, and thus their current fighting ability (Thomas & Cuthill 2002).

Although others noted that simakobu sometimes called in the early morning hours before dawn (Watanabe 1981, Kawamura & Megantara 1986), this is the first study to document a pronounced pre-dawn chorus. Previous studies have described the distribution of simakobu calls as either bimodal, with peaks in the morning and evening (Tenaza 1989), or as lacking an early morning peak (Schneider et al. 2008). This difference most likely reflects sampling effort (e.g., focal animal sampling, arriving at sleeping sites 30 minutes prior to dawn), as well as the use of clock time, which masks seasonal variation in sunrise times.

Contrary to our prediction, we found that dawn calls were significantly longer in duration than calls produced later in the day. Similar patterns have been described for the songs of male Kloss gibbons (Tenaza 1976), silvery gibbons (*Hylobates moloch*: Geissmann & Nijman 2006), and for red howler roars (Drubbel & Gautier 1993). Most studies have suggested that calls at dawn are the most energetically costly to produce since energy reserves are low due to prolonged fasting and/or low overnight temperatures (Montgomerie 1985; Cowlishaw 1996; Murphy et al. 2008). However, dawn may actually be the “cheapest” time to call because other costs are reduced, such as predation risk, acoustic transmission costs, and opportunity costs (reviewed in Staicer et al. 1996). Alternatively, the fact that dawn calls typically occur as part of a chorus could explain their long duration. In Kloss' gibbons, for example, songs produced as part of a chorus were longer than those sung alone (Tenaza 1976). Thus, males might be more motivated to call longer in the context of a chorus or may attempt to call longer than the previous caller to signal their superior quality to mates and competitors.

Whatever the reason, our results seem to indicate that the dawn chorus is the best time for simakobu males to assess their competitors via loud calls whereby males take advantage of the improved sound propagation (Waser & Waser 1977, Schneider et al. 2008) and increase the duration of their dawn calls to advertise their quality (Zahavi 1975, Grafen 1990). The fact that focal males produced dawn calls on ~70% of observation days suggests that there may be costs associated with *not* calling, such as an increased risk of aggressive encounters (cf. Whitehead 1987), and that males invest as much as possible in these early morning calls. This hypothesis found recent support in a study of another colobine monkey, the guereza. In this species, males only responded to dawn calls of a minimum duration, indicating that listeners were paying attention to this acoustic feature (Schel and Zuberbühler 2012).

Strategic Signals?

Unlike call duration, calling rate was not well predicted by our measures of energy status. Contrary to our prediction, adult male simakobu produced more loud calls on days when maximum temperatures were higher. We expected high temperatures to inhibit calling, when animals were stressed by the heat. In other species, animals reduce energetically expensive activities at temperatures exceeding 30°C (e.g., Sykes and colobus monkeys: Mueller et al 1983, chacma baboons: Hill 2006). While high temperatures exceeded 34°C in this study, we did not observe an effect of these hot days on calling rate. If loud calls were energetically costly, we would expect males to produce fewer calls on the hottest days, when overheated animals would be minimizing their physical exertion (reviewed in Terrien et al. 2011).

The circadian distribution of calling may help explain this result by showing that animals prefer to call at the coolest times of day. Consequently, it is likely that animals simply avoid calling during the hottest mid-day temperatures. Under these circumstances, though, we would expect to find no effect of maximum daytime temperatures, as was the case for two Sumatran primates, agile gibbons (*Hylobates agilis*) and siamangs (*Symphalangus syndactylus*: O'Brien et al. 2004). In our study, however, we found an increase in calling on hot days. However, when both maximum temperature and fruit availability were incorporated into a single model, maximum temperature was no longer significant, indicating that this factor has a relatively weak effect on calling rates. Thus, energy constraints do not appear to affect calling rates.

We did find evidence for seasonal variation in the fact that calling rate was negatively influenced by fruit availability. We predicted that if calling rate signaled energy status, then males would call more when more energy (i.e., fruit) was available in the environment. Such an effect of fruit availability on calling rate has been found for several gibbon species (Tenaza 1976, Raemaekers et al. 1984, Cowlishaw 1996). On the contrary, simakobu males called more when there was less fruit available. Similarly, in brown howlers (*Alouatta fusca*), loud call rates were lower when young leaves, their main food source, were less abundant (Chiarello 1995). This result suggests that males may use their calls to mitigate food competition. While energy intake is probably lower at these times, males may be calling more often in order to advertise their location and reduce the risks of energetically expensive chases and fights. Future research is needed to understand the role of loud calls in food defense.

In conclusion, unlike call duration, simakobu calling rate did not seem to reflect male energy status. A similar result was found for guereza roars, where males' roar lengths, but not rates (roars/chorus), were honest indicators of their fighting ability (Harris 2006). We hypothesize that call rates are instead linked to strategies involved in feeding and/or mate competition and reflect the motivation of the caller to repel rivals and attract mates (cf. Harris 2006). In this scenario, calls might still incur non-energy-related costs, such as increased predation risk or vulnerability to attack. Alternatively, calling throughout the day may simply be a statement that the area or group is currently being occupied and defended by an adult male, as has been suggested for red deer (Clutton-Brock and Albon 1979), rather than an honest signal of male quality.

Call duration, however, did appear to be an energetically costly signal limited by males' short-term energy reserves. Call duration might also provide information about differences in body size between callers, since the production of longer calls could require larger lung volume (Fitch and Hauser 2002). Furthermore, male ID was nearly always a significant factor in the mixed models, indicating that individual differences between males are pronounced and important. More research is needed to explore differences in the temporal and spectral properties of loud calls in relation to measures of male quality, such as body size or home range quality.

Tables and Figures

Table 5.1. Results of general linear model analysis of mean temperature and calling rate in 30-minute intervals for the three focal males.

	Fixed effects				Model	
Datasets	β	SE β	F	P	Mult. R^2	P
All times	-0.39	0.18	4.54	0.04	0.154	0.04
Pre-dawn excluded	-0.64	0.16	16.79	<0.01	0.412	<0.01

Table 5.2. Results of univariate generalized linear mixed model analysis of daily calling rate for the three focal males.

		Fixed factor				Random factor	
Variable	*N* days	*β*	SE *β*	*F*	*P*	*F*	*P*
Max temperature	80	0.38	0.10	12.88	<0.01	3.26	0.04
Rain	68	-0.16	0.13	1.40	0.24	1.24	0.30
Daily path length	48	-0.13	0.15	0.71	0.40	0.86	0.43
Physical condition	64	-0.19	0.12	2.31	0.13	2.51	0.09
Fruit availability	75	-0.48	0.11	18.91	<0.01	4.64	0.01

Fixed factor indicates the independent variable and random factor indicates individual ID.

Table 5.3. Results of univariate generalized linear mixed model analysis of call duration.

			Fixed factor				Random factor	
Variable	N calls	N males	β	SE β	F	P	F	P
Temperature (dawn)	29	3	-0.09	0.21	0.18	0.68	2.64	0.10
Temperature (post-dawn)	63	5	-0.28	0.12	5.31	0.02	2.67	0.04
Rain	81	6	-0.22	0.11	4.21	0.04	3.89	<0.01
Travel distance	59	3	0.20	0.14	2.05	0.16	0.62	0.54
Physical condition	92	3	0.18	0.10	3.30	0.07	3.54	0.03
Fruit availability	122	6	-0.02	0.09	0.07	0.80	6.59	<0.01
Dawn/Post-dawn	113	6	-0.35	0.08	17.59	<0.01	6.86	<0.01

Fixed factor indicates the independent variable and random factor indicates individual ID.

Table 5.4. Summary of predicted (P) and observed (O) relationships between predictor variables and dependent data sets.

	Temp		Rain		Travel distance		Dawn		Fruit availability		Physical condition	
Data set	P	O	P	O	P	O	P	O	P	O	P	O
Circadian dist.	-	-	-	n.s.								
Calling rate	-	+	-	n.s.	n.s.	n.s.			+	-	+	n.s.
Call duration	-	-	-	-	-	n.s.	-	+	+	n.s.	+	+*

Signs indicate statistically significant ($P<0.05$) positive (+) and negative (-) relationships between variables. n.s. denotes non-significant results. Statistical trends ($P<0.10$) indicated with *.

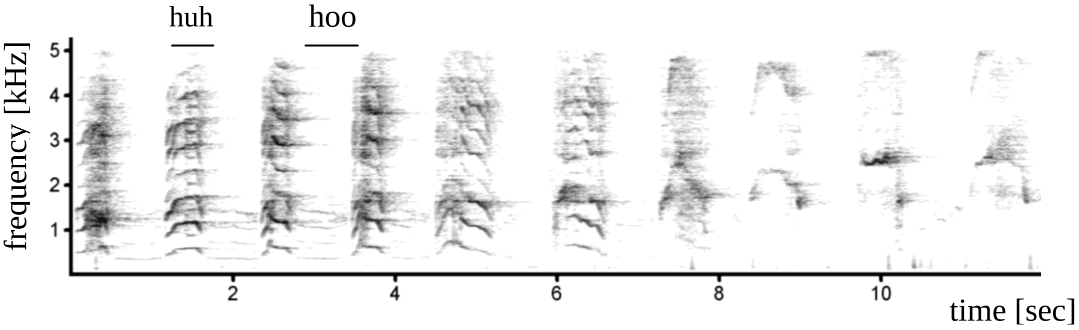


Fig. 5.1. Sample spectrogram of a complete simakobu loud call showing a series of 10 call units. All call units consist of a loud tonal bark syllable, often accompanied by a quieter gasp syllable in the call units at the start of the loud call.

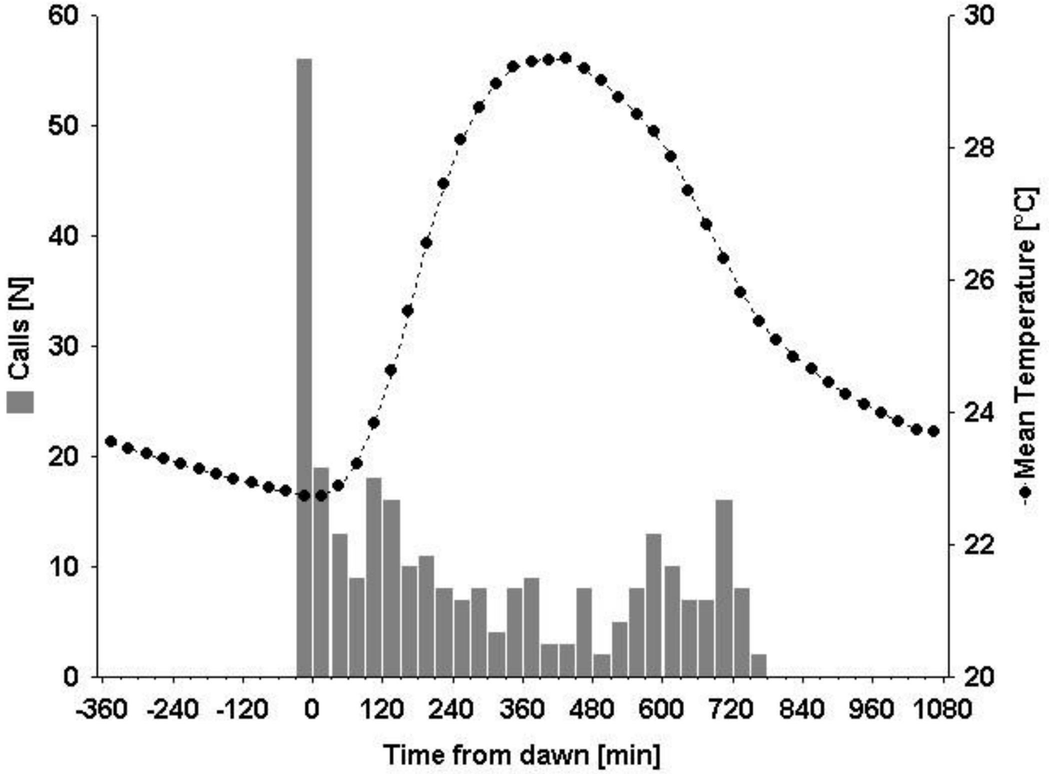


Fig. 5.2. Circadian distribution of loud calls (given in 30-minute intervals) produced by focal males during all-day follows relative to sunrise times and in relation to mean temperatures. Calls occurring before -30 or after 780 minutes excluded.

References

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227-267

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MH, White JS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127-135

Chiarello AG (1995) Role of loud calls in brown howlers, *Alouatta fusca*. Am J Primatol 36:213-222

Clutton-Brock TH, Albon SD (1979) The roaring of red deer and the evolution of honest advertisement. Behaviour 69:145-170

Cowlishaw G (1992) Song function in gibbons. Behaviour 121:131-153

Cowlishaw G (1996) Sexual selection and information content in gibbon song bouts. Ethology 102:272-284

Cucco M, Malacarne G (1997) The effect of supplemental food on time budget and body condition in the black redstart *Phoenicurus ochruros*. Ardea 85:211-221

da Cunha RGT, Jalles-Filho E (2007) The roaring of southern brown howler monkeys (*Alouatta guariba clamitans*) as a mechanism of active defence of borders. Folia Primatol 78:259-271

Delgado RA (2006) Sexual selection in the loud calls of male primates: signal content and function. Int J Primatol 27:5-25

Drubbel RV, Gautier JP (1993) On the occurrence of nocturnal and diurnal loud calls, differing in structure and duration, in red howlers (*Alouatta seniculus*) of French Guyana. Folia Primatol 60:195-209

Field A (2009) Discovering statistics using SPSS, third edition. SAGE Publications Ltd, London

Fischer J, Kitchen DM, Seyfarth RM, Cheney DL (2004) Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. Behav Ecol Sociobiol 56:140-148

Fitch WT, Hauser MD (2002) Unpacking" honesty": vertebrate vocal production and the evolution of acoustic signals. In: Simmons A, Fay RR, Popper AN (eds) Acoustic communication. Springer, New York, pp 65-13

Geissmann T, Nijman V (2006) Calling in wild silvery gibbons (*Hylobates moloch*) in Java (Indonesia): behavior, phylogeny, and conservation. Am J Primatol 68:1-19

Godfrey JD, Bryant DM (2000) State-dependent behaviour and energy expenditure: an experimental study of European robins on winter territories. J Anim Ecol 69:301-313

Gottlander K (1987) Variation in the song rate of the male pied flycatcher *Ficedula hypoleuca*: causes and consequences. Anim Behav 35:1037-1043

Grafen A (1990) Biological signals as handicaps. J Theor Biol 144:517-546

Hadi S, Ziegler T, Waltert M, Hodges JK (2009a) Tree diversity and forest structure in northern Siberut, Mentawai Islands, Indonesia. Trop Ecol 50:315-327

Hadi S, Ziegler T, Hodges JK (2009b) Group structure and physical characteristics of Simakobu monkeys (*Simias concolor*) on the Mentawai Island of Siberut, Indonesia. Folia Primatol 80:74-82

Harris TR (2006) Within-and among-male variation in roaring by black and white colobus monkeys (*Colobus guereza*): What does it reveal about function? Behaviour 143:197-218

Hill RA (2006) Thermal constraints on activity scheduling and habitat choice in baboons. Am J Phys Anthropol 129:242-249

Horwich RH, Gebhard K (1983) Roaring rhythms in black howler monkeys (*Alouatta pigra*) of Belize. Primates 24:290-296

Kacelnik A (1979) The foraging efficiency of great tits (*Parus major L.*) in relation to light intensity. Anim Behav 27:237-241

Kitchen DM, Seyfarth RM, Fischer J, Cheney DL (2003) Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). Behav Ecol Sociobiol 53:374-384

Koenig A, Borries C, Chalise MK, Winkler P (1997) Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). J Zool 243:215-235

Kunc HP, Wolf JBW (2008) Seasonal changes of vocal rates and their relation to territorial status in male Galápagos sea lions (*Zalophus wollebaeki*). Ethology 114:381-388

Lengagne T, Slater PJ (2002) The effects of rain on acoustic communication: tawny owls have good reason for calling less in wet weather. Proc Biol Sci 269:2121-2125

Mace R (1989) The relationship between daily routines of singing and foraging: an experiment on captive Great Tits *Parus major*. Ibis 131:415-420

Marsh CW (1981) Ranging behaviour and its relation to diet selection in Tana River red colobus (*Colobus badius rufomitratus*). J Zool 195:473-492

Mitani JC, Nishida T (1993) Contexts and social correlates of long-distance calling by male chimpanzees. Anim Behav 45:735-746

Mitani JC, Stuht J (1998) The evolution of nonhuman primate loud calls: acoustic adaptation for long-distance transmission. Primates 39:171-182

Molles LE, Vehrencamp SL (2001) Songbird cheaters pay a retaliation cost: evidence for auditory conventional signals. Proc Biol Sci 268:2013-2019

Montgomerie RD (1985) Why do birds sing at dawn? Abstracts of spoken papers, 19th Int Etholog Congr 1:242

Mueller EF, Kamau JMZ, Maloiy GMO (1983) A comparative study of basal metabolism and thermoregulation in a folivorous (*Colobus guereza*) and an omnivorous (*Cercopithecus mitis*) primate species. Comp Biochem Phys A 74:319-322

Murphy MT, Sexton K, Dolan AC, Redmond LJ (2008) Dawn song of the eastern kingbird: an honest signal of male quality? Anim Behav 75:1075-1084

Neumann C, Assahad G, Hammerschmidt K, Perwitasari-Farajallah D, Engelhardt A (2010) Loud calls in male crested macaques, *Macaca nigra*: a signal of dominance in a tolerant species. Anim Behav 79:187-193

O'Brien TG, Kinnaird MF, Nurcahyo A, Iqbal M, Rusmanto M (2004) Abundance and distribution of sympatric gibbons in a threatened Sumatran rain forest. Int J Primatol 25:267-284

Plavcan JM (2001) Sexual dimorphism in primate evolution. Am J Phys Anthropol 44:25-53

Prestwich KN (1994) The energetics of acoustic signaling in anurans and insects. Integr Comp Biol 34:625-643

Raemaekers JJ, Raemaekers PM, Haimoff EH (1984) Loud calls of the gibbon (*Hylobates lar*): repertoire, organisation and context. Behaviour 91:146-189

Reby D, McComb K (2003) Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. Anim Behav 65:519-530

Reid ML (1987) Costliness and reliability in the singing vigour of Ipswich sparrows. Anim Behav 35:1735-1743

Ryan MJ (1988) Energy, calling, and selection. Integr Comp Biol 28:885-898

Schel AM, Zuberbühler K (2012) Dawn chorusing in guereza colobus monkeys. Behav Ecol Sociobiol 66:361-373

Schneider C, Hodges JK, Fischer J, Hammerschmidt K (2008) Acoustic niches of Siberut primates. Int J Primatol 29:601-613

Sekulic R (1982) Daily and seasonal patterns of roaring and spacing in four red howler *Alouatta seniculus* troops. Folia Primatol 29:22-48

Staicer CA, Spector DA, Horn AG (1996) The dawn chorus and other diel patterns in acoustic signaling. In: Kroodsma DE, Miller EH (eds) Ecology and evolution of acoustic communication in birds. Comstock Publishing, Ithaca, NY, pp 426-453

Steenbeek R, Assink P, Wich SA (1999) Tenure related changes in wild Thomas's langurs II: loud calls. Behaviour 136:627-650

Teichroeb JA, Sicotte P (2010) The function of male agonistic displays in ursine colobus monkeys (*Colobus vellerosus*): male competition, female mate choice or sexual coercion? Ethology 116:366-380

Tenaza RR (1976) Songs, choruses and countersinging of Kloss' gibbons (*Hylobates klossii*) in Siberut Island, Indonesia. Z Tierpsychol 40:37-52

Tenaza RR (1989) Intergroup calls of male pig-tailed langurs (*Simias concolor*). Primates 30:199-206

Tenaza RR, Fuentes A (1995) Monandrous social organization of pigtailed langurs (*Simias concolor*) in the Pagai Islands, Indonesia. Int J Primatol 16:295-310

Terrien J, Perret M, Aujard F (2011) Behavioral thermoregulation in mammals: a review. Front Biosci 16:1428-1444

Thomas RJ (1999) Two tests of a stochastic dynamic programming model of daily singing routines in birds. Anim Behav 57:277-284

Thomas RJ (2002) The costs of singing in nightingales. Anim Behav 63:959-966

Thomas RJ, Cuthill IC (2002) Body mass regulation and the daily singing routines of European robins. Anim Behav 63:285-295

Vannoni E, McElligott AG (2009) Fallow bucks get hoarse: vocal fatigue as a possible signal to conspecifics. Anim Behav 78:3-10

Vehrencamp SL (2000) Handicap, index, and conventional signal elements of bird song. In: Espmark Y, Amundsen T, Rosenqvist G (eds) Animal signals: signalling and signal design in animal communication. Tapir Academic Press, Trondheim, pp 277-300

Waser PM (1977) Individual recognition, intragroup cohesion and intergroup spacing: evidence from sound playback to forest monkeys. Behaviour 60:28-74

Waser, PM, Waser MS (1977) Experimental studies of primate vocalization: specializations for long-distance propagation. Z Tierpsychol 43:239-263

Whitehead JM (1987) Vocally mediated reciprocity between neighbouring groups of mantled howling monkeys, *Alouatta palliata palliata*. Anim Behav 35:1615-1627

Whitehead JM (1989) The effect of the location of a simulated intruder on responses to long-distance vocalizations of mantled howler monkeys, *Alouatta palliata palliata*. Behaviour: 1/2:73-103

Whitten AJ (1982) The ecology of singing in Kloss gibbons (*Hylobates klossii*) on Siberut Island, Indonesia. Int J Primatol 3:33-51

Whitten AJ, Whitten JEJ (1982) Preliminary observations of the Mentawai macaque on Siberut Island, Indonesia. Int J Primatol 3:445-459

Wich SA, Nunn CL (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

Zahavi A (1975) Mate selection - a selection for a handicap. J Theor Biol 53:205-214

Zahavi A (1977) The cost of honesty (further remarks on the handicap principle). J Theor Biol 67:603-605

CHAPTER SIX:

Individual, Contextual and Age-Related Acoustic Variation in Simakobu (*Simias concolor*) Loud Calls

(With J Keith Hodges, Kurt Hammerschmidt)

Abstract

Primate loud calls have the potential to encode information about the identity, arousal, age, or physical condition of the caller, even at long distances. In this study, we conducted an analysis of the acoustic features of the loud calls produced by a species of Asian colobine monkey (simakobu, *Simias concolor*). Adult male simakobu produce loud calls spontaneously and in response to loud sounds and other loud calls, which are audible more than 500 m. Individual differences in calling rates and durations exist, but it is unknown what these differences signal and which other acoustic features vary among individuals. We aimed to describe the structure and usage of calls and to examine acoustic features that vary within and between individuals. We determined the context of 318 loud calls and analyzed 170 loud calls recorded from 11 adult males at an undisturbed site, Pungut, Siberut Island, Indonesia. Most calls (53%) followed the loud call of another male, 31% were spontaneous, and the remaining 16% followed a loud environmental disturbance. The fundamental frequency (F0) decreased while inter-unit intervals (IUI) increased over the course of loud call bouts, possibly indicating caller fatigue. Discriminant function analysis indicated that calls were not well discriminated by context, but spontaneous calls had higher peak frequencies, suggesting a higher level of arousal. Individual calls were distinct and individuals were mainly discriminated by IUI, call duration and

F0. Loud calls of older males had shorter IUI and lower F0, while middle-aged males had the highest peak frequencies. Overall, we found that calls were individually distinct and may provide information about the age, stamina and arousal of the calling male, and could thus be a way for males and females to assess competitors and mates from long distances.

Keywords: fundamental frequency · honest signal · long-distance communication · male-male competition · peak frequency

Introduction

Vocalizations are commonly used in long-distance animal communication, as sounds have the potential to carry information even at long range (Bradbury & Vehrencamp 1998). This is especially true in tropical forests where visibility is severely limited, and vocal signaling may be the primary means of communication among conspecifics (Waser & Waser 1977). Long-distance vocalizations (known as loud calls or long calls) are particularly widespread among non-human primates (reviewed in Wich et al. 2002, Oliveira & Ades 2004). These calls are loud, conspicuous vocalizations that carry over long distances and typically show specializations for transmission, including rapid rise times, broad frequency bandwidths, and relatively low frequencies (Waser & Waser 1977, Mitani & Stuht 1998).

Auditory signals may encode information about attributes of the sender, such as identity, sex, body size, age, rank, or physical condition (Clutton-Brock & Albon 1979, Reby et al. 1999, Fischer et al. 2004, Harris 2006, Ey et al. 2007a, Theis et al. 2007, Wyman et al. 2008). They may also contain information about the context of the call, such as the presence of food, predators, or social conflict (Seyfarth et al. 1980, Fichtel & Hammerschmidt 2002, Fischer et al. 2002, Wich et al. 2003a, Soltis et al. 2005). This information can be found in the spectral (i.e., frequency dimension) as well as temporal attributes of calls. Temporal features of calls vary with the lung capacity (and body size) of the caller as well as the control and timing of the emptying speed of air. Call frequencies are determined by the tension and size of the vocal folds as well as the filter function of the vocal tract (reviewed in Fitch & Hauser 1995, Ey et al. 2007a). For example, the fundamental frequency, the primary determinant of pitch, has been shown to vary with the caller's identity (e.g., African elephants, *Loxodonta africana*: McComb et al. 2003; Iberian wolves, *Canis lupus*: Palacios et al. 2007), body size (e.g., Japanese macaques, *Macaca fuscata*: Inoue 1988; hamadryas baboons, *Papio hamadryas*: Pfefferle & Fischer 2006, chacma baboons, *Papio ursinus*: Ey et al. 2007b), rank (e.g., chacma baboons: Fischer et al. 2004; chimpanzees, *Pan troglodytes*: Riede et al. 2007; fallow deer, *Dama dama*: Vannoni & McElligott 2008), and arousal (e.g., chacma baboons: Rendall 2003; humans: Hammerschmidt & Jürgens 2007; spotted hyenas, *Crocuta crocuta* Theis et al. 2007; African elephants: Soltis et al. 2009). Listeners might use some or all of this acoustic information to identify infanticidal males (e.g., lions, *Panthera leo*: McComb et al. 1993), differentiate neighbors from intruders (e.g., Thomas langurs: Wich et al. 2002), recognize the presence of predators (e.g., vervet monkeys, *Chlorocebus aethiops*: Seyfarth et al. 1980), or identify a strong competitor or high-quality mate (e.g., red deer, *Cervus elaphus*: Reby et al. 2005, Reby et al. 2010).

In the present study, we present an analysis of the acoustic features of the loud calls produced by a species of Asian colobine, simakobu (*Simias concolor*), on Siberut Island, Indonesia. Previous research suggests that these vocalizations function, in part, as honest advertisements of male energy status in this species (Chapter 5). In this species, adult males range separately in one-male groups with 2-5 adult females, and female dispersal is common (Chapter 2). Since groups meet and interact infrequently (Chapter four), loud calls are likely used by listeners to assess callers from long distances. While significant individual differences appear to exist in calling rates and call duration, it is unknown what these differences may signal and which other acoustic features vary among individuals. Simakobu loud calls are produced by males only and are audible from distances exceeding 500 m even in their dense rainforest habitat (Tenaza 1989, Erb pers. obs.). Loud calls are reported to occur in a number of contexts: 1) spontaneously, 2) in response to other calls, often as part of a chorus, 3) in response to loud environmental disturbances, such as tree falls or thunder, and 4) during intergroup encounters (Tenaza 1989). Males frequently produce loud calls just before dawn, and these predawn calls usually occur as a chorus of two or more callers (Watanabe 1981, Chapter 5).

Here, we describe the structure and usage of calls and to examine variation in acoustic features within and between individuals. We first determine the contexts in which loud calls are produced and provide a general description of their acoustic properties. We then test whether acoustic features change over the short-term, within a single call bout, presumably as a result of caller fatigue. Finally, we analyze variation across contexts, individuals, and age classes to identify the acoustic features that contribute most to their discrimination. If loud calls are honest signals of male competitive ability, we expect acoustic features to vary between individuals and males of different ages.

We focus on four acoustic parameters that have been shown to exhibit variation among callers and contexts: call duration, inter-unit interval, fundamental frequency and peak frequency. Based on sound production mechanisms as well as the results of previous research, we made several predictions. Over the course of a loud call, we expect that, as the lungs deflate, there will be a decrease in the fundamental frequency and an increase in the inter-unit interval (cf. Fitch & Hauser 1995, Fischer et al. 2004, Vannoni & McElligott 2009). We expect that calls produced in different contexts will be distinguished by the level of arousal of the caller, with more stressful or aversive states of the caller to be reflected in decreased inter-unit interval, increased duration and increased frequency characteristics (cf. Fichtel et al. 2001, , Manser 2001, Fichtel & Hammerschmidt 2002, Rendall 2003). Finally, we expect calls to convey differences in the relative ages of callers and predict that males will have longer calls with shorter inter-unit intervals and lower fundamental frequencies (cf. Fischer et al. 2004).

Methods

Study Site and Subjects

Research was carried out at the Pungut study site in the Peleonan Forest in northern Siberut, Indonesia (0°56’ – 1°03’S, 98°48’ – 98°51’E), a 10.7 km^2 area of hilly (altitude: ca. 25 – 190 m) primary evergreen rainforest. This area is managed by the Siberut Conservation Programme and is protected from hunting and logging through agreements with Indonesian officials and the local community. The climate is equatorial with mean monthly temperatures ranging from 21.5 and 31.7°C, and mean annual precipitation of 3601 mm (Chapter 3). In addition to simakobu, three other primate species inhabit the study area: Kloss’ gibbons (*Hylobates klossii*), Mentawai langurs (*Presbytis potenziani*), and Siberut macaques (*Macaca siberu*). With the exception of humans, mammalian predators do not occur on the Mentawai Islands, and potential predators of simakobu are limited to serpent eagles (*Spilornis cheela sipora*) and reticulated pythons (*Python reticulatus*) (Whitten & Whitten 1982).

Simakobu at this site reside in one-male groups (OMGs) with 3.0 females (range 2-5) and 7.9 individuals on average, as well as in all-male groups (AMGs) averaging 4.5 individuals (Chapter 2). Home ranges are small (<10 ha) and exhibit little overlap between adjacent groups (Chapter 4). Study subjects were 11 adult males residing in OMGs (N=10) and AMGs (N=1). Four of the study groups were habituated to observers in 2006/2007, and all individuals were identified (details in Chapter 2). Two of these groups (OMG-H and AMG-D) were followed beginning in February 2007, and most group members were habituated by May 2007. Two other habituated groups (OMG-A and OMG-E) were observed at the end of the study (June – December 2008). The remaining six OMGs (C, F, J, P, S, and Z) were unhabituated neighboring groups. They were contacted between July – August 2005 and February 2007 – December 2008 at irregular intervals.

Data Collection

Data were collected during the 25-month study period (July 2005 – August 2005 and February 2007 – December 2008) by WME and research assistants (see Acknowledgments). Groups were typically followed to sleeping trees in the evenings and relocated the following morning. Unhabituated groups were identified by distinctive features of the adult males and other easily-recognized group members. Individuals were identified by the shape and hair patterns of the tail, by the size and shape of the crest, and by the patterns and coloration of the facial hair.

During contact with groups, we employed all-occurrence sampling of loud calls (Altmann 1974). Whenever a loud call was heard, we recorded the following data: time, location (GPS point), stimulus (loud call, tree fall, thunder, airplane), and the caller(s)' identity and location. Recordings were made opportunistically by WME with a Marantz PMD-660 solid state recorder

(48 kHz sampling frequency, 16 bit; Marantz, Japan) and Sennheiser directional microphone (K6 power module and ME66 recording head; Sennheiser, Wedemark, Germany).

Acoustic Analysis

We accumulated a total of 661 loud call recordings during the study period. Prior to analysis, we visually inspected calls at a sample frequency of 11,025 Hz using Cool Edit 2000 (Syntrillium, Phoenix, AZ), and selected recordings that were not cut off or disturbed by background noise (e.g., birds, insects, other loud calls). Of the original sample, 186 calls were of sufficient quality for the acoustic analysis. Prior to the spectral analysis, we used a FFT filter (-30 dB) in Cool Edit to remove low-frequency (<100 Hz) and high-frequency (>5000 Hz) noise from recordings. We then used Avisoft SASLab Pro (Avisoft Bioacoustics, Berlin, Germany) to create spectrograms (FFT length: 1024 points, window: Hamming, frame size: 100% overlap: 93.75%).

Spectrograms were visually inspected to determine the start and end point for each call. Due to a high degree of variability in call units near the end of loud calls (e.g., some males continued vocalizing for several seconds or minutes following a loud call), it was often difficult to determine the end point of a particular call. To address this issue, we measured the duration of the interval between successive call units within a sample of 38 recordings made during the pilot study in 2005 and generated a histogram of these durations. From the histogram, we were able to identify a change point in the distribution at 2 seconds, and used this to define the end of loud calls. In other words, once the duration between two successive call units exceeded 2 seconds, this was considered to be the end of the call. Once the start and end point for each call was determined, we measured its duration and counted the number of call units it contained.

Simakobu loud calls were produced as a series of one- or two-syllable call units, each consisting of a loud noisy bark syllable (“huh”), typically accompanied by a quieter gasp syllable (“hoo”), particularly in the call units at the beginning of loud calls (Fig. 6.1). For the spectral analysis, each syllable of each call unit was saved as a separate file before generating the spectrograms in Avisoft (details above). The resultant spectrograms were then imported into LMA 2007, a custom software program. We used the interactive harmonic cursor tool to extract the acoustic parameters from the calls. In total, we examined six temporal and spectral acoustic parameters: call duration, inter-unit interval, as well as the fundamental frequency and peak frequency of the huh and hoo syllables (Table 6.1).

Data Analysis

Some of the spectral parameters could not be measured for both syllables in all call units. In order to minimize biases due to uneven sampling among calls, we randomly chose five huh and five hoo syllables from each loud call. In cases where fewer than five were available, data from all call units were used. A few calls exhibiting outliers in acoustic measures were replaced with more typical calls. Prior to analysis, we screened the data to look for any effects of recording distance on acoustic parameters (cf. Maciej et al. 2011). We found a negative trend ($P<0.10$) for the effect of distance on peak frequency when all recordings were included, but this relationship disappeared when we removed those calls recorded at distances exceeding 75 m. Thus, we excluded these calls ($N=16$) recorded from longer distances.

To examine whether the acoustic properties of vocalizations changed over the course of a single loud call, we selected calls with data available for most call units and both syllable types (mean: 90%, range: 81-100% complete). For this analysis, we calculated the relative position of each call unit, ranging from 0-1, with 1 indicating the last unit. For example, in a call with 10 units, the first unit position = 0.1, the second = 0.2, and so on. We then analyzed the relationship between call unit position and acoustic properties (fundamental frequency, peak frequency, and inter-unit interval).

Calls were assigned to the contexts noise, social, or spontaneous. Calls produced within five minutes of a loud disturbance, including thunder clap, tree fall, airplane, or branch break were assigned to the “noise” context. “Social” calls were defined as those produced within five minutes of another loud call. Calls produced in a chorus following a loud noise, however, were assigned to “noise”. Calls that occurred without any apparent auditory stimulus were classified as “spontaneous”.

To assess age-related variation, we compared calls across males residing in seven groups. Although their exact ages were not known, they could be ranked relative to each other. Three males (J, S, and Z) were classified as “older” because they were fully grown (head-body length) at the beginning of the study in 2005, and continued to reside in the same mixed-sex group for the duration of the study. Males in the “middle” class (A and H) reached adult head-body length and established mixed-sex groups in early 2007. “Younger” males (D and E) were not fully grown in 2007 and resided in all-male bands. In 2008, they were fully grown and began to produce loud calls. Thus, the average difference between age classes is estimated to exceed 1.5 years.

We performed discriminant function analyses (DFA) to test whether calls could be reliably classified according to context, caller identity and age class. To prevent results from being over-represented by males for whom more calls were available and to minimize the confounding effects of individual differences, we limited the sample for analysis of context to males who contributed at least one call to each of the three contexts and randomly selected up to 10 calls per male. For the DFA of individual differences and age classes, we selected up to 15 calls per male. When testing for individual differences, we included only those individuals who contributed at least six calls. Although we acknowledge that a higher number of calls per individual would have been better, we were limited by the overall sample size available.

For DFA, variables were entered using the direct method and call classification was cross-validated using the leave-one-out procedure. We checked for outliers and tested the assumption of homogeneity of covariance by plotting the first two functions to check for extreme values and confirm that the spread of points was similar among groups (cf. Quinn & Keough 2002). Following DFA, we conducted univariate general linear mixed models (LMM) using the Hochberg procedure to correct for multiple testing (Hochberg 1988). We recognize that ideally one would use one set of data for these sets of analyses; however, small sample sizes limited our ability to do this.

To analyze changes in acoustic properties within a loud call, we conducted univariate LMMs with call unit position as a fixed factor and the recording ID as a random factor. To analyze differences due to age and context, we entered individual ID as a random factor and the mean position of the call unit as a covariate. We further tested for interaction effects between our predictor variable and ID. When the covariate and interaction effects were not significant, we removed them from the models and reported results without these effects. Before conducting DFA, we checked for univariate and multivariate outliers following Tabachnick and Fidell 2001. We identified outliers in LMM analyses as cases with studentized residual scores exceeding an absolute value of 3.0 (cf. Kamilar et al. 2010). We re-ran those analyses without outliers and compared results. When the removal of outliers did not affect the patterns and significance of our results, we retained these cases and report test results with them. Statistical tests were performed using SPSS 19 (for DFA) and Statistica 9 (for LMM) with alpha set at $P < 0.05$.

Results

Contexts and Acoustic Properties of Loud Calls

Our description of the acoustic properties of calls was based on 170 full loud call recordings. For some calls, data for either huh or hoo syllables were not available; the sample size for huhs was 162 and for hoos was 160 calls. Calls were 15.5 s in duration on average and consisted of 15.9 call units (range 5-31), with an average inter-unit interval of 1.0 s (Table 6.2). In general, huh syllables showed higher frequency characteristics than hoo syllables. Fundamental frequency averaged 1310.4 ± 167.2 SD Hz in huh syllables, and 867.0 ± 143.2 SD Hz in hoo syllables. Similarly, peak frequency of huh syllables averaged 3798.4 ± 803.3 Hz, while hoo syllables averaged 3307.0 ± 666.4 Hz. We obtained sound pressure readings for 34 of these calls. Calls measured at 11-15 m (N=3) were 73.5-79.5 dB, while those measured at 16-20 m (N=7) ranged from 64.1-71.8. Even at distances exceeding 30 m, sound pressure levels were still high, ranging from 50.1-70.1 dB (N=5).

During the study period, we observed 318 loud calls while in close proximity (<50 m distance) to the caller. Of these, 167 (52.5%) followed the loud call of another male ("social" context), 99 (31.1%) were spontaneous, and 52 (16.4%) followed a loud disturbance ("noise" context: airplane: N=19, tree fall: N=19, thunder: N=4, branch break: N=1). Although we observed one loud call during one of the more than 50 intergroup encounters we witnessed (two groups <50 m apart), this call immediately followed a loud branch break, and did not appear to occur as part of an agonistic display or interaction between males.

Short-Term Changes in Acoustic Features

In order to describe changes that occurred during the progression of loud calls, we selected 22 calls with data available for most call units and both syllable types. Both the spectral and temporal properties of individual call units showed significant changes in relation to their position within loud calls, even after p-values were corrected for multiple testing (Table 6.3). For huh syllables, the fundamental frequency increased as the call progressed. For hoo syllables, on the other hand, fundamental frequency showed a decrease (Fig. 6.2a). Peak frequency increased in both huh and hoo syllables across the call. Finally, the interval between successive call units showed an increase from the start to finish of the loud call (Fig. 6.2b). These effects were strongest for inter-unit interval and fundamental frequency of the hoo syllables, indicated by the large F-values for these variables and high R^2 for the models.

Contextual Differences

To evaluate the variation in loud calls by context, we conducted a discriminant function analysis of 65 calls recorded from four males (Table 6.4). The first function accounted for 89.6% of the variance. The average correct assignment was 58.5% of cases and the cross-validation procedure yielded an average correct assignment of 41.5%, indicating there was substantial overlap between contexts (Fig. 6.3). Calls were correctly assigned (cross-validation values in parentheses) to “noise” in 19.0% (4.8%), “social” in 88.2% (64.7%), and “spontaneous” in 40.0% (40.0%) of cases (Table 6.5). Compared to their prior probabilities, calls produced in social and spontaneous contexts were correctly classified more than expected. Spontaneous calls are discriminated from noise and social via the discriminant function scores for the first function, while the second function shows little separation between the three groups (Fig. 6.3).

The variables that contributed most to the discrimination of contexts, indicated by their large loadings on the first function (>0. 45), were call duration and peak frequency of the huh syllable (Table 6.6). The LMM revealed a significant effect of context on peak frequency ($F_{2, 59} = 4.069$, $P = 0.022$), though duration produced only a statistical trend (Table 6.7). There were no significant interactions between context and individual, indicating that individuals showed similar patterns of loud call differences between contexts. Mean unit position also had no significant effect. In general, calls produced spontaneously showed higher peak frequencies than those made in other contexts (Fig. 6.4).

Individual Differences

To evaluate the variation in loud calls by individual males, we conducted a discriminant function analysis of 67 calls recorded from six males. The first two functions accounted for 93.8% of the variance (Function 1: 74.2%, Function 2: 19.6%). The assignment procedure of the discriminant function yielded an average correct assignment of 89.6% of cases, and the cross-validation procedure yielded an average correct assignment of 79.1%. Calls were correctly assigned to most males, with correct assignment scores ranging from 77.8% - 100% (60.0% – 100% cross-validated) for each individual (Table 6.8). Of the six variables entered into the analysis, three (inter-unit interval, duration and fundamental frequency of the hoo syllable) contributed to the discrimination of individuals, indicated by high loadings on the first two functions (Table 6.9).

Age Differences

To evaluate the variation in loud calls between males of different age classes, we conducted a discriminant function analysis of 68 calls from seven males (Table 6.4). The first function accounting for 73.7% of the variance (Fig. 6.6). The average correct assignment was 69.1%, with 60.3% of cross-validated cases correctly classified (Table 6.10). Males in the younger age class were correctly classified in 50.0% (37.5% cross-validated), those in the middle age class 76.7% (66.7%), and males in the older age class 72.7% (68.2%) of cases.

Inter-unit interval, peak frequency and fundamental frequency of the hoo syllable contributed most to the discrimination of age classes (Table 6.11). GLM analysis with Hochberg corrections revealed that inter-unit intervals increased with age (Table, 6.12, Fig. 6.7a); while fundamental frequency of the hoo syllable decreased (Table 6.12, Fig. 6.7b). Peak frequency of the hoo syllable also differed significantly across age classes (Table 6.12), and appeared to be highest for males in the middle age class (Fig. 6.7c). Mean unit position had no significant effect in any of the models.

Discussion

Like other species of Asian colobines, adult male simakobu produce loud calls that show specializations for long-distance transmission and distinct differences among individuals. Calls were high-amplitude and tonal, comprised redundant elements with modulating frequencies, and emphasized intermediate frequencies (1-4 kHz), features which promote long-distance propagation while reducing degradation during transmission (Wiley & Richards 1978). Individuals were well discriminated by both spectral and temporal features of their calls. This result is not surprising, given that human observers could quickly differentiate between callers, even at distances exceeding 200 m.

Simakobu loud calls were produced in relatively limited contexts. Unlike other species, simakobu calls were not given to predators or during agonistic encounters or fights between adult males (e.g., chacma baboons: Fischer et al. 2002, Thomas langurs: Wich et al. 2003a, guenons, *Cercopithecus* spp: Zuberbühler 2002). The fact that their calls do not serve as alarm calls is likely due to the relative paucity of predator species in the Mentawai Islands. Although humans do frequently hunt simakobu, they typically respond to humans by fleeing or hiding, and were never observed to call in response to the presence of humans, even during habituation. Despite previous reports of males producing loud calls during intergroup encounters (Tilson 1977, Tenaza 1989), we never observed this behavior in the more than 50 encounters we witnessed. Furthermore, loud calls were not accompanied by the running or jumping displays exhibited by other species (e.g., Nilgir langurs, *Trachypithecus johnii,* and Hanuman langurs, *Semnopithecus sp.*: Hohmann ; purple-faced langurs, *Trachypithecus vetulus*: Hohmann 1990; chacma baboons: Fischer et al. 2004; ursine colobus monkeys, *Colobus vellerosus*: Teichroeb and Sicotte 2010). These observations, together with the fact that calls typically elicit counter-calls from several hundred meters away, emphasize the role of these calls in long-distance between-group communication.

Overall, call contexts did not show distinct acoustic differences. This result probably indicates their universal function as advertisement signals, which signal the physical and physiological attributes of the caller rather than convey information about the external environment. The fact that simakobu loud calls are not used as alarm calls to predators further means that the ability for listeners to discriminate between contexts is less important.

Classification results should be interpreted with caution, however, as they may be sensitive to the number of contexts under consideration (Meise et al. 2011). The differences that do exist between contexts likely indicate the arousal or motivation of the caller. Spontaneous calls had higher peak frequencies than other calls, suggesting that the caller was more excited in these situations. Although we were unable to identify an auditory stimulus for these calls, it is possible that they may have been elicited by some visual or other cue of which observers were unaware.

In contrast, we found significant individual differences in simakobu loud calls. These acoustic differences between males likely reflect differences in age, body size, strength, physical condition and other features that influence a male's fighting ability. Like other studies, we found that the fundamental frequency contributed largely to the discrimination of individuals' calls (e.g., Thomas langurs: Steenbeek & Assink 2000, Wich et al. 2003a; Iberian wolves: Palacios et al. 2007; fallow deer: Vannoni & McElligott 2008; red-capped mangabeys, *Cercocebus torquatus*: Bouchet et al. 2012). The fundamental frequency is the primary determinant of perceived pitch and is controlled by vocal fold size and tension, with longer, thicker and more relaxed folds producing lower-pitched sounds (Fitch & Hauser 1995). Although vocal fold size is generally not tightly correlated with body size within age classes (Fitch & Hauser 2002 but see Pfefferle & Fischer 2006), the fundamental frequency may signal other aspects of male quality, including rank and age (e.g., chacma baboons: Fischer et al. 2004), physical condition (e.g., fallow deer: Vannoni & McElligott 2009), and even reproductive success (e.g., red deer: Reby & McComb 2003).

We also found that temporal aspects of calls were important in distinguishing individual males. Although these features are generally viewed as dynamic traits that vary with the arousal or motivation of the caller (cf. Rendall 2003), a number of studies have found distinct individual differences. Inter-unit intervals, for example, were among the most important features contributing to the loud calls of Thomas langur individuals (Steenbeek & Assink 2000), while call duration was important for distinguishing the loud calls of adult male chacma baboons (Fischer et al. 2002). Physiologically, call duration is related to lung capacity, and the size of the lungs, in turn, is closely related to body size (Fitch & Hauser 2002). Call duration can also signal the stamina of the caller, if calls are energetically difficult to produce (cf. Kitchen et al. 2003). Indeed, call duration has been linked to the age (e.g., chacma baboons: Fischer et al. 2004), rank (e.g., guerezas, *Colobus guereza*: Harris 2006), physical condition (e.g., fallow deer: Vannoni & McElligott 2009), and fighting ability (e.g., Thomas langurs: Wich et al. 2003b) of the caller.

Differences between individuals may be alternatively or additionally important for listeners to differentiate between familiar and unfamiliar individuals or between neighbors with whom relationships are decided. The discrimination between familiar and unfamiliar individuals by listeners has been documented in a number of species, and is commonly known as the dear enemy effect (reviewed in Temeles 1994). The ability to differentiate individuals this way is thought to reduce the time and energy spent in unnecessary contests with established neighbors, and allow territory holders to identify threatening intruders (e.g., Thomas langurs: Wich et al. 2002). Furthermore, neighboring males in established territories have typically interacted several times and dyadic relationships are often decided, so listeners can infer fighting ability based on previous experience (cf. Rubenstein & Hack 1992). Thus, listeners would benefit by recognizing unfamiliar calls as well as discriminating between the calls of familiar males. It is currently unknown whether simakobu have the ability to discriminate males on the basis of loud calls alone, but studies of another Asian colobine suggest that they might (Thomas langurs: Wich et al. 2002, 2004).

To test for possible effects of caller stamina and fatigue, we investigated changes in the acoustic structure over the course of a single loud call. As loud calls progressed, we found that call units showed significant changes. The delivery of the calls slowed as the interval between successive call units increased over time. Call units generally showed higher frequency characteristics later in the call, with higher peak frequency and higher fundamental frequency of huh syllables. This result is similar to the pattern found for the loud "wahoo" calls given by male baboons, where wahoos produced early in calling bouts had a higher F0 than those later in the bouts (Fischer et al. 2004). While loud calls in male baboons are accompanied by lengthy aggressive displays, simakobu loud calls do not involve this type of physical exertion. However, the loud calls of simakobu, though shorter, are delivered at a significantly faster rate (mean = 15.9 call units in 15.5 seconds) compared to baboon loud calling bouts (mean = 20 wahoos in 120 seconds). In baboons, these vocal changes appeared to indicate the exhaustion of the caller. This finding is also in line with previous research that found the duration of simakobu loud calls was affected by short-term changes in the energy status of the caller (Chapter 4). These results suggest that loud calls are energetically costly and may be honest signals of a male's competitive ability.

Despite an overall increase in frequency over a call bout, we also observed a significant decline in the fundamental frequency of the hoo syllables. This effect has also been documented in human speech and the vocalizations of vervet monkeys (*Cercopithecus aethiops*) and rhesus macaques (*Macaca mulatta*), and is due to the deflation of the lungs leading to a terminal decrease in the rate of vocal fold vibration (Fitch & Hauser 1995). In the vervets and macaques, this drop in fundamental frequency was also highly correlated with bout termination (Hauser

1997). Thus, listening males might use this information to assess when a neighbor's call is nearing its end and decide when to begin their vocal responses.

Possible long-term effects of the caller's strength and stamina were evaluated by examining the calls of males of different ages. We found that the fundamental frequency of the hoo was lowest and the inter-unit interval highest in the older age class. Similarly, in baboons, fundamental frequency decreased as adult males aged, even over periods as short as three years (Fischer et al. 2004). These older males also produced calls of longer duration. While total call duration did not discriminate between age classes in this study, the fact that the inter-unit interval increased suggests that the individual call units became longer. Since the wahoo calls of the baboon are produced as single vocalizations within an extended calling bout, they appear to be more comparable to call units rather than full loud calls of simakobu. As these older males typically also dropped in rank over time, the changes in the fundamental frequency and duration of their calls appeared to honestly signal a reduction in fighting ability, rather than old age per se. This is supported by the fact that these variables also changed over the course of a single loud call, perhaps indicating the caller's stamina and endurance.

Although we hadn't made any predictions about changes in peak frequency with age, we did find that the peak frequency of the hoo syllable was highest in males of the middle age class. In humans and squirrel monkeys, peak frequency was found to be the most important variable in the vocal expression of an aversive emotional state (Fichtel et al. 2001, Hammerschmidt & Jürgens 2007). In light of these studies, it is plausible that this acoustic feature indicates a greater degree of arousal in males of the middle age class and perhaps a greater motivation to fight. Our relative age classes appear to be broadly similar to the tenure categories used for Thomas langurs based on the length of tenure of the adult males and composition of groups (younger = all-male band/early tenure, middle = middle tenure, older = late tenure: *sensu* Steenbeek et al. 1999). Like the middle tenure on Thomas langurs, males assigned to our middle age class resided in stable groups with young infants. Males of this age/tenure may be more motivated to defend mates and infants, and this higher state of arousal may be signaled in the acoustic properties of their loud calls.

Overall, the results of our study indicate that loud calls are individually distinct and may provide information about the callers. These acoustic differences could, thus be a way for males and females to assess competitors and mates from long distances, since groups only meet and interact infrequently (Erb unpublished data). Listeners attending to the duration, inter-unit interval, fundamental frequency and peak frequency of calls could potentially assess the age, stamina, and arousal of the calling male. Playback experiments are needed to evaluate the salience of these features to listening males and females.

Tables and Figures

Table 6.1. Description of acoustic parameters and abbreviations.

Parameter	Description
Duration [s]	Duration from the start of the first unit until end of last unit*
Inter-unit interval (IUI) [s]	Duration of the interval between successive call units
Fundamental frequency (F0) [Hz]	Lowest frequency of a harmonic series
Peak frequency (Pf) [Hz]	Frequency with the highest amplitude

* last unit with inter-unit interval $\leq$ 2 s (see Methods).

Table 6.2. Descriptive statistics of acoustic parameters.

Variable	*N*	Mean	Min	Max	SD	CV
IUI [s]	170	1.00	0.69	1.48	0.165	16.485
Duration [s]	170	15.53	4.78	33.08	4.711	30.338
F0 (huh) [Hz]	162	1310.37	875.0	1905.8	167.197	12.759
Pf (huh) [Hz]	162	3798.39	2583.2	6466.0	803.267	21.148
F0 (hoo) [Hz]	160	866.97	461.0	1227.8	143.196	16.517
Pf (hoo) [Hz]	160	3306.99	1205.4	5714.0	666.421	20.152

Min = minimum value, Max = maximum value, SD = standard deviation, CV = coefficient of variation.

Table 6.3. Variation in relation to call unit position within the loud call. Results based on LMM with loud call recording as a random factor. N = 22 loud calls recorded from four males.

	Fixed effects					Random effects		Full model	
Variable	*F*	df	*P*	*β*	SE *β*	*F*	*P*	Mult R^2	*P*
IUI	127.421	1, 207	<0.001	0.502	0.044	8.178	<0.001	0.592	<0.001
F0 (huh)	70.155	1, 218	<0.001	0.445	0.053	3.462	<0.001	0.393	<0.001
Pf (huh)	26.448	1, 219	<0.001	0.278	0.054	5.023	<0.001	0.368	<0.001
F0 (hoo)	130.852	1, 188	<0.001	-0.294	0.036	58.060	<0.001	0.879	<0.001
Pf (hoo)	28.799	1, 190	<0.001	0.332	0.062	2.461	<0.001	0.291	<0.001

Table 6.4. Number of calls for each male in each context.

			Context		
ID	Age	N*	Noise	Social	Spontaneous
AL [1, 2]	Middle	23	2	18	3
CH		1	0	1	0
DG	Younger	3	0	3	0
EL [1, 2]	Younger	25	8	15	2
FR		2	1	1	0
HL [1, 2]	Middle	66	15	46	4
JK [2]	Older	11	3	7	0
PC		2	1	1	0
SM [1, 2]	Older	6	1	4	1
ZS [2]	Older	8	1	6	0
Unk		23			
Σ		170	32	102	10

Unk = unidentified caller; [1] indicates calls selected for contextual analysis; [2] indicates calls selected for individual analysis; * context could not be determined for some calls.

Table 6.5. Confusion matrix and classification results for discriminant function analysis of context.

Actual stimulus	Predicted stimulus			Total	Prior probability	% Classified	
	Noise	Social	Spontaneous			Original	Validated
Noise	4	17	0	21	0.32	19.0	4.8
Social	3	30	1	34	0.52	88.2	64.7
Spontaneous	0	6	4	10	0.15	40.0	40.0

Table 6.6. Structure matrix for discriminant function analysis of context.

	Factor loadings	
Variable	1	2
IUI	0.09	0.81
Duration	0.56	0.09
Pf (huh)	0.48	0.32
Pf (hoo)	0.28	-0.05
F0 (huh)	-0.25	-0.07
F0 (hoo)	-0.06	-0.60

Table 6.7. Variation in relation to call context. Results based on LMM with individual ID as a random factor. N = 65 loud calls recorded from four males.

	Fixed effects			Random effects		Full model	
Variable	*F*	df	*P*	*F*	*P*	Mult. R^2	*P*
IUI	0.472	2, 59	0.626	20.256	<0.001	0.519	<0.001
Duration	2.709	2, 59	0.075	3.266	0.027	0.215	0.012
F0 (huh)	0.392	2, 59	0.678	2.723	0.052	0.134	0.121
Pf (huh)	4.069	2, 59	**0.022**	8.629	<0.001	0.350	<0.001
F0 (hoo)	0.115	2, 59	0.891	43.831	<0.001	0.693	<0.001
Pf (hoo)	0.661	2, 59	0.520	5.884	0.001	0.248	0.004

Significant differences after Hochberg correction in bold.

Table 6.8. Confusion matrix and classification results for discriminant function analysis of individual ID.

Actual ID	Predicted ID						Total	Prior probability	% Classified	
	AL	EL	HL	JK	SM	ZS			Original	Validated
AL	14	1	0	0	0	0	15	0.22	93.3	80.0
EL	2	12	0	1	0	0	15	0.22	80.0	60.0
HL	0	0	15	0	0	0	15	0.22	100.0	86.7
JK	0	1	1	7	0	0	9	0.13	77.8	77.8
SM	0	1	0	0	5	0	6	0.09	83.3	83.3
ZS	0	0	0	0	0	7	7	0.10	100.0	100.0

Table 6.9. Structure matrix for discriminant function analysis of individual ID.

	Factor loadings				
Variable	1	2	3	4	5
IUI	0.70	-0.15	-0.11	0.24	0.13
Duration	-0.09	-0.48	-0.14	0.36	0.28
Pf (huh)	0.02	-0.010	0.74	0.67	0.00
Pf (hoo)	-0.05	0.26	-0.28	0.85	0.27
F0 (huh)	-0.01	0.01	0.50	-0.07	0.85
F0 (hoo)	-0.50	0.60	0.01	0.03	0.53

Table 6.10. Confusion matrix and classification results for discriminant function analysis of age class.

Actual Age	Predicted Age			Total	Prior probability	% Classified	
	Younger	Middle	Older			Original	Validated
Younger	8	5	3	16	0.24	50.0	37.5
Middle	2	23	5	30	0.44	76.7	66.7
Older	2	4	16	22	0.32	72.7	68.2

Table 6.11. Structure matrix for discriminant function analysis of age class.

	Factor loadings	
Variable	1	2
IUI	-0.60	0.01
Duration	-0.25	0.02
Pf (huh)	0.27	-0.17
Pf (hoo)	0.17	0.78
F0 (huh)	0.11	-0.46
F0 (hoo)	0.67	0.26

Table 6.12. Variation in relation to male age class. Results based on GLM. N = 68 loud calls recorded from seven males.

	Fixed effects			Full model	
Variable	*F*	df	*P*	Mult. R^2	*P*
IUI	10.855	2, 65	**<0.001**	0.250	<0.001
Duration	1.851	2, 65	0.165	0.054	0.165
F0 (huh)	2.663	2, 65	0.077	0.076	0.077
Pf (huh)	2.520	2, 65	0.088	0.072	0.088
F0 (hoo)	14.356	2, 65	**<0.001**	0.306	<0.001
Pf (hoo)	7.510	2, 65	**0.001**	0.188	0.001

Significant differences after Hochberg correction in bold.

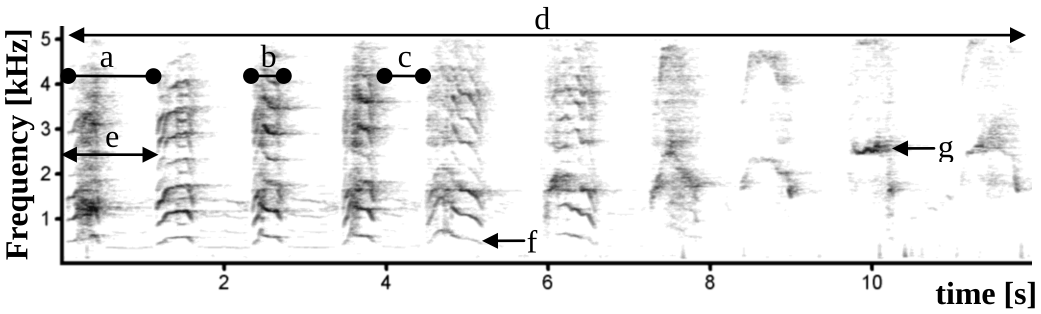
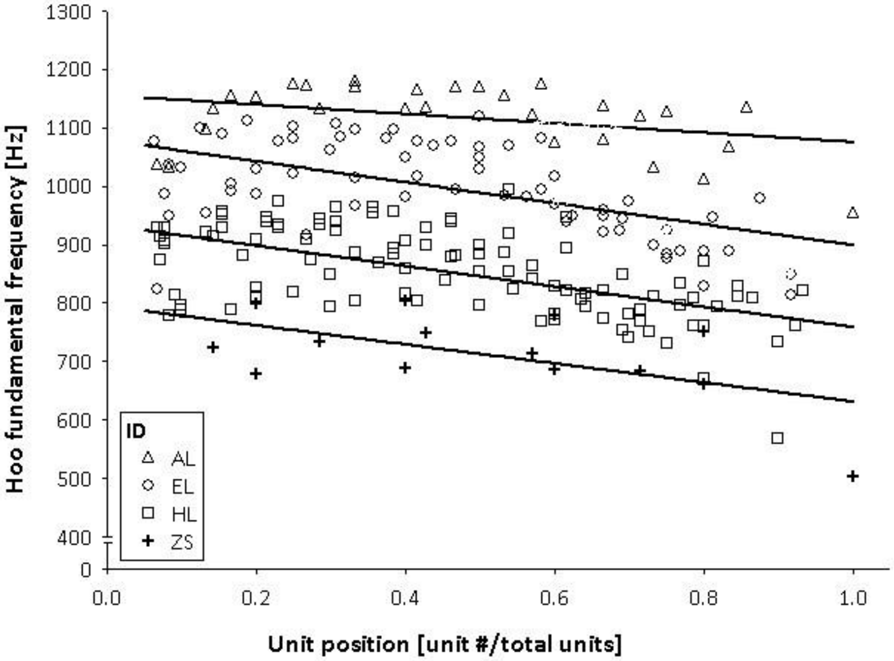
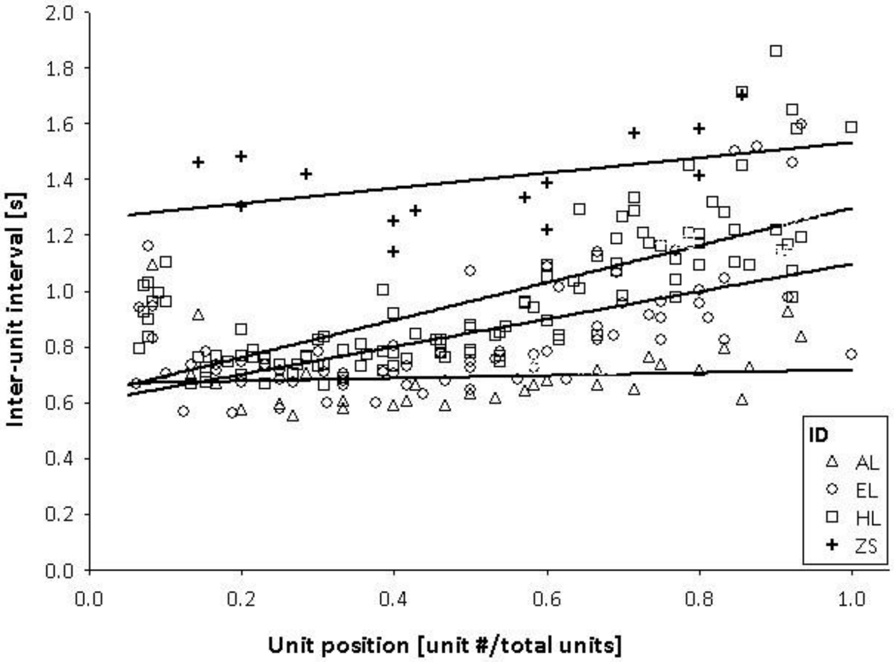


Fig. 6.1. Spectrogram of a simakobu loud call indicating parameters measured in the acoustic analysis: a = call unit, b = huh, c = hoo, d = duration, e = inter-unit interval, f = fundamental frequency, g = peak frequency.



(a)



(b)

Fig. 6.2. Changes in (a) fundamental frequency of the hoo syllable and (b) inter-unit interval as a function of call unit position. Best-fit lines for individual males provided for demonstration purposes only.

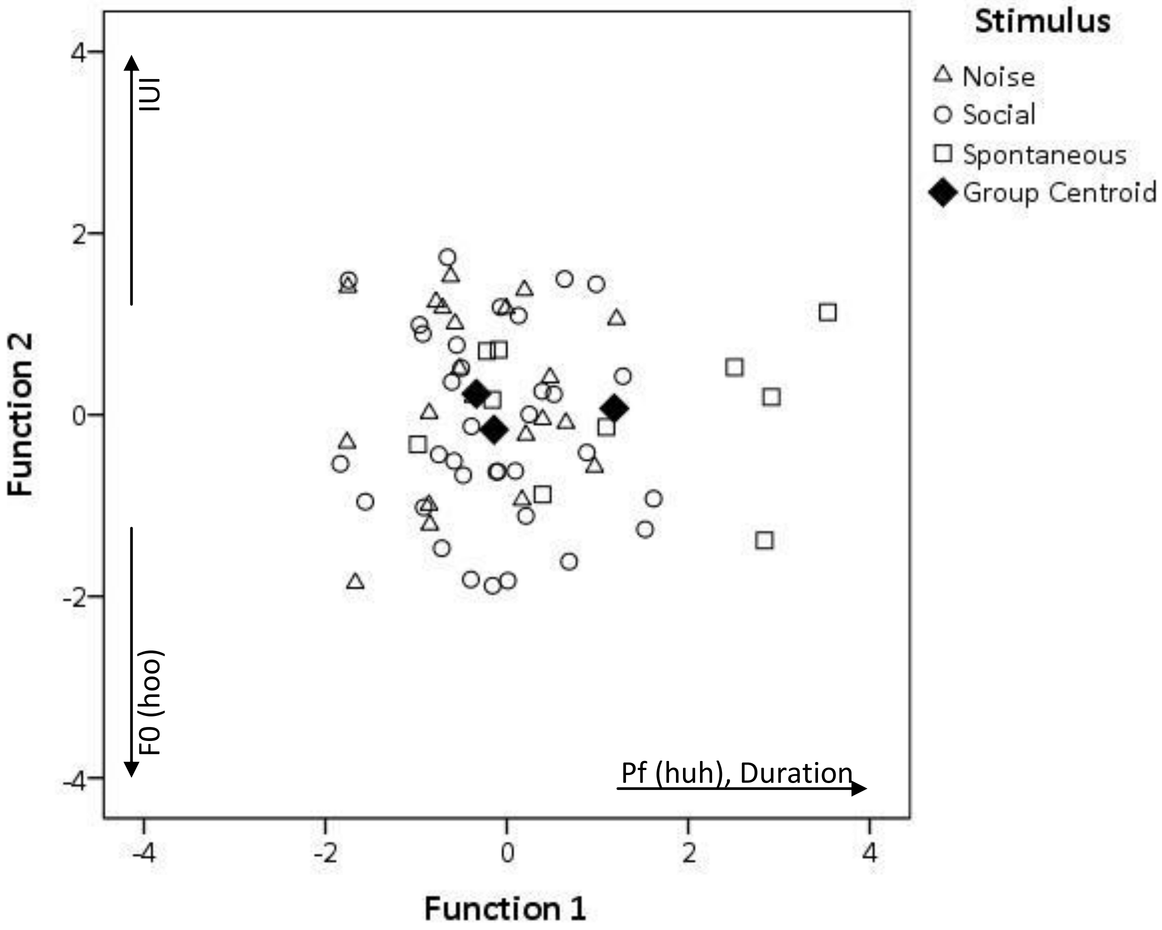


Fig. 6.3. Discriminant function scores for each context for the first two functions. Variables showing loadings with an absolute value >0.4 with each function are indicated.

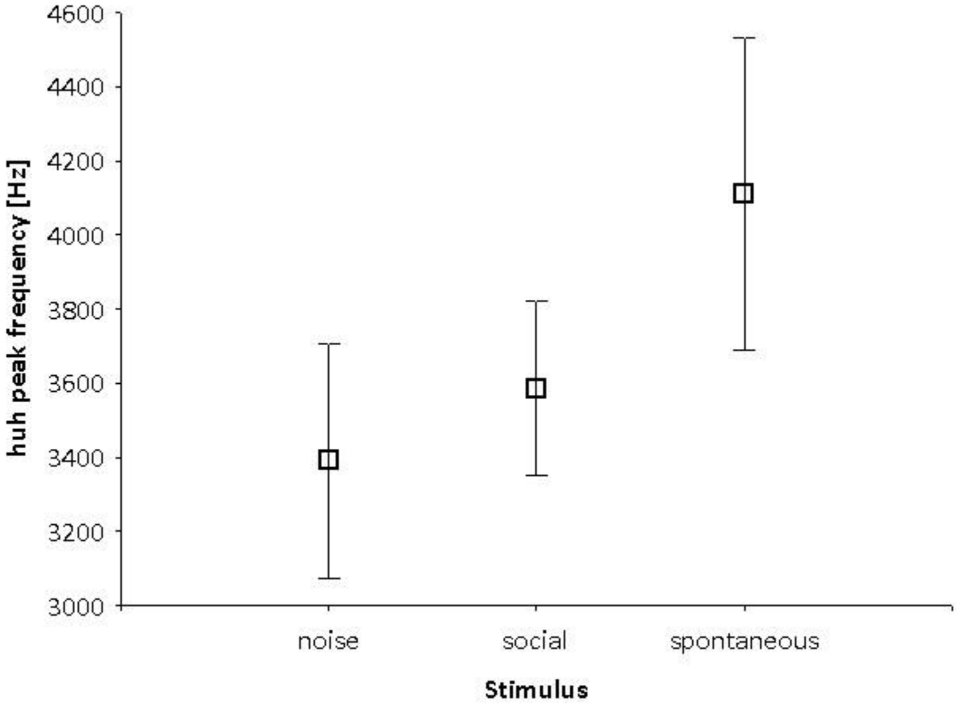


Fig. 6.4. Mean ± 95% confidence interval of peak frequency of huh syllables across contexts.

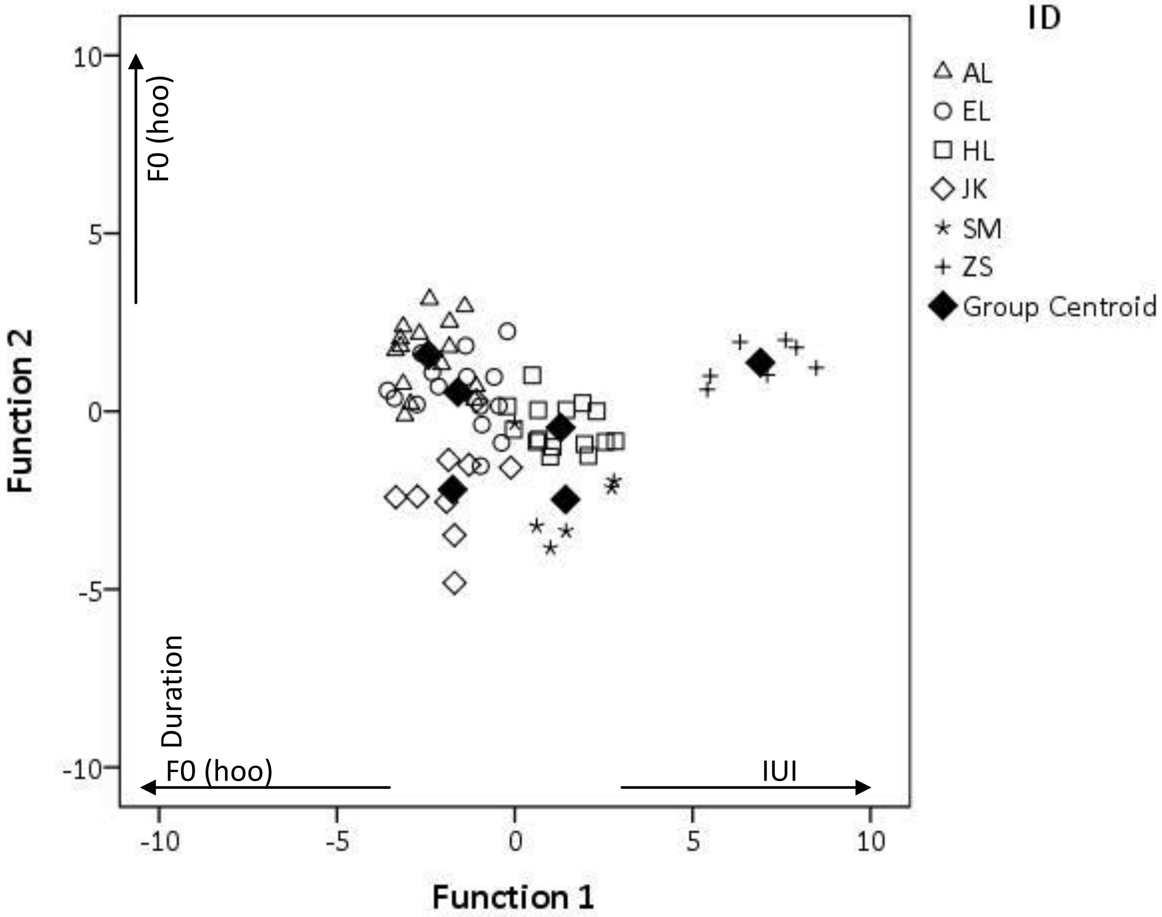


Fig. 6.5. Discriminant function scores for six individual males for the first two functions. Variables showing loadings with an absolute value >0.4 with each function are indicated.

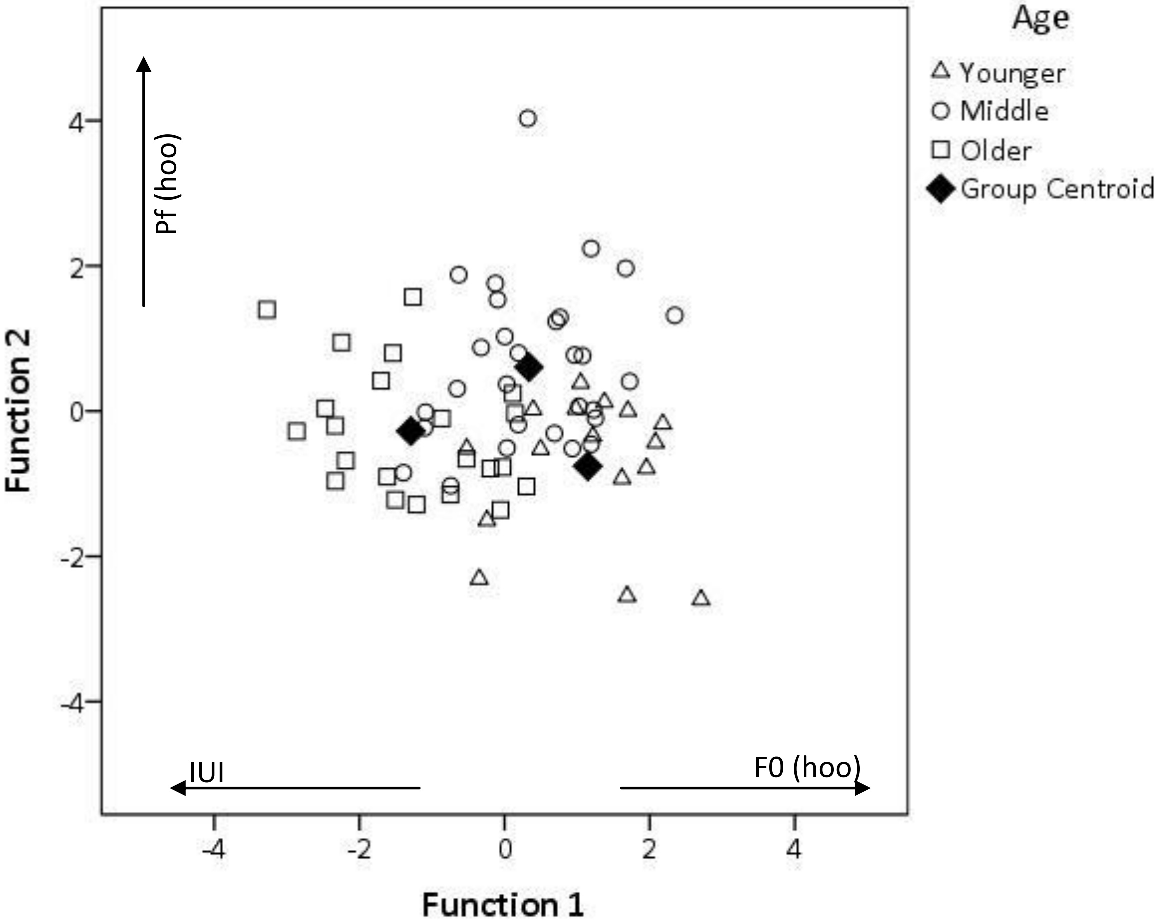


Fig. 6.6. Discriminant function scores for each age class for the first two functions. Variables showing loadings with an absolute value >0.4 with each function are indicated.

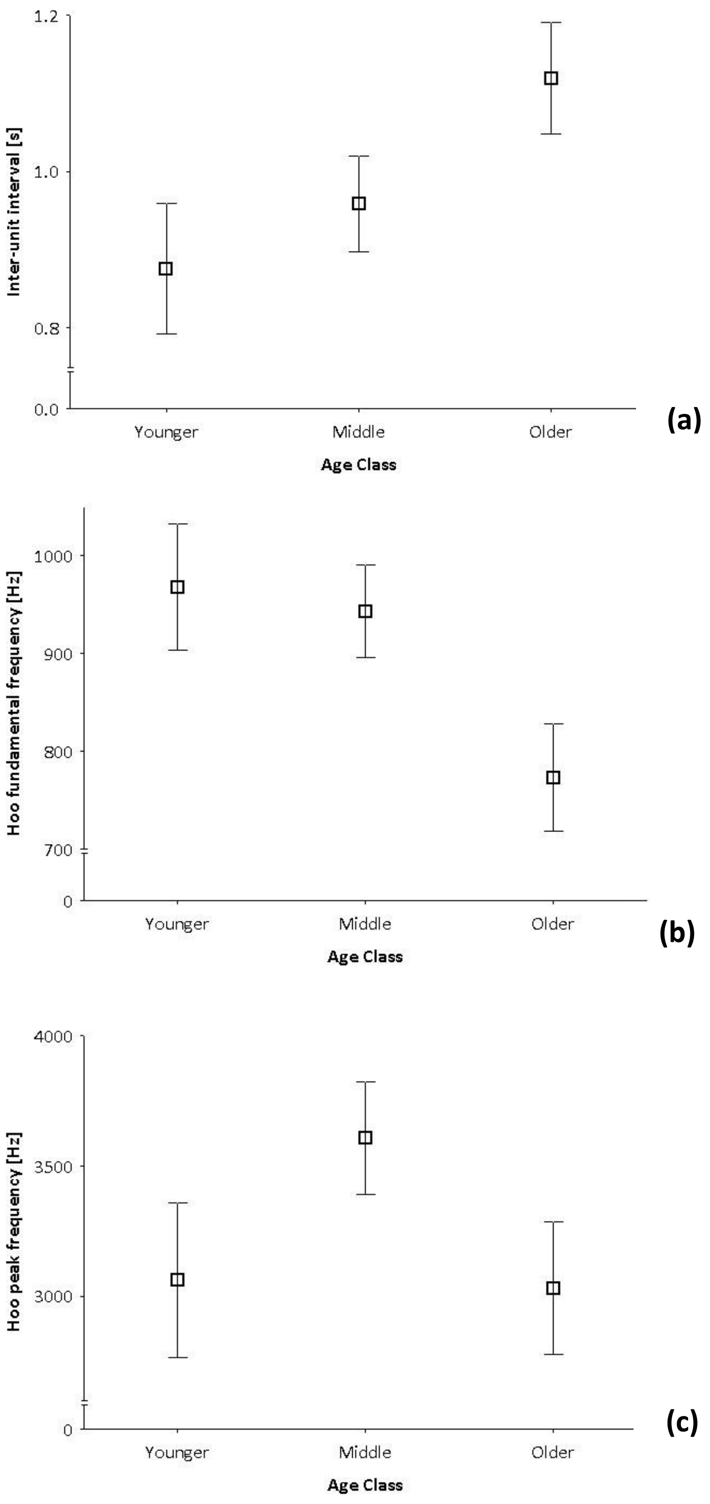


Fig. 6.7. Mean + 95% confidence interval of the parameters that varied significantly across age classes: a = inter-unit interval, b = fundamental frequency (hoo), c = peak frequency (hoo).

References

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227-267

Bouchet H, Blois-Heulin C, Pellier AS, Zuberbühler K, Lemasson A (2012) Acoustic variability and individual distinctiveness in the vocal repertoire of red-capped mangabeys (*Cercocebus torquatus*). J Comp Psychol 126:45-56

Bradbury JW, Vehrencamp SL (1998) Principles of animal communication. Sinauer Associates, Inc., Sunderland, MA

Clutton-Brock TH, Albon SD (1979) The roaring of red deer and the evolution of honest advertisement. Behaviour 69:145-170

Ey E, Pfefferle D, Fischer J (2007a) Do age- and sex-related variations reliably reflect body size in non-human primate vocalizations? A review. Primates 48:253-267

Ey E, Hammerschmidt K, Seyfarth RM, Fischer J (2007b) Age-and sex-related variations in clear calls of *Papio ursinus.* Int J Primatol 28:947-960

Fichtel C, Hammerschmidt K (2002) Responses of redfronted lemurs to experimentally modified alarm calls: Evidence for urgency-based changes in call structure. Ethology 108:763-778

Fichtel C, Hammerschmidt K, Jürgens U (2001) On the vocal expression of emotion. A multi-parametric analysis of different states of aversion in the squirrel monkey. Behaviour 138:97-116

Fischer J, Hammerschmidt K, Cheney DL, Seyfarth RM (2002) Acoustic features of male baboon loud calls: influences of context, age, and individuality. J Acoust Soc Am 111:1465-1474

Fischer J, Kitchen DM, Seyfarth RM, Cheney DL (2004) Baboon loud calls advertise male quality: Acoustic features and their relation to rank, age, and exhaustion. Behav Ecol Sociobiol 56:140-148

Fitch WT, Hauser MD (1995) Vocal production in nonhuman primates: Acoustics, physiology, and functional constraints on" honest" advertisement. Am J Primatol 37:191-219

Fitch WT, Hauser MD (2002) Unpacking" honesty": vertebrate vocal production and the evolution of acoustic signals. In: Simmons A, Fay RR, Popper AN (eds) Acoustic communication. Springer, New York, pp 65-137

Hammerschmidt K, Jürgens U (2007) Acoustical correlates of affective prosody. J Voice 21:531-540

Harris TR (2006) Within-and among-male variation in roaring by black and white colobus monkeys (*Colobus guereza*): What does it reveal about function? Behaviour 143:197-218

Hauser MD (1997) The evolution of communication. MIT Press, Cambridge, MA

Hochberg Y (1988) A sharper Bonferroni procecure for multiple tests of significance. Biometrika 75:800-802

Hohmann G (1990) Loud calls of male purple-faced langurs (*Presbytis senex*). Folia Primatol 55:200-206

Inoue M (1988) Age gradations in vocalization and body weight in Japanese monkeys (*Macaca fuscata*). Folia Primatol 51:76-86

Kitchen DM, Seyfarth RM, Fischer J, Cheney DL (2003) Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). Behav Ecol Sociobiol 53:374-384

Maciej P, Fischer J, Hammerschmidt K (2011) Transmission characteristics of primate vocalizations: implications for acoustic analyses. PLoS One 6:e23015

Manser MB (2001) The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. Proc Biol Sci 268:2315-2324

McComb K, Pusey A, Packer C, Grinnell J (1993) Female lions can identify potentially infanticidal males from their roars. Proc Biol Sci 252:59-64

McComb K, Reby D, Baker L, Moss C, Sayialel S (2003) Long-distance communication of acoustic cues to social identity in African elephants. Anim Behav 65:317-329

Meise K, Keller C, Cowlishaw G, Fischer J (2011) Sources of acoustic variation: implications for production specificity and call categorization in chacma baboon (*Papio ursinus*) grunts. J Acoust Soc Am 129:1631-1641

Mitani JC, Stuht J (1998) The evolution of nonhuman primate loud calls: acoustic adaptation for long-distance transmission. Primates 39:171-182

Oliveira DA, Ades C (2004) Long-distance calls in Neotropical primates. An Acad Bras Cienc 76:393-398

Palacios V, Font E, Márquez R (2007) Iberian wolf howls: acoustic structure, individual variation, and a comparison with North American populations. J Mammal 88:606-613

Pfefferle D, Fischer J (2006) Sounds and size: identification of acoustic variables that reflect body size in hamadryas baboons, *Papio hamadryas*. Anim Behav 72:43-51

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, New York

Reby D, Cargnelutti B, Joachim J, Aulagnier S (1999) Spectral acoustic structure of barking in roe deer (*Capreolus capreolus*). Sex-, age- and individual-related variations. C R Acad Sci III 322:271-279

Reby D, Charlton BD, Locatelli Y, McComb K (2010) Oestrous red deer hinds prefer male roars with higher fundamental frequencies. Proc Biol Sci 277:2747-2753

Reby D, McComb K (2003) Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. Anim Behav 65:519-530

Reby D, McComb K, Cargnelutti B, Darwin C, Fitch WT, Clutton-Brock T (2005) Red deer stags use formants as assessment cues during intrasexual agonistic interactions. Proc Biol Sci 272:941-947

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

Riede T, Arcadi AC, Owren MJ (2007) Nonlinear acoustics in the pant hoots of common chimpanzees (*Pan troglodytes*): vocalizing at the edge. J Acoust Soc Am 121:1758-1767

Rubenstein DI, Hack MA (1992) Horse signals: the sounds and scents of fury. Evol Ecol 6:254-260

Seyfarth RM, Cheney DL, Marler P (1980) Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. Science 210:801-803

Soltis J, Leighty KA, Wesolek CM, Savage A (2009) The expression of affect in African elephant (*Loxodonta africana*) rumble vocalizations. J Comp Psychol 123:222-225

Soltis J, Leong K, Savage A (2005) African elephant vocal communication II: rumble variation reflects the individual identity and emotional state of callers. Anim Behav 70:589-599

Steenbeek R, Assink P (2000) Individual differences in long-distance calls of male wild Thomas langurs (*Presbytis thomasi*). Folia Primatol 69:77-80

Steenbeek R, Assink P, Wich SA (1999) Tenure related changes in wild Thomas's langurs II: loud calls. Behaviour 136:627-650

Tabachnick BG, Fidell LS (1989) Using multivariate statistics. HarperCollins Publishers, Inc. New York

Teichroeb JA, Sicotte P (2010) The function of male agonistic displays in ursine colobus monkeys (*Colobus vellerosus*): Male competition, female mate choice or sexual coercion? Ethology 116:366-380

Temeles EJ (1994) The role of neighbours in territorial systems: when are they 'dear enemies'? Anim Behav 47:339-350

Tenaza RR (1989) Intergroup calls of male pig-tailed langurs (*Simias concolor*). Primates 30:199-206

Theis KR, Greene KM, Benson-Amram SR, Holekamp KE (2007) Sources of variation in the long-distance vocalizations of spotted hyenas. Behaviour 144:557-584

Tilson RL (1977) Social organization of simakobu monkeys (*Nasalis concolor*) in Siberut Island, Indonesia. J Mammal 58:202-212

Vannoni E, McElligott AG (2008) Low frequency groans indicate larger and more dominant fallow deer (*Dama dama*) males. PLoS One 3:e3113

Vannoni E, McElligott AG (2009) Fallow bucks get hoarse: vocal fatigue as a possible signal to conspecifics. Anim Behav 78:3-10

Waser PM, Waser MS (1977) Experimental studies of primate vocalization: specializations for long-distance propagation. Z Tierpsychol 43:239-263

Watanabe K (1981) Variations in group composition and population density of the two sympatric Mentawaian leaf-monkeys. Primates 22:145-160

Whitten AJ, Whitten JEJ (1982) Preliminary observations of the Mentawai macaque on Siberut Island, Indonesia. Int J Primatol 3:445-459

Wich SA, Assink PR, Becher F, Sterck EHM (2002) Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): the effect of familiarity. Behaviour 139:79-87

Wich SA, Assink PR, Sterck EHM (2004) Thomas langurs (*Presbytis thomasi*) discriminate between calls of young solitary versus older group-living males: a factor in avoiding infanticide? Behaviour 141:41-51

Wich SA, Koski S, de Vries H, van Schaik CP (2003) Individual and contextual variation in Thomas langur male loud calls. Ethology 109:1-13

Wich SA, van der Post DJ, Heistermann M, Möhle U, van Hooff JARAM, Sterck EHM (2003) Life-phase related changes in male loud call characteristics and testosterone levels in wild Thomas langurs. Int J Primatol 24:1251-1265

Wiley RH, Richards DG (1978) Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behav Ecol Sociobiol 3:69-94

Wyman MT, Mooring MS, McCowan B, Penedo MCT, Hart LA (2008) Amplitude of bison bellows reflects male quality, physical condition and motivation. Anim Behav 76:1625-1639

Zuberbühler K (2002) Effects of natural and sexual selection on the evolution of guenon loud calls. In: Glenn ME, Cords M (eds) The Guenons: diversity and adaptation in African monkeys. Springer, New York, pp 289-30

CHAPTER SEVEN:

Summary and Conclusions

In this dissertation, I aimed to investigate male-male competition and the use of loud calls by male simakobu residing in one-male groups. In species where females can be monopolized, males engage in contest competition to maintain exclusive access to a group (Emlen & Oring 1977). To achieve this, they can attempt to defend an area in which female range via aggressive intergroup encounters and long-distance vocalizations (Cheney 1987, Clutton-Brock 1989). In particular, I was interested in the use of loud calls as honest advertisements of male quality and fighting ability to deter rivals and attract females. To this end, I asked two main questions: 1) Are loud calls honest signals of male energy status? and 2) What acoustic features of calls signal male stamina and fighting ability? Because there is limited and often contradictory information available for this species, I first had to establish the social and spatial context of male-male competition. I, thus, asked: 3) What is the social organization and dispersal pattern of simakobu at the Pungut study site? 4) Are there seasonal differences in ecology and reproduction? and 5) What is the spatial distribution of groups and the nature of their relationships?

Simakobu Updated: A not-so-extreme Asian colobine

Contrary to previous assessments, the results of this study show that simakobu generally fit the Asian colobine pattern with respect to social organization, group size, and dispersal. I found OMGs with three adult females on average, but no adult male-female pairs (Chapter 2). In addition, I documented stable AMGs, which may also include juvenile females. Although this is the first time an AMG with more than two individuals as well as immature females has been documented for this species, AMGs are common among Asian colobines (Yeager & Kool 2000, Kirkpatrick 2011) and often contain juvenile females as well (e.g., proboscis monkeys, *Nasalis larvatus*: Boonratana 1993; Thomas langurs, *Presbytis thomasi*: Steenbeek et al. 2000; white-headed langurs, *Trachypithecus leucocephalus*: Jin et al. 2009). Overall, while at the small end of the spectrum, simakobu groups fit within the group size range for Asian colobines (cf. Kirkpatrick 2011).

Why, then, were adult male-female pairs so commonly encountered in the past? An inter-population comparison revealed that human disturbance was responsible (Chapter 2). I found that hunting pressure negatively affected adult sex ratios and immature numbers. Among primates, only a few studies have considered the impact of human disturbance on group composition (reviewed in Schwitzer et al. 2011). For example, red colobus (*Procolobus gordonorum*), black-and-white colobus (*Colobus angolensis*), and bearded saki (*Chiropotes satanas*) had smaller groups in areas with human disturbance (Marshall et al. 2005, Struhsaker 2008, Boyle & Smith 2010). In howler monkeys, the number of males per group decreased while the proportion of OMGs in the population increased in more disturbed habitats (*Alouatta palliata, A. pigra, A. seniculus,* reviewed in Arroyo-Rodríguez & Dias 2010). Overall, given the frequency and ease of hunting these animals, it is not surprising that these effects have been observed in nearly every simakobu population studied to date. These findings suggest that the small, apparently monogamous groups observed in previous studies resulted where hunting reduced the number of adult females in the population.

By documenting changes in group membership for five focal groups, I found that both males and females temporarily visited and transferred between groups (Chapter 2). Although male-biased dispersal is the norm for Old World monkeys (Greenwood 1980, Pusey & Packer 1987), female dispersal is a common Asian colobine trait (Sterck, 1998). Females may have used temporary visits to other groups to assess dispersal opportunities, and transfers to choose the highest quality mates. In contrast to the closely-related proboscis money (Yeager 1990), juvenile males are not present in OMGs. The lack of juvenile males in OMGs and the presence and immigration of young males in AMGs suggested that males may be dispersing from natal groups, and at an earlier age than their closest relatives. Adult male dispersals or take-overs were not observed during this study, and so this aspect of group formation is unknown. Male tenure length likely affects the frequency and timing of dispersal for all other age-sex classes, and long-term monitoring of known individuals and groups is needed to more fully understand these patterns.

In Chapter three, I aimed to assess the degree of reproductive seasonality of simakobu. Although earlier reports had suggested that births were restricted to just two or three months of the year, this appeared to be an unusual pattern for a Southeast Asian primate. Births were not significantly clustered across months, but there was a clear peak in September and October when 55% of births occurred that coincided with the wettest time of the year. Although the birth peak I observed was not unusual for Asian colobines in general, the equatorial location and aseasonal environment of this population predicted little or no birth peak. However, when pooled across study sites, simakobu births occurred in 10 calendar months, indicating that simakobu reproduction is not strictly seasonal. Conceptions were concentrated in March and April, following a peak in unripe fruit availability, and females seemed to conceive when their physical condition was best. The small sample size limits my interpretations; however, these observations suggest that simakobu may be capital breeders (Stearns 1992, Brockman & van Schaik 2005) with conceptions flexibly timed to females' recovery of energy reserves, though more births over several years are required to confirm this hypothesis.

Male-Male Competition in One-Male Groups

Adult male and female simakobu are clearly sexually dimorphic, as males are nearly 30% larger and have canines almost twice as long as females (Tenaza & Fuentes 1995, Hadi et al. 2009). Only adult males produce distinct loud calls and participate in aggressive intergroup encounters (Tenaza 1989a, Chapters 3-4). These observations indicate that male-male competition is likely operating in this species. The earlier observation that most simakobu groups comprised an adult male-female pair (Tilson 1977, Watanabe 1981, Tenaza & Fuentes 1995, reviewed in Chapters 1-2) seemed to present a paradox where apparently monogamous groups appeared to experience strong male-male competition. In Chapter two, I showed that, when undisturbed, simakobu do form one-male polygynous groups with two to five adult females. Among our study groups, one out of three adult males resided outside OMGs. Thus, the morphological and social pattern conforms well to predictions of sexual selection (cf. Plavcan & van Schaik 1992), and indicates the presence of contest competition among males to exclude rivals (Emlen & Oring 1977).

In species where females can be monopolized, males may exhibit territorial behavior in an attempt to defend females by defending the area in which they range (Emlen & Oring 1977). Male territorial behavior is common among Asian colobines (van Schaik et al. 1992), which form one-male groups and inhabit relatively small home range areas (Kirkpatrick 2011), and has thus been hypothesized to be related to the defense of females (Dunbar 1988, van Schaik et al. 1992). In Chapter four, I showed that simakobu home ranges were small, fewer than 10 ha, and exhibited limited overlap (0-13%) with other groups. Unlike the AMGs of other Asian colobines (e.g., Hanuman langurs, *Semnopithecus* sp.: Rajpurohit et al. 1995; Thomas langurs: Steenbeek et al. 2000; white-headed langurs: Qing Zhao pers. com.), simakobu AMGs did not range within large and flexible home ranges. Although they did not appear to actively defend a territory, they did occupy small home ranges that remained stable over a period of more than two years. Additional data on group tenure and ranging of simakobu AMGs are needed to investigate the significance of this apparently unusual pattern.

All OMGs maintained exclusive access to their core areas and adult males often responded aggressively to other groups, especially other adult males. The exclusive use of most of their home range area indicates that males are indirectly defending females through the defense of the area in which they range (Emlen & Oring 1977, van Schaik et al. 1992). Aggressive participation in intergroup encounters and loud call choruses are the most likely mechanisms by which males monopolize groups of females (Cheney 1987, Clutton-Brock 1989). However, this hypothesis remains to be directly tested in this species. More detailed analyses of home range use as well as comparison of aggressive behaviors and their outcomes at important feeding sites and during periods when receptive females and vulnerable infants are present are needed to determine the strategies males employ. Playback experiments testing for these effects would be particularly useful.

A male’s ability to monopolize access to a group of females depends not only on the size of the group and its spatial distribution, but is also influenced by the timing of their fertile periods (Emlen & Oring 1977, Pereira et al. 2000). Among primates, those species with less birth seasonality tend to exhibit more reproductive skew (Cowlishaw & Dunbar 1991, Nunn 1999a, Takahashi 2001). For example, in a study of 10 wild primate populations, van Noordwijk and van Schaik (2004) found that in six of eight seasonally breeding populations (those with at least 75% of births in a three-month period), paternity was shared with extra-group males; while paternity was monopolized by the resident male in the less seasonal populations. Thus, while simakobu group sizes and home range areas are small and adult males appear to be able to monopolize them, if female receptivity is highly synchronized, males might not be able maintain exclusive access and/or concentrate paternity (). In Chapter three, I found that simakobu exhibited a relatively non-seasonal pattern of reproduction, with just 55% of births concentrated in a three-month period (compared to the 75% benchmark used by van Noordwijk & van Schaik 2004). Given the results described above, it is thus likely that simakobu males are able to monopolize females in their groups and concentrate paternity. Nonetheless, the presence of sexual swellings in this species (Tenaza 1989b) may increase within-group synchrony, even in the absence of seasonal reproduction (Nunn 1999a, van Schaik et al. 2001). These swellings appear to be unique among Asian colobines, which usually have no external signs of receptivity (Kirkpatrick 2011). Furthermore, their occurrence in one-male groups is difficult to explain, as they are generally viewed as a means for females to confuse paternity among multiple males (Nunn 1999b). Detailed behavioral data on female receptivity and mating periods together with paternity analyses are needed to determine the success of male monopolization of females and the function of sexual swellings in this species.

Finally, the occurrence of female dispersal I described in Chapter two indicates the potential for female choice in this species. Female decisions for transfer may be influenced by the strength or fighting ability of the resident male, as in Thomas langurs (*Presbytis thomasi*: Sterck 1997). It remains unknown what factors influence dispersal decisions in simakobu, but it is possible that females use loud calls to assess the strength and quality of males. These acoustic signals may thus play a role in female choice, as has been suggested for Thomas langurs (Wich et al. 2003). If females choose males on the basis of their loud calls, males may use them to signal their fighting ability not only to repel their rivals but also to attract potential mates (Delgado 2006). Long-term monitoring of dispersal patterns in several groups combined with playback studies of loud calls varying in their acoustic characteristics are needed to evaluate this hypothesis.

The Honesty of Simakobu Loud Calls

Males in many primate species produce loud calls, conspicuous vocalizations that show specializations for transmission over long distances (Waser & Waser 1977, Mitani & Stuht 1998). Loud calls are common among Asian colobine males and are thought to play a role in group spacing and male competition (Delgado 2006). In Chapters five and six, I assessed the role of loud calls as honest advertisements of male quality and fighting ability, which might be used to deter rivals and attract mates. In these contexts, signalers may have an incentive to lie or exaggerate in order to manipulate receivers, and so signal reliability is thought to be maintained by various costs (Vehrencamp 2000, Searcy & Nowicki 2005). While other costs exist (see Vehrencamp 2000 for a review), in Chapter five I focused on “handicap” signals. Handicap signals are honest because they incur production costs to the sender, conveying accurate information about the caller’s health, condition, and current fighting ability (Zahavi 1975, Zahavi 1977, Grafen 1990).

Vocal displays, in particular, often incur energy costs (reviewed in Ryan 1988, Prestwich 1994). Although there is abundant evidence for the energetic costs of calls in a number of species, there is very little evidence in primates (Kappeler & van Schaik 2004). Primate loud calls may indicate a caller's willingness or motivation to defend important resources and/or mates (e.g., Whitehead 1989, Cowlishaw 1992, Harris 2006), but they also play a potential role in mate attraction and male-male competition as advertisements of fighting ability (e.g., Cowlishaw 1996, Wich & Nunn 2002, Fischer et al. 2004, Delgado 2006). In Chapter five, I studied simakobu loud calls to test the hypothesis that these vocal displays are energetically costly handicap signals. I found that call duration was negatively affected by short-term changes in energy status (Chapter 5), and that call acoustics showed significant changes over the course of a single bout, perhaps indicating the exhaustion of the caller. (Chapter 6) Together, these observations support the hypothesis that calls are energetically costly.

I also found a dramatic peak of calling in the 30-minute period before sunrise. Calls produced around this time were longer than those later in the day. These calls were typically produced as part of a chorus, which seemed to set the stage for direct comparison among callers. Intense chorusing by males at dawn is also common in birds, and a number of hypotheses have been proposed to explain this phenomenon, including physiological, social and environmental factors (reviewed in Staicer et al. 1996). Although I did not directly test all the existing hypotheses, this early morning period might represent the best time for males to advertise their energy status, since calls might signal the energy reserves that callers accumulated on the previous day, and thus their current fighting ability (Thomas & Cuthill 2002). The morning hours also have some of the best conditions for acoustic transmission of the day (Schneider et al. 2008). Thus, dawn calls can travel farther and provide more accurate and reliable information about the caller. The fact that focal males called on 67% of mornings indicates that there may be costs associated with not calling, such as the risk of aggressive encounters with other groups (cf. Whitehead 1987). Together, these finding support the hypothesis that these calls are used as assessment signals, and may play a role in mitigating physical contests between neighboring males. While muting or removal experiments like those done with birds (e.g., McDonald 1989) would provide the most convincing evidence for elucidating the role of loud calls in home range defense, similar experiments in primates are neither practical nor ethical. Playback experiments, however, could be used to determine the reactions of males and females to loud calls of different males. In particular, it would be interesting to compare the reactions of cycling and non-cycling females to calls with variable acoustic properties (cf. Reby et al. 2010).

Unlike call durations, daily calling rates did not show indications that they were energy-limited (Chapter 5). Calling rates were negatively influenced by fruit availability, which suggests that they may be related to feeding competition, perhaps signaling the motivation of the caller to repel rivals and attract mates (cf. Harris 2006). Alternatively, calling throughout the day may simply be a statement that the territory is currently occupied and defended (cf. Clutton-Brock & Albon 1979). It is further possible that calling rates are indirectly tied to fruit availability if reproduction is affected by seasonal fluctuations in food resources. I did find a clear birth peak in September and October than coincided with a peak in fruit feeding (Chapter 3), providing some indirect support for this idea. In order to thoroughly evaluate these possibilities, however, a more detailed study of loud call production in space and time is needed. Data on calling rates in different parts of the home range and during periods of mating, conception and birth would help elucidate loud call function in these contexts. Once again, playback studies from different home range areas and in different social and reproductive contexts would prove useful.

Acoustic analyses confirmed my observations in the field, that individual loud calls were acoustically distinct and could be differentiated on the basis of both temporal and spectral characteristics. I found that call duration was an important variable in discriminating callers. As this feature is related to lung capacity and thus body size (Fitch & Hauser 2002), it may provide information about the caller's fighting ability (e.g., Thomas langurs: Wich et al. 2003). The fundamental frequency also contributed largely to the discrimination among males. This acoustic feature is controlled by the size and tension of the vocal folds (Fitch & Hauser 1995), and thus has the potential to signal aspects of male quality including rank and age (e.g., chacma baboons, *Papio ursinus*: Fischer et al. 2004), physical condition (fallow deer, *Dama dama*: Vannoni & McElligott 2009), and even reproductive success (e.g., red deer, *Cervus elaphus*: Reby & McComb 2003). Overall, these acoustic features contribute to the function of loud calls as honest "index" signals. Unlike handicap signals, index signals are constrained by physical and physiological factors, thereby providing honest information about the age, size or strength of the signaler (Vehrencamp 2000, Maynard Smith & Harper 2003).

Age could also be an important factor influencing loud call acoustic through the long-term effects of caller strength and stamina. As males aged, and likely experienced a decline in fighting ability, their calls decreased in patch and increased in duration. However, males in the middle age class produced calls with higher peak frequency compared to younger and older males. As this acoustic feature is an important variable in the expression of an aversive emotional state (squirrel monkeys, *Saimiri sciureus*: Fichtel et al. 2001, humans: Hammerschmidt & Jürgens 2007), this result may indicate higher arousal in these males and perhaps a greater motivation to fight.

Overall, these results indicate that loud calls may provide information about the age, size, stamina and fighting ability of the callers. These acoustic differences could thus be a way for males and females to discriminate neighbors from strangers (e.g., Wich et al. 2002), identify previous rivals (e.g., Rubenstein & Hack 1992), and assess competitors and mates from long distances (e.g., Reby et al. 2010). Their hypothesized role in between-group communication was supported by the observation that their acoustic features promote long-distance propagation while reducing degradation as well as the fact that more than 50% of calls were produced in response to another male loud call (Chapter 6). Playback experiments are needed to assess the salience of these features to listening males and females.

Implications for Simakobu Conservation

Simakobu are a critically endangered species Whittaker & Mittermeier 2008) and one of the 25 most endangered primates (Mittermeier et al. 2009). They are endemic to the Mentawai Islands of Indonesia, where their wild population numbers fewer than 20,000 individuals (estimate = 6700-17,300), representing a decline of 33-75% in 20 years (Whittaker 2006). The extinction of several simakobu populations has been documented throughout the Mentawai Islands. At Grukna, in northern Siberut, where simakobu were thriving with an estimated population density of 220 individuals/km^2 in 1978 (Watanabe 1981), no animals could be found in 1990 (Tenaza & Fuentes 1995). Similarly, entire simakobu populations were driven to extinction on at least two islets of South Pagai (Yanuar et al. 1998). These losses were apparently related to human disturbance in these areas. Indeed, heavy hunting and commercial logging have been identified as the major threats to their long-term survival (Whittaker 2006).

Evaluating the relative impacts of habitat disturbance and hunting pressure is a critical issue for conservation management (Cowlishaw & Dunbar 2000). In Chapter two, I showed that hunting pressure negatively affected the sex ratio and number of immatures in mixed-sex groups, and likely explains the preponderance of small monogamous groups described in many populations (see Chapter 2). Among the Mentawai primates, simakobu are considered the best tasting and easiest to hunt, and are thus the most hunted (Mitchell & Tilson 1986). These observations indicate that hunting may be the greatest extinction risk for simakobu, and call for increased conservation action and education to reduce hunting rates throughout the Mentawai Islands.

Conclusions

Overall, results from this study have revealed that, rather than being an exceptional primate, simakobu appear to fit comfortably within the Asian colobine range of group size and composition, dispersal, reproduction, ranging, and male competition. The occurrence of conspicuous sexual swellings in one-male groups as well as stable all-male groups with small home ranges, however, seem to deviate from the basic pattern in other primates and Asian colobine species, and the significance of these observations remains a puzzle. Simakobu show morphological and behavioral signs of strong male-male competition, which influences ranging patterns, intergroup interactions, and loud call behavior. Males attempt to monopolize females and appear to aggressively defend at least part of the area in which they range. They produce loud calls several times each day, and despite very small home range areas, groups meet only once or twice per week. This suggests that males use loud calls to signal their presence and fighting ability to defend females and/or the resources within their home ranges. Loud calls may function as honest signals of male condition, age, and strength, which are likely used by males and females alike to assess rivals and mates. Future research is needed to fully investigate the role of loud calls as part of a strategy by males to defend females, food resources, and/or infants.

References

Arroyo-Rodríguez V, Dias PAD (2010) Effects of habitat fragmentation and disturbance on howler monkeys: a review. Am J Primatol 72:1-16

Boonratana R (1993) The ecology and behaviour of the proboscis monkey (*Nasalis larvatus*) in the Lower Kinabatangan, Sabah. Mahidol University, Bangkok. PhD thesis

Boyle SA, Smith AT (2010) Behavioral modifications in northern bearded saki monkeys (*Chiropotes satanas chiropotes*) in forest fragments of central Amazonia. Primates 51:43-51

Brockman DK, van Schaik CP (2005) Seasonality and reproductive function. In Brockman DK, van Schaik CP (eds), Seasonality in primates: Studies of living and extinct human and non-human primates. Cambridge University Press, Cambridge, pp 269-305

Cheney DL (1987) Interactions and relationships between groups. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 267-281

Clutton-Brock TH (1989) Review lecture: mammalian mating systems. Proc R Soc Lond B 236:339-372

Clutton-Brock TH, Albon SD (1979) The roaring of red deer and the evolution of honest advertisement. Behaviour 69:145-170

Cowlishaw G (1992) Song function in gibbons. Behaviour 121:131-153

Cowlishaw G (1996) Sexual selection and information content in gibbon song bouts. Ethology 102:272-284

Cowlishaw G, Dunbar RIM (1991) Dominance rank and mating success in male primates. Anim Behav 41:1045-1056

Cowlishaw G, Dunbar RIM (2000) Primate conservation biology. University of Chicago Press, Chicago

Delgado RA (2006) Sexual selection in the loud calls of male primates: signal content and function. Int J Primatol 27:5-25

Dunbar RIM (1988) Primate social systems. Cornell University Press, Ithaca, New York

Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223

Fichtel C, Hammerschmidt K, Jürgens U (2001) On the vocal expression of emotion. A multi-parametric analysis of different states of aversion in the squirrel monkey. Behaviour 138:97-116

Fischer J, Kitchen DM, Seyfarth RM, Cheney DL (2004) Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. Behav Ecol Sociobiol 56:140-148

Fitch WT, Hauser MD (1995) Vocal production in nonhuman primates: acoustics, physiology, and functional constraints on" honest" advertisement. Am J Primatol 37:191-219

Fitch WT, Hauser MD (2002) Unpacking" honesty": vertebrate vocal production and the evolution of acoustic signals. In: Simmons A, Fay RR, Popper AN (eds) Acoustic communication. Springer, New York, pp 65-137

Grafen A (1990) Biological signals as handicaps. J Theor Biol 144:517-546

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140-1162

Hadi S, Ziegler T, Hodges JK (2009) Group structure and physical characteristics of Simakobu monkeys (*Simias concolor*) on the Mentawai Island of Siberut, Indonesia. Folia Primatol 80:74-82

Hammerschmidt K, Jürgens U (2007) Acoustical correlates of affective prosody. J Voice 21:531-540

Harris TR (2006) Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). Behav Ecol Sociobiol 61:317-329

Jin T, Wang DZ, Zhao Q, Yin LJ, Qin DG, Ran WZ, Pan WS (2009) Social organization of white-headed langurs (*Trachypithecus leucocephalus*) in the Nongguan Karst Hills, Guangxi, China. Am J Primatol 71:206-213

Kappeler PM, van Schaik CP (2004) Sexual selection in primates: review and selective preview. In: Kappeler PM, van Schaik CP (eds) Sexual selection in primates: new and comparative perspectives. Cambridge University Press, New York, pp 3-20

Kirkpatrick RC (2011) The Asian colobines: diversity among leaf-eating monkeys. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf R (eds) Primates in perspective. Oxford University Press, New York, pp 189-202

Marshall AR, Topp-Jørgensen JE, Brink H, Fanning E (2005) Monkey abundance and social structure in two high-elevation forest reserves in the Udzungwa Mountains of Tanzania. Int J Primatol 26:127-145

Maynard Smith J, Harper D (2003) Animal signals. Oxford University Press, New York

McDonald MV (1989) Function of song in Scott's seaside sparrow, *Ammodramus maritimus peninsulae*. Anim Behav 38:468-485

Mitani JC, Stuht J (1998) The evolution of nonhuman primate loud calls: acoustic adaptation for long-distance transmission. Primates 39:171-182

Mitchell AH, Tilson RL (1986) Restoring the balance: traditional hunting and primate conservation in the Mentawai Islands, Indonesia. In: Else JG, Lee PC (eds) Primate ecology and conservation. Cambridge University Press, Cambridge, pp 249-260

Mittermeier RA, Wallis J, Rylands AB, Ganzhorn JU, Oates JF, Williamson EA, Palacios E, Heyman EW, Kierulff MCM, Yongcheng L, Supriatna J, Roos C, Walker S, Cortes-Ortiz L, Schwitzer C (2009) Primates in peril: the world's 25 most endangered primates 2008-2010. IUCN/SSC Primate Specialist Group, International Primatological Society, and Conservation International, Arlington, VA

Nunn CL (1999a) The number of males in primate social groups: a comparative test of the socioecological model. Behav Ecol Sociobiol 46:1-13

Nunn CL (1999b) The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. Anim Behav 58:229-246

Pereira ME, Clutton-Brock TH, Kappeler PM (2000) Understanding male primates. In: Kappeler PM (ed) Primate males: causes and consequences of variation in group composition. Cambridge University Press, New York, pp 271-277

Plavcan JM, van Schaik CP (1992) Intrasexual competition and canine dimorphism in anthropoid primates. Yearb Phys Anthropol 87:461-477

Prestwich KN (1994) The energetics of acoustic signaling in anurans and insects. Integr Comp Biol 34:625-643

Pusey AE, Packer C (1987) Dispersal and philopatry. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. The University of Chicago Press, Chicago, pp 250-266

Rajpurohit LS, Sommer V, Mohnot SM (1995) Wanderers between harems and bachelor bands: male Hanuman langurs (*Presbytis entellus*) at Jodhpur in Rajasthan. Behaviour 132:255-299

Reby D, Charlton BD, Locatelli Y, McComb K (2010) Oestrous red deer hinds prefer male roars with higher fundamental frequencies. Proc R Soc B 277:2747-2753

Reby D, McComb K (2003) Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. Anim Behav 65:519-530

Rubenstein DI, Hack MA (1992) Horse signals: the sounds and scents of fury. Evol Ecol 6:254-260

Ryan MJ (1988) Energy, calling, and selection. Integr Comp Biol 28:885-898

Schneider C, Hodges JK, Fischer J, Hammerschmidt K (2008) Acoustic niches of Siberut primates. Int J Primatol 29:601-613

Searcy WA, Nowicki S (2005) The evolution of animal communication: reliability and deception in signaling systems. Princeton University Press, Princeton

Schwitzer C, Glatt L, Nekaris KA, Ganzhorn JU (2011) Responses of animals to habitat alteration: an overview focussing on primates. Endang Species Res 14: 31-38

Staicer CA, Spector DA, Horn AG (1996) The dawn chorus and other diel patterns in acoustic signaling. In: Kroodsma DE, Miller EH (eds) Ecology and evolution of acoustic communication in birds. Comstock Publishing, Ithaca, NY, pp 426-453

Stearns, SC (1992) The evolution of life histories. Oxford University Press, New York.

Steenbeek R, Sterck EHM, de Vries H, van Hooff JARAM (2000) Costs and benefits of the one-male, age-graded, and all-male phases in wild Thomas's langur groups. In: Kappeler PM (ed) Primate males: causes and consequences of variation in group composition. Cambridge University Press, Cambridge, pp 130-145

Sterck EHM (1997) Determinants of female dispersal in Thomas langurs. Am J Primatol 42:179-198

Sterck EHM (1998) Female dispersal, social organization, and infanticide in langurs: are they linked to human disturbance? Am J Primatol 44:235-254

Struhsaker TT (2008) Demographic variability in monkeys: implications for theory and conservation. Int J Primatol 29:19-34

Takahashi H (2001) Influence of fluctuation in the operational sex ratio to mating of troop and non-troop male Japanese macaques for four years on Kinkazan Island, Japan. Primates 42:183-191

Tenaza RR (1989a) Intergroup calls of male pig-tailed langurs (*Simias concolor*). Primates 30:199-206

Tenaza RR (1989b) Female sexual swellings in the Asian colobine *Simias concolor*. Am J Primatol 17:81-86

Tenaza RR, Fuentes A (1995) Monandrous social organization of pigtailed langurs (*Simias concolor*) in the Pagai Islands, Indonesia. Int J Primatol 16:295-310

Thomas RJ, Cuthill IC (2002) Body mass regulation and the daily singing routines of European robins. Anim Behav 63:285-295

Tilson RL (1977) Social organization of simakobu monkeys (*Nasalis concolor*) in Siberut Island, Indonesia. J Mammal 58:202-212

Vannoni E, McElligott AG (2009) Fallow bucks get hoarse: vocal fatigue as a possible signal to conspecifics. Anim Behav 78:3-10

van Noordwijk MA, van Schaik CP (2004) Sexual selection and the careers of primate males: paternity concentration, dominance-acquisition tactics and transfer decisions. In: Kappeler PM, van Schaik CP (eds) Sexual selection in primates: new and comparative perspectives. Cambridge University Press, New York, pp 208-229

van Schaik CP, Assink PR, Salafsky N (1992) Territorial behavior in Southeast Asian langurs: resource defense or mate defense. Am J Primatol 26:233-242

van Schaik CP, van Noordwijk MA, Nunn CL (2001) Sex and social evolution in primates. In Lee PC (ed) Comparative primate socioecology. Cambridge University Press, New York, pp 204-231

Vehrencamp SL (2000) Handicap, index, and conventional signal elements of bird song. In: Espmark Y, Amundsen T, Rosenqvist G (eds) Animal signals: signalling and signal design in animal communication. Tapir Academic Press, Trondheim, pp 277-300

Waser, PM, Waser MS (1977) Experimental studies of primate vocalization: specializations for long-distance propagation. Z Tierpsychol 43:239-263

Watanabe K (1981) Variations in group composition and population density of the two sympatric Mentawaian leaf-monkeys. Primates 22:145-160

Whitehead JM (1987) Vocally mediated reciprocity between neighbouring groups of mantled howling monkeys, *Alouatta palliata palliata*. Anim Behav 35:1615-1627

Whitehead JM (1989) The effect of the location of a simulated intruder on responses to long-distance vocalizations of mantled howler monkeys, *Alouatta palliata palliata*. Behaviour: 1/2:73-103

Whittaker DJ (2006) A conservation action plan for the Mentawai primates. Primate Conserv 20:95-105

Whittaker DJ, Mittermeier RA (2008) *Simias concolor*. In: IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. <www.iucnredlist.org>. Downloaded on 30 March 2012

Wich SA, Nunn CL (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

Wich SA, Assink PR, Becher F, Sterck EHM (2002) Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): the effect of familiarity. Behaviour 139:79-87

Wich SA, van der Post DJ, Heistermann M, Möhle U, van Hooff JARAM, Sterck EHM (2003) Life-phase related changes in male loud call characteristics and testosterone levels in wild Thomas langurs. Int J Primatol 24:1251-1265

Yanuar A, Fuentes A, Studd K (1998) A short report on the current status of the Mentawai snub-nosed langur (*Simias concolor concolor*) on Simalegu Island, South Pagai, Mentawai, Indonesia. Trop. Biodiv 5:299-305

Yeager CP (1990) Proboscis monkey (*Nasalis larvatus*) social organization: group structure. Am J Primatol 20:95-106

Yeager CP, Kool K (2000) The behavioral ecology of Asian colobines. In: Whitehead PF, Jolly CJ (eds) Old World monkeys. Cambridge University Press, Cambridge, pp 496-521

Zahavi A (1975) Mate selection-a selection for a handicap. J Theor Biol 53:205-214

Zahavi A (1977) The cost of honesty (further remarks on the handicap principle). J Theor Biol 67:603-605

Bibliography

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227-267

Andersson MB (1994) Sexual selection. Princeton University Press, Princeton

Arroyo-Rodríguez V, Dias PAD (2010) Effects of habitat fragmentation and disturbance on howler monkeys: a review. Am J Primatol 72:1-16

Ashton PS, Givnish TJ, Appanah S (1988) Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. Am Nat, 132, 44-66

Batschelet E (1981) Circular statistics in biology. Academic Press, New York

Beyer HL (2004) Hawth's analysis tools for ArcGIS . Available at http://www.spatialecology.com/htools

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MH, White JS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127-135

Boonratana R (1993) The ecology and behaviour of the proboscis monkey (*Nasalis larvatus*) in the Lower Kinabatangan, Sabah. Mahidol University, Bangkok. PhD thesis

Boonratana R (2000) Ranging behavior of proboscis monkeys (*Nasalis larvatus*) in the Lower Kinabatangan, Northern Borneo. Int J Primatol 21:497-518

Borries C, Lu A, Ossi-Lupo K, Larney E, Koenig A (2011) Primate life histories and dietary adaptations: a comparison of Asian colobines and macaques. Am J Phys Anthropol 144:286-299

Bouchet H, Blois-Heulin C, Pellier AS, Zuberbühler K, Lemasson A (2012) Acoustic variability and individual distinctiveness in the vocal repertoire of red-capped mangabeys (*Cercocebus torquatus*). J Comp Psychol 126:45-56

Boyle SA, Smith AT (2010) Behavioral modifications in northern bearded saki monkeys (*Chiropotes satanas chiropotes*) in forest fragments of central Amazonia. Primates 51:43-51

Bradbury JW, Vehrencamp SL (1998) Principles of animal communication. Sinauer Associates, Inc., Sunderland, MA

Brockman DK, van Schaik CP (2005) Seasonality and reproductive function. In: Brockman DK, van Schaik CP (eds) Seasonality in primates: Studies of living and extinct human and non-human primates. Cambridge University Press, Cambridge, pp 269-305

Cheney DL (1987) Interactions and relationships between groups. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 267-281

Chiarello AG (1995) Role of loud calls in brown howlers, *Alouatta fusca*. Am J Primatol 36:213-222

Clutton-Brock TH (1989) Review lecture: mammalian mating systems. Proc R Soc Lond B 236:339-372

Clutton-Brock TH, Albon SD (1979) The roaring of red deer and the evolution of honest advertisement. Behaviour 69:145-170

Cowlishaw G (1992) Song function in gibbons. Behaviour 121:131-153

Cowlishaw G (1996) Sexual selection and information content in gibbon song bouts. Ethology 102:272-284

Cowlishaw G, Dunbar RIM (1991) Dominance rank and mating success in male primates. Anim Behav 41:1045-1056

Cowlishaw G, Dunbar RIM (2000) Primate conservation biology. University of Chicago Press, Chicago

Cucco M, Malacarne G (1997) The effect of supplemental food on time budget and body condition in the black redstart *Phoenicurus ochruros*. Ardea 85:211-221

Curtin SH (1980) Dusky and banded leaf monkeys. In: Chivers DJ (ed) Malayan forest primates: ten years' study in tropical rain forest. Plenum Press, New York, pp 107-145

Curtin SH, Chivers DJ. (1978) Leaf-eating primates of peninsular Malaysia: the siamang and the dusky leaf-monkey. In: Montgomery GG (ed) The ecology of arboreal folivores. Smithsonian Institution Press, Washington, DC, pp 441-464

da Cunha RGT, Jalles-Filho E (2007) The roaring of southern brown howler monkeys (*Alouatta guariba clamitans*) as a mechanism of active defence of borders. Folia Primatol 78:259-271

Darwin C (1871) The descent of man and selection in relation to sex. John Murray, London

Delgado RA (2006) Sexual selection in the loud calls of male primates: signal content and function. Int J Primatol 27:5-25

Di Bitetti MS, Janson CH (2000) When will the stork arrive? Patterns of birth seasonality in neotropical primates. Am J Primatol 50:109-130

Drent RH, Daan S (1980) The prudent parent: energetic adjustments in avian breeding. In Klomp H, Woldendrop JW (eds) The integrated study of bird populations. North Holland, New York, pp 225-252

Dunbar RIM (1988) Primate social systems. Cornell University Press, Ithaca, New York

Drubbel RV, Gautier JP (1993) On the occurrence of nocturnal and diurnal loud calls, differing in structure and duration, in red howlers (*Alouatta seniculus*) of French Guyana. Folia Primatol 60:195-209

Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223

Erb WM, Borries C, Lestari NS, Ziegler T (2012) Demography of simakobu (*Simias concolor*) and the impact of human disturbance. Am J Primatol 74:580-590

Ey E, Hammerschmidt K, Seyfarth RM, Fischer J (2007b) Age-and sex-related variations in clear calls of *Papio ursinus.* Int J Primatol 28:947-960

Ey E, Pfefferle D, Fischer J (2007a) Do age- and sex-related variations reliably reflect body size in non-human primate vocalizations? A review. Primates 48:253-267

Fashing PJ (2001) Male and female strategies during intergroup encounters in guerezas (*Colobus guereza*): evidence for resource defense mediated through males and a comparison with other primates. Behav Ecol Sociobiol 50:219-230

Fichtel C, Hammerschmidt K (2002) Responses of redfronted lemurs to experimentally modified alarm calls: Evidence for urgency-based changes in call structure. Ethology 108:763-778

Fichtel C, Hammerschmidt K, Jürgens U (2001) On the vocal expression of emotion. A multi-parametric analysis of different states of aversion in the squirrel monkey. Behaviour 138:97-116

Field A (2009) Discovering statistics using SPSS, third edition. SAGE Publications Ltd, London

Fischer J, Hammerschmidt K, Cheney DL, Seyfarth RM (2002) Acoustic features of male baboon loud calls: influences of context, age, and individuality. J Acoust Soc Am 111:1465-1474

Fischer J, Kitchen DM, Seyfarth RM, Cheney DL (2004) Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. Behav Ecol Sociobiol 56:140-148

Fitch WT, Hauser MD (1995) Vocal production in nonhuman primates: Acoustics, physiology, and functional constraints on" honest" advertisement. Am J Primatol 37:191-219

Fitch WT, Hauser MD (2002) Unpacking" honesty": vertebrate vocal production and the evolution of acoustic signals. In: Simmons A, Fay RR, Popper AN (eds) Acoustic communication. Springer, New York, pp 65-13

Fretwell SD, Lucas HL (1969) On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheor 19:16-36

Fuentes A (1994) The socioecology of the Mentawai Island langur (*Presbytis potenziani*). University of California at Berkeley, Berkley. PhD thesis

Fuentes A, Ray E (1996) Humans, habitat loss and hunting: the status of the Mentawai Islands primates on Sipora and Pagai Islands. Asian Primates 5:5-9

Ganzhorn JU, Klaus S, Ortmann S, Schmid J (2003) Adaptations to seasonality: some primate and nonprimate examples. In: Kappeler PM, Pereira ME (eds), Primate life histories and socioecology. The University of Chicago Press, Chicago and London, pp 132-148

Geissmann T, Nijman V (2006) Calling in wild silvery gibbons (*Hylobates moloch*) in Java (Indonesia): behavior, phylogeny, and conservation. Am J Primatol 68:1-19

Gibson L, Koenig A (2012) Neighboring groups and habitat edges modulate range use in Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*). Behav Ecol Sociobiol 66:633-643

Godfrey JD, Bryant DM (2000) State-dependent behaviour and energy expenditure: an experimental study of European robins on winter territories. J Anim Ecol 69:301-313

Gottlander K (1987) Variation in the song rate of the male pied flycatcher *Ficedula hypoleuca*: causes and consequences. Anim Behav 35:1037-1043

Grafen A (1990) Biological signals as handicaps. J Theor Biol 144:517-546

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140-1162

Grueter CC, van Schaik CP (2010) Evolutionary determinants of modular societies in colobines. Behav Ecol 21:63-71

Gurmaya KJ (1986) Ecology and behavior of *Presbytis thomasi* in Northern Sumatra. Primates 27:151-172

Hadi S, Ziegler T, Hodges JK (2009) Group structure and physical characteristics of Simakobu monkeys (*Simias concolor*) on the Mentawai Island of Siberut, Indonesia. Folia Primatol 80:74-82

Hadi S, Ziegler T, Waltert M, Hodges JK (2009) Tree diversity and forest structure in northern Siberut, Mentawai Islands, Indonesia. Trop Ecol 50:315-327

Hadi S, Ziegler T, Waltert M, Syamsuri F, Mühlenberg M, Hodges JK (2012) Habitat use and trophic niche overlap of two sympatric colobines, *Presbytis potenziani* and *Simias concolor,* on Siberut Island, Indonesia. Int J Primatol 33:218-232

Hammerschmidt K, Jürgens U (2007) Acoustical correlates of affective prosody. J Voice 21:531-540

Harris TR (2006) Within-and among-male variation in roaring by black and white colobus monkeys (*Colobus guereza*): What does it reveal about function? Behaviour 143:197-218

Harris TR (2006) Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). Behav Ecol Sociobiol 61:317-329

Hauser MD (1997) The evolution of communication. MIT Press, Cambridge, MA

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965-1978

Hill RA (2006) Thermal constraints on activity scheduling and habitat choice in baboons. Am J Phys Anthropol 129:242-249

Hochberg Y (1988) A sharper Bonferroni procecure for multiple tests of significance. Biometrika 75:800-802

Hohmann G (1990) Loud calls of male purple-faced langurs (*Presbytis senex*). Folia Primatol 55:200-206

Hohmann G, Vogl L (1991) Loud calls of male Nilgiri langurs (*Presbytis johnii*): age-, individual-, and population-specific differences. Int J Primatol 12:503-524

Horwich RH, Gebhard K (1983) Roaring rhythms in black howler monkeys (*Alouatta pigra*) of Belize. Primates 24:290-296

Inoue M (1988) Age gradations in vocalization and body weight in Japanese monkeys (*Macaca fuscata*). Folia Primatol 51:76-86

Janson CH, Verdolin J (2005) Seasonality of primate births in relation to climate. In: Brockman DK, van Schaik CP (eds) Seasonality in primates: studies of living and extinct human and non-human primates. Cambridge University Press, Cambridge, pp 307-349

Jin T, Wang DZ, Zhao Q, Yin LJ, Qin DG, Ran WZ, Pan WS (2009) Social organization of white-headed langurs (*Trachypithecus leucocephalus*) in the Nongguan Karst Hills, Guangxi, China. Am J Primatol 71:206-213

Jönsson KI (1997) Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78:57-66

Kacelnik A (1979) The foraging efficiency of great tits (*Parus major L.*) in relation to light intensity. Anim Behav 27:237-241

Kappeler PM, van Schaik CP (2004) Sexual selection in primates: review and selective preview. In: Kappeler PM, van Schaik CP (eds) Sexual selection in primates: new and comparative perspectives. Cambridge University Press, New York, pp 3-20

Kawamura S, Megantara EN (1986) Observation of primates in logged forest on Sipora Island, Mentawai. Kyoto University Research Report of Studies on Asian Non-Human Primates 5:1-12

Kirkpatrick RC (2007) The Asian colobines: diversity among leaf-eating monkeys. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK (eds) Primates in perspective. Oxford University Press, New York, pp 186-200

Kirkpatrick RC (2011) The Asian colobines: diversity among leaf-eating monkeys. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf R (eds) Primates in perspective. Oxford University Press, New York, pp 189-202

Kirkpatrick RC, Grueter CC (2010) Snub-nosed monkeys: multilevel societies across varied environments. Evol Anthropol 19:98-113

Kitchen DM, Seyfarth RM, Fischer J, Cheney DL (2003) Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). Behav Ecol Sociobiol 53:374-384

Koenig A, Borries C, Chalise MK, Winkler P (1997) Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). J Zool 243:215-235

Kunc HP, Wolf JBW (2008) Seasonal changes of vocal rates and their relation to territorial status in male Galápagos sea lions (*Zalophus wollebaeki*). Ethology 114:381-388

Lancaster JB, Lee RB (1965) The annual reproductive cycle in monkeys and apes. In: DeVore I (ed) Primate behavior: field studies of monkeys and apes. Holt, Rinehart and Winston, New York, pp 486-513

Lee PC, Majluf P, Gordon IJ (1991) Growth, weaning and maternal investment from a comparative perspective. J Zool 225:99-114

Lengagne T, Slater PJ (2002) The effects of rain on acoustic communication: tawny owls have good reason for calling less in wet weather. Proc Biol Sci 269:2121-2125

Leutenegger W, Lubach G (1987) Sexual dimorphism, mating system, and effect of phylogeny in de Brazza's monkey (*Cercopithecus neglectus*). Am J Primatol 13:171-179

Lewis RJ, Kappeler PM (2005) Seasonality, body condition, and timing of reproduction in *Propithecus verreauxi verreauxi* in the Kirindy Forest. Am J Primatol 67:347-364

Lindburg DG (1987) Seasonality of reproduction in primates. In: Mitchell EJ (ed), Comparative primate biology Vol. 2B. Alan R. Liss, New York, pp 167-218

Lowe MJ (2007) Downloaded on March 3, 2011 from http://commons.wikimedia.org/wiki/File:Mentawai_Islands_Map.png

Mace R (1989) The relationship between daily routines of singing and foraging: an experiment on captive Great Tits *Parus major*. Ibis 131:415-420

Maciej P, Fischer J, Hammerschmidt K (2011) Transmission characteristics of primate vocalizations: implications for acoustic analyses. PLoS One 6:e23015

Manser MB (2001) The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. Proc Biol Sci 268:2315-2324

Marsh CW (1981) Ranging behaviour and its relation to diet selection in Tana River red colobus (*Colobus badius rufomitratus*). J Zool 195:473-492

Marsh CW (1981) Diet choice among red colobus (*Colobus badius rufomitratus*) on the Tana river, Kenya. Folia Primatol 35:147-178

Marshall AJ (2010) Effect of habitat quality on primate populations in Kalimantan: gibbons and leaf monkeys as case studies. In: Gursky-Doyen S, Supriatna J (eds) Indonesian primates. Springer, New York, pp 157-177

Marshall AR, Topp-Jørgensen JE, Brink H, Fanning E (2005) Monkey abundance and social structure in two high-elevation forest reserves in the Udzungwa Mountains of Tanzania. Int J Primatol 26:127-145

Maynard Smith J, Harper D (2003) Animal signals. Oxford University Press, New York

Mbora DNM, Meikle DB (2004) The value of unprotected habitat in conserving the critically endangered Tana River red colobus (*Procolobus rufomitratus*). Biol Conserv 120:91-99

McComb K, Pusey A, Packer C, Grinnell J (1993) Female lions can identify potentially infanticidal males from their roars. Proc Biol Sci 252:59-64

McComb K, Reby D, Baker L, Moss C, Sayialel S (2003) Long-distance communication of acoustic cues to social identity in African elephants. Anim Behav 65:317-329

McDonald MV (1989) Function of song in Scott's seaside sparrow, *Ammodramus maritimus peninsulae*. Anim Behav 38:468-485

McNab BK (1978) Energetics of arboreal folivores: physiological problems and ecological consequences of feeding on an ubiquitous food supply. In: Montgomery GG (ed) The ecology of arboreal folivores. Smithsonian Institution Press, Washington, DC, pp 153-162

Meise K, Keller C, Cowlishaw G, Fischer J (2011) Sources of acoustic variation: implications for production specificity and call categorization in chacma baboon (*Papio ursinus*) grunts. J Acoust Soc Am 129:1631-1641

Miller CT, Paciulli LM (2002) Patterns of lateralized hand use in an arboreal primate, *Simias concolor*. Am J Primatol 56:231-236

Mitani JC, Nishida T (1993) Contexts and social correlates of long-distance calling by male chimpanzees. Anim Behav 45:735-746

Mitani JC, Stuht J (1998) The evolution of nonhuman primate loud calls: acoustic adaptation for long-distance transmission. Primates 39:171-182

Mitchell AH, Tilson RL (1986) Restoring the balance: traditional hunting and primate conservation in the Mentawai Islands, Indonesia. In: Else JG, Lee PC (eds) Primate ecology and conservation. Cambridge University Press, Cambridge, pp 249-260

Mittermeier RA (1987) Effect of hunting on rain forest primates. In: Marsh CW, Mittermeier RA (eds) Primate conservation in the tropical rain forest. Alan R. Liss, New York, pp 109-146

Mittermeier RA, Wallis J, Rylands AB, Ganzhorn JU, Oates JF, Williamson EA, Palacios E, Heyman EW, Kierulff MCM, Yongcheng L, Supriatna J, Roos C, Walker S, Cortes-Ortiz L, Schwitzer C (2009) Primates in peril: the world's 25 most endangered primates 2008-2010. IUCN/SSC Primate Specialist Group, International Primatological Society, and Conservation International, Arlington, VA

Molles LE, Vehrencamp SL (2001) Songbird cheaters pay a retaliation cost: evidence for auditory conventional signals. Proc Biol Sci 268:2013-2019

Montgomerie RD (1985) Why do birds sing at dawn? Abstracts of spoken papers, 19th Int Etholog Congr 1:242

Moore J (1984) Female transfer in primates. Int J Primatol 5:537-589

Mueller EF, Kamau JMZ, Maloiy GMO (1983) A comparative study of basal metabolism and thermoregulation in a folivorous (*Colobus guereza*) and an omnivorous (*Cercopithecus mitis*) primate species. Comp Biochem Phys A 74:319-322

Murai T (2006) Mating behaviors of the proboscis monkey (*Nasalis larvatus*). Am J Primatol 68:832-837

Murphy MT, Sexton K, Dolan AC, Redmond LJ (2008) Dawn song of the eastern kingbird: an honest signal of male quality? Anim Behav 75:1075-1084

National Research Council, US (1981) Techniques for the study of primate population ecology. National Academy Press, Washington, D.C.

Neumann C, Assahad G, Hammerschmidt K, Perwitasari-Farajallah D, Engelhardt A (2010) Loud calls in male crested macaques, *Macaca nigra*: a signal of dominance in a tolerant species. Anim Behav 79:187-193

Newton PN, Dunbar RIM (1994) Colobine monkey society. In: Davies AG, Oates JF (eds) Colobine monkeys: their ecology, behaviour and evolution. Cambridge University Press, Cambridge, pp 311-346

Nunn CL (1999) The number of males in primate social groups: a comparative test of the socioecological model. Behav Ecol Sociobiol 46:1-13

Nunn CL (1999) The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. Anim Behav 58:229-246

Oates JF (1996) Habitat alteration, hunting and the conservation of folivorous primates in African forests. Aust J Ecol 21:1-9

O'Brien TG, Kinnaird MF, Nurcahyo A, Iqbal M, Rusmanto M (2004) Abundance and distribution of sympatric gibbons in a threatened Sumatran rain forest. Int J Primatol 25:267-284

Oliveira DA, Ades C (2004) Long-distance calls in Neotropical primates. An Acad Bras Cienc 76:393-398

Paciulli LM (2004) The effects of logging, hunting, and vegetation on the densities of the Pagai, Mentawai Island primates State University of New York at Stony Brook, Stony Brook. PhD thesis

Paciulli LM (2010) The relationship between nonhuman primate densities and vegetation on the Pagai, Mentawai Islands, Indonesia. In: Gursky-Doyen S, Supriatna J (eds), Indonesian primates. Springer, New York, pp 199-215

Palacios V, Font E, Márquez R (2007) Iberian wolf howls: acoustic structure, individual variation, and a comparison with North American populations. J Mammal 88:606-613

Pereira ME, Clutton-Brock TH, Kappeler PM (2000) Understanding male primates. In: Kappeler PM (ed) Primate males: causes and consequences of variation in group composition. Cambridge University Press, New York, pp 271-277

Pfefferle D, Fischer J (2006) Sounds and size: identification of acoustic variables that reflect body size in hamadryas baboons, *Papio hamadryas*. Anim Behav 72:43-51

Phiapalath P, Borries C, Suwanwaree P (2011) Seasonality of group size, feeding, and breeding in wild red-shanked douc langurs (Lao PDR). Am J Primatol 73:1134-1144

PHPA (1995) Siberut National Park integrated conservation and development plan (1995-2020). Biodiversity Conservation Project, Jakarta

Pinto LP, Costa CM, Strier KB, da Fonseca GA (1993) Habitat, density and group size of primates in a Brazilian tropical forest. Folia Primatol 61:135-143

Plavcan JM (2001) Sexual dimorphism in primate evolution. Am J Phys Anthropol 44:25-53

Plavcan JM, van Schaik CP (1992) Intrasexual competition and canine dimorphism in anthropoid primates. Yearb Phys Anthropol 87:461-477

Prestwich KN (1994) The energetics of acoustic signaling in anurans and insects. Integr Comp Biol 34:625-643

Pusey AE, Packer C (1987) Dispersal and philopatry. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. The University of Chicago Press, Chicago, pp 250-266

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, New York

Quinten MC, Waltert M, Syamsuri F, Hodges JK (2010) Peat swamp forest supports high primate densities on Siberut Island, Sumatra, Indonesia. Oryx 44:147-151

Raemaekers JJ, Raemaekers PM, Haimoff EH (1984) Loud calls of the gibbon (*Hylobates lar*): repertoire, organisation and context. Behaviour 91:146-189

Rajpurohit LS, Sommer V, Mohnot SM (1995) Wanderers between harems and bachelor bands: male Hanuman langurs (*Presbytis entellus*) at Jodhpur in Rajasthan. Behaviour 132:255-299

Reby D, McComb K (2003) Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. Anim Behav 65:519-530

Reby D, Cargnelutti B, Joachim J, Aulagnier S (1999) Spectral acoustic structure of barking in roe deer (*Capreolus capreolus*). Sex-, age- and individual-related variations. C R Acad Sci III 322:271-279

Reby D, Charlton BD, Locatelli Y, McComb K (2010) Oestrous red deer hinds prefer male roars with higher fundamental frequencies. Proc Biol Sci 277:2747-2753

Reby D, McComb K, Cargnelutti B, Darwin C, Fitch WT, Clutton-Brock T (2005) Red deer stags use formants as assessment cues during intrasexual agonistic interactions. Proc Biol Sci 272:941-947

Reid ML (1987) Costliness and reliability in the singing vigour of Ipswich sparrows. Anim Behav 35:1735-1743

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

Riede T, Arcadi AC, Owren MJ (2007) Nonlinear acoustics in the pant hoots of common chimpanzees (*Pan troglodytes*): vocalizing at the edge. J Acoust Soc Am 121:1758-1767

Rodgers AR, Carr AP, Beyer HL, Smith L, Kie JG (2007) HRT: home range tools for ArcGIS. Version 1.1. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada

Rubenstein DI, Hack MA (1992) Horse signals: the sounds and scents of fury. Evol Ecol 6:254-260

Rudran R (1973) Adult male replacement in one-male troops of purple-faced langurs (*Presbytis senex senex*) and its effect on population structure. Folia Primatol 19:166-192

Ruhiyat Y (1983) Socio-ecological study of *Presbytis aygula* in West Java. Primates 24:344-359

Ryan MJ (1988) Energy, calling, and selection. Integr Comp Biol 28:885-898

Schel AM, Zuberbühler K (2012) Dawn chorusing in guereza colobus monkeys. Behav Ecol Sociobiol 66:361-373

Schneider C, Hodges JK, Fischer J, Hammerschmidt K (2008) Acoustic niches of Siberut primates. Int J Primatol 29:601-613

Schwitzer C, Glatt L, Nekaris KA, Ganzhorn JU (2011) Responses of animals to habitat alteration: an overview focussing on primates. Endang Species Res 14: 31-38

Searcy WA, Nowicki S (2005) The evolution of animal communication: reliability and deception in signaling systems. Princeton University Press, Princeton

Seyfarth RM, Cheney DL, Marler P (1980) Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. Science 210:801-803

Smith R, Jungers WL (1997) Body mass in comparative primatology. J Hum Evol 32:523-559

Soltis J, Leighty KA, Wesolek CM, Savage A (2009) The expression of affect in African elephant (*Loxodonta africana*) rumble vocalizations. J Comp Psychol 123:222-225

Soltis J, Leong K, Savage A (2005) African elephant vocal communication II: rumble variation reflects the individual identity and emotional state of callers. Anim Behav 70:589-599

Staicer CA, Spector DA, Horn AG (1996) The dawn chorus and other diel patterns in acoustic signaling. In: Kroodsma DE, Miller EH (eds) Ecology and evolution of acoustic communication in birds. Comstock Publishing, Ithaca, NY, pp 426-453

Stanford CB (1991) Social dynamics of intergroup encounters in the capped langur (*Presbytis pileata*). Am J Primatol 25:35-47

Stanford CB (1998) Chimpanzee and red colobus: the ecology of predator and prey. Harvard University Press, Cambridge

Stearns SC (1989) Trade-offs in life-history evolution. Funct Ecol 3:259-268

Stearns SC (1992) The evolution of life histories. Oxford University Press, New York.

Steenbeek R, Assink P (2000) Individual differences in long-distance calls of male wild Thomas langurs (*Presbytis thomasi*). Folia Primatol 69:77-80

Steenbeek R, Assink P, Wich SA (1999) Tenure related changes in wild Thomas's langurs II: loud calls. Behaviour 136:627-650

Steenbeek R, Sterck EHM, de Vries H, van Hooff JARAM (2000) Costs and benefits of the one-male, age-graded, and all-male phases in wild Thomas's langur groups. In Kappeler PM (ed) Primate males: causes and consequences of variation in group composition. Cambridge University Press, Cambridge, pp 130-145

Sterck EHM (1997) Determinants of female dispersal in Thomas langurs. Am J Primatol 42:179-198

Sterck EHM (1998) Female dispersal, social organization, and infanticide in langurs: are they linked to human disturbance? Am J Primatol 44:235-254

Sterck EHM, Willems EP, van Hooff JARAM, Wich SA (2005) Female dispersal, inbreeding avoidance and mate choice in Thomas langurs (*Presbytis thomasi*). Behaviour 142:845-868

Sterner KN, Raaum RL, Zhang YP, Stewart CB, Disotell TR (2006) Mitochondrial data support an odd-nosed colobine clade. Mol Phylogenet Evol 40:1-7

Struhsaker TT (2008) Demographic variability in monkeys: implications for theory and conservation. Int J Primatol 29:19-34

Struhsaker TT, Marshall AR, Detwiler K, Siex K, Ehardt C, Lisbjerg DD, Butynski TM (2004) Demographic variation among Udzungwa red colobus in relation to gross ecological and sociological parameters. Int J Primatol 25:615-658

Tabachnick BG, Fidell LS (1989) Using multivariate statistics. HarperCollins Publishers, Inc. New York

Takahashi H (2001) Influence of fluctuation in the operational sex ratio to mating of troop and non-troop male Japanese macaques for four years on Kinkazan Island, Japan. Primates 42:183-191

Teichroeb JA, Sicotte P (2010) The function of male agonistic displays in ursine colobus monkeys (*Colobus vellerosus*): male competition, female mate choice or sexual coercion? Ethology 116:366-380

Temeles EJ (1994) The role of neighbours in territorial systems: when are they 'dear enemies'? Anim Behav 47:339-350

Tenaza RR (1976) Songs, choruses and countersinging of Kloss' gibbons (*Hylobates klossii*) in Siberut Island, Indonesia. Z Tierpsychol 40:37-52

Tenaza RR (1987) The status of primates and their habitats in the Pagai Islands, Indonesia. Prim Conserv 8:104-110

Tenaza RR (1989) Female sexual swellings in the Asian colobine *Simias concolor.* Am J Primatol 17:81-86

Tenaza RR (1989) Intergroup calls of male pig-tailed langurs (*Simias concolor*). Primates 30:199-206

Tenaza RR, Fuentes A (1995) Monandrous social organization of pigtailed langurs (*Simias concolor*) in the Pagai Islands, Indonesia. Int J Primatol 16:295-310

Terrien J, Perret M, Aujard F (2011) Behavioral thermoregulation in mammals: a review. Front Biosci 16:1428-1444

Theis KR, Greene KM, Benson-Amram SR, Holekamp KE (2007) Sources of variation in the long-distance vocalizations of spotted hyenas. Behaviour 144:557-584

Thomas RJ (1999) Two tests of a stochastic dynamic programming model of daily singing routines in birds. Anim Behav 57:277-284

Thomas RJ (2002) The costs of singing in nightingales. Anim Behav 63:959-966

Thomas RJ, Cuthill IC (2002) Body mass regulation and the daily singing routines of European robins. Anim Behav 63:285-295

Tilson RL (1977) Social organization of simakobu monkeys (*Nasalis concolor*) in Siberut Island, Indonesia. J Mammal 58:202-212

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man, 1871-1971. Aldine-Atherton, Chicago, pp 136-179

Tutin CEG, Fernandez M (1984) Nationwide census of gorilla (*Gorilla g. gorilla*) and chimpanzee (*Pan t. troglodytes*) populations in Gabon. Am J Primatol 6:313-336

Vannoni E, McElligott AG (2008) Low frequency groans indicate larger and more dominant fallow deer (*Dama dama*) males. PLoS One 3:e3113

Vannoni E, McElligott AG (2009) Fallow bucks get hoarse: vocal fatigue as a possible signal to conspecifics. Anim Behav 78:3-10 van Noordwijk MA, van Schaik CP (1999) The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, *Macaca fascicularis.* Primates 40:105-130

van Noordwijk MA, van Schaik CP (2004) Sexual selection and the careers of primate males: paternity concentration, dominance-acquisition tactics and transfer decisions. In: Kappeler PM, van Schaik CP (eds) Sexual selection in primates: new and comparative perspectives. Cambridge University Press, New York, pp 208-229

van Schaik CP, Assink PR, Salafsky N (1992) Territorial behavior in Southeast Asian langurs: resource defense or mate defense. Am J Primatol 26:233-242

van Schaik CP, van Noordwijk MA (1985) Interannual variability in fruit abundance and the reproductive seasonality in Sumatran Long-tailed macaques (*Macaca fascicularis*). J Zool 206:533-549

van Schaik CP, van Noordwijk MA, Nunn CL (2001) Sex and social evolution in primates. In Lee PC (ed) Comparative primate socioecology. Cambridge University Press, New York, pp 204-231

Vehrencamp SL (2000) Handicap, index, and conventional signal elements of bird song. In: Espmark Y, Amundsen T, Rosenqvist G (eds) Animal signals: signalling and signal design in animal communication. Tapir Academic Press, Trondheim, pp 277-300

Walter H (1994) Vegetation of the earth and ecological systems of the geo-biosphere. Springer, Berlin

Waltert M, Abegg C, Ziegler T, Hadi S, Priata D, Hodges JK (2008) Abundance and community structure of Mentawai primates in the Peleonan Forest, North Siberut, Indonesia. Oryx 42:375-379

Waser PM (1977) Individual recognition, intragroup cohesion and intergroup spacing: evidence from sound playback to forest monkeys. Behaviour 60:28-74

Waser PM, Waser MS (1977) Experimental studies of primate vocalization: specializations for long-distance propagation. Z Tierpsychol 43:239-263

Watanabe K (1981) Variations in group composition and population density of the two sympatric Mentawaian leaf-monkeys. Primates 22:145-160

Watts DP (1998) Seasonality in the ecology and life histories of mountain gorillas (*Gorilla gorilla beringei*). Int J Primatol 19:929-948

Whitehead JM (1987) Vocally mediated reciprocity between neighbouring groups of mantled howling monkeys, *Alouatta palliata palliata*. Anim Behav 35:1615-1627

Whitehead JM (1989) The effect of the location of a simulated intruder on responses to long-distance vocalizations of mantled howler monkeys, *Alouatta palliata palliata*. Behaviour: 1/2:73-103

Whittaker DJ (2005) New population estimates for the endemic Kloss's gibbon *Hylobates klossii* on the Mentawai Islands, Indonesia. Oryx 39:458-461

Whittaker DJ (2006) A conservation action plan for the Mentawai primates. Primate Conserv 20:95-105

Whittaker DJ, Mittermeier RA (2008) *Simias concolor*. In: IUCN 2011. IUCN Red List of Threatened Species. Version 2011.1. Downloaded on September 25, 2011 from http://www.iucnredlist.org

Whittaker DJ, Ting N, Melnick DJ (2006) Molecular phylogenetic affinities of the simakobu monkey (*Simias concolor*). Mol Phylogenet Evol 39:887-892

Whitten AJ (1982) The gibbons of Siberut. J. M. Dent & Sons Ltd., London

Whitten AJ (1982) A numerical analysis of tropical rain forest, using floristic and structural data, and its application to an analysis of gibbon ranging behaviour. J Ecol 70:249-271

Whitten AJ (1982) The ecology of singing in Kloss gibbons (*Hylobates klossii*) on Siberut Island, Indonesia. Int J Primatol 3:33-51

Whitten AJ, Whitten JEJ (1982) Preliminary observations of the Mentawai macaque on Siberut Island, Indonesia. Int J Primatol 3:445-459

Wich SA, Assink PR, Becher F, Sterck EHM (2002) Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): the effect of familiarity. Behaviour 139:79-87

Wich SA, Assink PR, Becher F, Sterck EHM (2002) Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): the effect of location. Behaviour 139:65-78

Wich SA, Assink PR, Sterck EHM (2004) Thomas langurs (*Presbytis thomasi*) discriminate between calls of young solitary versus older group-living males: a factor in avoiding infanticide? Behaviour 141:41-51

Wich SA, Koski S, de Vries H, van Schaik CP (2003) Individual and contextual variation in Thomas langur male loud calls. Ethology 109:1-13

Wich SA, Nunn CL (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

Wich SA, Sterck EHM (2007) Familiarity and threat of opponents determine variation in Thomas langur (*Presbytis thomasi*) male behaviour during between-group encounters. Behaviour 144:1583-1598

Wich SA, van der Post DJ, Heistermann M, Möhle U, van Hooff JARAM, Sterck EHM (2003) Life-phase related changes in male loud call characteristics and testosterone levels in wild Thomas langurs. Int J Primatol 24:1251-1265

Wiley RH, Richards DG (1978) Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behav Ecol Sociobiol 3:69-94

Williams GC (1966) Adaptation and natural selection. Princeton University Press, Princeton

Winkler P, Loch H, Vogel C (1984) Life history of Hanuman langurs (*Presbytis entellus*): Reproductive parameters, infant mortality, and troop development. Folia Primatol 43:1-23

Wolf KE (1984) Reproductive competition among co-resident male silvered leaf monkeys (*Presbytis cristata*). Yale University, New Haven, PhD thesis

WorldClim (2000) "WorldClim." Downloaded on November 16, 2010 from http://www.worldclim.org/tiles.php

Wyman MT, Mooring MS, McCowan B, Penedo MCT, Hart LA (2008) Amplitude of bison bellows reflects male quality, physical condition and motivation. Anim Behav 76:1625-1639

Yanuar A, Fuentes A, Studd K (1998) A short report on the current status of the Mentawai snub-nosed langur (*Simias concolor concolor*) on Simalegu Island, South Pagai, Mentawai, Indonesia. Trop. Biodiv 5:299-305

Yeager CP (1990) Proboscis monkey (*Nasalis larvatus*) social organization: group structure. Am J Primatol 20:95-106

Yeager CP, Kool K (2000) The behavioral ecology of Asian colobines. In: Whitehead PF, Jolly CJ (eds) Old World monkeys. Cambridge University Press, Cambridge, pp 496-521

Zahavi A (1975) Mate selection - a selection for a handicap. J Theor Biol 53:205-214

Zahavi A (1977) The cost of honesty (further remarks on the handicap principle). J Theor Biol 67:603-605

Zuberbühler K (2002) Effects of natural and sexual selection on the evolution of guenon loud calls. In: Glenn ME, Cords M (eds) The Guenons: diversity and adaptation in African monkeys. Springer, New York, pp 289-30

Zucker EL, Clarke MR (2003) Longitudinal assessment of immature-to-adult ratios in two groups of Costa Rican *Alouatta palliata*. Int J Primatol 24:87-101