Preface

The impact of predation on the morphology, behavior, and ecology of animals has long been recognized by the primatologist community (Altmann, 1956; Burtt, 1981; Curio, 1976; Hamilton, 1971; Kruuk, 1972). Recent thorough reviews of adaptations of birds and mammals to predation have emphasized the complex role that predation threat has played in modifying proximate behaviors such as habitat choice to avoid predator detection, degree and type of vigilance, and group size and defense, as well as ultimate factors including the evolution of warning systems, coloration, and locomotor patterns (Thompson et al., 1980; Sih, 1987; Lima & Dill, 1990; Curio, 1993; Caro, 2005).

From the late 1960s, primatologists have adopted similar techniques to analyze the impacts of predation on the social systems of monkeys and apes (Crook & Gartlan, 1966; Eisenberg et al., 1972; Goss-Custard et al., 1972; Clutton-Brock, 1974; van Schaik & van Hooff, 1983). The fact that actual predation was witnessed but rarely fueled a debate regarding whether predation or food acquisition played a more important role in primate evolution (Wrangham, 1980; van Schaik, 1983; Anderson, 1986; Janson, 1987; Wrangham, 1987; Rodman, 1988; Janson, 1998). More recent studies are more subtle in their design, and have worked from a hypothetical framework that an animal's being eaten is more costly than its missing a meal; they have thus attempted to quantify how animals perceive and act upon predation risk rather than the act of predation itself (Cords, 1990; Boesch, 1994; Isbell, 1994; Cowlishaw, 1997; Hill & Dunbar, 1998; Cowlishaw, 1998). Other investigations have been founded on how primate cognitive abilities and complex social learning aid them in avoiding predators (Seyfarth et al., 1980; Bshary and Noë , 1997; Zuberbühler et al. , 1999; Zuberbühler, 2000; Shultz et al., 2004). These, and a multitude of other studies, are beginning to elucidate our understanding of the impact of predation on primate evolution. Or are they?

We have conducted research on nocturnal primates for more than ten years. Immersed as we have been in the literature of nocturnal primatology we recognize a spectrum of diversity amongst the nocturnal primates in their social organization, cognitive behavior, and ecology (Charles-Dominique, 1978; Bearder, 1999; Müller and Thalmann, 2000). Our studies on tarsiers and lorises showed that these species were highly social and that resource distribution was not

sufficient to explain why they defied the supposed "stricture" of being solitary (Gursky, 2005a; Nekaris, 2006). Furthermore, our animals defied another supposed "rule" — namely, that all nocturnal primates should avoid predators by crypsis (Charles-Dominique, 1977). Even recent reviews of primate social organization and predation theory included one-sentence write-offs, excluding nocturnal primates from discussions of primate social evolution on the basis that crypsis is their only mechanism of predator avoidance (Kappeler, 1997; Stanford, 2002).

An analysis of the mammalian literature shows this type of generalization to be crude at best. Small mammals are known to have extraordinarily high rates of predation, and a plethora of studies of rodents, insectivores, and lagomorphs, among others, have shown that predation is a viable and powerful ecological force (Lima & Dill, 1990; Caro, 2005). Furthermore, although researchers have long considered it critical to include prosimian studies in a general theoretical framework concerning the evolution of the order Primates (Charles-Dominique & Martin, 1970; Cartmill, 1972; Oxnard et al., 1990), a pervading view contends that prosimians are too far removed from humans for the former's behavior to shed any light on the patterns of behavior seen in anthropoids (Kappeler & van Schaik, 2002; Stanford, 2002).

Such notions are perhaps fueled by a paucity of predation research on prosimians in general. This lack of literature may relate to the fact that the study of nocturnal primates is still in the descriptive rather than the theoretical phase; with so many species still being described, data collection on endangered species may begin with recording basic parameters of the diet and home range of these animals (Bearder, 1999). Furthermore, any study of nocturnal and cathemeral primates that goes beyond collecting radio-tracking fixes has proved to be a challenge; much more difficult has been the actual observation of predation events (Sterling et al., 2000). However, an excellent review by Goodman et al. demonstrates the dramatic effect predation can have on lemurs, and it remains the most highly quoted resource on lemur predation, despite that it was published in 1993. Studies of referential signaling aid in dispelling the view that prosimians are primitive and not worthy of comparison with monkeys and apes (Oda, 1998; Fichtel & Kappeler, 2002). A handful of studies further reveal that prosimians are not always cryptic and may engage in social displays toward predators (Sauther, 1989; Schülke, 2001; Bearder et al., 2002; Gursky, 2005b).

In addition to the above cited works, our colleagues regaled us with tales of lemurs, bushbabies, and lorises that demonstrate how these animals employ numerous tactics against predators beyond crypsis. Their observations showed that strategies of nocturnal and cathemeral primates they studied were not unlike antipredator strategies exhibited by the better-studied diurnal primates — conclusions that contradict the popular view (Stanford, 2002). The anecdotal nature of many of these observations, however, suggested that an outlet was needed to report them; thus the idea for this volume was formed.

The original goal of this volume was to synthesize current research on the anti-predator behavior of nocturnal and cathemeral primates. We quickly realized, however, that although we could, in this volume, emphasize these less-studied

species, we would fall into the same trap as previous researchers if we did not consider primates as an order. Thus, the seventeen chapters in this volume consider anti-predator strategies exhibited across primates including: crypsis, alarm calling (referential or otherwise), mobbing behavior, production of toxins, group cohesion, behavioral modification due to environmental factors (habitat choice, sleeping site choice, visibility, moonlight), and vigilance, among others. This volume is organized into three sections: predation theory, anti-predator strategies of nocturnal and cathemeral primates, and anti-predator strategies of diurnal primates. Although we have divided it in this manner, we hope the reader can see the common theoretical and behavioral threads that unite these primate studies as emphasized here.

The two chapters of Section One bring together an immense volume of literature and observations on two important areas of primate predation studies. Zuberbühler fuels a discussion on the effect of predation on primate cognitive evolution with examples from long-term research by himself and colleagues at the Taï forest in West Africa. The studies at the site benefited from complementary observations of the predators themselves — a component often lacking in primate fieldwork. Zuberbühler's comprehensive experience of this ecological system leads him to the controversial conclusion that at Taï, predation does not drive traditionally recognized traits such as group size, body size, life history etc. Rather, it has selected for the evolution of sophisticated cognitive processes, including semantic predator-specific calls, amongst the sympatric primates. This straying from typical predation theory is also emphasized by Hart in her biogeographical analysis of primate predation. Hart's comprehensive dataset of inferred and observed instances of predation on primates allowed her to search for regional patterns to predation. Although primates in some regions (the Neotropics and Madagascar) seem to be more heavily preyed upon than in others (Africa and Asia), Hart found the overall scarcity of data a limiting factor in interpreting them. She did uncover, however, that primates of all body sizes, activity cycles, and ecological niches as determined by strata were preyed upon. This study reminds us that the range of primates from small-bodied nocturnal primates to large-bodied apes cannot be removed from our consideration of predation theory.

Section Two on cathemeral and nocturnal primates contains two major areas: reviews from long-term studies of multiple species, and specific field studies of one or more species. Dollar et al., in line with Zuberbühler, contribute the first research project directly aimed at analyzing the foraging strategies of the largest Malagasy predator — the fossa. Their research shows, contradictorily to the findings of Hart, that although the fossa is capable of taking many species, the taxon most likely to fall victim to it is *Lepilemur*, possibly due to that primate's predictable pattern of sleeping in tree holes, slow locomotion, and solitary lifestyle. Indeed, in her contribution Nash sheds further light on factors that might influence the desirability of *Lepilemur* as a prey item. *Lepilemur* at Nash's study site did not significantly moderate its behavior in relation to different quantities of moonlight, as did many nocturnal mammals. Although they did reduce their time in the highest part of the canopy during moonlit times, perhaps as a device to avoid aerial

predators, in general, Nash proposes, their nutrient-poor diet does not allow for much behavioral flexibility.

Karpanty & Wright, Scheumann et al., and Colquhoun present informative reviews on lemur predation that link to other theoretical perspectives in this volume. Karpanty & Wright synthesize an enormous dataset on lemur predation collected over nineteen years in Ranomafana National Park. *Ad libitum* observations, combined with playback experiments, analyses of predator scats, and systematic fieldwork, aided in formulating a picture of the impact of predation on the rainforest primate community. Although some lemurs relied on the traditional pattern of crypsis, others were highly vocal. Furthermore, they found that both activity pattern and body size *did* have an effect on predation, again in contradiction to Hart. Scheumann et al. review the scanty body of studies on lemur predation and examine their own long-term studies in northwestern Madagascar. They find that, as in the Taï forest, predation clearly has had an impact on cognitive evolution in lemurs, with numerous lemurs using predator-specific referential signals that appear to be socially learned. Body size not only seems to relate to predation risk, but also seems to influence what types of predator strategies lemurs use to combat potential predators. Colquhoun reviews the anti-predator strategies of cathemeral primates, which, due to their potential for activity in the day or night, may need a defense system against a greater array of predators. He suggests that in these small, group-living primates crypsis may play a role; however, cathemerality is not fully understood amongst most of the larger-bodied taxa. For the better-studied *Eulemur*, all of which are sexually dichromatic, he puts forth the interesting hypothesis that this coloration may be a form of polymorphic strategy to counter apostatic predation. All three of these studies are excellent illustrations for revaluating the "crypsis only" view.

Ultimate strategies for avoiding predation are explored by Crompton & Sellers Hagey et al., and Nekaris et al. Crompton & Sellers consider the function of the unique locomotor pattern exhibited by many nocturnal primates: vertical clinging and leaping. By showing that galagos, tarsiers, and some lemurs are capable of leaping far beyond their average distance, they suggest that, from an energetic perspective, the most likely selective factor influencing this ability would be confounding, avoiding, or escaping from a predator. Hagey et al. present long-awaited data on the function and composition of the brachial gland of *Nycticebus.* Their study confirms that small levels of toxic compounds are indeed present in the gland, possibly having evolved as a complex chemical signal to conspecifics and as a toxin for immobilizing prey. The ecological ramifications of chemical communication are presented by Nekaris et al. Novel field data on West African pottos and Sri Lankan slender lorises are compared to revaluate the role that crypsis supposedly plays in the anti-predator strategies of these primates. Although the authors report that lorises engaged in noisy displays and were faster and more vocal than the relatively cryptic pottos, they also describe the prevalence of olfactory communication in all taxa. Comparing their work with the mammalian literature in general, they stress the olfactory capabilities of predators and warn against dismissing olfactory communication as cryptic.

Bearder & Gursky both present data from long-term field studies on strategies that nocturnal primates employ to cope with danger. Both papers reinforce elements presented by Scheumann et al. and by Zuberbühler in that both find evidence for referential signaling. In his paper on calling patterns in two species of galagos, Bearder not only describes, for the first time, the large array of alarm calls emitted by these species, but also contextualizes them. Not only are the calls acoustically distinct, based on the level of fear or arousal of the emitter, they also vary in speed and intensity. Although calls may not have predator-specific contexts, they were situation-specific and were uttered according to the level of danger. Similarly, Gursky discovered that tarsiers incorporate a wide range of tactics to cope with potential predators. Systematic presentation of avian and terrestrial predator models allowed for detailed observations on how spectral tarsiers react in the presence of a potential predator. Not surprisingly, although some predators elicited cryptic responses from them, tarsiers also vocalized, banded together and mobbed predators, again contradicting the view of the cryptic prosimians.

The studies of diurnal primates have been grouped together in Section Three, but certain themes continue throughout these studies. Long-term studies of *Lemur catta* allow for a review by Gould & Sauther supplemented with novel data. These data emphasize that ring-tailed lemurs, like other well-studied diurnal primates, form larger groups and increase vigilance in areas of vulnerability and during vulnerable times of the year (during and after weaning). Referential signaling is also evident, reinforcing the postulation of Scheumann et al. that this cognitive system is characteristic of lemurs. In line with Dollar et al., Gil da Costa approached the predator and prey relationship between harpy eagles and howler monkeys. In a unique situation whereby harpy eagles were released into an area from which they had been extirpated, Gil da Costa was able to analyze both the eagles' and the monkeys' tactics. Whereas monkeys immediately adopted strategies such as group repositioning and vigilance, the eagles too adopted their own mechanisms, learning situations where stealth or attack would improve their capture rate. This study shows how quickly primates and prey can adapt in only one generation.

Long-term field studies on estimating predation risk are presented by Enstam and by Hill & Weingrill. Enstam reviews the impact on predation risk on cercopithecines and illustrates the importance of the study of multiple aspects of habitat structure rather than ecosystem type alone in order to estimate risk. She demonstrates through her own studies of vervet and patas monkeys that even with a highly flexible suite of anti-predator strategies, these primates still can suffer high predation pressure. We have stressed throughout this review that studies of predation on nocturnal primates are in their infancy. In their chapter Hill & Weingrill reiterate this point for diurnal primates and provide elegant guidelines for the measurement of predation risk in terrestrial environments. By focusing on their work with chacma baboons, they show how baboons respond behaviorally to habitat-specific levels of predation risk, even in environments where predators are scarce. These results suggest a deeper ultimate impact of predation on the primate behavior.

The volume is concluded with a review by Treves & Palmqvist. When we were organizing this volume, our colleagues asked us if we would include humans. The scope of understanding the development of *Homo* as a predator would require a volume in its own right. However, Treves & Palmqvist attempt to reconstruct the interactions of hominins prior to *Homo ergaster*, particularly with respect to them as prey to mammalian carnivores. By reconstructing the hunting habits and the diets of paleocarnivores, Treves & Palmqvist suggest that strong group cohesion, vigilance, and last but not least, extreme crypsis, would have characterized early hominin anti-predator strategies.

Many of the contributors to this volume stress how the study of predation, in whichever form it takes, is still at an early stage. A number of the authors outline areas of further study or present compelling hypotheses worthy of additional testing. Although this book focuses mainly on prosimians, we hope that the unifying themes running through all the essays will aid the reader in considering predation theory in a broader light. These studies show that species, regardless of their activity rhythm, body size, or brain size, do not engage in uniform or predictable strategies. At the very least we hope that this volume will dispel a myth as well as encourage a new spectrum of research on primate anti-predator strategies.

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2
Predation on Primates: A Biogeographical Analysis

D. Hart

Introduction

Measuring the magnitude of predation has been deemed an important task in clarifying aspects of primate ecology (Terborgh & Janson, 1986). This goal is in keeping with a general theoretical shift noted by Sih et al. (1985) toward acknowledgment that predation often has a greater impact than resource competition on individual animals through behavior and life history; on prey populations through size and stability; and on ecosystems through diversity and relative abundance patterns. Biogeography, as a comparative observational science dealing with spatial and temporal scales too large for experimentation, seeks patterns of biodiversity upon which theories may be formulated (Brown & Lomolino, 1996). Primate predation studies benefit from a biogeographical approach when primates and their predators are assessed from the standpoint of four major regions: Africa, Madagascar, Asia, and the Neotropics. Since predation is thought to have affected morphological, ecological, and behavioral traits in primates (Hart, 2000; Zuberbühler & Jenny, 2002), a comparison of the four regions may facilitate identification of broad biogeographic patterns that are associated with predation.

Erroneous assumptions concerning predation as a demographic variable find their way into published comments. One commonplace, but erroneous, assumption is that "mortality due to predation appears to be negligible" (Dunbar, 1988, p.53). Opinions have ranged from a belief that the role of predation in primate evolution is minimal (Raemakers & Chivers, 1980; Wrangham, 1980; Cheney & Wrangham, 1987) to theories that predation is a powerful force in shaping social patterns (van Schaik, 1983; Terborgh & Janson, 1986; Dunbar, 1988; Hart, 2000; Hart & Sussman, 2005). Recent reviews and studies on topics such as the vulnerability of baboons to predation (Cowlishaw, 1994), ecological patterns of predation on primates (Isbell, 1994a), the status of predation research (Boinski & Chapman, 1995), predation rate versus predation risk (Hill & Dunbar, 1998), and the influence of predation on arboreal primates (Treves, 1999) have expanded theoretical discussion of this topic. Nonetheless, because observation of predation in the primate literature is often anecdotal rather than quantitative, there has been a

tendency to underestimate the pervasive influence predation has on the behavior and ecology of primates (Caine, 1990).

Large-scale patterns in predation have been discussed in broad theoretical terms but never assessed using quantified data. Moreover, there have been few attempts to recruit research carried out on various predators as an aid to understanding the impact of predation on primates. Predator-prey relationships are best studied from the perspective of the predator (Washburn et al., 1965; Cheney & Wrangham, 1987; Isbell, 1994; Boinski & Chapman, 1995; Mitani et al., 2001). Observation of only one group of one species (the typical parameters of primate research) provides limited data and often skews the perception of predation, whereas fieldwork on predatory species gives an ecosystemic view of several trophic levels. The home range of a solitary predator usually overlaps numerous prey groups and species; while the predator hunts on a daily basis, it may only occasionally attack the primate group under study. Primatologists have rarely viewed their subjects as prey, and the inclusion of predators into the realm of primate ecology has not been common. To that end, I conducted a meta-analysis of predation on primates that can serve as a basis for objective review of this topic.

Methods

Meta-analysis is the branch of statistics wherein data from various sources are combined (Halvorsen, 1986). Because the broad overview of data collected in my study is a first attempt to quantify the entire spectrum of predation on primates, a descriptive numerical summary is needed to deal with the data in manageable form (Sokal & Rohlf, 1981; Mansfield, 1986). Since it was not possible to collect data from all research sites in a random sampling, I collected raw data and used descriptive statistics throughout to summarize these data. Frequency distributions are used for comparison of variables, and summaries based on percentages are employed to interpret specific issues.

Primate data were categorized as follows: (1) by geographic region: Africa, Madagascar, Asia, and the Neotropics; (2) by body size divided into two categories: because body weights of primates extend along a continuum from 60 g to 169.5 kg, I selected a reasonable arbitrary weight division of under and over 2 kg to separate small-bodied from large-bodied primates; (3) by stratum generally occupied: arboreal or terrestrial; and (4) by daily activity cycle: diurnal or nocturnal (a decision to limit the activity cycles to these two divisions was based on the realization that more precise divisions, such as cathemeral, would constitute very small fractions of the data set).

For each primate prey, the equivalent data on its predator were also collated as follows: (1) by broad predator categories: felids, raptors, canids and hyaenids, small carnivores (which included the vivverid, herpestid, and mustelid families), reptiles, or unidentified (if the predator left a dead or dying primate but was not itself observed); (2) by geographic region: Africa, Madagascar, Asia, and the

Neotropics; (3) by weight in kilograms (predators ranged from *Vanga curvirostris*, weighing 72 g, to *Crocodylus palustris*, weighing 227 kg); (4) by stratum occupied: aerial, arboreal, terrestrial, or aquatic; and (5) by daily activity cycle: diurnal or nocturnal.

Data were drawn from both published and unpublished sources (viz., the scientific literature and my own questionnaires) based on the fieldwork of primate researchers, ornithologists, herpetologists, and mammalogists. Data were derived from observed predation events and studies of predation that have produced quantitative results. The latter are heavily dependent on predator research and offer information on the entire spectrum of prey in the diet of many of the 174 primate predator species identified by Hart (2000). Along with other food items, primate remains—ranging from the smallest (*Microcebus*) to the largest (*Gorilla*)—have been found in predator scats, pellets, nests, and dens.

One hundred and seventy-four predator species identified in this meta-analysis were divided into five broad categories: *felids* (21 species of wild cats), *raptors* (82 species of hawks, eagles, owls, and other predatory birds), *canids* and *hyaenids* (10 species of wild dogs and jackals and 3 species of hyenas), *small carnivores* (22 species of civets, genets, mongoose, the fossa, and a tropical weasel, among others), and *reptiles* (36 species of snakes, crocodilians, and monitor lizards). Ecology rather than taxonomy was emphasized in the predator categories; for instance, taxonomically the hyenas are more closely related to felids than canids, but the predation strategies of dogs and hyenas (i.e., pack hunting and coursing after prey) justify combining the two carnivore families.

While all categories of primate mortality are pertinent and deserve further research, the meta-analysis described in this chapter was deliberately limited to the relationship between primates and the groups of carnivorous animals that are predatory by definition. Neither an analysis of human predation on non-human primates nor predation by primates on other primates was attempted. There is a large body of literature detailing human exploitation of primates (see Mittermeier, 1987; Mittermeier & Cheney, 1987; Peres, 1990; Alvard & Kaplan, 1991; Alvard, 1994; Oates, 1994, 1996; McRae, 1997; Redmond, 1998; McNeil, 1999). Less is known about the effects of non-human primate predation on other primates. Chimpanzees, orangutans, baboons, blue monkeys (*Cercopithecus mitis*), capuchin monkeys (*Cebus spp*.), red-fronted brown lemurs (*Eulemur fulvus rufus*), and dwarf lemurs (*Microcebus coquereli*) have been observed hunting and eating smaller primates (see Hart, 2000). A few instances of primates preying on other primates are relatively well studied, particularly chimpanzee predation (Uehara et al., 1992; Stanford et al., 1994; Stanford, 1995; Stanford & Wrangham, 1998). At Gombe National Park in Tanzania, chimpanzee predation on red colobus (*Procolobus badius*) is extensive, alleged to account for "an annual harvest of from 16.8 to 32.9% of the red colobus population, depending on the number of male chimpanzees and the precise size of the red colobus population in a given year" (Stanford et al., 1994, p. 221).

Results

A total of 3,592 primate mortalities and unsuccessful predation attempts were identified. This establishes a baseline for understanding the biogeographical patterns of predation on primates. General patterns will be examined prior to discussing the four regions separately.

Figure 2.1 is an overall representation of 3,592 instances of predation cited in questionnaires and literature, classified by geographic region and predator category. Table 2.1 separates the predation incidents into unsuccessful attacks ($n = 679$, 18.9%), successful predations ($n = 2,229$, 62.1%), and suspected predations ($n = 684$, 19.0%). (See (Hart, 2000) for data sources and a discussion of the number of reported predation events as a function of the number of sources from which they were collected.) Felids and raptors accounted for the most predations on primates (34.6%, $n = 1,243$ and 40.7%, $n = 1,461$, respectively), followed by unidentified predators (9.0%, $n = 323$), canids and hyaenids (7.0%, $n = 253$), reptiles (5.4%, $n = 194$), and small carnivores (3.3%, $n = 118$).

Table 2.1 requires explanation lest the reader equate the number of predation events listed with the number of identified primate predator species. There is no direct cause and effect relationship between these two variables because the number of predation events is not random but, rather, the outcome of studies directed at specific primates or predators. Thus, the data on unsuccessful attacks, successful predations, and suspected predations by felids, raptors, canids and hyaenids, small carnivores, and reptiles are representative of those primates or predator species that

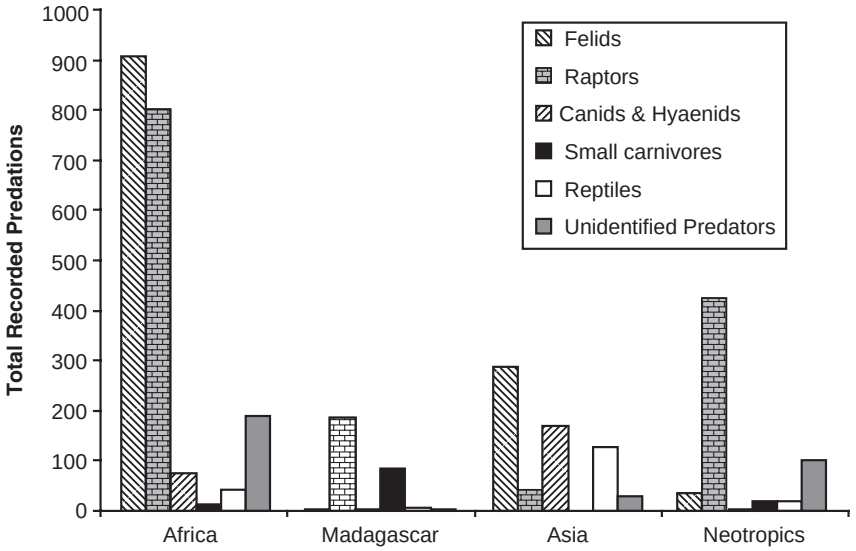


FIGURE 2.1. Overall magnitude of recorded predation on primates (Data source: Hart, 2000)

TABLE 2.1. Summary of recorded predations from questionnaires and literature (Data source: Hart, 2000).

Region and Predator	Unsuccessful Attacks	Successful Attacks	Suspected Predation	Number of Identified Predator Species
AFRICA				
Felid	66	725	123	7
Raptor	199	573	36	22
Canid & hyaenid	26	40	10	7
Small carnivore	4	9	0	9
Reptile	4	36	3	12
Unidentified	5	37	149	–
Total Africa	**304**	**1420**	**321**	**57**
MADAGASCAR				
Felid	0	3	1	–
Raptor	18	158	10	17
Canid & hyaenid	0	3	0	–
Small carnivore	5	63	17	7
Reptile	0	6	0	5
Unidentified	0	0	2	–
Total Madagascar	**23**	**233**	**30**	**29**
ASIA				
Felid	8	254	27	8
Raptor	13	26	4	15
Canid & hyaenid	13	58	100	6
Small carnivore	0	0	0	3
Reptile	2	41	83	7
Unidentified	0	10	19	–
Total Asia	**36**	**389**	**233**	**39**
NEOTROPICS				
Felid	10	20	6	6
Raptor	263	146	15	30
Canid & hyaenid	1	1	1	1
Small carnivore	15	3	2	4
Reptile	11	7	1	13
Unidentified	16	10	75	–
Total Neotropics	**316**	**187**	**100**	**54**
TOTAL	**679**	**2229**	**684**	

have been studied. On the other hand, the number of predator species associated with primate predation derives from both anecdotal and quantitative observations.

After making an initial assessment to gauge the magnitude of recorded predation in the four geographic regions, I eliminated data on suspected predations from further analysis. I based this decision on a simple rationale that there was an inherent margin of error built into the "suspected" classification. Even with the most conservative approach to judging suspected predation, it would be problematic to combine these data with those gathered from eyewitness observations and results from controlled studies. At this point in the meta-analysis I also combined

the data from the remaining two classes—unsuccessful attacks and successful predations—since these categories were empirical in nature.

After graphing the magnitude of recorded predation, the next stage of data analysis explores primate predation separately in each geographical region and, further, attempts to isolate the variables that determine which groupings of primate species are preyed upon. In all four regions I examine the possible combinations of primate body size, stratum occupied, and activity cycle to see whether there are primates that are exempt from predation. Data indicate that none of the characteristics examined protects primates from predators. Although the exact rates of predation are often unknown, it is apparent from these data that primates are preyed upon if they are small or large, nocturnal or diurnal, arboreal or terrestrial.

Africa

African felids and raptors together accounted for the highest frequencies of primate predation, 53.7%, $n = 1, 563$ (Figure 2.2). That more than half of all reported predation events can be attributed to felids and raptors in one region is most likely an artifact of the greater quantity of questionnaire returns and scientific articles based on field research in Africa than in other regions. Leopards are opportunistic ambush hunters that are a key predator of primates, particularly in African tropical rainforests (Boesch, 1991, 1992; Zuberbühler & Jenny, 2002). Two major studies in the Taï forest calculated relatively similar percentages of primates in leopard diets; Zuberbühler & Jenny, (2002) estimated that 27.9% ($n = 64$) of the leopard diet consisted of primates; Hoppe-Dominik (1984) estimated 24.2% ($n = 61$). Outside of rainforest habitat, leopards are also major predators of primates. During a study of vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya, Isbell (1990) lost 45.0% ($n = 23$) of her study population to leopards in one year.

Other African wild cats also prey on primates. In the Mahale mountains of Tanzania, for example, lions (*Panthera leo*) appear to be major predators of primates (Tsukahara, 1993). Until recently, predation as a mortality factor for Mahale chimps was assumed to be negligible. However, this assumption has been challenged by evidence of chimpanzee hair, bones, and teeth in 4 out of 11 samples of lion feces collected over a four-month period. As another example, two lionesses near Mana Pools in Zimbabwe were known to favor baboons as prey. Over a six-year period, a safari guide in the area observed the lionesses killing six baboons (T. Williamson, pers. comm.).

African raptors have numerous failed predation attempts on primates ($n = 199$). This figure is borne out by observations of frequent unsuccessful attacks on Diana monkeys (*Cercopithecus diana*) by crowned hawk-eagles (*Stephanoaetus coronatus*, Figure 2.3) (Zuberbühler et al., 1997). The crowned hawk-eagle is one of the largest of the African eagles and is immensely powerful (Steyn, 1973; Williams & Arlott, 1980; Brown et al., 1982). Its thick tarsi, robust toes, and long talons enable it to kill large prey; with an average adult weight of 3.6 kg, the eagle routinely subdues animals four to five times its own size (Brown, 1971; Steyn, 1973, 1983; Brown et al., 1982; Tarboton, 1989). The crowned hawk-eagle

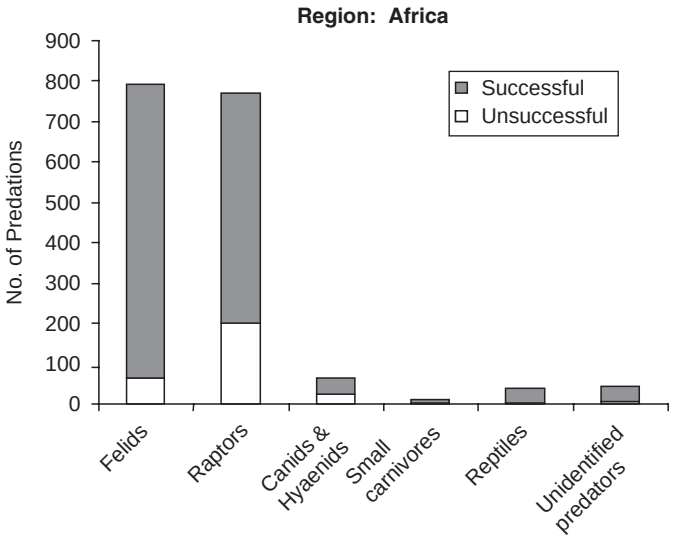


FIGURE 2.2. Comparison of successful and unsuccessful attacks by six categories of predators in Africa (Data source: Hart, 2000)

may be a primate specialist. Studies of this raptor in the Kibale forest of Uganda found high percentages of primates in eagle diets; Skorupa (1989) noted that 87.9% ($n = 29$) of eagle prey were monkeys, and Struhsaker & Leakey (1990) estimated this figure to be 83.7% ($n = 41$). Mitani et al., (2001) determined that primates composed the vast majority of crowned hawk-eagle prey items (82%, $n = 74$) in the Ngogo study site in Kibale during a 37-month study. At another research site in the Kiwengoma Forest Reserve, Tanzania, the skeletal remains found in one crowned hawk-eagle nest were "90% dominated by blue monkey" (Msuya, 1993, p.120). The geographic range of this raptor is extensive throughout the tropical belt of Africa. New research is finding that crowned hawk eagles exert much the same predation pressure on monkeys across different parts of their range (cf. Mitani et al., 2001; Shultz, 2001, 2002).

There are no arboreal-nocturnal primates weighing more than 2 kg in Africa, and there are no terrestrial-diurnal primates weighing less than 2 kg. (Of course, no terrestrial-nocturnal primates exist of any weight in any region.) Predation was recorded in the remaining four ecological categories identified in Figure 2.4. The single data point representing small, arboreal-diurnal primates refers to predation on the talapoin monkey (*Miopithecus talapoin*), the only African primate species in this category. The remaining three groups are dominated by guenons, mangabeys, and colobus in the arboreal-diurnal, over-2-kg category; arboreal-nocturnal primates under 2 kg refer to galagos and lorisids; terrestrial-diurnal primates over 2 kg include apes and baboons.

There are some interesting patterns that can be inferred from Figure 2.4. More terrestrial primate genera ($n = 7$) have evolved in Africa than other regions, and

FIGURE 2.3. Forest-hunting raptors, such as the African crowned hawk-eagle, are the major and most competent predators on primates (Steve Bird/Birdseekers Tours)

Africa is the only region in which there are more terrestrial-diurnal than arboreal-diurnal genera. Some of the information contained in Figure 2.4 likely represents an artifact of the numerous studies carried out on terrestrial primate species weighing over 2 kg, particularly baboons and chimpanzees. But it is difficult to say whether the 806 predations recorded in this category might also reflect an abundance of terrestrial primates, or might even point to a striking difference between arboreal and terrestrial primates as far as vulnerability to predators.

Madagascar

Corresponding information for Madagascar (Figure 2.5) shows an emphasis on raptor and small carnivore predation. Madagascar is the only region in which

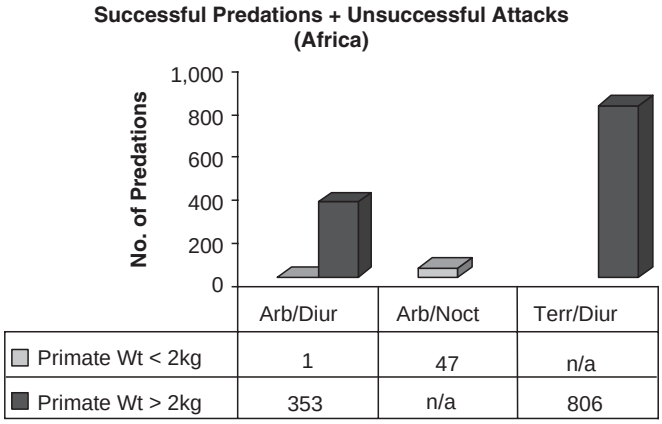


FIGURE 2.4. Comparison of recorded predation on African primates weighing <2 kg and >2 kg in three ecological groups; n/a denotes no primate species exist in that category (Data source: Hart, 2000)

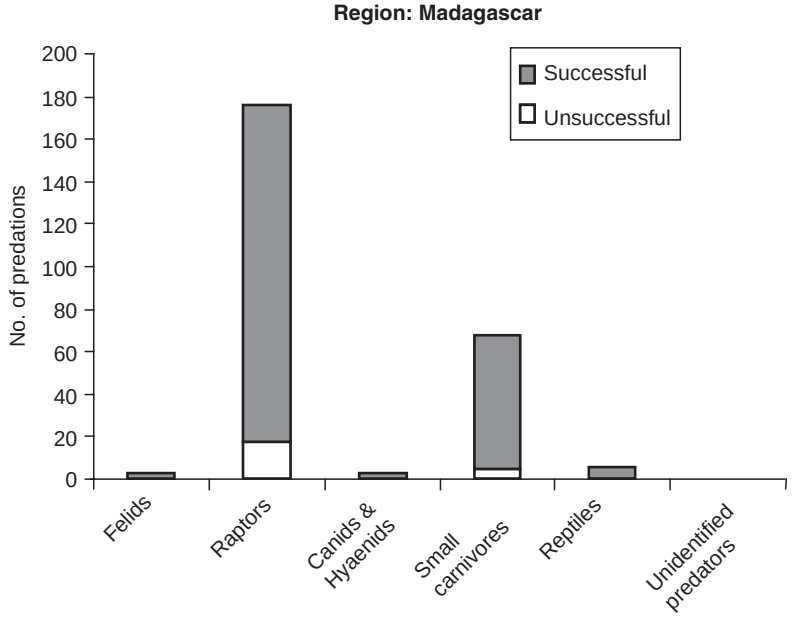


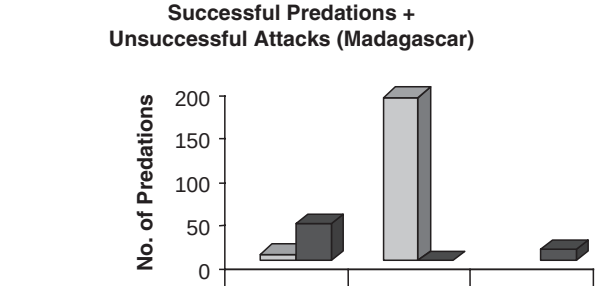
FIGURE 2.5. Comparison of successful and unsuccessful attacks by six categories of predators in Madagascar (Data source: Hart, 2000)

small carnivores (specifically, the fossa, *Cryptoprocta ferox*) are important as primate predators. Indeed, more than half of the predation data for all four regions included in the small carnivore category of Table 2.1 refer to the fossa. This is

easily attributed to the fossa's unique status on the island of Madagascar. No wild cats are indigenous to the island, and the fossa (a viverrid that weighs 20 kg and resembles a small North American puma) occupies the ecological niche of the island's absent felids. (The few instances of felid predation shown in Figure 2.5 are due to feral cats.) Some studies reveal that small carnivores, such as the fossa, may not target any particular age or sex of primate prey (Wright et al., 1997, 1998). Wright et al. (1998) described fossa as "equal opportunity" predators; deaths due to fossa predation in three groups of Milne-Edward's sifakas (*Propithecus diadema edwardsi*) were spread over all age and sex classes.

The fossa is the only species of small carnivore that has been the subject of repeated studies that have the objective of understanding the ecological relationship between a predator and its primate prey (Rasolonandrasana, 1994; Rasoloarison et al., 1995; Goodman et al., 1997; Wright et al., 1997). It is interesting to speculate that many of the small, fast-moving, arboreal carnivores may have the same capacity as fossa to inflict heavy predation on arboreal primates. At least six other species of these small carnivores prey on Madagascar primate fauna; they are Indian civet (*Viverricula indica*), Malagasy civet (*Fossa fossana*), narrow-striped mongoose (*Mungotictis decemlineata*), ring-tailed mongoose (*Galidia elegans*), Malagasy brown-tailed mongoose (*Salanoia concolor*), and broad-striped mongoose (*Galidictis spp*.). Small carnivores may be important predators on primates in other regions also, but no quantitative information exists on diets of African, Asian, or Neotropical small carnivores that have been identified as primate predators.

Malagasy prosimians (Figure 2.6) occupy five of the ecological groupings identified here. Arboreal-diurnal primates weighing less than 2 kg are represented only by bamboo lemurs (*Hapalemur spp*.); those over 2 kg include *Propithecus, Indri*, *Varecia*, and *Eulemur*. (For the purpose of comparison, cathemeral species,



	Arb/Diur	Arb/Noct	Terr/Diur
Primate Wt < 2kg	8	190	n/a
Primate Wt > 2kg	43	0	14

FIGURE 2.6. Comparison of recorded predation on Malagasy primates weighing <2 kg and >2 kg in three ecological groups; n/a denotes no primate species exist in that category; 0 denotes no predation events were reported (Data source: Hart, 2000)

such as *Eulemur*, were analyzed with arboreal-diurnal species.) The category of arboreal-nocturnal primates weighing less than 2 kg is occupied by the *Cheirogaleidae*. The terrestrial-diurnal, over-2-kg category is filled by the ring-tailed lemur (*Lemur catta*). The aye-aye (*Daubentonia madagascariensis*) is the only primate in Madagascar that is arboreal-nocturnal and weighs more than 2 kg. Except for *Daubentonia*, predation has been recorded for all other families of Malagasy primates.

Nocturnal raptors (the Malagasy owls) and the diurnal Madagascar harrier hawk (*Polyboroides radiatus*) are frequent predators on prosimians (Goodman et al., 1991; Goodman & Langrand, 1993; Goodman et al., 1993a, 1993b; Karpanty & Goodman, 1999; Brockman, 2003). The increasing number of studies that document Malagasy raptor diets has served to reveal the extent to which primates incur predation. Diurnal raptors, such as the Madagascar harrier hawk, are major predators of Verreaux's sifaka (*Propithecus verreauxi*), even though the primates are two to three times the size of the raptor (Karpanty & Goodman, 1999). Henst's goshawks (*Accipiter henstii*) weigh only 1.2 kg but successfully prey on large-bodied, arboreal-diurnal species as well as small-bodied, nocturnal primates (Goodman et al., 1998; Karpanty, 2003).

There is conspicuously high predation on small, arboreal-nocturnal primates in Madagascar. This may reflect the fact that Madagascar is the only region in which more nocturnal than diurnal primate genera have evolved. Ornithological research has made it apparent that small nocturnal primates on Madagascar constitute a prey base for many species of endemic owls, for example, *Tyto soumagnei, Otus rutilus*, and *Asio madagascariensis*, along with the Malagasy subspecies of barn owl (*Tyto alba affinis*) (Goodman et al., 1991; Goodman & Langrand, 1993; Goodman et al., 1993a, 1993b).

Asia

Leopards and tigers (*Panthera tigris*) incur a substantial impact on Asian primates. A good example comes from research in the Periyar Tiger Reserve, South India, where 81.4% ($n = 79$) of the leopard diet from September 1991–September 1994 consisted of Nilgiri langur (*Trachypithecus johnii*) (Srivastava et al., 1996). In Meru-Betiri Reserve, Indonesia, langurs and macaques were the predominant food of the leopard (56.9%, $n = 33$) in a study carried out by Seidensticker and Suyono (1980). Perhaps less intuitive than the leopard's reliance on primate prey is the tiger's penchant for primates. Tigers are usually assumed to take only very large ungulate prey. Nevertheless, Hanuman langurs (*Presbytis entellus*) are frequent prey of tigers in the forest of Ranthambhore, India, where the monkeys are often captured when moving between trees (Thapar, 1986). Schaller (1967) calculated that langurs made up 7.0% ($n = 21$) of the tiger diet in Kanha Park, India; Sunquist (1981) studied the composition of tiger diets in Chitawan Park, Nepal, finding that 5.7% ($n = 7$) consisted of langurs. Two recent studies carried out in Bangladesh and India indicate that rhesus macaques (*Macaca mulatta*) and langurs were the third highest components in tiger diets (Reza et al., 2001; Sankar & Johnsingh, 2002).

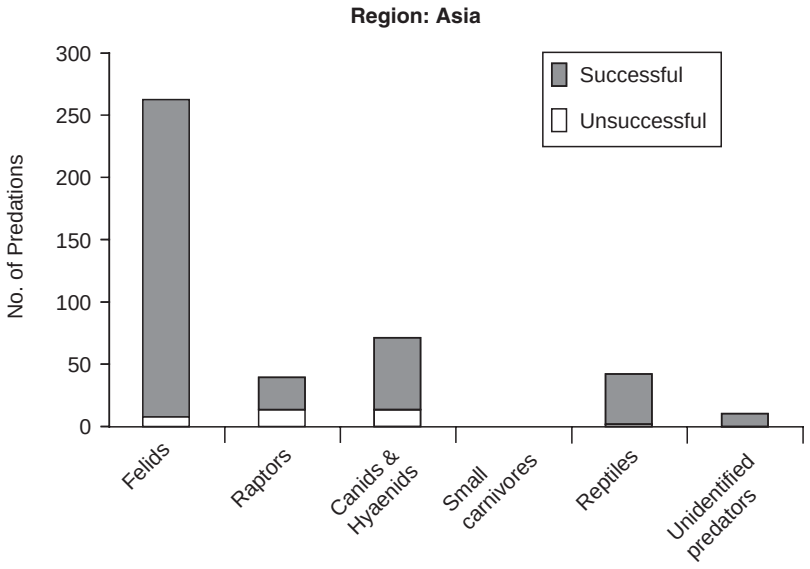


FIGURE 2.7. Comparison of successful and unsuccessful attacks by six categories of predators in Asia (Data source: Hart, 2000)

With regard to currently available data on primate predators, canids and hyaenids are not heavily represented in any region. Nevertheless, Asian canids—the golden jackal (*Canis aureus*) and the dhole (*Cuon alpinus*)—figure prominently as predators (Johnsingh, 1980; Newton, 1985; Stanford, 1989; D'Cunha, 1996; see Figure 2.7). Several Asian canids not previously considered primate predators have been identified in recent years. N. Itoigawa (pers. comm.) related that he has received anecdotal reports concerning red fox (*Vulpes vulpes*) and raccoon dog (*Nyctereutes procyonoides*) predation on Japanese macaques *(Macaca fuscata)*.

Wolves (*Canis lupus*) still exist in Saudi Arabia and other parts of Southwest Asia and are known to be quintessential opportunists throughout their nearly global range. Remains of *Papio hamadryas* were found in wolf scats in the Arabian Peninsula (Biquand et al., 1994). The decline in large Asian carnivores has been dramatic over the last several decades, but in the early 1970s wolves and Asian black bears (*Selenarctos thibetanus*) in Nepal were alleged to prey on Hanuman langurs (Bishop, 1975).

Asia is also notable for a relatively high incidence of reptile predation on primates. There are more reptile predations ($n = 43$) in Asia than in other geographic regions, although Africa has nearly as many ($n = 40$). When "suspected" reptile predations are added to successful and unsuccessful categories (refer to Table 2.1), the Asian figure ($n = 126$) is nearly three times higher than the figure for Africa

($n = 43$), over six times higher than that of the Neotropics ($n = 19$), and twenty-one times greater than the number for Madagascar ($n = 6$).

The first quantitative study of large tropical snake diets was published less than a decade ago (Shine et al., 1998). Specimens of *Python reticulatus* (an Asian snake in which females routinely reach a length of 7 m) were examined for stomach contents within the context of commercial exploitation for the skin trade. Although large ungulate prey were more easily identified in the hindgut than smaller primate species, Shine et al. (1998) calculated that 3.4% ($n = 14$) of the identifiable remains of food in the python alimentary tracts consisted of macaques and langurs. Pythons are also known to consume small, nocturnal Asian primates (Wiens & Zitzmann, 1999). During a study of slow loris (*Nycticebus coucang*) in Indonesia, weak signals from a radio-collared focal animal were traced to dense ferns on the forest floor. When these signals continued over a three-day period from such an unlikely location for an arboreal primate, researchers investigated and found a reticulated python. The signals were being emitted from the interior of the python, which had swallowed the loris.

Compared to other regions, the level of primate predation by raptors in Asia is low. Probably correlated with this minimal level is the fact that fewer raptor species have been identified as primate predators in Asia than other regions. Another reason may be a lack of field studies on South and Southeast Asian raptors. (Other than the Philippine eagle, *Pithecophaga jeffery*, I found no literature on the diets of Asian raptor species known to prey on primates.) If a similar body of field research becomes available for Asian raptors, as now exists for African birds of prey, this picture may change.

Asian primates (Figure 2.8) occupy only three of the ecological groups identified here: arboreal-diurnal primates over 2 kg in weight (*Pongo, Presbytis*, *Trachypithecus*, *Nasalis*, and others), terrestrial-diurnal primates over 2 kg

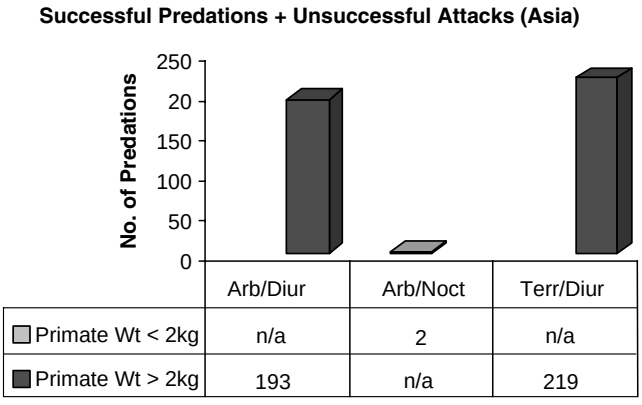


FIGURE 2.8. Comparison of recorded predation on Asian primates weighing <2 kg and >2 kg in three ecological groups; n/a denotes no primate species exist in that category (Data source: Hart, 2000)

(*Macaca*), and arboreal-nocturnal primates under 2 kg (*Tarsius, Nycticebus*, *Loris*). The large diurnal species are preyed on by leopards, tigers, dholes, jackals, crocodiles, and snakes, but until recently there were so few studies on small, nocturnal Asian primates (Rasmussen, 1997) that only two incidents were available for examination at the time of this meta-analysis. There are three genera of prosimians in Asia, half the number found in Africa and Madagascar, but the current surge in field research on nocturnal Asian primates has greatly expanded knowledge about predation on these species (see Wiens and Zitzmann, 1999, 2003; Gursky, 2002, 2003, 2005; Lakshmi and Mohan, 2002; Nekaris, 2003; Nekaris and Jayewardene, 2004).

The Neotropics

Figure 2.9 represents an overview of primate predation in the Neotropics. The paucity of felid predation is readily apparent despite the fact that two large cat species: jaguar (*Panthera onca*) and puma (*Felis concolor*), and four small felids: ocelot (*F. pardalis*), jaguarundi (*F. yagouroundi*), margay (*F. wiedii*), and oncilla (*F. tigrina*), have been identified as primate predators.

A variety of small hawk and falcon species inhabit Central and South American forests. Neotropical raptor species are twice as numerous as Old World species mainly because of the ubiquitous small forest falcons of the genus *Micrastur*. Thiollay (1985) describes the hunting techniques of small rainforest hawks and falcons as a combination of active and inactive behaviors; sitting motionless

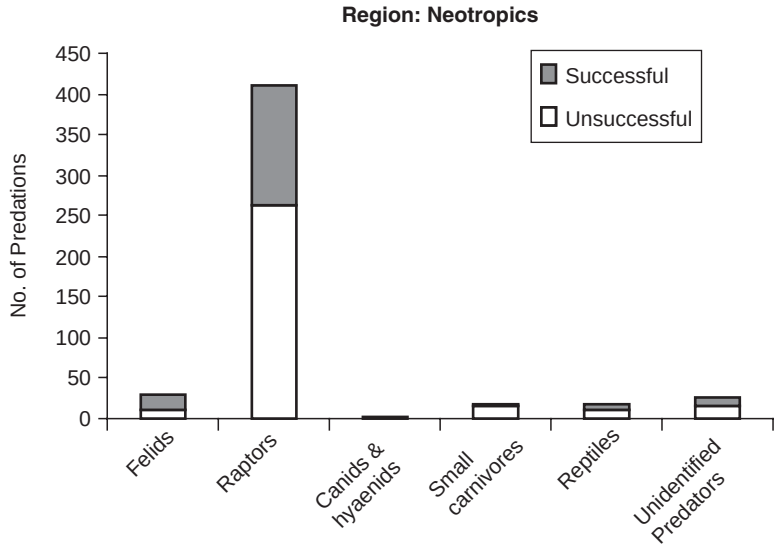
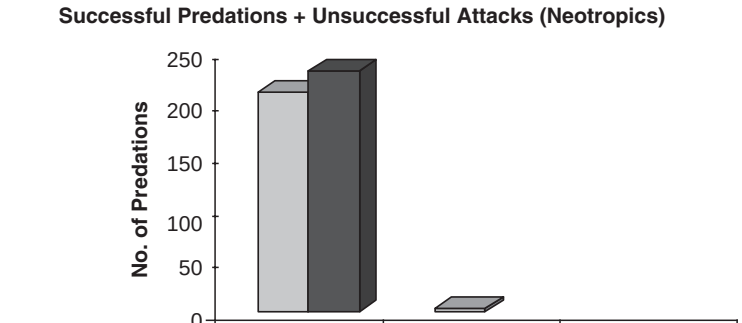


FIGURE 2.9. Comparison of successful and unsuccessful attacks by six categories of predators in the Neotropics (Data source: Hart, 2000)

FIGURE 2.10. The harpy eagle is the premier raptor of the Neotropics (Used by permission of R.W. Sussman)

and inconspicuous, they intersperse inactivity with occasional swift, soundless flights from tree to tree. Some species, such as the collared forest falcon (*M. semitorquatus*), pursue active hunting. This raptor actually runs along branches in pursuit of prey (Thiollay, 1985). Many of the predation attempts by Neotropical hawks, falcons, and toucans are unsuccessful, but this does not deter frequent attacks on callitrichids and very young squirrel monkeys (Terborgh, 1983; Boinski, 1987; Goldizen, 1987; Mitchell et al., 1991).

The harpy eagle (*Harpia harpyja*, Figure 2.10) is one of the largest and strongest raptors in the world (Brown & Amadon, 1989). This species exhibits the same short, broad wings and relatively long, graduated tail as the crowned hawk-eagle of



	Arb/Diur	Arb/Noct	Terr/Diur
Primate Wt < 2kg	209	2	n/a
Primate Wt > 2kg	230	n/a	n/a

FIGURE 2.11. Comparison of recorded predation on Neotropical primates weighing <2 kg and >2 kg in three ecological groups; n/a denotes no primate species exist in that category (Data source: Hart, 2000)

Africa. Ecological equivalents, the two raptors have garnered similar reputations as premier predators on monkeys (Izor, 1985).

There are two features of the Neotropical primate component not found in other regions (Figure 2.11): it lacks a terrestrial species and it has only a single nocturnal genus. Considerable predation is recorded for small and large arboreal-diurnal Neotropical primates, i.e., the callitrichids and the cebids. The only New World primate that is arboreal and nocturnal is *Aotus,* the owl monkey, for which a small number of predations by owls has been recorded (Wright, 1985; Brooks, 1996). There are no Neotropical primates inhabiting other ecological divisions identified here.

Estimated Predation Rates

Estimated predation rate (EPR), the percentage of a primate population killed annually by predators, provides a valuable insight into the effect predation has on a primate group. Additionally, EPR calculations measure the effect of predator mortality on all components of the population, including the reproductively active portion. This is an important caveat since estimated rates of predation on immature primates (infant and juvenile age classes) may be higher in comparison to adults. Janson and van Schaik (1993) compared immature versus mature primates and estimated the predation rate was 3–17 times higher for immature individuals than for adults in species of cercopithecines and 3–6 times higher in cebids.

Figure 2.12 displays mean estimated predation rates for four regions. Madagascar has the highest mean EPR (8.9 %, $n = 6$), and Asia has the lowest (3.0 %, $n = 19$). Mean EPRs for Africa and the Neotropics are 5.6% ($n = 57$) and 6.7% ($n = 14$), respectively. Estimated predation rates ranged from zero to

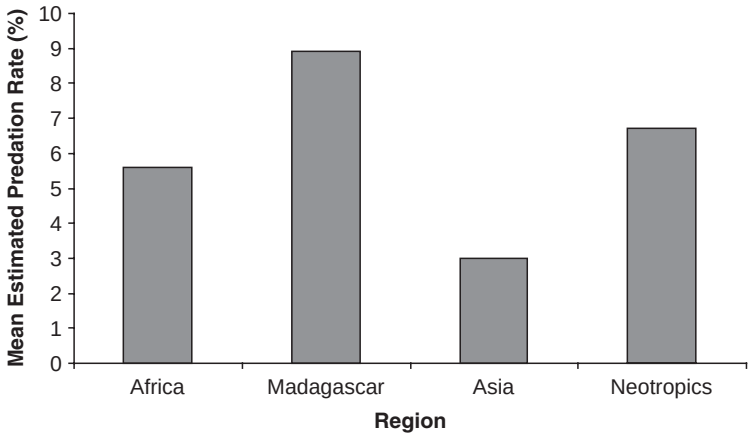


FIGURE 2.12. Comparison of mean estimated predation rates by region (Data sources: Hart, 2000; Mitani et al., 2001; Shultz, 2003)

TABLE 2.2. Estimated predation rates for primate weight and ecological groupings (Data sources: Hart, 2000; Mitani et al., 2001; Shultz, 2003).

Primates < 2 kg Arboreal Diurnal ($n = 7$)	Primates < 2 kg Arboreal Nocturnal ($n = 4$)	Primates > 2 kg Arboreal Diurnal ($n = 38$)	Primates > 2 kg Terrestrial Diurnal ($n = 44$)
Mean EPR	Mean EPR	Mean EPR	Mean EPR
7.0%	15.8%	5.4%	4.4%
Range	Range	Range	Range
1.0–15.0%	8.6–25.0%	0–18.0%	0–15.0%

25.0% in this sample. The inclusion of a zero predation rate is due to calculations by questionnaire respondents who lost no study animals to predators over a number of years. (Of course, it is possible that aberrant conditions existed at these study sites, such as the eradication of predators in the area or human disturbance causing predators to disperse.) The highest rate in the sample is 25.0% of a *Microcebus* population lost to predation each year (Goodman et al., 1993c). This EPR is based on predation by two genera of owls and does not include additive predation by diurnal raptors, snakes, or small carnivores. The high reproductive potential of *Microcebus* counteracts what would seem to be an intolerable level of predation (Goodman et al., 1993c; Hill & Dunbar, 1998). Unlike most primate species, some Malagasy prosimians (including *Microcebus*) produce an average of two infants twice per year (Martin, 1972). The mouse lemur is able to sustain a predation rate of 25.0% because, for a primate, it has a very high reproductive potential (Goodman et al., 1993c).

In Table 2.2 estimated predation rates for primates are summarized from the perspective of ecological groupings used in this chapter. The highest predation rate was incurred by small, arboreal-nocturnal primates. This may be partially reflective of the 25.0% EPR calculated for mouse lemurs; in addition, the sample

sizes are very small for two of the categories ($n = 4, n = 7$) and relatively large for the other two ($n = 38, n = 44$).

Frequency of Occurrence of Primates in Predator Diets

Frequency of occurrence is defined as the number of individual prey animals of one taxon relative to all prey eaten (Rabinowitz & Nottingham, 1986). Expressed as a percentage of all food intake by a predator, frequencies of occurrence can be estimated using various methods. (Table 2.3 lists these techniques along with the number of studies in the data set that used each sampling method.) Boshoff et al. (1994) give an excellent explanation of how frequencies of occurrence provide a good approximation of the composition and species richness of prey; any biases can be assumed to be common to all samples, so comparison between samples is valid.

It should be noted that frequencies of occurrence of primates in predator diets are based on conservative estimates. These methods usually result in underestimates since biases against finding the remains of young, small, or nocturnally active prey are exacerbated by several processes (Rice, 1986; Thapar, 1986). Primates are often underrepresented when frequencies of occurrence are calculated from direct observation of kills or examination of prey carcasses due to the rapidity with which small carcasses are consumed by large carnivores (Schaller, 1972; Eloff, 1973; Floyd et al., 1978; Bothma & Le Riche, 1986). Furthermore, the chance that skeletal remains pass through the digestive tract of a carnivore in recognizable form is greater for large prey animals than for smaller ones (Muckenhirn, 1972). Even when the largest primates fall prey to a carnivore, the remains disappear rapidly in tropical climates. All traces of a western lowland gorilla killed by a leopard in Gabon were nearly gone three or four days after death due to consumption by the primary predator, scavengers, and insects (Tutin & Benirschke, 1991). A similar amount of time was noted for the disappearance of a chimpanzee carcass after leopard predation in the Taï forest, Côte d'Ivoire (Boesch, 1991). Fecal samples from predators are also difficult to collect in tropical forests because they may be destroyed within hours by dung beetles and trigonid bees; only those containing large amounts of fur or those placed in sunny areas survive a few days (Emmons, 1987).

The most commonly used methods (fecal sampling, pellet/regurgitation sampling, analysis of nest or den remains, and analysis of prey carcasses) provide

TABLE 2.3. Frequency of occurrence sampling methods (Data source: Hart, 2000).

Type of Sampling Method	Number of Studies
Stomach contents	3
Fecal sampling	33
Pellets and regurgitations	8
Nest and den remains	38
Analysis of prey carcasses	9
Direct observation of kills	5

information on food ingested over an extended period of time and are non-invasive, unlike analysis of stomach contents, which involves dissection of the predator. Direct observation of kills has the advantage of providing indisputable confirmation of predation rather than scavenging, but it requires both perseverance and luck. As a sampling method it yields more limited information since only one meal at a time can be identified. Another drawback to direct observation is that prey are often alerted to predators or made more vigilant when human observers are present (Isbell & Young, 1993). Observing the kill of a secretive, nocturnal predator, such as the leopard, is particularly problematic. Despite nearly half of the vervet population under study falling victim to leopards during one year at Amboseli National Park, Kenya, no monkeys were killed within sight of researchers (Isbell, 1990). The sampling of feces, regurgitations, nest or den remains, and prey carcasses provides an estimate of the minimum number of preyed-upon individuals of one taxon, and it requires a tedious cleaning and reconstruction process (Figure 2.13). Nest and den remains yield excellent data for compilation of predator diets since several nesting cycles result in large build-ups of prey bones within and below raptor nests (Sanders et al., 2003; Shultz et al., 2004). The larger the collection of nest and den remains the greater the accuracy of dietary content.

The percentage of a predator's diet composed of primates ranged widely in the data set described here. At the upper end of a continuum, nest remains of forest-hunting African crowned hawk-eagles identified 80–90% of their diet as primates

FIGURE 2.13. Leopard scat containing two gorilla hind digits was found by researchers in the Central African Republic; one intact toe has been removed from the fecal matter and is clearly visible on the right (Used by permission of Michael Fay)

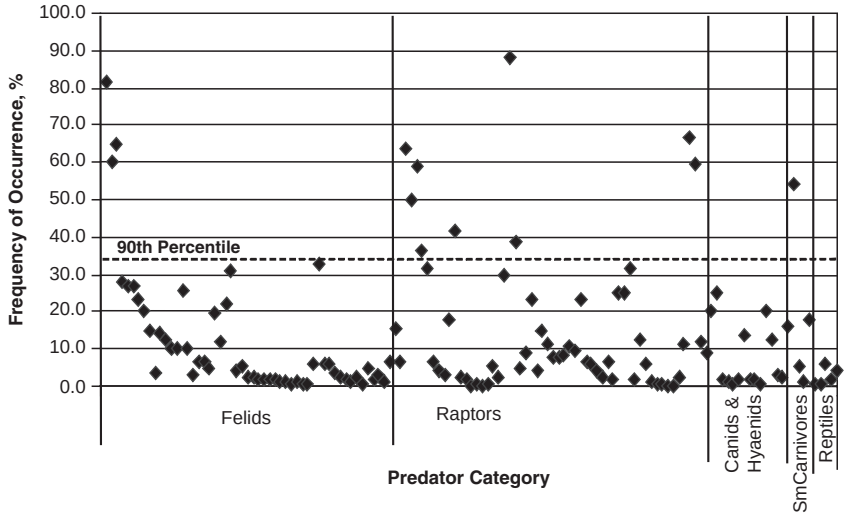


FIGURE 2.14. Frequency of occurrence of primates in predator diets. Each point represents data from a field study on a species of felid, raptor, canid and hyaenid, small carnivore, or reptile plotted as a percentage of primates found in the diet of a single predator. Median values: felids, 5.2%, $n = 53$; raptors, 7.6%, $n = 59$; canids and hyaenids, 2.0%, $n = 13$; small carnivores, 10.6%, $n = 4$; reptiles, 3.0%, $n = 6$ (Data source: Hart, 2000)

of various species (Skorupa, 1989; Struhsaker & Leakey, 1990; Msuya, 1993; Mitani et al., 2001). At the lower end a study of Verreaux's eagles (*Aquila verreauxii*), an African savanna raptor, estimated only 0.05% ($n = 27$) of the diet was composed of primates (Boshoff et al., 1991). Frequencies of occurrence were available from 96 studies on 35 species of predators. More data were collated on felid and raptor diets containing primates than for other predators (Figure 2.14). Extensive research is available analyzing the total range of hyena and wild canid prey, mostly large savanna ungulate species (Estes & Goddard, 1967; Henschel & Tilson, 1988; Johnsingh, 1980, 1983; Kruuk, 1970, 1972; Kruuk & Turner, 1967; Mills & Biggs, 1989), so it is plausible to compare them with felids and raptors in Figure 2.14. Reptile and small carnivore species inhabiting the same geographic ranges as primates have not been the focus of many studies intended to generate information on diet composition (reptiles $n = 5$, small carnivores $n = 4$). Taking this into consideration, however, it is still apparent that felids and raptors are major predator groups where the killing of primates is concerned. Only felids, raptors, and one small carnivore, the fossa, have frequencies of occurrence that fall above the 90th percentile.

In Figures 2.15–2.18 means were determined for the percentage of primates in the diets of different predator groups by first averaging each separate species' frequency of occurrence percentages and then calculating the mean for all species within each predator group. These means are presented separately for Africa, Madagascar, Asia, and the Neotropics to facilitate comparison across regions.

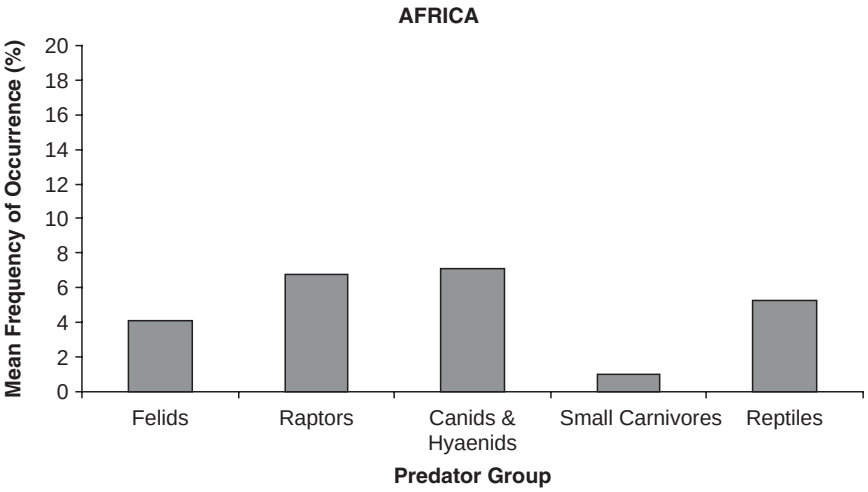


FIGURE 2.15. Five groups of African predators are compared by frequency of occurrence of primates in their diets. Number of identified primate predators in Africa: felids, $n = 7$; raptors, $n = 22$; canids and hyaenids, $n = 7$; small carnivores, $n = 9$; reptiles, $n = 12$ (Data sources: Hart, 2000; Mitani et al., 2001; Shultz, 2002; Zuberbühler & Jenny, 2002)

In Africa (Figure 2.15) there is a relatively narrow range of percentages of primate prey among the five predator groups; the highest mean component of primates occurs in canid and hyaenid diets (7.1%, $n = 2$ species), and the lowest occurs in small carnivore diets (1.0%, $n = 1$ species). Within the narrow range, raptor diets averaged 6.8% primate prey ($n = 7$ species), reptiles 5.3% ($n = 2$ species), and felids 4.1% ($n = 4$ species).

Frequency of occurrence of primates in Malagasy predator diets (Figure 2.16) reveals an emphasis on raptor and small carnivores. Mean raptor frequency of occurrence was 17.2% ($n = 6$ species), and mean small carnivore frequency was 25.1% ($n = 1$ species). Seventeen raptor species have been identified as primate predators in this region (58.6% of the total predator component). This is the highest ratio of raptor to total predator numbers in any region. The highest estimated predation rates in any region are also due to Malagasy birds of prey.

The frequency with which primates appear in the diets of Asian predators (Figure 2.17) is similar to Africa except that felids have a much higher mean frequency of primates in their diets (15.0%, $n = 2$ species). Raptors averaged 4.4% primate prey ($n = 1$ species), canids and hyaenids 4.0% ($n = 3$ species), and reptiles 4.1% ($n = 2$ species). No frequency of occurrence data were available for small carnivores in Asia.

Neotropical raptors have the highest mean percentage of primates in their diets (36.6%, $n = 2$ species) of any predator group in any region. All other predator consumption of primates in the Neotropics is negligible by comparison. Figure 2.18 also presents an apparent association between the number of identified Neotropical raptor species that prey on primates ($n = 30$) and these high

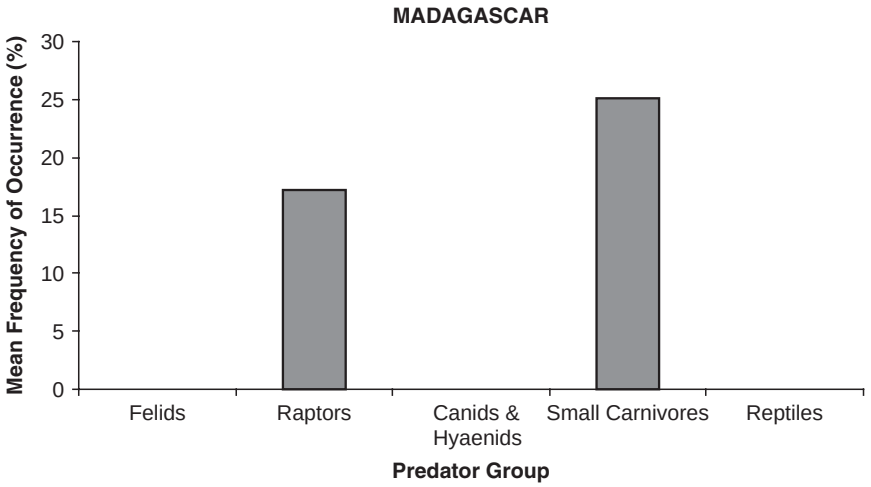


FIGURE 2.16. Five groups of Malagasy predators are compared by frequency of occurrence of primates in their diets. Number of identified primate predators in Madagascar: felids, $n = 0$; raptors, $n = 17$; canids and hyaenids, $n = 0$; small carnivores, $n = 7$; reptiles, $n = 5$ (Data sources: Karpanty & Goodman, 1999; Hart, 2000; Thorstrom & La Marca, 2000)

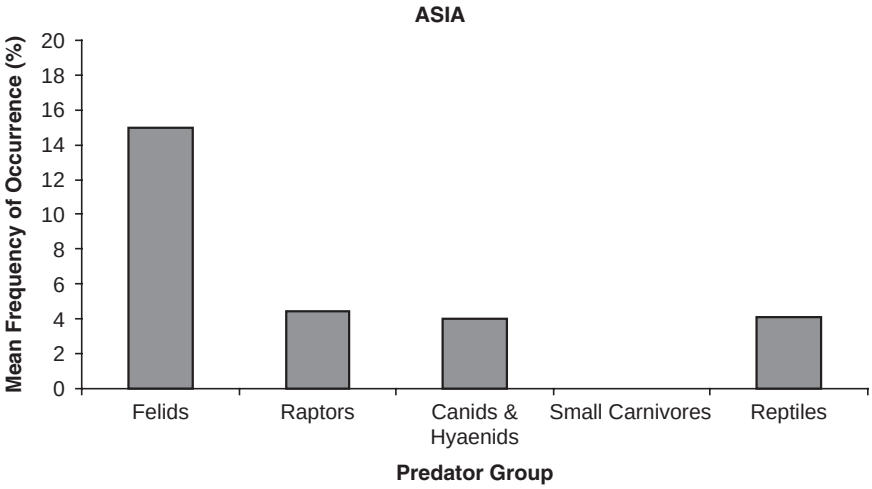


FIGURE 2.17. Five groups of Asian predators are compared by frequency of occurrence of primates in their diets. Number of identified primate predators in Asia: felids, $n = 8$; raptors, $n = 15$; canids and hyaenids, $n = 6$; small carnivores, $n = 3$; reptiles, $n = 7$ (Data sources: Hart, 2000; Reza et al., 2001; Sankar & Johnsingh, 2002; Uhde & Sommer, 2002)

frequencies of occurrence. The mean primate component in raptor diets in the Neotropics is more than twice as high as this figure in Madagascar, more than four times higher than Africa's, and more than eight times higher than the figure in

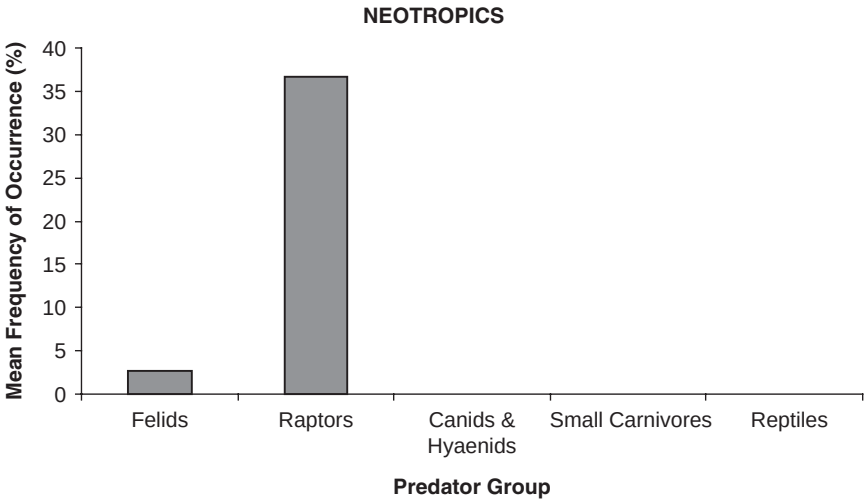


FIGURE 2.18. Five groups of Neotropical predators are compared by frequency of occurrence of primates in their diets. Number of identified primate predators in the Neotropics: felids, $n = 6$; raptors, $n = 30$; canids and hyaenids, $n = 1$; small carnivores, $n = 4$; reptiles, $n = 13$ (Data source: Hart, 2000)

Asia. Therefore, while there are more Neotropical raptor species, they also prey on many more primates than raptors of other regions.

Discussion

Biogeographical associations and insights have emerged from this meta-analysis despite the necessary reliance on preliminary and non-random data. What are the biogeographical patterns that account for links between primate regions and certain types of predation? With some exceptions, there appears to be a possibility of two primate predation patterns based on frequency of occurrence data. One pattern is apparent in Africa and Asia and consists of modest levels of predation spread among many predator taxa. It may be that shared predators (the leopard, lion, cheetah, striped hyena, and several species of canids) in combination with shared primate taxa (Catarrhini) enhance the perceived similarity between the two regions.

The other pattern found in Madagascar and the Neotropics consists of heavy predation by a narrower range of predators. High levels of raptor predation define a common link between Madagascar and the Neotropics. The four highest mean frequencies of primates in individual predator species diets were raptors indigenous to Madagascar and the Neotropics—Henst's goshawks, Madagascar long-eared owls (*Asio madagascariensis*), harpy eagles, and Guiana crested eagles (*Morphnus guianensis*). There is a complete absence of wild felids, canids, or

hyaenids in Madagascar. While this pattern is not paralleled in the Neotropics, especially concerning wild cat species, there are no hyaenids, and only one wild canid predator—the coyote (*Canis latrans*)—is suspected to be a primate predator in Central America. Nevertheless, it would be presumptuous to infer indelible patterns from the analysis in this chapter, due to the many limiting factors. Perhaps the most limiting factor is that extensive research efforts are made on certain species of primate predators while other identified predators remain known only through anecdotal reports. This lack of random data collection skews the picture of primate predation to an unknown degree.

Primates are "generalist" prey in the sense that, as a taxon, they range in size from 60 g to 169.5 kg, they inhabit geographic ranges throughout the tropics, subtropics, and a few temperate forests, they range from completely arboreal to wholly terrestrial, and they include both nocturnal and diurnal species. Their successful radiation into many ecological niches carried with it the potential to interact with many predators. The 174 primate predators identified in Hart (2000) include many opportunistic feeders. While there are key primate predators among these species, there are no examples of predators with a rigidly narrow food base that forces them to prey only on primates.

Co-evolution between predators and their primate prey is most visible from the behavioral and morphological adaptations in primates that are traceable to specific predators (Terborgh, 1983). For example, primate polyspecific associations are limited to geographic regions inhabited by monkey-eating raptors (e.g., harpy eagles of the Neotropics and crowned hawk-eagles of Central and West Africa), which are predators that provide a strong incentive for aggregation (Gautier-Hion et al., 1983; Terborgh, 1990a). Terborgh (1983) discussed the relationship between body size and methods of escape from raptor predation among Neotropical primates at Cocha Cashu, Peru. He identified three distinct strategies adopted by primates: crypsis, group living, and escape from predators through an increase in size. The smallest primates (tamarins and marmosets) spend many hours per day in safe hiding places; medium-sized *Cebus* and *Saimiri* seek protection in groups. The remaining evolutionary adaptation in Terborgh's model, that of size increase, applies to adults of the largest Neotropical species, i.e., *Ateles, Brachyteles, Lagothrix*, and *Alouatta*. These primates often rest in conspicuous exposed perches in the canopy, from which they scan for harpy and Guiana crested eagles. Although the two raptors are known as capable predators of the largest Neotropical primates, they do not pass up primates of any size. Harpy eagles prey most frequently on *Cebus* (Voous, 1969); Guiana crested eagles even prey on infant tamarins (Vasquez & Heymann, 2001).

Consistently high predation rates on primates may indicate long-term predator-prey relationships. Many years of recording leopard predation on vervets at Amboseli have produced an estimated predation rate of 11.0–15.0% (Cheney & Wrangham, 1987; Isbell, 1990). Owl predation on mouse lemurs (Goodman et al., 1993b) was estimated to be 25.0% annually. However, a "high" estimated predation rate is not the only, or necessarily most important, criterion for determining the levels at which certain predators may kill primates for food. The estimated

predation rates for crowned hawk-eagle exploitation of red colobus, black and white colobus, mangabey, and blue monkeys in the Kibale forest range from 0.3–3.0%, depending on the species of primate, but the frequency of occurrence of primates in the diet of the eagle pairs under study was 83.7% (Struhsaker & Leakey, 1990). Thus, frequency of occurrence of primates in the diet of a predator may be a more precise measure of the predator-prey relationship than EPR since the latter can be calculated as the collective effect from many predators in an ecosystem. Frequencies of occurrence, on the other hand, present a clear connection between the predator and its prey.

Primates have been observed to be secondary prey in some geographic locations and primary prey for the same predator species in another (Brown, 1966; Seidensticker & Suyono, 1980). Differences may exist in levels of predation on primates due to richness of other fauna or because other prey species have been eliminated by natural or human-induced causes. Seidensticker (1983, 1985, 1991) examined field studies containing reliable data in order to identify the environmental correlates in which primates account for a major portion of African and Asian leopard diets. He credits primate body size and availability of ungulate prey as key factors: If there were abundant ungulate species in the 20–50-kg range, leopards ate few primates; if ungulates in this size class were present but at low density, leopards had intermediate numbers of primates (i.e., <30%) in their diet; if this size class of ungulate was missing from the faunal composition, leopards had high proportions of primates in their diet. In four cases this pattern is substantiated: (1) Seidensticker & Suyono (1980) discovered that *Trachypithecus cristata* and *Macaca fascicularis* were the predominant food of tiger, leopard, and dhole in Meru-Betiri Reserve, Indonesia, because small ungulates have been extirpated by humans. Primates in the reserve are the substitute for a range of other prey normally available to large Asian carnivores. (2) In the Periyar Tiger Reserve, India, where Nilgiri langur account for 81.4% of the leopard diet, there is an absence of large ungulate species such as chital (*Axis axis*), hog deer (*A. porcinus*), and swamp deer (*Cervus duvanceli*). Ungulates weighing 20–50 kg are also not available to leopards; the Nilgiri tahr (*Hemitragus hylocrius*) exists only in isolated pockets, and sambar (*Cervus unicolor*) is the major prey item in the diet of a competing predator, the pack-hunting dhole (Srivastava et al., 1996). (3) At another site in India, Eravikulam National Park, where small ungulates, such as Nilgiri tahr, sambar, and barking deer (*Muntiacus muntjak*) were common, the remains of these animals occurred in 94.0% of tiger droppings collected for analysis and in 77.0% of leopard droppings. Remains of Nilgiri langurs appeared in no tiger droppings and in 27.0% of leopard droppings (Rice, 1986). In addition, all leopard sightings occurred within the home ranges of tahr, and leopards were seen hunting tahr in 36.0% of the sightings (Rice, 1986). (4) Niokolo-Koba National Park in Senegal does not contain dense concentrations of ungulates, and Guinea baboons (*Papio papio*) are the commonest large herbivore (Byrne, 1982). A high risk of predation from healthy populations of both diurnal African hunting dogs (*Lycaon pictus*) and nocturnal predators, such as leopards, lions, and spotted hyenas (*Crocuta crocuta*), was inferred from baboon behavior and social structure, specifically through

frequent alarm vocalizations, extreme wariness of open spaces, and unusually high numbers in baboon troops. In addition, a paucity of secure sleeping sites may increase the likelihood that considerable predation on baboons occurs. Baboons are "likely to be more important in the diet of all large predators than would be the case in East Africa" (Byrne, 1982, p. 308).

Studies of geographically variable interactions have been credited with furthering an understanding of how evolution affects predator-prey systems (Abrams, 2000). Before true comparisons can further our understanding of the evolutionary ecology of primate predation, however, it will be necessary to study many more predator species throughout the four regions in which primates exist. When more of this critical information is forthcoming, the biogeographic emphasis can then shift from the search for mere associations to that of statistical correlations that may exist between predation and primate ecology, morphology, and behavior. That said, the four regional analyses, in which all possible combinations of primate body size, stratum occupied, and activity cycle were examined for any ecological groups that might be exempt from predation (see Figures 2.4, 2.6, 2.8, and 2.11), indicate the extent and all-encompassing character of predation on primates. There were no variable combinations of body size, stratum, activity cycle, or geographic region that protected primates from predators. Even without knowledge of the exact rates of predation, it is safe to hypothesize that primates are preyed upon no matter what size they are or what ecological variables they exhibit.

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2
Predation on Primates: A Biogeographical Analysis

D. Hart

Introduction

Measuring the magnitude of predation has been deemed an important task in clarifying aspects of primate ecology (Terborgh & Janson, 1986). This goal is in keeping with a general theoretical shift noted by Sih et al. (1985) toward acknowledgment that predation often has a greater impact than resource competition on individual animals through behavior and life history; on prey populations through size and stability; and on ecosystems through diversity and relative abundance patterns. Biogeography, as a comparative observational science dealing with spatial and temporal scales too large for experimentation, seeks patterns of biodiversity upon which theories may be formulated (Brown & Lomolino, 1996). Primate predation studies benefit from a biogeographical approach when primates and their predators are assessed from the standpoint of four major regions: Africa, Madagascar, Asia, and the Neotropics. Since predation is thought to have affected morphological, ecological, and behavioral traits in primates (Hart, 2000; Zuberbühler & Jenny, 2002), a comparison of the four regions may facilitate identification of broad biogeographic patterns that are associated with predation.

Erroneous assumptions concerning predation as a demographic variable find their way into published comments. One commonplace, but erroneous, assumption is that "mortality due to predation appears to be negligible" (Dunbar, 1988, p.53). Opinions have ranged from a belief that the role of predation in primate evolution is minimal (Raemakers & Chivers, 1980; Wrangham, 1980; Cheney & Wrangham, 1987) to theories that predation is a powerful force in shaping social patterns (van Schaik, 1983; Terborgh & Janson, 1986; Dunbar, 1988; Hart, 2000; Hart & Sussman, 2005). Recent reviews and studies on topics such as the vulnerability of baboons to predation (Cowlishaw, 1994), ecological patterns of predation on primates (Isbell, 1994a), the status of predation research (Boinski & Chapman, 1995), predation rate versus predation risk (Hill & Dunbar, 1998), and the influence of predation on arboreal primates (Treves, 1999) have expanded theoretical discussion of this topic. Nonetheless, because observation of predation in the primate literature is often anecdotal rather than quantitative, there has been a

tendency to underestimate the pervasive influence predation has on the behavior and ecology of primates (Caine, 1990).

Large-scale patterns in predation have been discussed in broad theoretical terms but never assessed using quantified data. Moreover, there have been few attempts to recruit research carried out on various predators as an aid to understanding the impact of predation on primates. Predator-prey relationships are best studied from the perspective of the predator (Washburn et al., 1965; Cheney & Wrangham, 1987; Isbell, 1994; Boinski & Chapman, 1995; Mitani et al., 2001). Observation of only one group of one species (the typical parameters of primate research) provides limited data and often skews the perception of predation, whereas fieldwork on predatory species gives an ecosystemic view of several trophic levels. The home range of a solitary predator usually overlaps numerous prey groups and species; while the predator hunts on a daily basis, it may only occasionally attack the primate group under study. Primatologists have rarely viewed their subjects as prey, and the inclusion of predators into the realm of primate ecology has not been common. To that end, I conducted a meta-analysis of predation on primates that can serve as a basis for objective review of this topic.

Methods

Meta-analysis is the branch of statistics wherein data from various sources are combined (Halvorsen, 1986). Because the broad overview of data collected in my study is a first attempt to quantify the entire spectrum of predation on primates, a descriptive numerical summary is needed to deal with the data in manageable form (Sokal & Rohlf, 1981; Mansfield, 1986). Since it was not possible to collect data from all research sites in a random sampling, I collected raw data and used descriptive statistics throughout to summarize these data. Frequency distributions are used for comparison of variables, and summaries based on percentages are employed to interpret specific issues.

Primate data were categorized as follows: (1) by geographic region: Africa, Madagascar, Asia, and the Neotropics; (2) by body size divided into two categories: because body weights of primates extend along a continuum from 60 g to 169.5 kg, I selected a reasonable arbitrary weight division of under and over 2 kg to separate small-bodied from large-bodied primates; (3) by stratum generally occupied: arboreal or terrestrial; and (4) by daily activity cycle: diurnal or nocturnal (a decision to limit the activity cycles to these two divisions was based on the realization that more precise divisions, such as cathemeral, would constitute very small fractions of the data set).

For each primate prey, the equivalent data on its predator were also collated as follows: (1) by broad predator categories: felids, raptors, canids and hyaenids, small carnivores (which included the vivverid, herpestid, and mustelid families), reptiles, or unidentified (if the predator left a dead or dying primate but was not itself observed); (2) by geographic region: Africa, Madagascar, Asia, and the

Neotropics; (3) by weight in kilograms (predators ranged from *Vanga curvirostris*, weighing 72 g, to *Crocodylus palustris*, weighing 227 kg); (4) by stratum occupied: aerial, arboreal, terrestrial, or aquatic; and (5) by daily activity cycle: diurnal or nocturnal.

Data were drawn from both published and unpublished sources (viz., the scientific literature and my own questionnaires) based on the fieldwork of primate researchers, ornithologists, herpetologists, and mammalogists. Data were derived from observed predation events and studies of predation that have produced quantitative results. The latter are heavily dependent on predator research and offer information on the entire spectrum of prey in the diet of many of the 174 primate predator species identified by Hart (2000). Along with other food items, primate remains—ranging from the smallest (*Microcebus*) to the largest (*Gorilla*)—have been found in predator scats, pellets, nests, and dens.

One hundred and seventy-four predator species identified in this meta-analysis were divided into five broad categories: *felids* (21 species of wild cats), *raptors* (82 species of hawks, eagles, owls, and other predatory birds), *canids* and *hyaenids* (10 species of wild dogs and jackals and 3 species of hyenas), *small carnivores* (22 species of civets, genets, mongoose, the fossa, and a tropical weasel, among others), and *reptiles* (36 species of snakes, crocodilians, and monitor lizards). Ecology rather than taxonomy was emphasized in the predator categories; for instance, taxonomically the hyenas are more closely related to felids than canids, but the predation strategies of dogs and hyenas (i.e., pack hunting and coursing after prey) justify combining the two carnivore families.

While all categories of primate mortality are pertinent and deserve further research, the meta-analysis described in this chapter was deliberately limited to the relationship between primates and the groups of carnivorous animals that are predatory by definition. Neither an analysis of human predation on non-human primates nor predation by primates on other primates was attempted. There is a large body of literature detailing human exploitation of primates (see Mittermeier, 1987; Mittermeier & Cheney, 1987; Peres, 1990; Alvard & Kaplan, 1991; Alvard, 1994; Oates, 1994, 1996; McRae, 1997; Redmond, 1998; McNeil, 1999). Less is known about the effects of non-human primate predation on other primates. Chimpanzees, orangutans, baboons, blue monkeys (*Cercopithecus mitis*), capuchin monkeys (*Cebus spp.*), red-fronted brown lemurs (*Eulemur fulvus rufus*), and dwarf lemurs (*Microcebus coquereli*) have been observed hunting and eating smaller primates (see Hart, 2000). A few instances of primates preying on other primates are relatively well studied, particularly chimpanzee predation (Uehara et al., 1992; Stanford et al., 1994; Stanford, 1995; Stanford & Wrangham, 1998). At Gombe National Park in Tanzania, chimpanzee predation on red colobus (*Procolobus badius*) is extensive, alleged to account for "an annual harvest of from 16.8 to 32.9% of the red colobus population, depending on the number of male chimpanzees and the precise size of the red colobus population in a given year" (Stanford et al., 1994, p. 221).

Results

A total of 3,592 primate mortalities and unsuccessful predation attempts were identified. This establishes a baseline for understanding the biogeographical patterns of predation on primates. General patterns will be examined prior to discussing the four regions separately.

Figure 2.1 is an overall representation of 3,592 instances of predation cited in questionnaires and literature, classified by geographic region and predator category. Table 2.1 separates the predation incidents into unsuccessful attacks ($n = 679$, 18.9%), successful predations ($n = 2,229$, 62.1%), and suspected predations ($n = 684$, 19.0%). (See (Hart, 2000) for data sources and a discussion of the number of reported predation events as a function of the number of sources from which they were collected.) Felids and raptors accounted for the most predations on primates (34.6%, $n = 1,243$ and 40.7%, $n = 1,461$, respectively), followed by unidentified predators (9.0%, $n = 323$), canids and hyaenids (7.0%, $n = 253$), reptiles (5.4%, $n = 194$), and small carnivores (3.3%, $n = 118$).

Table 2.1 requires explanation lest the reader equate the number of predation events listed with the number of identified primate predator species. There is no direct cause and effect relationship between these two variables because the number of predation events is not random but, rather, the outcome of studies directed at specific primates or predators. Thus, the data on unsuccessful attacks, successful predations, and suspected predations by felids, raptors, canids and hyaenids, small carnivores, and reptiles are representative of those primates or predator species that

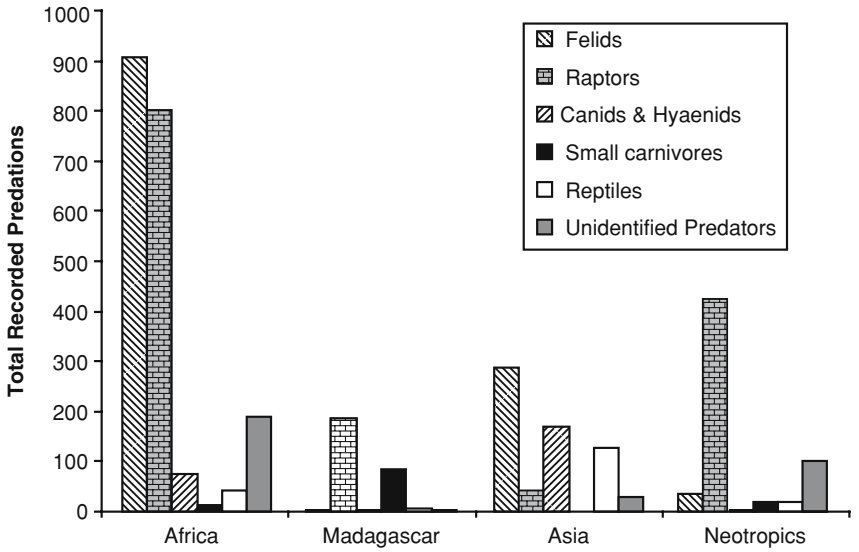


FIGURE 2.1. Overall magnitude of recorded predation on primates (Data source: Hart, 2000)

TABLE 2.1. Summary of recorded predations from questionnaires and literature (Data source: Hart, 2000).

Region and Predator	Unsuccessful Attacks	Successful Attacks	Suspected Predation	Number of Identified Predator Species
AFRICA				
Felid	66	725	123	7
Raptor	199	573	36	22
Canid & hyaenid	26	40	10	7
Small carnivore	4	9	0	9
Reptile	4	36	3	12
Unidentified	5	37	149	–
Total Africa	**304**	**1420**	**321**	**57**
MADAGASCAR				
Felid	0	3	1	–
Raptor	18	158	10	17
Canid & hyaenid	0	3	0	–
Small carnivore	5	63	17	7
Reptile	0	6	0	5
Unidentified	0	0	2	–
Total Madagascar	**23**	**233**	**30**	**29**
ASIA				
Felid	8	254	27	8
Raptor	13	26	4	15
Canid & hyaenid	13	58	100	6
Small carnivore	0	0	0	3
Reptile	2	41	83	7
Unidentified	0	10	19	–
Total Asia	**36**	**389**	**233**	**39**
NEOTROPICS				
Felid	10	20	6	6
Raptor	263	146	15	30
Canid & hyaenid	1	1	1	1
Small carnivore	15	3	2	4
Reptile	11	7	1	13
Unidentified	16	10	75	–
Total Neotropics	**316**	**187**	**100**	**54**
TOTAL	**679**	**2229**	**684**	

have been studied. On the other hand, the number of predator species associated with primate predation derives from both anecdotal and quantitative observations.

After making an initial assessment to gauge the magnitude of recorded predation in the four geographic regions, I eliminated data on suspected predations from further analysis. I based this decision on a simple rationale that there was an inherent margin of error built into the "suspected" classification. Even with the most conservative approach to judging suspected predation, it would be problematic to combine these data with those gathered from eyewitness observations and results from controlled studies. At this point in the meta-analysis I also combined

the data from the remaining two classes—unsuccessful attacks and successful predations—since these categories were empirical in nature.

After graphing the magnitude of recorded predation, the next stage of data analysis explores primate predation separately in each geographical region and, further, attempts to isolate the variables that determine which groupings of primate species are preyed upon. In all four regions I examine the possible combinations of primate body size, stratum occupied, and activity cycle to see whether there are primates that are exempt from predation. Data indicate that none of the characteristics examined protects primates from predators. Although the exact rates of predation are often unknown, it is apparent from these data that primates are preyed upon if they are small or large, nocturnal or diurnal, arboreal or terrestrial.

Africa

African felids and raptors together accounted for the highest frequencies of primate predation, 53.7%, $n = 1, 563$ (Figure 2.2). That more than half of all reported predation events can be attributed to felids and raptors in one region is most likely an artifact of the greater quantity of questionnaire returns and scientific articles based on field research in Africa than in other regions. Leopards are opportunistic ambush hunters that are a key predator of primates, particularly in African tropical rainforests (Boesch, 1991, 1992; Zuberbühler & Jenny, 2002). Two major studies in the Taï forest calculated relatively similar percentages of primates in leopard diets; Zuberbühler & Jenny, (2002) estimated that 27.9% ($n = 64$) of the leopard diet consisted of primates; Hoppe-Dominik (1984) estimated 24.2% ($n = 61$). Outside of rainforest habitat, leopards are also major predators of primates. During a study of vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya, Isbell (1990) lost 45.0% ($n = 23$) of her study population to leopards in one year.

Other African wild cats also prey on primates. In the Mahale mountains of Tanzania, for example, lions (*Panthera leo*) appear to be major predators of primates (Tsukahara, 1993). Until recently, predation as a mortality factor for Mahale chimps was assumed to be negligible. However, this assumption has been challenged by evidence of chimpanzee hair, bones, and teeth in 4 out of 11 samples of lion feces collected over a four-month period. As another example, two lionesses near Mana Pools in Zimbabwe were known to favor baboons as prey. Over a six-year period, a safari guide in the area observed the lionesses killing six baboons (T. Williamson, pers. comm.).

African raptors have numerous failed predation attempts on primates ($n = 199$). This figure is borne out by observations of frequent unsuccessful attacks on Diana monkeys (*Cercopithecus diana*) by crowned hawk-eagles (*Stephanoaetus coronatus*, Figure 2.3) (Zuberbühler et al., 1997). The crowned hawk-eagle is one of the largest of the African eagles and is immensely powerful (Steyn, 1973; Williams & Arlott, 1980; Brown et al., 1982). Its thick tarsi, robust toes, and long talons enable it to kill large prey; with an average adult weight of 3.6 kg, the eagle routinely subdues animals four to five times its own size (Brown, 1971; Steyn, 1973, 1983; Brown et al., 1982; Tarboton, 1989). The crowned hawk-eagle

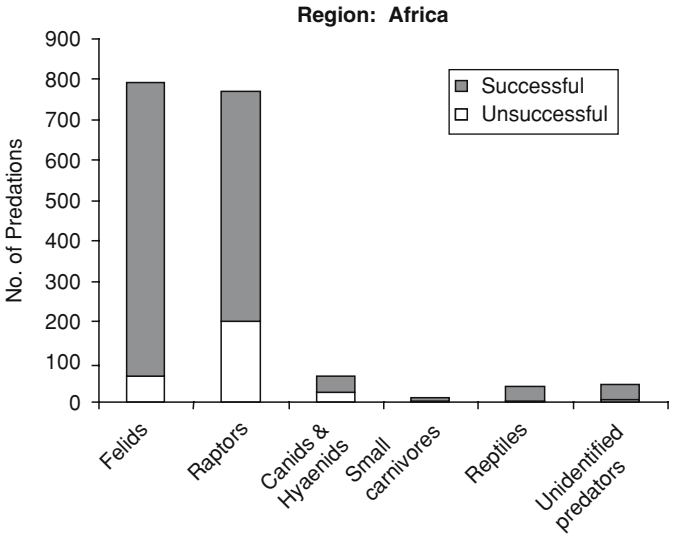


FIGURE 2.2. Comparison of successful and unsuccessful attacks by six categories of predators in Africa (Data source: Hart, 2000)

may be a primate specialist. Studies of this raptor in the Kibale forest of Uganda found high percentages of primates in eagle diets; Skorupa (1989) noted that 87.9% ($n = 29$) of eagle prey were monkeys, and Struhsaker & Leakey (1990) estimated this figure to be 83.7% ($n = 41$). Mitani et al., (2001) determined that primates composed the vast majority of crowned hawk-eagle prey items (82%, $n = 74$) in the Ngogo study site in Kibale during a 37-month study. At another research site in the Kiwengoma Forest Reserve, Tanzania, the skeletal remains found in one crowned hawk-eagle nest were "90% dominated by blue monkey" (Msuya, 1993, p.120). The geographic range of this raptor is extensive throughout the tropical belt of Africa. New research is finding that crowned hawk eagles exert much the same predation pressure on monkeys across different parts of their range (cf. Mitani et al., 2001; Shultz, 2001, 2002).

There are no arboreal-nocturnal primates weighing more than 2 kg in Africa, and there are no terrestrial-diurnal primates weighing less than 2 kg. (Of course, no terrestrial-nocturnal primates exist of any weight in any region.) Predation was recorded in the remaining four ecological categories identified in Figure 2.4. The single data point representing small, arboreal-diurnal primates refers to predation on the talapoin monkey (*Miopithecus talapoin*), the only African primate species in this category. The remaining three groups are dominated by guenons, mangabeys, and colobus in the arboreal-diurnal, over-2-kg category; arboreal-nocturnal primates under 2 kg refer to galagos and lorisids; terrestrial-diurnal primates over 2 kg include apes and baboons.

There are some interesting patterns that can be inferred from Figure 2.4. More terrestrial primate genera ($n = 7$) have evolved in Africa than other regions, and

FIGURE 2.3. Forest-hunting raptors, such as the African crowned hawk-eagle, are the major and most competent predators on primates (Steve Bird/Birdseekers Tours)

Africa is the only region in which there are more terrestrial-diurnal than arboreal-diurnal genera. Some of the information contained in Figure 2.4 likely represents an artifact of the numerous studies carried out on terrestrial primate species weighing over 2 kg, particularly baboons and chimpanzees. But it is difficult to say whether the 806 predations recorded in this category might also reflect an abundance of terrestrial primates, or might even point to a striking difference between arboreal and terrestrial primates as far as vulnerability to predators.

Madagascar

Corresponding information for Madagascar (Figure 2.5) shows an emphasis on raptor and small carnivore predation. Madagascar is the only region in which

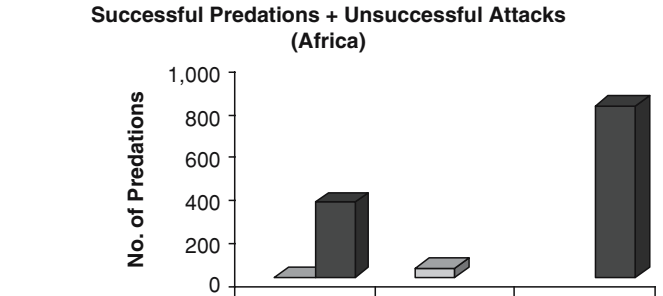


FIGURE 2.4. Comparison of recorded predation on African primates weighing <2 kg and >2 kg in three ecological groups; n/a denotes no primate species exist in that category (Data source: Hart, 2000)

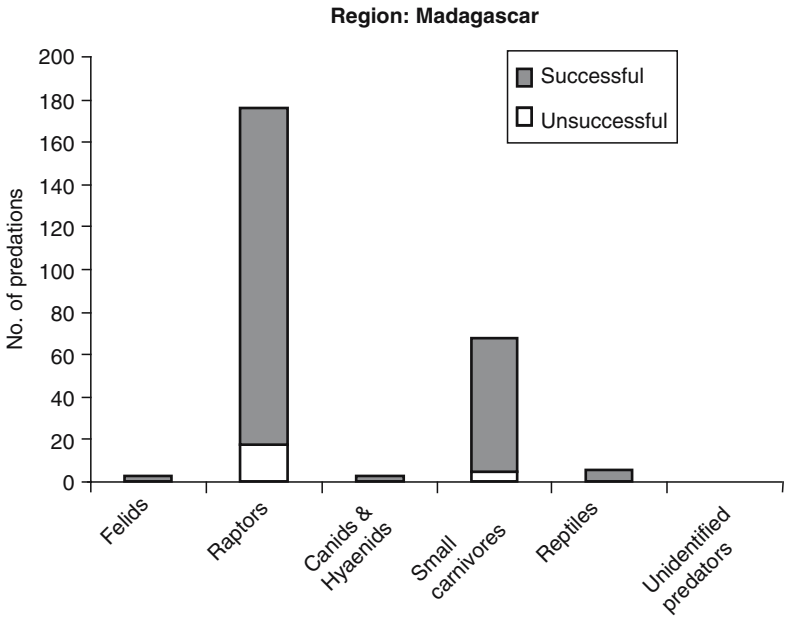


FIGURE 2.5. Comparison of successful and unsuccessful attacks by six categories of predators in Madagascar (Data source: Hart, 2000)

small carnivores (specifically, the fossa, *Cryptoprocta ferox*) are important as primate predators. Indeed, more than half of the predation data for all four regions included in the small carnivore category of Table 2.1 refer to the fossa. This is

easily attributed to the fossa's unique status on the island of Madagascar. No wild cats are indigenous to the island, and the fossa (a viverrid that weighs 20 kg and resembles a small North American puma) occupies the ecological niche of the island's absent felids. (The few instances of felid predation shown in Figure 2.5 are due to feral cats.) Some studies reveal that small carnivores, such as the fossa, may not target any particular age or sex of primate prey (Wright et al., 1997, 1998). Wright et al. (1998) described fossa as "equal opportunity" predators; deaths due to fossa predation in three groups of Milne-Edward's sifakas (*Propithecus diadema edwardsi*) were spread over all age and sex classes.

The fossa is the only species of small carnivore that has been the subject of repeated studies that have the objective of understanding the ecological relationship between a predator and its primate prey (Rasolonandrasana, 1994; Rasoloarison et al., 1995; Goodman et al., 1997; Wright et al., 1997). It is interesting to speculate that many of the small, fast-moving, arboreal carnivores may have the same capacity as fossa to inflict heavy predation on arboreal primates. At least six other species of these small carnivores prey on Madagascar primate fauna; they are Indian civet (*Viverricula indica*), Malagasy civet (*Fossa fossana*), narrow-striped mongoose (*Mungotictis decemlineata*), ring-tailed mongoose (*Galidia elegans*), Malagasy brown-tailed mongoose (*Salanoia concolor*), and broad-striped mongoose (*Galidictis spp*.). Small carnivores may be important predators on primates in other regions also, but no quantitative information exists on diets of African, Asian, or Neotropical small carnivores that have been identified as primate predators.

Malagasy prosimians (Figure 2.6) occupy five of the ecological groupings identified here. Arboreal-diurnal primates weighing less than 2 kg are represented only by bamboo lemurs (*Hapalemur spp*.); those over 2 kg include *Propithecus, Indri*, *Varecia*, and *Eulemur*. (For the purpose of comparison, cathemeral species,

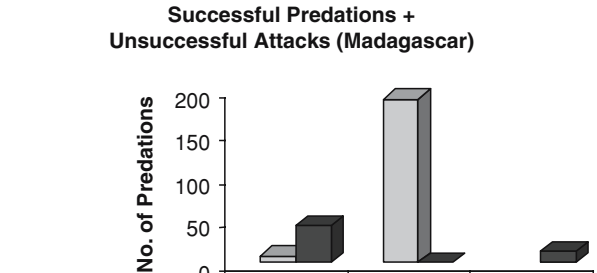


FIGURE 2.6. Comparison of recorded predation on Malagasy primates weighing <2 kg and >2 kg in three ecological groups; n/a denotes no primate species exist in that category; 0 denotes no predation events were reported (Data source: Hart, 2000)

such as *Eulemur*, were analyzed with arboreal-diurnal species.) The category of arboreal-nocturnal primates weighing less than 2 kg is occupied by the *Cheirogaleidae*. The terrestrial-diurnal, over-2-kg category is filled by the ring-tailed lemur (*Lemur catta*). The aye-aye (*Daubentonia madagascariensis*) is the only primate in Madagascar that is arboreal-nocturnal and weighs more than 2 kg. Except for *Daubentonia*, predation has been recorded for all other families of Malagasy primates.

Nocturnal raptors (the Malagasy owls) and the diurnal Madagascar harrier hawk (*Polyboroides radiatus*) are frequent predators on prosimians (Goodman et al., 1991; Goodman & Langrand, 1993; Goodman et al., 1993a, 1993b; Karpanty & Goodman, 1999; Brockman, 2003). The increasing number of studies that document Malagasy raptor diets has served to reveal the extent to which primates incur predation. Diurnal raptors, such as the Madagascar harrier hawk, are major predators of Verreaux's sifaka (*Propithecus verreauxi*), even though the primates are two to three times the size of the raptor (Karpanty & Goodman, 1999). Henst's goshawks (*Accipiter henstii*) weigh only 1.2 kg but successfully prey on large-bodied, arboreal-diurnal species as well as small-bodied, nocturnal primates (Goodman et al., 1998; Karpanty, 2003).

There is conspicuously high predation on small, arboreal-nocturnal primates in Madagascar. This may reflect the fact that Madagascar is the only region in which more nocturnal than diurnal primate genera have evolved. Ornithological research has made it apparent that small nocturnal primates on Madagascar constitute a prey base for many species of endemic owls, for example, *Tyto soumagnei, Otus rutilus*, and *Asio madagascariensis*, along with the Malagasy subspecies of barn owl (*Tyto alba affinis*) (Goodman et al., 1991; Goodman & Langrand, 1993; Goodman et al., 1993a, 1993b).

Asia

Leopards and tigers (*Panthera tigris*) incur a substantial impact on Asian primates. A good example comes from research in the Periyar Tiger Reserve, South India, where 81.4% ($n = 79$) of the leopard diet from September 1991–September 1994 consisted of Nilgiri langur (*Trachypithecus johnii*) (Srivastava et al., 1996). In Meru-Betiri Reserve, Indonesia, langurs and macaques were the predominant food of the leopard (56.9%, $n = 33$) in a study carried out by Seidensticker and Suyono (1980). Perhaps less intuitive than the leopard's reliance on primate prey is the tiger's penchant for primates. Tigers are usually assumed to take only very large ungulate prey. Nevertheless, Hanuman langurs (*Presbytis entellus*) are frequent prey of tigers in the forest of Ranthambhore, India, where the monkeys are often captured when moving between trees (Thapar, 1986). Schaller (1967) calculated that langurs made up 7.0% ($n = 21$) of the tiger diet in Kanha Park, India; Sunquist (1981) studied the composition of tiger diets in Chitawan Park, Nepal, finding that 5.7% ($n = 7$) consisted of langurs. Two recent studies carried out in Bangladesh and India indicate that rhesus macaques (*Macaca mulatta*) and langurs were the third highest components in tiger diets (Reza et al., 2001; Sankar & Johnsingh, 2002).

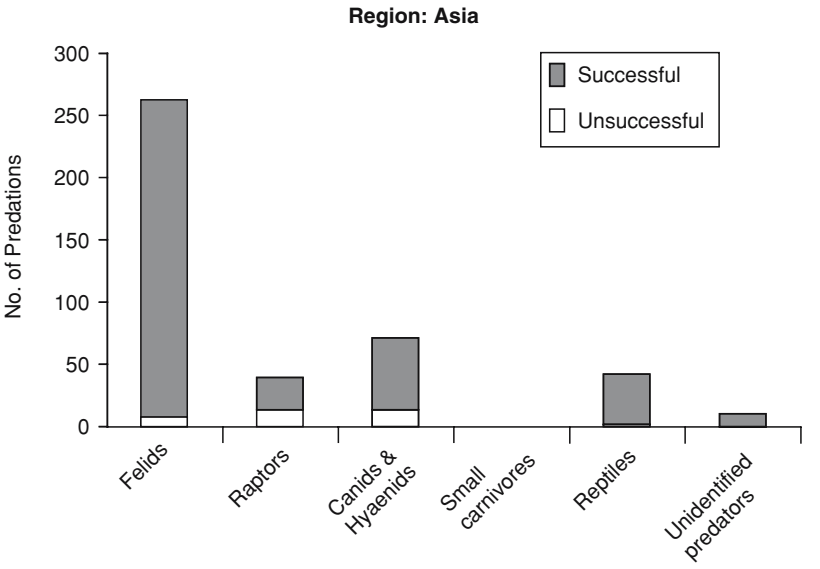


FIGURE 2.7. Comparison of successful and unsuccessful attacks by six categories of predators in Asia (Data source: Hart, 2000)

With regard to currently available data on primate predators, canids and hyaenids are not heavily represented in any region. Nevertheless, Asian canids—the golden jackal (*Canis aureus*) and the dhole (*Cuon alpinus*)—figure prominently as predators (Johnsingh, 1980; Newton, 1985; Stanford, 1989; D'Cunha, 1996; see Figure 2.7). Several Asian canids not previously considered primate predators have been identified in recent years. N. Itoigawa (pers. comm.) related that he has received anecdotal reports concerning red fox (*Vulpes vulpes*) and raccoon dog (*Nyctereutes procyonoides*) predation on Japanese macaques *(Macaca fuscata)*.

Wolves (*Canis lupus*) still exist in Saudi Arabia and other parts of Southwest Asia and are known to be quintessential opportunists throughout their nearly global range. Remains of *Papio hamadryas* were found in wolf scats in the Arabian Peninsula (Biquand et al., 1994). The decline in large Asian carnivores has been dramatic over the last several decades, but in the early 1970s wolves and Asian black bears (*Selenarctos thibetanus*) in Nepal were alleged to prey on Hanuman langurs (Bishop, 1975).

Asia is also notable for a relatively high incidence of reptile predation on primates. There are more reptile predations ($n = 43$) in Asia than in other geographic regions, although Africa has nearly as many ($n = 40$). When "suspected" reptile predations are added to successful and unsuccessful categories (refer to Table 2.1), the Asian figure ($n = 126$) is nearly three times higher than the figure for Africa

($n = 43$), over six times higher than that of the Neotropics ($n = 19$), and twenty-one times greater than the number for Madagascar ($n = 6$).

The first quantitative study of large tropical snake diets was published less than a decade ago (Shine et al., 1998). Specimens of *Python reticulatus* (an Asian snake in which females routinely reach a length of 7 m) were examined for stomach contents within the context of commercial exploitation for the skin trade. Although large ungulate prey were more easily identified in the hindgut than smaller primate species, Shine et al. (1998) calculated that 3.4% ($n = 14$) of the identifiable remains of food in the python alimentary tracts consisted of macaques and langurs. Pythons are also known to consume small, nocturnal Asian primates (Wiens & Zitzmann, 1999). During a study of slow loris (*Nycticebus coucang*) in Indonesia, weak signals from a radio-collared focal animal were traced to dense ferns on the forest floor. When these signals continued over a three-day period from such an unlikely location for an arboreal primate, researchers investigated and found a reticulated python. The signals were being emitted from the interior of the python, which had swallowed the loris.

Compared to other regions, the level of primate predation by raptors in Asia is low. Probably correlated with this minimal level is the fact that fewer raptor species have been identified as primate predators in Asia than other regions. Another reason may be a lack of field studies on South and Southeast Asian raptors. (Other than the Philippine eagle, *Pithecophaga jeffery*, I found no literature on the diets of Asian raptor species known to prey on primates.) If a similar body of field research becomes available for Asian raptors, as now exists for African birds of prey, this picture may change.

Asian primates (Figure 2.8) occupy only three of the ecological groups identified here: arboreal-diurnal primates over 2 kg in weight (*Pongo, Presbytis*, *Trachypithecus*, *Nasalis*, and others), terrestrial-diurnal primates over 2 kg

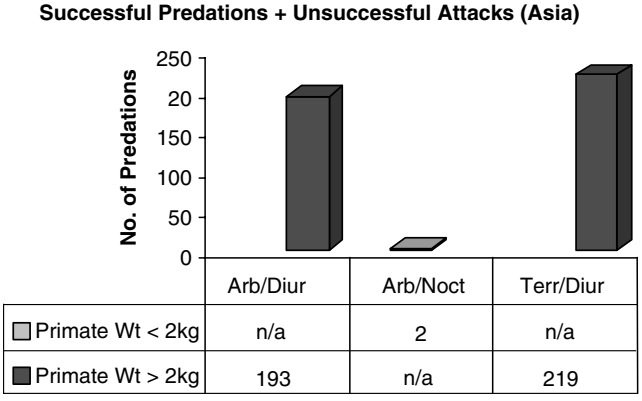


FIGURE 2.8. Comparison of recorded predation on Asian primates weighing <2 kg and >2 kg in three ecological groups; n/a denotes no primate species exist in that category (Data source: Hart, 2000)

(*Macaca*), and arboreal-nocturnal primates under 2 kg (*Tarsius, Nycticebus*, *Loris*). The large diurnal species are preyed on by leopards, tigers, dholes, jackals, crocodiles, and snakes, but until recently there were so few studies on small, nocturnal Asian primates (Rasmussen, 1997) that only two incidents were available for examination at the time of this meta-analysis. There are three genera of prosimians in Asia, half the number found in Africa and Madagascar, but the current surge in field research on nocturnal Asian primates has greatly expanded knowledge about predation on these species (see Wiens and Zitzmann, 1999, 2003; Gursky, 2002, 2003, 2005; Lakshmi and Mohan, 2002; Nekaris, 2003; Nekaris and Jayewardene, 2004).

The Neotropics

Figure 2.9 represents an overview of primate predation in the Neotropics. The paucity of felid predation is readily apparent despite the fact that two large cat species: jaguar (*Panthera onca*) and puma (*Felis concolor*), and four small felids: ocelot (*F. pardalis*), jaguarundi (*F. yagouroundi*), margay (*F. wiedii*), and oncilla (*F. tigrina*), have been identified as primate predators.

A variety of small hawk and falcon species inhabit Central and South American forests. Neotropical raptor species are twice as numerous as Old World species mainly because of the ubiquitous small forest falcons of the genus *Micrastur*. Thiollay (1985) describes the hunting techniques of small rainforest hawks and falcons as a combination of active and inactive behaviors; sitting motionless

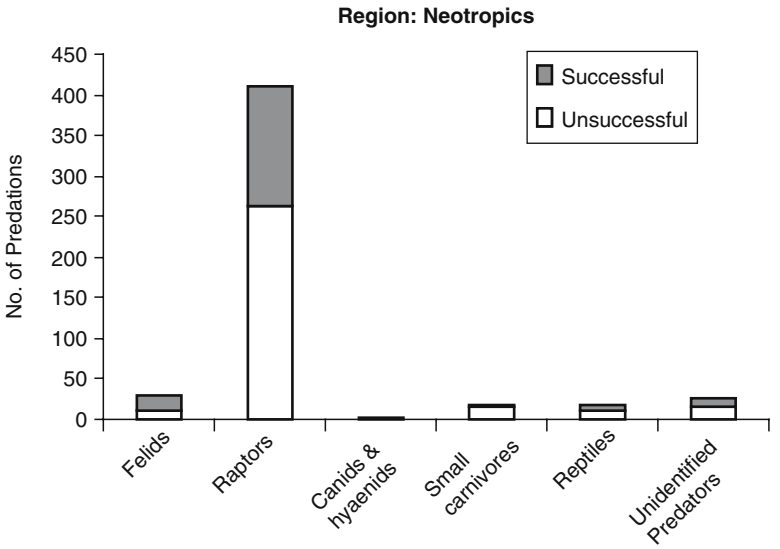
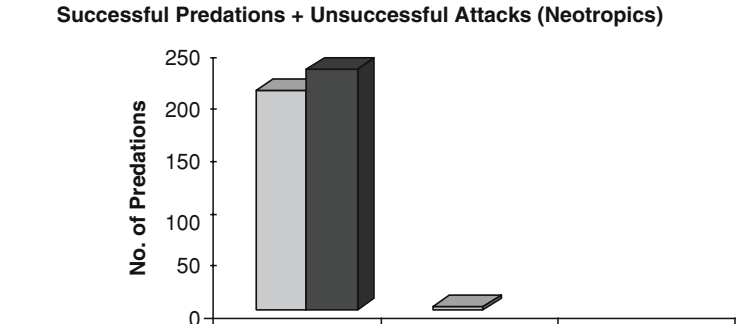


FIGURE 2.9. Comparison of successful and unsuccessful attacks by six categories of predators in the Neotropics (Data source: Hart, 2000)

FIGURE 2.10. The harpy eagle is the premier raptor of the Neotropics (Used by permission of R.W. Sussman)

and inconspicuous, they intersperse inactivity with occasional swift, soundless flights from tree to tree. Some species, such as the collared forest falcon (*M. semitorquatus*), pursue active hunting. This raptor actually runs along branches in pursuit of prey (Thiollay, 1985). Many of the predation attempts by Neotropical hawks, falcons, and toucans are unsuccessful, but this does not deter frequent attacks on callitrichids and very young squirrel monkeys (Terborgh, 1983; Boinski, 1987; Goldizen, 1987; Mitchell et al., 1991).

The harpy eagle (*Harpia harpyja*, Figure 2.10) is one of the largest and strongest raptors in the world (Brown & Amadon, 1989). This species exhibits the same short, broad wings and relatively long, graduated tail as the crowned hawk-eagle of



	Arb/Diur	Arb/Noct	Terr/Diur
Primate Wt < 2kg	209	2	n/a
Primate Wt > 2kg	230	n/a	n/a

FIGURE 2.11. Comparison of recorded predation on Neotropical primates weighing <2 kg and >2 kg in three ecological groups; n/a denotes no primate species exist in that category (Data source: Hart, 2000)

Africa. Ecological equivalents, the two raptors have garnered similar reputations as premier predators on monkeys (Izor, 1985).

There are two features of the Neotropical primate component not found in other regions (Figure 2.11): it lacks a terrestrial species and it has only a single nocturnal genus. Considerable predation is recorded for small and large arboreal-diurnal Neotropical primates, i.e., the callitrichids and the cebids. The only New World primate that is arboreal and nocturnal is *Aotus,* the owl monkey, for which a small number of predations by owls has been recorded (Wright, 1985; Brooks, 1996). There are no Neotropical primates inhabiting other ecological divisions identified here.

Estimated Predation Rates

Estimated predation rate (EPR), the percentage of a primate population killed annually by predators, provides a valuable insight into the effect predation has on a primate group. Additionally, EPR calculations measure the effect of predator mortality on all components of the population, including the reproductively active portion. This is an important caveat since estimated rates of predation on immature primates (infant and juvenile age classes) may be higher in comparison to adults. Janson and van Schaik (1993) compared immature versus mature primates and estimated the predation rate was 3–17 times higher for immature individuals than for adults in species of cercopithecines and 3–6 times higher in cebids.

Figure 2.12 displays mean estimated predation rates for four regions. Madagascar has the highest mean EPR (8.9 %, $n = 6$), and Asia has the lowest (3.0 %, $n = 19$). Mean EPRs for Africa and the Neotropics are 5.6% ($n = 57$) and 6.7% ($n = 14$), respectively. Estimated predation rates ranged from zero to

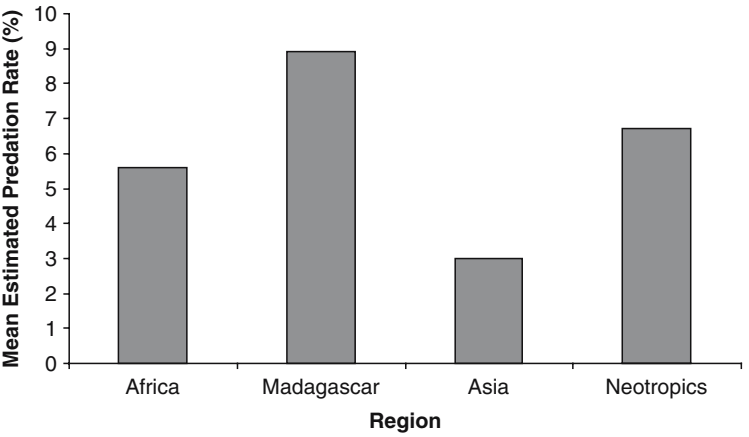


FIGURE 2.12. Comparison of mean estimated predation rates by region (Data sources: Hart, 2000; Mitani et al., 2001; Shultz, 2003)

TABLE 2.2. Estimated predation rates for primate weight and ecological groupings (Data sources: Hart, 2000; Mitani et al., 2001; Shultz, 2003).

Primates < 2 kg Arboreal Diurnal ($n = 7$)	Primates < 2 kg Arboreal Nocturnal ($n = 4$)	Primates > 2 kg Arboreal Diurnal ($n = 38$)	Primates > 2 kg Terrestrial Diurnal ($n = 44$)
Mean EPR	Mean EPR	Mean EPR	Mean EPR
7.0%	15.8%	5.4%	4.4%
Range	Range	Range	Range
1.0–15.0%	8.6–25.0%	0–18.0%	0–15.0%

25.0% in this sample. The inclusion of a zero predation rate is due to calculations by questionnaire respondents who lost no study animals to predators over a number of years. (Of course, it is possible that aberrant conditions existed at these study sites, such as the eradication of predators in the area or human disturbance causing predators to disperse.) The highest rate in the sample is 25.0% of a *Microcebus* population lost to predation each year (Goodman et al., 1993c). This EPR is based on predation by two genera of owls and does not include additive predation by diurnal raptors, snakes, or small carnivores. The high reproductive potential of *Microcebus* counteracts what would seem to be an intolerable level of predation (Goodman et al., 1993c; Hill & Dunbar, 1998). Unlike most primate species, some Malagasy prosimians (including *Microcebus*) produce an average of two infants twice per year (Martin, 1972). The mouse lemur is able to sustain a predation rate of 25.0% because, for a primate, it has a very high reproductive potential (Goodman et al., 1993c).

In Table 2.2 estimated predation rates for primates are summarized from the perspective of ecological groupings used in this chapter. The highest predation rate was incurred by small, arboreal-nocturnal primates. This may be partially reflective of the 25.0% EPR calculated for mouse lemurs; in addition, the sample

sizes are very small for two of the categories ($n = 4, n = 7$) and relatively large for the other two ($n = 38, n = 44$).

Frequency of Occurrence of Primates in Predator Diets

Frequency of occurrence is defined as the number of individual prey animals of one taxon relative to all prey eaten (Rabinowitz & Nottingham, 1986). Expressed as a percentage of all food intake by a predator, frequencies of occurrence can be estimated using various methods. (Table 2.3 lists these techniques along with the number of studies in the data set that used each sampling method.) Boshoff et al. (1994) give an excellent explanation of how frequencies of occurrence provide a good approximation of the composition and species richness of prey; any biases can be assumed to be common to all samples, so comparison between samples is valid.

It should be noted that frequencies of occurrence of primates in predator diets are based on conservative estimates. These methods usually result in underestimates since biases against finding the remains of young, small, or nocturnally active prey are exacerbated by several processes (Rice, 1986; Thapar, 1986). Primates are often underrepresented when frequencies of occurrence are calculated from direct observation of kills or examination of prey carcasses due to the rapidity with which small carcasses are consumed by large carnivores (Schaller, 1972; Eloff, 1973; Floyd et al., 1978; Bothma & Le Riche, 1986). Furthermore, the chance that skeletal remains pass through the digestive tract of a carnivore in recognizable form is greater for large prey animals than for smaller ones (Muckenhirn, 1972). Even when the largest primates fall prey to a carnivore, the remains disappear rapidly in tropical climates. All traces of a western lowland gorilla killed by a leopard in Gabon were nearly gone three or four days after death due to consumption by the primary predator, scavengers, and insects (Tutin & Benirschke, 1991). A similar amount of time was noted for the disappearance of a chimpanzee carcass after leopard predation in the Taï forest, Côte d'Ivoire (Boesch, 1991). Fecal samples from predators are also difficult to collect in tropical forests because they may be destroyed within hours by dung beetles and trigonid bees; only those containing large amounts of fur or those placed in sunny areas survive a few days (Emmons, 1987).

The most commonly used methods (fecal sampling, pellet/regurgitation sampling, analysis of nest or den remains, and analysis of prey carcasses) provide

TABLE 2.3. Frequency of occurrence sampling methods (Data source: Hart, 2000).

Type of Sampling Method	Number of Studies
Stomach contents	3
Fecal sampling	33
Pellets and regurgitations	8
Nest and den remains	38
Analysis of prey carcasses	9
Direct observation of kills	5

information on food ingested over an extended period of time and are non-invasive, unlike analysis of stomach contents, which involves dissection of the predator. Direct observation of kills has the advantage of providing indisputable confirmation of predation rather than scavenging, but it requires both perseverance and luck. As a sampling method it yields more limited information since only one meal at a time can be identified. Another drawback to direct observation is that prey are often alerted to predators or made more vigilant when human observers are present (Isbell & Young, 1993). Observing the kill of a secretive, nocturnal predator, such as the leopard, is particularly problematic. Despite nearly half of the vervet population under study falling victim to leopards during one year at Amboseli National Park, Kenya, no monkeys were killed within sight of researchers (Isbell, 1990). The sampling of feces, regurgitations, nest or den remains, and prey carcasses provides an estimate of the minimum number of preyed-upon individuals of one taxon, and it requires a tedious cleaning and reconstruction process (Figure 2.13). Nest and den remains yield excellent data for compilation of predator diets since several nesting cycles result in large build-ups of prey bones within and below raptor nests (Sanders et al., 2003; Shultz et al., 2004). The larger the collection of nest and den remains the greater the accuracy of dietary content.

The percentage of a predator's diet composed of primates ranged widely in the data set described here. At the upper end of a continuum, nest remains of forest-hunting African crowned hawk-eagles identified 80–90% of their diet as primates

FIGURE 2.13. Leopard scat containing two gorilla hind digits was found by researchers in the Central African Republic; one intact toe has been removed from the fecal matter and is clearly visible on the right (Used by permission of Michael Fay)

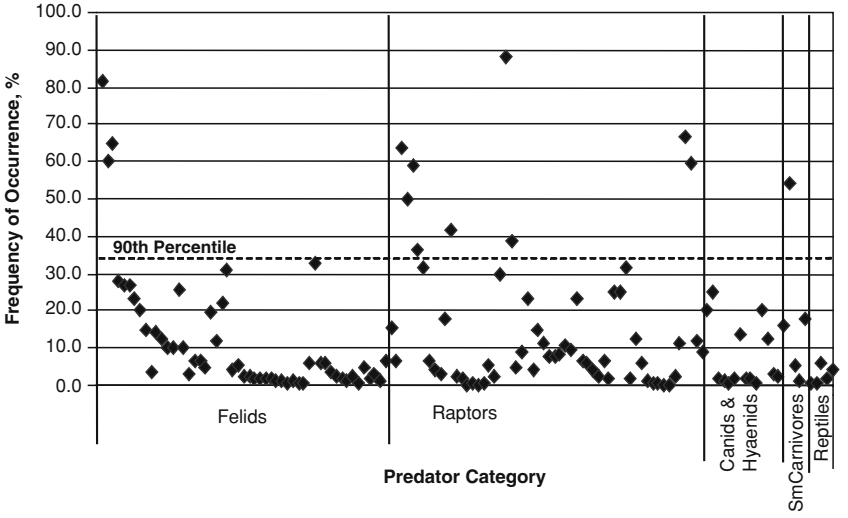


FIGURE 2.14. Frequency of occurrence of primates in predator diets. Each point represents data from a field study on a species of felid, raptor, canid and hyaenid, small carnivore, or reptile plotted as a percentage of primates found in the diet of a single predator. Median values: felids, 5.2%, $n = 53$; raptors, 7.6%, $n = 59$; canids and hyaenids, 2.0%, $n = 13$; small carnivores, 10.6%, $n = 4$; reptiles, 3.0%, $n = 6$ (Data source: Hart, 2000)

of various species (Skorupa, 1989; Struhsaker & Leakey, 1990; Msuya, 1993; Mitani et al., 2001). At the lower end a study of Verreaux's eagles (*Aquila verreauxii*), an African savanna raptor, estimated only 0.05% ($n = 27$) of the diet was composed of primates (Boshoff et al., 1991). Frequencies of occurrence were available from 96 studies on 35 species of predators. More data were collated on felid and raptor diets containing primates than for other predators (Figure 2.14). Extensive research is available analyzing the total range of hyena and wild canid prey, mostly large savanna ungulate species (Estes & Goddard, 1967; Henschel & Tilson, 1988; Johnsingh, 1980, 1983; Kruuk, 1970, 1972; Kruuk & Turner, 1967; Mills & Biggs, 1989), so it is plausible to compare them with felids and raptors in Figure 2.14. Reptile and small carnivore species inhabiting the same geographic ranges as primates have not been the focus of many studies intended to generate information on diet composition (reptiles $n = 5$, small carnivores $n = 4$). Taking this into consideration, however, it is still apparent that felids and raptors are major predator groups where the killing of primates is concerned. Only felids, raptors, and one small carnivore, the fossa, have frequencies of occurrence that fall above the 90th percentile.

In Figures 2.15–2.18 means were determined for the percentage of primates in the diets of different predator groups by first averaging each separate species' frequency of occurrence percentages and then calculating the mean for all species within each predator group. These means are presented separately for Africa, Madagascar, Asia, and the Neotropics to facilitate comparison across regions.

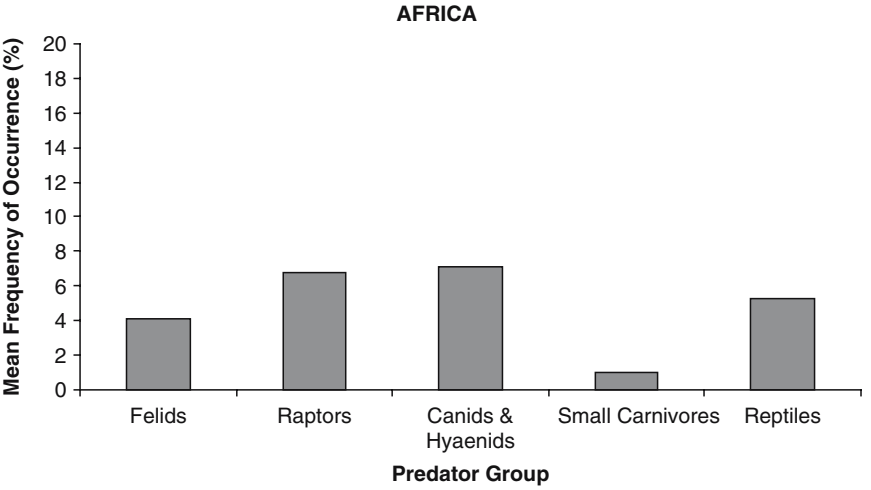


FIGURE 2.15. Five groups of African predators are compared by frequency of occurrence of primates in their diets. Number of identified primate predators in Africa: felids, $n = 7$; raptors, $n = 22$; canids and hyaenids, $n = 7$; small carnivores, $n = 9$; reptiles, $n = 12$ (Data sources: Hart, 2000; Mitani et al., 2001; Shultz, 2002; Zuberbühler & Jenny, 2002)

In Africa (Figure 2.15) there is a relatively narrow range of percentages of primate prey among the five predator groups; the highest mean component of primates occurs in canid and hyaenid diets (7.1%, $n = 2$ species), and the lowest occurs in small carnivore diets (1.0%, $n = 1$ species). Within the narrow range, raptor diets averaged 6.8% primate prey ($n = 7$ species), reptiles 5.3% ($n = 2$ species), and felids 4.1% ($n = 4$ species).

Frequency of occurrence of primates in Malagasy predator diets (Figure 2.16) reveals an emphasis on raptor and small carnivores. Mean raptor frequency of occurrence was 17.2% ($n = 6$ species), and mean small carnivore frequency was 25.1% ($n = 1$ species). Seventeen raptor species have been identified as primate predators in this region (58.6% of the total predator component). This is the highest ratio of raptor to total predator numbers in any region. The highest estimated predation rates in any region are also due to Malagasy birds of prey.

The frequency with which primates appear in the diets of Asian predators (Figure 2.17) is similar to Africa except that felids have a much higher mean frequency of primates in their diets (15.0%, $n = 2$ species). Raptors averaged 4.4% primate prey ($n = 1$ species), canids and hyaenids 4.0% ($n = 3$ species), and reptiles 4.1% ($n = 2$ species). No frequency of occurrence data were available for small carnivores in Asia.

Neotropical raptors have the highest mean percentage of primates in their diets (36.6%, $n = 2$ species) of any predator group in any region. All other predator consumption of primates in the Neotropics is negligible by comparison. Figure 2.18 also presents an apparent association between the number of identified Neotropical raptor species that prey on primates ($n = 30$) and these high

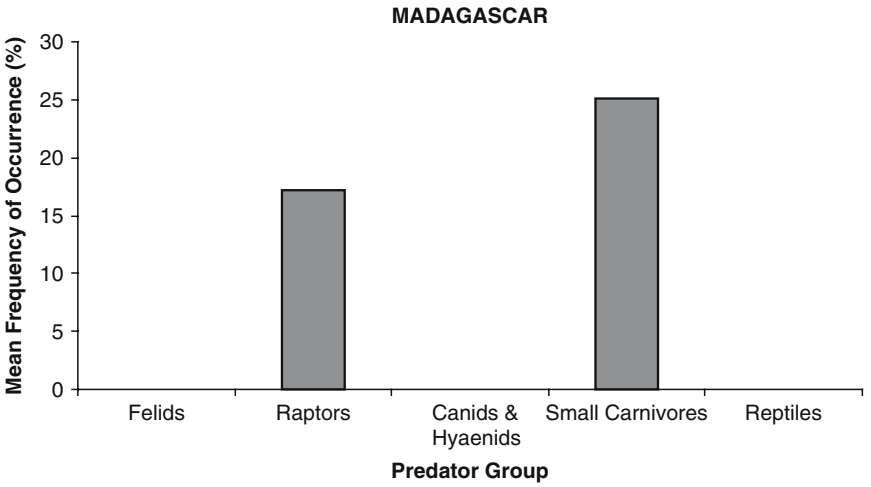


FIGURE 2.16. Five groups of Malagasy predators are compared by frequency of occurrence of primates in their diets. Number of identified primate predators in Madagascar: felids, $n = 0$; raptors, $n = 17$; canids and hyaenids, $n = 0$; small carnivores, $n = 7$; reptiles, $n = 5$ (Data sources: Karpanty & Goodman, 1999; Hart, 2000; Thorstrom & La Marca, 2000)

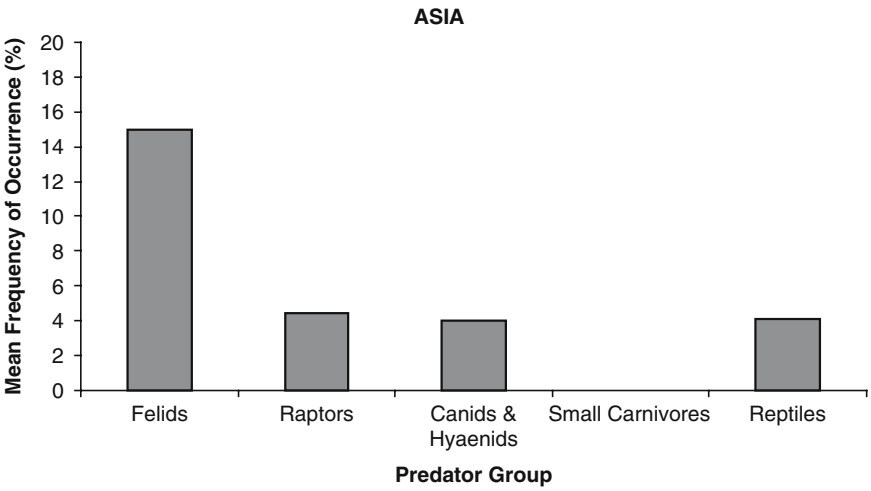


FIGURE 2.17. Five groups of Asian predators are compared by frequency of occurrence of primates in their diets. Number of identified primate predators in Asia: felids, $n = 8$; raptors, $n = 15$; canids and hyaenids, $n = 6$; small carnivores, $n = 3$; reptiles, $n = 7$ (Data sources: Hart, 2000; Reza et al., 2001; Sankar & Johnsingh, 2002; Uhde & Sommer, 2002)

frequencies of occurrence. The mean primate component in raptor diets in the Neotropics is more than twice as high as this figure in Madagascar, more than four times higher than Africa's, and more than eight times higher than the figure in

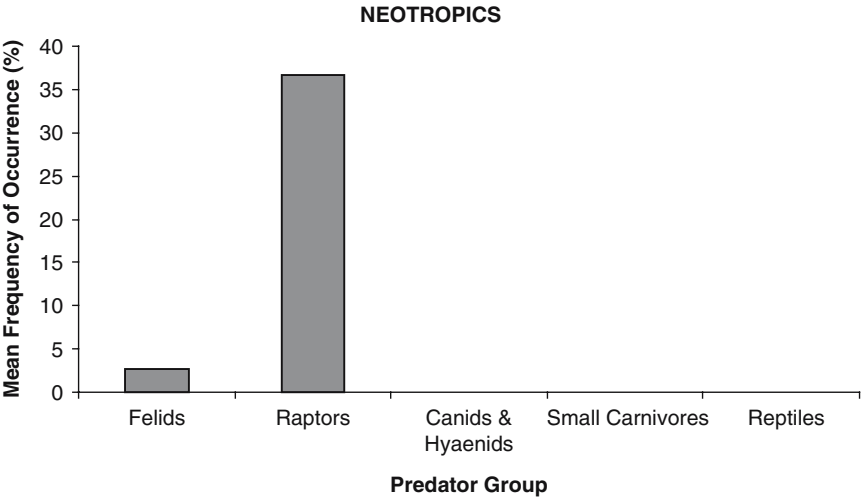


FIGURE 2.18. Five groups of Neotropical predators are compared by frequency of occurrence of primates in their diets. Number of identified primate predators in the Neotropics: felids, $n = 6$; raptors, $n = 30$; canids and hyaenids, $n = 1$; small carnivores, $n = 4$; reptiles, $n = 13$ (Data source: Hart, 2000)

Asia. Therefore, while there are more Neotropical raptor species, they also prey on many more primates than raptors of other regions.

Discussion

Biogeographical associations and insights have emerged from this meta-analysis despite the necessary reliance on preliminary and non-random data. What are the biogeographical patterns that account for links between primate regions and certain types of predation? With some exceptions, there appears to be a possibility of two primate predation patterns based on frequency of occurrence data. One pattern is apparent in Africa and Asia and consists of modest levels of predation spread among many predator taxa. It may be that shared predators (the leopard, lion, cheetah, striped hyena, and several species of canids) in combination with shared primate taxa (Catarrhini) enhance the perceived similarity between the two regions.

The other pattern found in Madagascar and the Neotropics consists of heavy predation by a narrower range of predators. High levels of raptor predation define a common link between Madagascar and the Neotropics. The four highest mean frequencies of primates in individual predator species diets were raptors indigenous to Madagascar and the Neotropics—Henst's goshawks, Madagascar long-eared owls (*Asio madagascariensis*), harpy eagles, and Guiana crested eagles (*Morphnus guianensis*). There is a complete absence of wild felids, canids, or

hyaenids in Madagascar. While this pattern is not paralleled in the Neotropics, especially concerning wild cat species, there are no hyaenids, and only one wild canid predator—the coyote (*Canis latrans*)—is suspected to be a primate predator in Central America. Nevertheless, it would be presumptuous to infer indelible patterns from the analysis in this chapter, due to the many limiting factors. Perhaps the most limiting factor is that extensive research efforts are made on certain species of primate predators while other identified predators remain known only through anecdotal reports. This lack of random data collection skews the picture of primate predation to an unknown degree.

Primates are "generalist" prey in the sense that, as a taxon, they range in size from 60 g to 169.5 kg, they inhabit geographic ranges throughout the tropics, subtropics, and a few temperate forests, they range from completely arboreal to wholly terrestrial, and they include both nocturnal and diurnal species. Their successful radiation into many ecological niches carried with it the potential to interact with many predators. The 174 primate predators identified in Hart (2000) include many opportunistic feeders. While there are key primate predators among these species, there are no examples of predators with a rigidly narrow food base that forces them to prey only on primates.

Co-evolution between predators and their primate prey is most visible from the behavioral and morphological adaptations in primates that are traceable to specific predators (Terborgh, 1983). For example, primate polyspecific associations are limited to geographic regions inhabited by monkey-eating raptors (e.g., harpy eagles of the Neotropics and crowned hawk-eagles of Central and West Africa), which are predators that provide a strong incentive for aggregation (Gautier-Hion et al., 1983; Terborgh, 1990a). Terborgh (1983) discussed the relationship between body size and methods of escape from raptor predation among Neotropical primates at Cocha Cashu, Peru. He identified three distinct strategies adopted by primates: crypsis, group living, and escape from predators through an increase in size. The smallest primates (tamarins and marmosets) spend many hours per day in safe hiding places; medium-sized *Cebus* and *Saimiri* seek protection in groups. The remaining evolutionary adaptation in Terborgh's model, that of size increase, applies to adults of the largest Neotropical species, i.e., *Ateles, Brachyteles, Lagothrix*, and *Alouatta*. These primates often rest in conspicuous exposed perches in the canopy, from which they scan for harpy and Guiana crested eagles. Although the two raptors are known as capable predators of the largest Neotropical primates, they do not pass up primates of any size. Harpy eagles prey most frequently on *Cebus* (Voous, 1969); Guiana crested eagles even prey on infant tamarins (Vasquez & Heymann, 2001).

Consistently high predation rates on primates may indicate long-term predator-prey relationships. Many years of recording leopard predation on vervets at Amboseli have produced an estimated predation rate of 11.0–15.0% (Cheney & Wrangham, 1987; Isbell, 1990). Owl predation on mouse lemurs (Goodman et al., 1993b) was estimated to be 25.0% annually. However, a "high" estimated predation rate is not the only, or necessarily most important, criterion for determining the levels at which certain predators may kill primates for food. The estimated

predation rates for crowned hawk-eagle exploitation of red colobus, black and white colobus, mangabey, and blue monkeys in the Kibale forest range from 0.3–3.0%, depending on the species of primate, but the frequency of occurrence of primates in the diet of the eagle pairs under study was 83.7% (Struhsaker & Leakey, 1990). Thus, frequency of occurrence of primates in the diet of a predator may be a more precise measure of the predator-prey relationship than EPR since the latter can be calculated as the collective effect from many predators in an ecosystem. Frequencies of occurrence, on the other hand, present a clear connection between the predator and its prey.

Primates have been observed to be secondary prey in some geographic locations and primary prey for the same predator species in another (Brown, 1966; Seidensticker & Suyono, 1980). Differences may exist in levels of predation on primates due to richness of other fauna or because other prey species have been eliminated by natural or human-induced causes. Seidensticker (1983, 1985, 1991) examined field studies containing reliable data in order to identify the environmental correlates in which primates account for a major portion of African and Asian leopard diets. He credits primate body size and availability of ungulate prey as key factors: If there were abundant ungulate species in the 20–50-kg range, leopards ate few primates; if ungulates in this size class were present but at low density, leopards had intermediate numbers of primates (i.e., <30%) in their diet; if this size class of ungulate was missing from the faunal composition, leopards had high proportions of primates in their diet. In four cases this pattern is substantiated: (1) Seidensticker & Suyono (1980) discovered that *Trachypithecus cristata* and *Macaca fascicularis* were the predominant food of tiger, leopard, and dhole in Meru-Betiri Reserve, Indonesia, because small ungulates have been extirpated by humans. Primates in the reserve are the substitute for a range of other prey normally available to large Asian carnivores. (2) In the Periyar Tiger Reserve, India, where Nilgiri langur account for 81.4% of the leopard diet, there is an absence of large ungulate species such as chital (*Axis axis*), hog deer (*A. porcinus*), and swamp deer (*Cervus duvanceli*). Ungulates weighing 20–50 kg are also not available to leopards; the Nilgiri tahr (*Hemitragus hylocrius*) exists only in isolated pockets, and sambar (*Cervus unicolor*) is the major prey item in the diet of a competing predator, the pack-hunting dhole (Srivastava et al., 1996). (3) At another site in India, Eravikulam National Park, where small ungulates, such as Nilgiri tahr, sambar, and barking deer (*Muntiacus muntjak*) were common, the remains of these animals occurred in 94.0% of tiger droppings collected for analysis and in 77.0% of leopard droppings. Remains of Nilgiri langurs appeared in no tiger droppings and in 27.0% of leopard droppings (Rice, 1986). In addition, all leopard sightings occurred within the home ranges of tahr, and leopards were seen hunting tahr in 36.0% of the sightings (Rice, 1986). (4) Niokolo-Koba National Park in Senegal does not contain dense concentrations of ungulates, and Guinea baboons (*Papio papio*) are the commonest large herbivore (Byrne, 1982). A high risk of predation from healthy populations of both diurnal African hunting dogs (*Lycaon pictus*) and nocturnal predators, such as leopards, lions, and spotted hyenas (*Crocuta crocuta*), was inferred from baboon behavior and social structure, specifically through

frequent alarm vocalizations, extreme wariness of open spaces, and unusually high numbers in baboon troops. In addition, a paucity of secure sleeping sites may increase the likelihood that considerable predation on baboons occurs. Baboons are "likely to be more important in the diet of all large predators than would be the case in East Africa" (Byrne, 1982, p. 308).

Studies of geographically variable interactions have been credited with furthering an understanding of how evolution affects predator-prey systems (Abrams, 2000). Before true comparisons can further our understanding of the evolutionary ecology of primate predation, however, it will be necessary to study many more predator species throughout the four regions in which primates exist. When more of this critical information is forthcoming, the biogeographic emphasis can then shift from the search for mere associations to that of statistical correlations that may exist between predation and primate ecology, morphology, and behavior. That said, the four regional analyses, in which all possible combinations of primate body size, stratum occupied, and activity cycle were examined for any ecological groups that might be exempt from predation (see Figures 2.4, 2.6, 2.8, and 2.11), indicate the extent and all-encompassing character of predation on primates. There were no variable combinations of body size, stratum, activity cycle, or geographic region that protected primates from predators. Even without knowledge of the exact rates of predation, it is safe to hypothesize that primates are preyed upon no matter what size they are or what ecological variables they exhibit.

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