

11 • Predation risk and antipredator adaptations in white-faced sakis, *Pithecia pithecia*

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Introduction

The risk of predation poses a constant threat to the lives of primates living in natural habitats, and the study of its influence on many aspects of primate life has a long legacy in the history of primatology (Crook and Gartlan 1967, Eisenberg *et al.* 1972, Hart 2000, Kummer 1967, Terborgh 1983, Terborgh and Janson 1986). While these studies have been largely theoretical in nature, it seems clear that a number of different biological, ecological, and behavioral variables interact to constitute a given species' response to the threat of predation. Thus, for example, large body size may reduce the number of potential predators, a species may avoid areas where the density of predators (i.e., risk) is high, or small-bodied species may adopt a cryptic strategy in an effort to escape detection. Socially, individuals may give alarm calls to warn other members of the group in the event of danger, and/or manipulate their spatial proximity to other group members under different risk regimes (i.e., area or conditions of high vs. low risk, see Ydenberg 1998).

While problems exist in the interpretation of how these adaptations have evolved in concert with other social characteristics, it is difficult to imagine that the threat of being eaten represents anything but a strong selective force in the lives of nonhuman primates. Indeed, it is difficult to conceive of an ecological variable more closely related to individual fitness than the threat of death. However, predation is rarely observed directly, and this fact has led some to suggest that it may be of little consequence for the evolution of social structure (e.g., Cheney and Wrangham 1987). It is true that primatologists are limited to secondary sources of data (playback experiments, estimates of vigilance, alarm calling) when studying predation, and that there have been very few studies conducted from the predator's point of view (e.g., Emmons 1987, Rettig

1978, Wright *et al.* 1997, and see Sautner, Chapter 7 (this volume). A recent comprehensive treatment of predator-prey relationships across primates incorporates salient variables such as predator behavior, body size, and habitat type (Hart 2000).

There are, however, sound reasons for thinking that secondary sources of data are sufficient, and in some cases even better than witnessing actual predation events. Students of predation have begun to realize that the persistent threat of predation may be more important than actual predation attempts themselves (for a review, see Lima and Dill 1990). Indeed, Lima (1986) has suggested that changes in individual behavior due to risk may have a larger impact on demography than actual deaths due to predation. Peckarsky *et al.* (1993) have shown that the perceived threat of predation can impact the activity, growth, and fecundity of animals in natural habitats. Experimental studies in the field and in the laboratory indicate that risk is such an important factor in the lives of foraging animals that they often behave as if a predator is constantly present (Lima and Dill 1990, Ydenberg 1998). Thus, sources of data, apart from actual predation events, have plenty to teach us about the importance of risk, even if we never see a predation attempt at all.

Attempts to assess the importance of predation as an organizing influence for social structure and social behavior across primates have met with mixed results. Boiniski *et al.* (2000) have recently suggested that attempting to predict the evolutionary, ecological, and behavioral significance of predation by employing cross-species comparisons may be premature. They list a number of reasons for this view, including the paucity of reliable data devoid of preconceived notions about how predator and prey should behave (a predictable consequence of theory preceding the accumulation of data). In addition to this well supported point of view, we would argue that half of the equation pertinent to the question at hand has been largely ignored. Studies of the behavior and ecology of predators that threaten primates have lagged far behind both the collection of relevant primatological data and the generation of theory purported to use these data in a hypothetical framework. Examining half of the data relevant to predator-prey interactions between primates and their predators can only result in an incomplete understanding of these interactions and their influence on the lives of both predator and prey.

Despite the fact that they appear to exhibit a range of different anti-predator adaptations, no data exist on the specifics of these

Table 11.1. Potential saki monkey predators documented from this region of eastern Venezuela

Species	Common name	Venezuelan name
<i>Morphus guianensis</i>	Crested Eagle	Águila Monera
<i>Buteo albonotatus</i>	Zone-tailed Hawk	Gavián Negro
<i>Heterospizias meridionalis</i>	Savanna Hawk	Gavián Pira Venado
<i>Harpia haliaeetus solitarius</i>	Solitary Eagle	Águila Solitaria
<i>Harpia harpyja</i>	HarpY Eagle	Águila Harpia
<i>Spizaelus ornatus</i>	Ornate Hawk Eagle	Águila de Penacho
<i>Leopardus wiedii</i>	Margay	Gato Tigre
<i>Leopardus pardalis</i>	Ocelot	Tigrillo
<i>Panthera onca</i>	Jaguar	Tigre
<i>Leopardus tigrinus</i>	Oncilla	Tigrillo
<i>Hephalurus yaguarundi</i>	Jaguarundi	Yaguarundi
<i>Eira barbara</i>	Tayra	Guache, Guanico
<i>Eumeces murinus</i>	Green anaconda	Anaconda
<i>Boa constrictor</i>	Red-tailed boa	Boa

Source: Linares, 1998; Phelps and de Schauensee, 1978; I. Balbás personal communication)

patterns for any of the pithecin monkeys (sakis and uakaris). At an average body weight of 1.77 kg ($n=3$ adults, Glander and Norconk, unpublished data), white-faced sakis are potential prey for a number of avian and terrestrial predators (Table 11.1). The avian predators are large hawks and eagles. Among these only the harpy eagle (*Harpia harpyja*) has been studied extensively. Retting (1978) noted that harpy eagles in Guyana routinely take large primates such as red howler monkeys and that white-faced saki remains were found beneath harpy nests. They perch high in the tallest trees of the canopy but ambush prey within the canopy and subcanopy. Harpy eagles may be locally extinct in the study area due to habitat fragmentation (Alvarez-Cordero, personal communication). The conservation status of the other raptor species in the area of the lake is completely unknown. We have observed the zone-tailed hawk (*Buteo albonotatus*) and the crested eagle (*Morphus guianensis*), although we often observe raptors without being able to identify them to species. Zone-tailed hawks inhabit savanna habitats and secondary forest edges feeding on reptiles, birds, and small mammals. Crested eagles soar high in search of potential food but

also ambush prey in the canopy and subcanopy. They have been reported to prey on primates as large as young adult spider monkeys (Julliot 1994).

Undoubtedly, the jaguar (*Panthera onca*), ocelot (*Leopardus pardalis*), and the red-tailed boa (*Boa constrictor*) are the primary terrestrial threats to white-faced sakis. All of these species have been observed in the study area. Jaguars have been recorded preying on a group of red howlers on a nearby island (Pretz *et al.* 1992), and jaguar tracks, as well as those of other felids, are occasionally observed along exposed banks during the dry season (personal observation). In addition, because sakis have been observed going to the water's edge to drink during the dry season (Harrison 1998), the green anaconda (*Eunectes murinus*) must be considered a potential threat during this time of year.

Smaller felids and large mustelids may also pose a threat to juvenile or elderly individuals. Tayra (*Eira barbara*) have been locally observed, are accomplished climbers, and have been known to take juvenile primates (Defler 1980). Margay (*Leopardus wiedii*), jaguarundi (*Hepailurus yagouaroundi*), and oncilla (*Leopardus tigrinus*) are small felids that have been observed in the lake region, and all are capable of taking small-bodied mammals. Felids and other terrestrial mammals are more often temporary than permanent residents on small Guri Lake islands. Sakis have never been seen to swim between islands, but most other vertebrates (including felids and snakes) have been observed swimming in the lake.

In this chapter we present field data on a suite of antipredator behaviors in wild white-faced sakis, *Pithecia pithecia*, and the consequences of these behaviors for foraging individuals. We use patterns of alarm calls, group responses to perceived predator risk, and data on intragroup spacing and habitat use in an effort to describe the particular way in which white-faced sakis respond to the threat of predation. We view such baseline, descriptive ecological data as a fundamental precursor to the generation of theoretical approaches to foraging and social behavior.

Methods

Study site

Our research takes place on islands in Guri Lake, Bolívar State, eastern Venezuela. Guri Lake is a catchment area for the Raúl Leoni Hydroelectric Dam. The lake covers an area of 4200 km² and contains more than 100 islands, many of which are completely

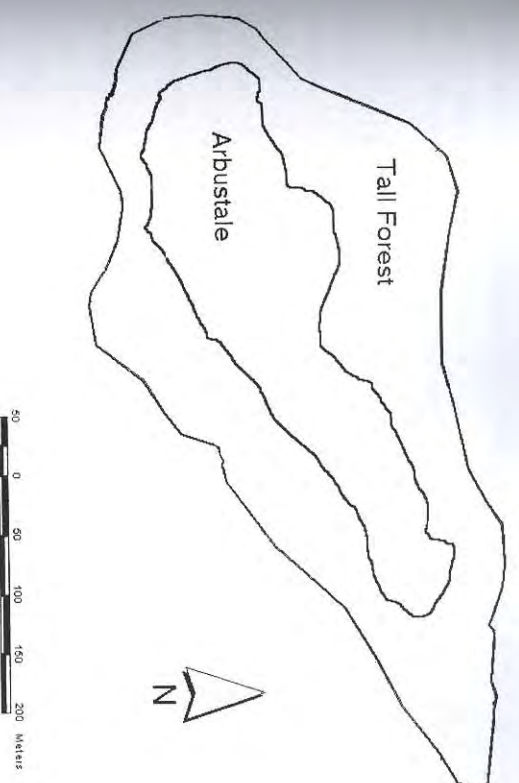


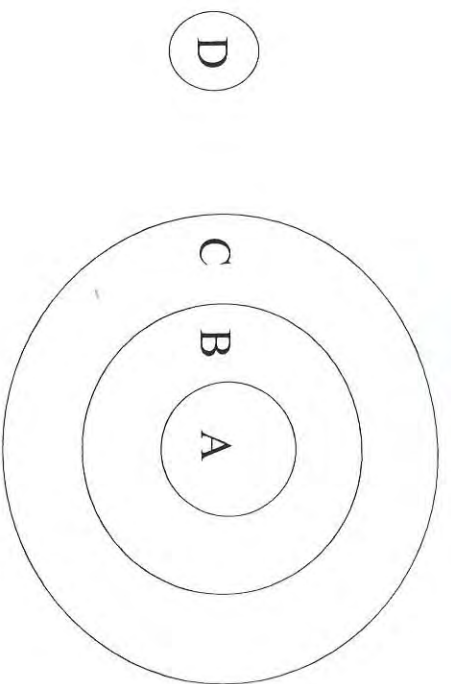
Fig. 11.1. Schematic map of the study island showing the distribution of the two major forest types, tall forest and low scrub forest, or arbustale.

forested. Flooding of the basin was completed in 1986 isolating the primates on the islands to which they had dispersed. Four primate species live in forests in and around the lake: *Pithecia pithecia*, *Chiropotes satanus*, *Alouatta seniculus*, and *Cebus olivaceus*. The present study was conducted on Isla Redonda (7° 45' N, 62° 52' W) in the northern section of the lake. The 15-ha island is composed of both tall, dry tropical forest and lower 'arbustale' forest in the center of the island (Fig. 11.1). In addition to white-faced sakis, the island is also inhabited by a single group of red howlers and several solitary howler individuals. Detailed descriptions of the island have been published elsewhere (Aymard *et al.* 1997, Norconk 1996, Parolin 1993). The climate is tropical with rainfall mediated by the Intertropical Convergence Zone, resulting in distinct wet (May–October) and dry (November–April) seasons. The study island receives an annual average rainfall of 1100 mm (EDELCA: Electrificación del Caroní, unpublished data).

Subjects

White-faced sakis are sexually dichromatic (males bearing white faces), with about 500 g difference in body weight between adult males and females (males larger than females). Group size during the years from which the present data are drawn has fluctuated between a maximum of nine individuals (five males, four females) and a minimum of five individuals (two males, three females). All individuals were fully habituated to human observation.

2. Weighted index of centrality. The Centrality (CI) for each individual is equal to the sum of the number of samples in each of the four zones, divided by the number of samples. The zones are labeled A, B, C, and D. Zones A, B, and C are concentric circles around a group of individuals. Zone D is the area outside the concentric circles but within a 15 m radius of the center are assigned



$$CI = \frac{\sum 4nA + 3nB + 2nC + nD}{nA + nB + nC + nD}$$

Data collection

We present data collected during the years 1991-93, 1995, and 1997-99. Study periods varied in length from 3 months to 12 months. Alarm call data were collected as all-occurrence samples. We recorded the age and sex of the initial caller, whether or not the call was echoed, and how many times it was echoed. We also recorded the duration of the event and group response, that is, whether or not the sakis shifted position in the canopy (moved up or down) and whether the predator was mobbed or chased. We identified the predators as avian or terrestrial and identified them to species when possible.

Data on intragroup spacing were collected using both focal animal and group scan sampling methods (Altmann 1974) during the wet season of 1993 from 12 June to 5 September. A single focal animal was sampled for an entire day, and focal animals were rotated to ensure an even representation in the database. Every 20 minutes, we recorded the focal animal's activity (feed, rest, or travel), the type of food item taken when feeding, and the number and identity of other group members within 5 m (near neighbors). We also recorded the distance to each animal relative to the observer with a visual estimate of distance in meters and a direction taken as a compass bearing (Fig. 11.2). To avoid biasing the sample

Table 11.2. Frequency and percent of total observations of alarm calls given to classes of predators

Predator class	Frequency	Percentage of total observations	Number of species of predator
Vulture	174	77.0	2
Raptor	11	4.9	2
Snake	6	2.7	1
Felid	2	0.9	1
Unknown	33	14.6	—
Total	226	100.0	6

in favor of individuals that were easily seen, we discarded any samples that contained fewer than seven of the nine individuals in the group. A test of possible temporal autocorrelation that would bias the samples resulted in no significant change in the outcome of statistical analysis.

The Law of Cosines was applied to group scans *a posteriori* to calculate interindividual distance of animals relative to the focal animal:

$$c^2 = a^2 + b^2 - 2ab(\cos\alpha)$$

where a is the distance between the observer and individual (a), b is the distance between the observer and individual (b), and α is the angle between a and b . These individual estimates were plotted and used to derive a measure of each animal's relative position within the group using a Centrality Index (CI) following the method of Barton and Whiten (1993). All data were analyzed using SPSS v.10.

Results

Alarm calls

We recorded 226 separate occasions when white-faced sakis uttered alarm calls in response to predators (Table 11.2). Of these, 90.3% ($n = 204$) were directed at avian threats. The remainder (9.7%; $n = 22$) were directed at terrestrial predators. The potential predators were identified on 193 (85.4%) occasions, the vast majority of which (77%; $n = 174$) were common vultures. Crested eagles were spotted on three occasions and hawks on four occasions. The most common terrestrial threat was the red-tailed boa (3%; $n = 6$).

There was a strong sex bias in the tendency to utter alarm calls

($\chi^2 = 16.2$; $df = 1$; $p < 0.01$) with males calling significantly more than expected. However, juveniles were also significantly more likely to utter alarm calls than adults ($\chi^2 = 23.4$; $df = 1$; $p < 0.01$). In fact, the two juveniles in the group accounted for more than half of all alarm calls uttered (51.8%, 117 calls). Both of these trends are the result of the juvenile male, TX, being responsible for nearly 40% of all calls uttered.

Fifty-five percent of all calls were echoed by group members, and of these, 31% were echoed only once, 15% were echoed by other individuals twice, and 2.5% were echoed more than five times.

Group spacing

Vigilance behavior is difficult to measure in white-faced sakis due to their saltatory locomotion, as well as a high level of overall social vigilance (*sensu* Boinski 2000). As a result, it is difficult to tease apart a heightened sense of awareness due to feeding or social behavior/territorial behavior from vigilance related specifically to predation. However, if animals on the periphery of the group are more vigilant, they should: (a) be the first to give an alarm call when a predator is detected, and (b) give more alarm calls than animals in the core of the group. The animals with the three lowest centrality index scores (i.e., those most peripheralized) gave 68% of all initial alarm calls. There was no relationship between the total number of calls for each individual and that individual's position in the group.

We tested the effect of the median number of near neighbors (individuals within 5 m of the focal subject) on the tendency to utter alarm calls and found no significant association (Kendall's $\tau = 0.12$; $\rho > 0.05$; $n = 9$ individuals).

With respect to foraging success and predation risk, we examined whether the trends in centrality indices and/or near neighbor measures influenced an individual's foraging success. Only when feeding on insects was an individual's position within the group associated with its ability to access resources ($n = 9$, $\tau = 0.556$, $\rho < 0.05$). Sakis feed on insects rarely (opportunistically); hence, this association may be an artifact of small sample size. Next, we compared an individual's median number of near neighbors to the frequency with which it fed on each of the three food classes. Feeding frequencies did not vary with the number of other individuals within 5 m (fruit: $n = 9$, $\tau = -0.12$, $\rho > 0.05$; leaves: $n = 9$, $\tau = 0.29$, $\rho > 0.05$; insects: $n = 9$, $\rho = 0.34$, $\rho > 0.05$). Hence, neither group geometry (judged by centrality index scores), social distance (judged by

appear to have an effect on foraging success for individual white-faced sakis.

Group response

White-faced sakis generally maintain their position in the canopy (i.e., do not move lower or higher) under all but the strongest of threats (91.2%, $n = 206$ alarm bouts). However, strong threats (real or perceived) lead them to change their position in the canopy and change their foraging behavior in drastic fashion. Long bouts of change their foraging behavior, directed at a strong threat occurred on alarm calling, or mobbing, in duration from 1.9 minutes to four occasions. These bouts ranged in duration from 1.9 minutes to 88 minutes. The behavior of the sakis during these mobbing events provides insight into the overall white-faced saki response to strong threat of predation. For example, on 25/6/99 at 06:10 h, shortly after leaving their sleeping trees, all members of the group began alarm-calling at a small felid (probably an oncilla). The entire group followed the predator over 200 m to the north side of the island, constantly alarming as they traveled. The mobbing lasted for over 20 minutes, after which the group climbed into several tall trees and remained motionless and extremely vigilant for 92 minutes. This incident resulted in their first feeding bout of the day being delayed nearly 2 h. On a second occasion, 18/12/91 the group alarmed for 20 minutes to a boa constrictor in a feeding tree.

Responses such as these are similar when confronted by a strong threat (real or perceived). For example, during the wet season of 1997, several howler monkeys died on the island from what may have been toxification from feeding on *Coccoloba striata* leaves (Polygonaceae). The death of the first individual attracted dozens of avian carrion feeders (including the 3.5 kg king vulture, *Sarcorampus papa*) flying very low over the northeast end of the island. In contrast to the response to terrestrial threats, the sakis did not mob these potential threats; rather, they descended into the low, dense understory, spread themselves evenly over an area of about 1 ha, and remained motionless for 2 h and 13 min. Each individual remained very still and none uttered an alarm call, despite the presence of so many large birds flying low over the canopy. They eventually descended nearly to the ground and silently moved away, despite the continued presence of the vultures. In total, more than 3 h passed before the group resumed feeding. While this situation was extreme, it seems clear that sakis rarely mob avian predators unless they are very small hawks who have alighted in the canopy.

possibility of expanding the models to include three dimensions. The original models were developed from the study of large herds and terrestrial baboons where individuals are threatened by attack in two dimensions, whereas arboreal taxa are threatened by attack in three dimensions.

Enhanced vigilance is thought to occur to the detriment of foraging success. Despite the fact that alarm calling varied predictably with group geometry and social distance, these differences did not translate into differential foraging success for individual sakis. It is possible that our chosen estimate of feeding (time spent feeding on each of three resource classes) does not provide the proper resolution for distinguishing fine-grained differences in foraging success. However, Norronk *et al.* (1999) used a fine-grained measure of intake (timed feeding events normalized by wet and dry food weights) to examine individual female foraging success given incidents of contest competition. They found that only when feeding on the rarest resources of unusually high nutrient quality could any differences in feeding success be discerned. If there are individual differences in feeding competition in white-faced sakis, our preliminary analyses suggest that it may be due to ecological reasons other than predation risk and/or social reasons other than contest competition.

Group responses to predation have been described for a number of platyrrhines. We described two different types of group response in Venezuelan white-faced sakis. When threatened by terrestrial threats, at least those posed by small felids and boas, sakis will mob and/or chase these predators through the forest. A period of extensive inactivity usually follows such events. Such mobbing events may be unusual for small-bodied primates living in small groups. Indeed, most species that are reported to mob and chase predators are large-bodied taxa living in large troops (chimpanzees: Hiraiwa-Hasegawa *et al.* 1986, baboons: Altmann and Altmann 1970, Iwamoto *et al.* 1996), though small cats are occasionally mobbed by smaller taxa (Passamani 1995).

Faced with strong avian threat, white-faced sakis tend to employ an extreme mode of cryptic evasion, whereby they descend to thick undergrowth and freeze for extended periods of time. This 'freezing' behavior has been described for a number of primate species (Gautier-Hion 1973, Izawa 1978, Wahome *et al.* 1993), most of them with relatively small body size.

As discussed above, we found that individual white-faced sakis vary little in their foraging success relative to several ecological and

social variables. As a group, however, cryptic predator evasion can have a drastic effect on daily food intake. In the future, we hope to be able to compare pre-attack and post-attack foraging effort for individuals and for the group as a whole. We suspect that such lengthy periods of time with no feeding might be compensated for in several ways. First, sakis may feed at higher rates once feeding resumes. Second, they may concentrate on especially high-quality resources in the aftermath of a predator scare. Finally, daily activity budgets may be altered such that less time is devoted to nonfeeding activities such as rest, grooming, and play, and they may forage later into the afternoon.

Conclusion

White-faced sakis appear to employ a combination of detection and evasion to combat the threat of predation depending on the type of predator involved and the severity of the threat. Small terrestrial, arboreal, and perched avian predators, and snakes tend to evoke a mobbing response, whereas other strong avian threats lead to cryptic evasion. Unfortunately, we have no data on group response when faced with the most serious threats (hairy eagle and jaguar), though we suspect both would elicit an evasive response.

We found no evidence to suggest that different individual risk regimes lead to variable foraging success. However, extended periods of cryptic evasion undoubtedly affect the foraging success of all individuals in a group. Future work is needed to understand how sakis recoup lost foraging effort following serious predator attacks.

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Eat or be Eaten

Predator Sensitive Foraging Among Primates

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