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Predation and Predation Attempts on Red Titi Monkeys *(Callicebus discolor)* and Equatorial Sakis *(Pithecia aequatorialis)* in Amazonian Ecuador

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Key Words
Predation · *Harpia harpyja* · *Callicebus discolor* · *Pithecia aequatorialis* · Antipredator behaviour · Amazonia

Abstract
Anecdotal reports of predation as well as observed predation attempts and rates of animal disappearance provide some of the most relevant data for evaluating the influence that predation risk may have on primate behavioural ecology. Here, we report rates of disappearance from six groups of red titi monkeys *(Callicebus discolor)* and two groups of equatorial sakis *(Pithecia aequatorialis)* followed over a period of four and a half years at a lowland site in Amazonian Ecuador. We also describe the first direct observation of a harpy eagle *(Harpia harpyja)* preying upon a titi monkey, as well as 3 unsuccessful attacks by tayras *(Eira barbara)* on titi monkeys and 4 unsuccessful attacks by various raptors on sakis. Our data indicate that pitheciid primates may face a wider array of possible predators than previously recognized, and that titi monkeys and sakis are susceptible to different major classes of predators. Our observations also suggest differences in the sex role during predator defence that could be related to the evolution and maintenance of monogamous systems.

Introduction

The risk of predation is thought to strongly influence primate behaviour and grouping patterns [van Schaik, 1983; Terborgh and Janson, 1986]. Although attacks by predators are significant events in the life histories of most primate species, pre-

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dation on arboreal mammals is rarely observed in the wild [Cheney and Wrangham, 1987; Isbell, 1994; Stanford, 2002]. Therefore, field studies that examine predation risk to primates are particularly challenging [Hill and Dunbar, 1998; Janson, 1998], and it has been primarily anecdotal reports of predation that have provided some of the most relevant data on the influence that predation risk may have on primate socioecology [Isbell, 1994; Boinski and Chapman, 1995].

In the absence of data on actual predation events, predation attempts and rates of animal disappearance become important proxies for evaluating the role of predation as an evolutionary pressure influencing primate socioecology [Isbell, 1994]. This may be particularly true for small-bodied primate taxa, since it is assumed that the risks of predation may be higher than in larger-bodied species. Titi monkeys (*Callicebus* spp.) are the smallest of the pitheciids, with adults weighing approximately 1 kg, whereas sakis (*Pithecia* spp.) weigh 2 or 3 times more [Norconk et al., 2007; Di Fiore and Fernandez-Duque, unpubl. data]. In lowland Ecuador, both taxa live in socially monogamous groups, characterized by the presence of only 1 reproductive adult male, 1 reproductive adult female and a few young [Di Fiore et al., 2007; Fernandez-Duque and Di Fiore, unpubl. data]. Subadult titi monkeys disperse when they are approximately 3 years old [Bossuyt, 2002], whereas there is some indication that the peripheralization of sakis that may precede dispersal occurs when they are between 3 and 4 years [Norconk, 2006]. Given that the 2 taxa live in small groups, they offer a good opportunity to evaluate how differences in size may be related to inter-taxon patterns of predation and their antipredator behaviour [Ferrari, 2009].

Titis and sakis face a variety of potential predators in lowland Ecuador. The region hosts at least 21 species of raptors including 9 falcon species, 5 owl species and 7 species of hawks and eagles [Blake, 2007]. Two of the eagles *(Harpia harpyja, Spizaëtus ornatus)* have been reported to feed on several different species of Neotropical primates [Fowler and Cope, 1964; Rettig, 1978; Klein et al., 1988; Eason, 1989; Boinski and Chapman, 1995; Martins et al., 2005]. In addition, several mammalian carnivores known to be primate predators are found at the site [Peetz et al., 1992; Miranda et al., 2005; Ludwig et al., 2007; Matsuda and Izawa, 2008; Ferrari, 2009; Bezerra et al., 2009]. Several snakes are also thought to be likely predators of pitheciids [Ferrari et al., 2004; Cisneros-Heredia et al., 2005].

We report here 1 successful and 7 unsuccessful predation events on red titi monkeys and equatorial sakis in Amazonian Ecuador.

Materials and Methods

The study area is located at the Tiputini Biodiversity Station (76° 08′ W, 0° 38′ S), located within the Yasuní National Park and Biosphere Reserve in the Ecuadorian Amazon. The primate community of 10 different species has been studied extensively [Di Fiore, 2001; Carrillo-Bilbao et al., 2005; Di Fiore and Fleischer, 2005; Di Fiore et al., 2007; Fernandez-Duque et al., 2008; Di Fiore et al., 2009]. Between July 2004 and December 2008, researchers in the area spent approximately 25,000 h in the forest studying 7 primate species. Every time the researchers found a primate group, they recorded the time, location, composition and individual identity of all group members seen, plus the modal behaviour of the group. Researchers also recorded detailed notes on all observed predation attempts, including the time, number of prey and predators observed, predator taxa, and all vocalizations and behaviours during and after the

encounter. We were in contact with two groups of sakis for 1,937 h and with six groups of red titi monkeys for 2,223 h. More detailed information was gathered while conducting behavioural follows of titis and sakis [Di Fiore et al., 2007]. The number of contact hours with each of the groups was not evenly distributed (table 1), since the number of groups under investigation has expanded over the years. At least 1 individual from each group was fitted with a radio collar following procedures used successfully with owl monkeys in Argentina [Fernandez-Duque and Rotundo, 2003]. All procedures were approved by the corresponding authorities in Ecuador and the USA.

Results

Titi Monkey Rates of Disappearance and Predator Encounters

Eight individuals from six different groups of *C. discolor* disappeared during the study (table 1). We infer that 5 of these animals died, 2 were adults who disappeared and their radio collars were found on the ground, and another 2 were young individuals (13 months) unlikely to have dispersed. The adult female of group G had been observed 2 days before we found her collar on the ground. The collar had some hairs attached to it, but we could not find any bones or body remains near it. The clasp was still shut and there was a small bite mark on the antenna. The fifth individual was an adult female with an injured leg; we assume that she probably died since she had been in the group for several years prior to her disappearance and was never observed again (table 1). The remaining 3 individuals were all approaching the age when dispersal seems to occur.

Harpy Eagle Attack

On January 26, 2008 at 09.45 h, one of the authors (R.S.) heard at least 2 titis producing loud calls [chirrup-pumping, chirrup-panting pumping: Robinson, 1979]. He then found a harpy eagle holding and eating a red titi monkey. The eagle stood on a fallen log 1 m from the ground, and less than 15 m away from the 2 vocalizing individuals. The animals stopped calling and moved out of sight when the observer approached. This group was not one of our habituated study groups. The eagle also fled first to a 2-metre-high perch, and then to a 10-metre-high perch where it stayed for a few minutes before moving off. When we found the carcass on the following day, it had no eyes or skin on the head, and it had a large wound near the neck that the eagle was feeding from when encountered. Bleeding claw marks on the back were also evident. Given its size, we estimated that the titi was a subadult or an adult, but we could not determine its sex, nor were we able to recover any body parts that could help with sex identification.

Tayra Encounters

On December 4, 2007 at 17.05 h, both members of titi monkey group K began alarm calling as they moved towards a gap created by a fallen tree. While calling, they moved quickly into a vine tangle and remained out of view. Two tayras then appeared from the direction that the titis had been facing when they started alarm calling. The tayras began to cross the gap on one of the branches of the fallen tree, moving in the direction of the monkeys. When the tayras saw the researcher (A.G.L.), they moved off in the opposite direction.

Table 1. Study groups for each species, years followed, hours followed, and presumed fate of the individuals of different age-sex classes that disappeared during this time

Species	Group	Years followed	Hours followed	Age-sex categories[1]	Presumed fate
Callicebus discolor	K	5	1,372	adult female	dead
				subadult male	dispersed
				juveniles (13 months)	dead
	H	3	281	subadult	dispersed
	L	3	234	juvenile (13 months)	dead
	B	3	165	subadult female	dispersed
	G	1	142	adult female	suspected predation
	P	1	29	adult male	suspected predation
Pithecia aequatorialis	M	5	1,839	juvenile (13 months)	dead
				subadult male	dispersed (confirmed)
	D		98	adult male	unknown

[1] Adult: reproducing individual; subadult: >18 months (titis) or >3 years (sakis) and still in natal group; juvenile: 6–18 months (titis), 1–3 years (sakis); infants: 0–6 months (titis), <12 months (sakis).

On February 2, 2007 at 13.42 h, the same group was resting relatively low in the canopy (<3 m). Two tayras were observed moving towards the titis while chasing a medium-sized rodent (*Myoprocta* sp.) along the trail. The tayras did not initially notice the researcher (A.G.L.). The adult male titi started alarm calling and looking towards the tayras. One of the tayras looked at the monkeys and climbed 1 m up on a tree in front of them; the other tayra and the rodent were out of view by then. The titis continued alarm calling and moved quickly towards a vine tangle in the middle canopy (approximately 8 m). The tayra then noticed the researcher and left the area. The titis continued vocalizing for approximately 10 more minutes while out of view in the vine tangle.

Finally, on May 21, 2007 at 08.16 h, while observing titi monkey group B, A.G.L. heard an infant vocalizing agitatedly and immediately noticed a tayra approaching the infant in the same tree. The adult titi male moved quickly towards the infant and started making loud calls and showing piloerection. The infant climbed on the male's back, and the male then moved quickly to an adjacent tree. The male continued vocalizing while staring at the tree with the tayra; the juvenile and adult female in the group, who were nearby but out of view, also gave alarm calls. The tayra oriented towards the male, but did not go into the tree the male had entered and left the area soon thereafter.

Saki Rates of Disappearance and Predator Encounters

Between July 2004 and December 2008, the adult male and 1 infant disappeared from saki group M (table 1). A researcher found the adult male dead, apparently due to natural causes [Di Fiore et al., 2007]. The fate of the infant is unknown, but was presumed dead given its young age.

The first predation attempt occurred on February 21, 2006 at 07.07 h, when an assistant saw a bird (species unknown) diving into the tree where the adult male, adult female, and juvenile were feeding. The 3 individuals left the tree immediately and alarm-called repeatedly for approximately 10 min. On February 24, 2006 at 09.14 h, a large raptor (species unknown) swooped over 1 of the individuals in the group within the forest subcanopy. An alarm vocalization was heard and the assistant then observed the saki monkey dropping quickly to lower branches. On October 20, 2006 at 12.30 h, while A.G.L. was observing a juvenile saki, it gave an alarm call, jumped backwards and off the branch on which it was standing, and fell to the ground from a height of approximately 10 m. It ran on the ground until it was less than 3 m from A.G.L., always with its head oriented upwards, and then it quickly climbed a liana 0.5 m high while alarm calling and looking up. When a second researcher approached, they both noticed a large eagle (species unidentified) flying from the area where the juvenile had originally been standing. After flying to within 2 m of the monkey, the bird changed direction and flew away. Finally, on July 25, 2007 at 12.05 h, another researcher saw a raptor dive towards the infant of the same group. The infant again escaped the attack by dropping to lower branches. At that moment, the adult male started alarm calling, and it approached the bird, while the adult female moved towards the infant and the infant climbed on the female's back. The subadult male (a putative sibling or half-sibling of the infant) approached the adult male from a neighbouring tree and joined him in vocalizing. Both males then moved towards the raptor while vocalizing; the female with the infant on her back remained at a distance of at least 5 m. The animals continued to vocalize and remained alert for at least 15 min.

Discussion

Predators of Pitheciids

Published reports of predation on *Callicebus* sp. are rare, but our long-term project suggests that titi monkeys may face a range of natural predators. We have reported here the first observed case of predation of titi monkeys by harpy eagles. It is possible that titi monkeys are not common prey items in the harpy eagle diet, since most studies report harpy eagles typically taking somewhat larger animals as prey [Rettig, 1978; Izor, 1985; Eason, 1989; Peres, 1990; Sherman, 1991; Galetti and de Carvalho, 2000; Ferrari and Port-Carvalho, 2003; Martins et al., 2005]. The harpy eagle's feeding behaviour we observed is similar to reports of harpy eagles while preying on other primates. The titi monkey was badly injured on the head, and in the report of Martins et al. [2005], the necropsy suggested that cerebral wounds probably caused by the eagle's beak may have been the cause of death.

Direct observations have been made of predation on titis by *Boa constrictor* [at this same site in 2003: Cisneros-Heredia et al., 2005], capuchin monkeys [*Cebus* sp.: Lawrence, 2003; Sampaio and Ferrari, 2005], crested eagles *(Morphnus guianensis),* and ornate hawk-eagles [Terborgh, 1983]. Additionally, the remains of titis have been found in faecal samples of ocelots [Bianchi, 2001; Bianchi and Mendes, 2007], and margays [Defler, 2004]. Our observations suggest that tayras might also constitute an important threat. Tayras, well adapted to running and climbing along branches [Presley, 2000], have been reported to prey upon several species of arboreal primates

of similar or smaller size, including common marmosets *(Callithrix jacchus),* squirrel monkeys *(Saimiri sciureus),* and tamarins *(Saguinus* spp., *Leontopithecus rosalia)* [Galef Jr. et al., 1976; Franklin et al., 2007; Bezerra et al., 2009]. Still, the number of unsuccessful attacks we witnessed indicate that tayras may not be extremely efficient primate predators [Ferrari, 2009]. Given that the presence of a researcher apparently caused the early termination of 2 of the 3 witnessed interactions between titis and tayras, it is necessary to consider the possible impact of this factor in evaluating predation rates. Ideally, the success of a predator would be evaluated by habituating and studying the predator itself [Isbell, 1994].

We do not know of any other reports of predation or attempted predation on equatorial sakis. In the case of other pitheciines, most records of predation involve either raptors or snakes [Ferrari, 2009]. There are reports of successful predation by harpy eagles of both Guianan white-faced sakis *(Pithecia pithecia)* and bearded sakis *(Chiropotes utahicki, Chiropotes satanas),* as well as reports of remains being encountered in proximity to harpy eagle nests [Rettig, 1978; Martins et al., 2005]. Although our observations show that raptors may be one of the main predators of equatorial sakis, in agreement with what has been reported for Neotropical primates [Hart, 2007], the presence of researchers could have affected the number of encounters our saki subjects had with other classes of predators, such as mammals. Given that the observer's presence and the timing of observation in primate field studies are important factors that influence predation rate on primates [Isbell and Young, 1993], our presence may have had a different effect on mammals than on birds of prey.

Antipredator Behaviour of Pitheciids

It has been suggested that the antipredator behaviour of titis primarily involves crypsis and hiding [Terborgh, 1983; Ferrari, 2009], and in 2 of the 3 encounters with tayras observed in this study, titi monkeys hid in vine tangles. Nonetheless, behaviours such as loud alarm calling and mobbing were also seen during the encounters reported above, as well as in other predation reports [Cisneros-Heredia et al., 2005; Sampaio and Ferrari, 2005]. Behaviours such as alarm calls, mobbing, and counterattacks against predators may be effective ways of distracting or discouraging predators so that other group members (presumed to be close kin) can disperse or escape [Cheney and Wrangham, 1987; Shahuano Tello et al., 2002]. In that regard, it is noteworthy that these behaviours were only present in the presence of infants, and that both titi and saki males approached the predator while giving loud calls. Interestingly, in the case of the sakis, the subadult male joined the adult male in confronting a predator, while the female and the infant remained behind. Our data suggest that a sex difference in aggressive defence is also present in these 2 species as has been reported for other primates [Isbell, 1994; Arlet and Isbell, 2009]. Moreover, the fact that the males were explicitly aggressive when an infant was at risk might suggest that males play a crucial role in the survival of their offspring. This is of special interest for sakis, believed to show only low levels of direct male parental investment, and it gives more importance to the maternally initiated babysitting with a pair-bonded male seen in our study group with 3 different infants [Schmitt et al., 2005; Fernandez-Duque and Di Fiore, unpubl. data].

It has been suggested that monogamy is most likely to develop where male care of offspring is advantageous [Kleiman, 1977], although extensive paternal care may

only develop after the advent of strong pair-bonding between particular males and females [Dunbar, 1995a, b]. It is still unclear, however, whether male protection against predators might be advantageous enough to be a key selective force behind the evolution of monogamy, as Dunbar [1988] has suggested. The tendency for some species to form larger groups in response to the pressure of predation [van Schaik and Hörstermann, 1994; Hill and Lee, 1998] and the fact that males in many non-monogamous species also defend their group's offspring [Anderson, 1986; Isbell, 1994; Arlet and Isbell, 2009] are strong arguments against male antipredation services being an important general factor driving the evolution of monogamy. Nonetheless, the role of the males in reducing predation risk may be more important for sakis, a species in which direct care of offspring by males is minimal. Alternatively, some researchers have suggested that monogamy and male-female pair bonding reflect adaptations to the risk of infanticide from extragroup males [van Schaik and Dunbar, 1990; van Schaik and Kappeler, 2003], although there is little evidence as yet to suggest that the risk of male infanticide may be significant for any monogamous platyrrhine. Further long-term study is needed to evaluate the relative importance of different male services (direct care, protection against infanticide, and predation defence) in the expression of monogamy among sakis and titis.

Our data also indicate that although both equatorial sakis and red titi monkeys live in relatively small socially monogamous groups and face the same predator community, there may be some differences in patterns of predation on these 2 taxa and in their respective antipredator behaviour, which might be explained by differences in body size and use of different forest strata [Ferrari, 2009]. In our study, sakis were observed interacting more often with birds of prey, whereas titis encountered carnivores more frequently. The sakis used mainly the top of the canopies for travelling and foraging and, as such, they are perhaps easier to detect by flying birds of prey. On the other hand, titis spend most of the time in the understorey moving slowly among vine tangles and high-density vegetation [Carrillo-Bilbao et al., 2005], which may make them less conspicuous and impose limitations on the detection ability of aerial predators, but which may also increase the probability of encountering semi-terrestrial mammals.

Even after 5 years of fieldwork with titi monkeys and sakis, the amount of data we have collected on confirmed predation events is limited and should be considered with caution. Our experience, however, is not different from what has been reported by other primatologists, who seldom witness predation directly. It seems clear that little progress will be made in understanding patterns of predation on wild nonhuman primates until dramatically different research approaches are employed that can provide direct insight into animals' perceptions of predation risk and antipredator behaviour and into the biology of predators themselves.

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References

Anderson CM (1986). Predation and primate evolution. *Primates* 27: 15–39.

Arlet ME, Isbell LA (2009). Variation in behavioral and hormonal responses of adult male gray-cheeked mangabey *(Lophocebus albigena)* to crowned eagles *(Stephanoaetus coronatus)* in Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology* 63: 491–199. See http://anthropology.ucdavis.edu/people/lynne-a.-isbell-1/pdf/Arlet%20and%20Isbell%20BES%202009.pdf

Bezerra BM, Barnett AA, Souto A, Jones G (2009). Predation by the tayra on the common marmoset and the pale-throated three-toed sloth. *Journal of Ethology* 27: 91–96.

Bianchi RC (2001). *Estudo comparativo da dieta da jaguatirica,* Leopardus pardalis *(Linnaeus, 1758), em Mata Atlântica.* Disseration, Universidade Federal do Espírito Santo, Vitória.

Bianchi RDC, Mendes SL (2007). Ocelot *(Leopardus pardalis)* predation on primates in Caratinga Biological Station, Southeast Brazil. *American Journal of Primatology* 69: 1173–1178.

Blake JG (2007). Neotropical forest bird communities: a comparison of species richness and composition at local and regional scales. *The Condor* 109: 237–255.

Boinski S, Chapman C (1995). Predation on primates: Where are we and what's next? *Evolutionary Anthropology* 4: 1–3.

Bossuyt F (2002). Natal dispersal of titi monkeys *(Callicebus moloch)* at Cocha Cashu, Manu National Park, Peru. *American Journal of Physical Anthropology* 34: 47.

Carrillo-Bilbao G, Di Fiore A, Fernandez-Duque E (2005). Dieta, forrajeo y presupuesto de tiempo en cotoncillos *(Callicebus discolor)* del Parque Nacional Yasuní en la Amazonia Ecuatoriana. *Neotropical Primates* 13: 7–11.

Cheney D, Wrangham RW (1987). Predation. In *Primate Societies* (Smuts BB, Cheney DL, Seyfarth RM, Struhsaker TT, eds.), pp 227–239. Chicago, University of Chicago Press.

Cisneros-Heredia D, Leon-Reyes A, Seger S (2005). *Boa constrictor* predation on a titi monkey, *Callicebus discolor. Neotropical Primates* 13: 11–12.

Defler T (2004). *Primates de Colombia*. Bogotá, Conservación International.

Di Fiore A (2001). Investigación ecológica y de comportamiento de primates en el Parque Nacional Yasuní. In *Conservación y desarollo sostenible del Parque Nacional Yasuní y su área de influencia: memorias del seminario-taller Yasuní* (Jorgenson J, Coello Rodríguez M, eds.), pp 165–173. Quito, Simbioe.

Di Fiore A, Fernandez-Duque E, Hurst D (2007). Adult male replacement in socially monogamous equatorial saki monkeys *(Pithecia aequatorialis). Folia Primatologica* 78: 88–98.

Di Fiore A, Fleischer RC (2005). Social behavior, reproductive strategies, and population genetic structure of *Lagothrix poeppigii*. *International Journal of Primatology* 26: 1137–1173.

Di Fiore A, Link A, Schmitt CA, Spehar SN (2009). Dispersal patterns in sympatric woolly and spider monkeys: integrating molecular and observational data. *Behaviour* 146: 437–470.

Dunbar RIM (1988). *Primate Social Systems.* London, Chapman & Hall.

Dunbar RIM (1995a). The mating system of the callitrichid primates. 1. Conditions for the coevolution of pair bonding and twinning. *Animal Behaviour* 50: 1057–1070.

Dunbar RIM (1995b). The mating system of callitrichid primates. 2. The impact of helpers. *Animal Behaviour* 50: 1071–1089.

Eason P (1989). Harpy eagle attempts predation on adult howler monkey. *The Condor* 91: 469–470.

Fernandez-Duque E, Di Fiore A, Carrillo-Bilbao G (2008). Behavior, ecology, and demography of *Aotus vociferans* in Yasuni National Park, Ecuador. *International Journal of Primatology* 29: 421–431.

Fernandez-Duque E, Rotundo M (2003). Field methods for capturing and marking azarai night monkeys. *International Journal of Primatology* 24: 1113–1120.

Ferrari SF (2009). Predation risk and antipredator strategies. In *South American Primates: Comparative Perspectives in the Study of Behavior, Ecology, and Conservation* (Garber PA, Estrada A, Bicca-Marques JC, Heymann EK, Strier KB, eds.), pp 251–277. New York, Springer.

Ferrari SF, Pereira WLA, Santos RR, Veiga LM (2004). Fatal attack of *Boa constrictor* on a bearded saki *(Chiropotes satanas utahicki)*. *Folia Primatologica* 75: 111–113.
Ferrari SF, Port-Carvalho M (2003). Predation of an infant collared peccary by a harpy eagle in Eastern Amazonia. *Wilson Bulletin* 15: 103–104.
Fowler J, Cope J (1964). Notes on the harpy eagle in British Guiana. *The Auk* 81: 257–273.
Franklin SP, Hankerson SJ, Baker AJ, Dietz JM (2007). Golden lion tamarin sleeping-site use and pre-retirement behavior during intense predation. *American Journal of Primatology* 69: 325–335.
Galef Jr BG, Mittermeier RA, Bailey RC (1976). Predation by the tayra *(Eira barbara)*. *Journal of Mammalogy* 57: 760–761.
Galetti M, de Carvalho O (2000). Sloths in the diet of a harpy eagle nestling in eastern Amazon. *Wilson Bulletin* 112: 535–536.
Hart D (2007). Predation on primates: a biogeographical analysis. In *Primate Anti-Predator Strategies* (Gursky S, Nekaris KAI, eds.), pp 27–59. Chicago, Springer.
Hill R, Dunbar R (1998). An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping behaviour. *Behaviour* 135: 411–430.
Hill RA, Lee PC (1998). Predation risk as an influence on group size in cercopithecoid primates: implications for social structure. *Journal of Zoology* 245: 447–456.
Isbell L (1994). Predation on primates: ecological patterns and evolutionary consequences. *Evolutionary Anthropology* 3: 61–71.
Isbell LA, Young TP (1993). Human presence reduces predation in a free-ranging vervet monkey population in Kenya. *Animal Behaviour* 45: 1233–1235.
Izor RJ (1985). Sloths and other mammalian prey of the harpy eagle. In *Conservation and Ecology of the Armadillos, Sloths and Vermilinguas* (Montogomery GG, ed.), pp 343–346. Washington, Smithsonian Institution Press.
Janson C (1998). Testing the predation hypothesis for vertebrate sociality: prospects and pitfalls. *Behaviour* 135: 389–410.
Kleiman DG (1977). Monogamy in mammals. *The Quarterly Review of Biology* 52: 39–69.
Klein BC, Harper LH, Bierregaard RO, Powell GVN (1988). The nesting and feeding behavior of the ornate hawk-eagle near Manaus, Brazil. *The Condor* 90: 239–241.
Lawrence J (2003). Preliminary report on the natural history of brown titi monkeys *(Callicebus brunneus)* at Los Amigos Research Station, Madre de Dios, Peru. *American Journal of Physical Anthropology* Supplement 36: 136.
Ludwig G, Aguiar LM, Miranda JMD, Teixeira GM, Svoboda WK, Malanski LS, Shiozawa MM, Hilst CLS, Navarro IT, Passos FC (2007). Cougar predation on black-and-gold howlers on Mutum Island, Southern Brazil. *International Journal of Primatology* 28: 39–46.
Martins SS, Lima EM, Silva Jr JS (2005). Predation of a bearded saki *(Chiropotes utahicki)* by a harpy eagle *(Harpia harpyja)*. *Neotropical Primates* 13: 7–10.
Matsuda I, Izawa K (2008). Predation of wild spider monkeys at La Macarena, Colombia. *Primates* 49: 65–68.
Miranda J, Bernardi I, Abreu K, Passos F (2005). Predation on *Alouatta guariba clamitans* Cabrera (Primates, Atelidae) by *Leopardus pardalis* (Linnaeus) (Carnivora, Felidae). *Revista Brasileira de Zoologia* 22: 793–795.
Norconk MA (2006). Long-term study of group dynamics and female reproduction in Venezuelan *Pithecia pithecia*. *International Journal of Primatology* 27: 653–674.
Norconk M (2007). Sakis, uakaris, and titi monkeys: behavioral diversity in a radiation of primate seed predators. In *Primates in Perspective* (Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK, eds.), pp 123–138. New York, Oxford University Press.
Peetz A, Norconk M, Kinzey W (1992). Predation by jaguar on howler monkeys *(Alouatta seniculus)* in Venezuela. *American Journal of Primatology* 28: 223–228.
Peres C (1990). A harpy eagle successfully captures an adult male red howler monkey. *Wilson Bulletin* 102: 560–561.
Presley SJ (2000). *Eira barbara*. *Mammalian Species* 636: 1–6.
Rettig N (1978). Breeding behavior of the harpy eagle *(Harpia harpyja)*. *The Auk* 95: 629–643.
Robinson J (1979). An analysis of the organization of vocal communication in the titi monkey *Callicebus moloch*. *Zeitschrift für Tierpsychologie* 49: 381–405.
Sampaio DT, Ferrari SF (2005). Predation of an infant titi monkey *(Callicebus moloch)* by a tufted capuchin *(Cebus apella)*. *Folia Primatologica* 76: 113–115.
Schmitt C, Di Fiore A, Hurst D, Fernandez-Duque E (2005). *Maternally-Initiated Babysitting by Wild Adult Male Equatorial Sakis* (Pithecia aequatorialis) *in Yasuní National Park, Ecuador.* 1st Annual NYCEP Symposium: 'Monkeys: Old and New', New York.
Shahuano Tello NS, Huck M, Heymann EW (2002). *Boa constrictor* attack and successful group defence in moustached tamarins, *Saguinus mystax*. *Folia Primatologica* 73: 146–148.
Sherman PT (1991). Harpy eagle predation on a red howler monkey. *Folia Primatologica* 56: 53–56.

Stanford CB (2002). Avoiding predators: expectations and evidence in primate antipredator behavior. *International Journal of Primatology* 23: 741–757.
Terborgh J (1983). *Five New World Primates: A Study in Comparative Ecology*. Princeton, Princeton University Press.
Terborgh J, Janson C (1986). The socioecology of primate groups. *Annual Review of Ecology and Systematics* 17: 111–135.
van Schaik CP (1983). Why are diurnal primates living in groups? *Behaviour* 87: 120–144.
Van Schaik CP, Dunbar RIM (1990). The evolution of monogamy in large primates: a new hypothesis and some crucial tests. *Behaviour* 115: 30–61.
van Schaik CP, Hörstermann M (1994). Predation risk and the number of adult males in a primate group: a comparative test. *Behavioral Ecology and Sociobiology* 35: 261–272.
Van Schaik CP, Kappeler PM (2003). The evolution of social monogamy in primates. In *Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals* (Reichard UH, Boesch C, eds.), pp 59–80. Cambridge, University of Cambridge.