WASHINGTON UNIVERSITY

Department of Anthropology

Dissertation Committee:

Robert W. Sussman, Chairperson
Glenn Conroy
Charles Hildeboldt
Jonathan Losos
Jane Phillips-Conroy
Thomas Pilgram
D. Tab Rasmussen

PRIMATES AS PREY

ECOLOGICAL, MORPHOLOGICAL AND BEHAVIORAL RELATIONSHIPS BETWEEN PRIMATE SPECIES AND THEIR PREDATORS

by

Donna Lee Hart

A dissertation presented to the
Graduate School of Arts and Sciences
of Washington University in
partial fulfillment of the
requirements for the degree
of Doctor of Philosophy

May 2000

Saint Louis, Missouri

UMI Number: 9972669

Bell & Howell Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

ABSTRACT

Predation is acknowledged to be an issue of fundamental importance in the study of primates. However, while predation has been discussed in theoretical terms, little quantified data exist on the subject. This thesis combines the research of primatologists with the findings of their counterparts who study large and small predatory mammals, raptors, and reptiles to assemble a database on primate mortality due to predation.

There are 176 confirmed or potential predators of primates in the four geographic regions inhabited by primates (Africa, Madagascar, Asia, and the Neotropics). From questionnaires and the scientific and natural history literature, approximately 3600 successful, unsuccessful, and suspected predation events were identified. No variables of body size, nocturnal or diurnal activity cycles, or strata could be identified that exempted primates from predation. However, the evolution of larger body size in arboreal primates may have conferred some protection from raptors and small carnivores.

Frequencies of occurrence of primates in predator diets were used to identify eleven species of predators that could be deemed "primate specialists." An analysis of the estimated predation rates of primate species indicated that small, nocturnal, arboreal primates may undergo higher rates of predation than other categories of primates. When primate anti-predator strategies were placed within the context of sequential behaviors of hunting predators, primates were especially adept in offsetting predation in the early stages of the predators' actions. When primates were compared to other prey species (particularly ungulates) inhabiting the same biomes and preyed on by the same predators, some similarities in rates of predation were apparent between the two groups.

ACKNOWLEDGMENTS

My acknowledgments are a joy to write. So many people have helped me to accomplish the task of finishing this dissertation that I am in awe of my academic mentors, family, and friends.

Thanks, especially, to Bob Sussman who has been as much friend as advisor during the years I have been in graduate school at Washington University. I had always admired and respected Bob's academic, philosophical, and ethical opinions even before knowing him as professor and advisor. Bob's interest in primate conservation brought me to Washington University and his interest in predation on primates launched my research into this topic.

My husband, Al Bruns, was the most supportive spouse through this process that anyone could imagine. My love for him only increased during the preparation of my dissertation. I am extremely fortunate to have had the good sense 20 years ago to find someone with a truly giving nature (and such a good sense of humor during middle-of-the-night computer crashes and other crises).

Friends – particularly Sharon Dunn-Smith, Mary Willis, Shimelis Beyene, Barbara Rain, and my sister, Diane Telle – were there for me every minute of every day. I cannot adequately express the appreciation I feel toward them. Sharon's devotion during my research and data accumulation stages while we both worked for the International Wildlife Coalition was amazing. That the same commitment continued after we were no longer co-workers, and she had embarked on her own academic career, is a tribute to her loyalty and friendship. Sharon ... from the bottom of my heart ... thank you for all the hours of copying, typing, literature searches, bibliographic entries, and just plain hard work. You are the ultimate friend.

Mary and Shimelis – fellow graduate students at Washington University – became intimate, dearest friends; their addition to my life ranks as the best outcome of graduate school. Mary and I have shared everything for the past ten years – from the "Great Donut Dissertation" quest to moments of despair. Shimelis will always be considered a part of my family; holiday and family celebrations are forever linked with him.

Barb has listened to me thinking out loud for hours – providing the needed balance of love, spirituality, and fun to my life. Morning telephone calls from my sister, Diane, were the spark that started my day's work. Also, many thanks to Sheila Coleman who has kept my life in order during some very chaotic years. And thanks to all other friends and family for love and support.

In addition, I want to express appreciation to the International Wildlife Coalition for encouraging me to embark on a Ph.D. while I served as a Vice-President. I value my career in wildlife conservation and the enthusiasm everyone at IWC expressed for my academic goals.

Thank you to the members of my committee – Jane Phillips-Conroy, Glenn Conroy, Charles Hildeboldt, Tom Pilgram, Tab Rasmussen, and Jonathan Losos – for advice and support. Scooter, thank you for your timely editorial help, thoughtful suggestions, and your friendship.

Thanks also to the contributors of data collected on primate predation. These are acknowledged in Appendix 5 of the dissertation. I want to especially thank Richard Wrangham for sharing his questionnaire on predation, Steve Goodman for many hours spent with me at the Field Museum of Natural History in Chicago, and Julian Kerbis-Peterhans for his dissertation and slides.

And thanks to Alex, the ultimate feline predator -- bane to voles in the pasture and deer mice in the barn, but pure inspiration to anyone studying predation!

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I.

INTRODUCTION: THEORETICAL VIEWS ON PREDATION

"In these lofty forests, ... the Great Philippine Eagle has made his home, with no enemies to trouble him. He is well known to the natives as a robber of their poultry and small pigs, but chiefly as a destroyer of monkeys, which are the only animals sufficiently abundant in the forests to support such a large bird." (Seth-Smith 1910, p. 286)

Predation is a fundamentally important issue in primate ecology. However, insights to predation based on empirical data have been lacking, tending to make it a controversial topic. As a result, a theoretical dichotomy currently exists regarding the impact of predation as a selective force on primate adaptations.

Some researchers question the role predation has played in primate evolution (Eisenberg et al. 1972, Bourliere 1979, Dittus 1979, Wrangham 1979, 1980, Cheney and Wrangham 1987). Conversely, others have postulated that patterns of primate sociality resulted from predation pressure (Terborgh 1983, Moore 1984, van Schaik 1983, Terborgh and Janson 1986, Dunbar 1988) and that major behavioral, morphological, and ecological adaptations have evolved as a result of predation (Tilson 1977, Harvey et al. 1978, Busse 1980, Tutin et al. 1983, Sussman and Kinzey 1984, Anderson 1986a, Caine 1993).

Predation as a demographic parameter often is discounted by primate researchers under the assumption that few instances have been observed or recorded (Hall 1966, Altmann 1974, Hausfater and Hrdy 1984, Cheney and Wrangham 1987, Hrdy et al. 1995). The significance of apparent anti-predator morphological, social, and behavioral patterns is disputed because most of these adaptations also can be explained plausibly as responses to sexual selection or feeding competition (Struhsaker 1969, Wrangham 1980). Because observation of predation in the scientific literature may be anecdotal rather than quantitative, there has been a tendency to minimize possible impacts and frequencies, as well as to underestimate the pervasive influence predation has on the behavior and ecology of primates (Caine 1990). 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 and Chapman 1995), predation rate versus predation risk (Hill and Dunbar 1998), and the influence of predation on arboreal primates (Treves 1999) have expanded theoretical discussion of this topic.

Analyses suggest to some researchers that predation has played a key role in the evolution of basic primate attributes, such as group living (Alexander 1974, Terborgh 1983, van Schaik 1983, van Schaik et al. 1983b, Stacey 1986, Terborgh and Janson 1986). Much discussion has also centered around the related topics of group size (e.g., van Schaik and van Hooff 1983, van Schaik et al. 1983a, Stacey 1986, Terborgh and Janson 1986, Rodman 1988, Ferrari and Lopes Ferrari 1990) and polyspecific associations (e.g., Gartlan and Struhsaker 1972, Waser 1980a, 1984, Gautier-Hion et al. 1983, Buchanan-Smith 1990, Terborgh 1990a). Large primate groups are considered beneficial because vigilance is enhanced (van Schaik and van Hooff 1983, Caine 1987, Hardie and Buchanan-Smith 1997), but off-setting this benefit is increased competition for resources

(Wrangham 1980). Attempts to test for correlations between levels of predation and number of individuals within groups showed positive correlations between estimated rate of predation and group size (Anderson1986a, Isbell 1994a). This positive correlation was substantiated by one field study (van Schaik and van Noordwijk 1985), but other primates living in small groups, e.g., callitrichids, sustain relatively high degrees of predation (Terborgh 1983, Sussman and Kinzey 1984, Goldizen 1987, Caine 1993) as do nocturnal prosimians (Goodman et al. 1993c).

Some authors (e.g., Crook 1970, Leutenegger and Kelly 1977) focused on predation as an explanation for the existence of multi-male primate groups. However, in some instances conspicuous males are selected by predators (Stacey 1986, Boesch and Boesch 1989, Struhsaker and Leakey 1990). While one study found correlates between the number of males in a group and the level of predation (Anderson 1986a), another found no correlation (Cheney and Wrangham 1987).

Low and high predation levels, of course, are relative terms. Nonetheless, Hill and Lee (1998) have assigned qualitative definitions to low, medium, and high predation risk: Low risk entails the presence of predators but no actual or attempted predation has been observed or suspected; medium predation risk is associated with occasional predation attempts but infrequent predation observed or suspected; high predation risk involves frequent or regular, actual or attempted predation observed and suspected.

"[S]uccessful predation is a rare event -- at most it can occur only once in the lifetime of a prey" (Terborgh 1983, p. 197). Whatever the overall impact of successful predation may be, it does not modify the behavioral strategies of a primate living at constant *risk* from successful predation (Dunbar 1988).

There has been little attempt to recruit research carried out on predator species as an aid to understanding the impact of predation on primates. Primatologists may have relied on limited viewpoints, therefore, when discussing predation (Anderson 1986a, Cheney and Wrangham 1987, Isbell 1994a, Boinski and Chapman 1995.) Significant changes in field research methodology have been called for, such as night observations and the study/habituation of predators along with primate groups, to accomplish an accurate appraisal of predation (Busse 1980, Isbell 1994a). The integration of research on predatory animals may answer some of the myriad questions regarding predation on primates, such as: Are primates frequent prey for species of felids, diurnal and nocturnal birds of prey, canids, hyaenids, small carnivores or reptiles? What are the correlates of predation levels on primates, e.g., habitat, group size, age, sex, morphology? What is the relative predation pressure on primates occupying different ecological niches? Which predators emphasize which species of primates in their diets? What are the factors common to primates and other prey taxa? What are the behavioral adaptations highlighting co-evolution of primates and their predators? From the fossil record, how may predation have affected early hominids, themselves vulnerable primates living in open woodland?

To date, no comprehensive attempt has been made to collect and summarize published and non-published empirical or anecdotal records of actual predation events in the wild. This thesis is designed (a) to assess the proximate impact of predators upon primate populations through a study of predation data; and (b) to identify the ultimate morphological, behavioral, and ecological adaptations that may have evolved between predators and their primate prey. I hypothesize that some predatory species specialize on primates as a resource base and that many others kill primates opportunistically. As a result, primates have co-evolved with predators and possess the capacity to offset a certain level of predation-induced mortality through their ecological niches, behavior patterns, and unique morphological adaptations.

One hundred seventy-six species of potential primate predators have been identified: raptors, felids, canids, hyaenids, ursids, small carnivores, reptiles, and sharks. The scientific literature dealing with these species was reviewed for quantitative and qualitative references to primates as prey. Questionnaires to field researchers were used to collect an additional set of quantitative and qualitative data. In addition, the primate repertoire of anti-predator behaviors was compiled and placed in the context of ethological research on predators.

In Chapter II, I review the wide range of predators that prey on primates, both currently and in the fossil record. The extent of successful and unsuccessful predation events observed by qualified researchers and naturalists is presented quantitatively in Chapter III. In Chapter IV, I analyze predation data collected through questionnaires and literature searches. Information on predators is used to provide a counterbalance to primate research and allows cross-checking between the two fields, a technique useful in establishing more accurate estimates of the level and impact of predation. Direct observation of predatory species, as well as fecal analyses, stomach contents, and prey remains in nests, dens, or feeding sites (information regularly gathered in studies of predatory animals) provides a valuable base of quantitative data from which to assess predation on primates. In Chapter V, I give a narrower discussion of the broad categories found in the previous chapter, focusing on the predators that are "primate specialists." In Chapter VI, I use body weight data on primates and predators to explore size relationships and size increase as an anti-predation strategy. In Chapter VII, I integrate primate defense strategies into the context of responses to sequential events initiated by their predators. For a wider perspective, in Chapter VIII, I compare primate predation rates with other mammalian prey species. In the final chapter, I summarize my findings and conclusions concerning primates and their predators.

CHAPTER II.

A REVIEW OF THE MORPHOLOGY, ECOLOGY, AND BEHAVIOR OF PREDATORS

> *"The extraordinary habit of monkeys leaving trees when attacked by* [dholes] *... is common also in the case of the Nilgiri Black Langur on these hills, and a good account of this curious trait will be found ... published in 1876; no explanation is however offered for such peculiar behaviour. That wild dogs profit by this failing is evident from the fact that I have on more than one occasion in the Kundahs found black monkey fur in wild dog droppings."* (Phythian-Adams 1939, p. 653)

Predation is a complex interaction of processes between predator and prey. Interactions occur on the levels of behavior, physiology, cognitive learning, and ecological adaptations, few of which are overt or measurable (Bryden 1976). Within the ecological constraints of habitat and prey density, predatory behaviors are shaped by natural selection to maximize nutrient intake (Sunquist and Sunquist 1989). The effects of predation are eventually apparent in the population dynamics of both predator and prey species (Bryden 1976).

Current theory holds that under natural conditions (i.e., an environment devoid of human perturbations caused by agriculture or technology) prey delimit the ultimate size of predator populations (Kruuk 1986). It is unlikely that the reverse is true, i.e., that predators ever regulate the size of prey populations under natural conditions (Vezina 1985). Predators are responsible, however, for many aspects of the morphology and behavior of their prey (Bertram 1978, 1979). If anti-predator defenses have evolved in conjunction with predators, populations of prey species will not be unduly affected by predation under normal environmental conditions (Kruuk 1986). If, however, coevolution has not occurred between predators and prey (e.g., in the case of introduced species), prey may be lacking proper defenses and could suffer high mortality to the point of extinction (Kruuk 1986).

It is paradigmatic in the ethological literature that predation can best be studied from the perspective of the predator. A look at primate predation from the viewpoint of predator research can expand knowledge on this important aspect of primate demography. Primatologists concur that progress in understanding the importance of predation on primates will come from this approach (Anderson 1986a, Cheney and Wrangham 1987, Isbell 1994a, Boinski and Chapman 1995). For example, one of the highest rates of predation was recorded at Gombe National Park, Tanzania, during extensive observation of chimpanzees (*Pan troglodytes*) preying on red colobus monkeys (*Colobus badius*) (Busse 1977, Stanford et al. 1994a).

Primates are preyed upon by diurnal raptors, owls and other predatory birds, felids, canids, hyaenids, ursids, viverrids, herpestids, mustelids, procyonids, marsupials, large and small crocodiles, snakes, monitor lizards, and tegus. These predators range in size from small predatory birds weighing under 100 g (*Vanga curvirostris*, the Malagasy hook-billed vanga) to giant reptiles weighing in excess of 200 kg (*Crocodylus palustris*, the mugger crocodile).

One hundred seventy-six known or potential species of predators are considered in this study; each one exhibits a distinct morphological, ecological, and behavioral relationship to its primate prey. Appendix 1 contains a listing of these predatory species and the sources from which they were identified. Taxonomy of predatory animals is derived from the following sources: birds (Brown and Amadon 1989, Howard and Moore 1991, Howell and Webb 1995), mammals (Corbet and Hill 1991, Nowak 1991, 1999), reptiles (Mattison 1988, Ross 1989, Frank and Ramus 1995), and sharks (Ellis 1996).

The following data are contained in Tables 2.1-2.9:

- Table 2.1. Diurnal raptors, owls, and other birds known or suspected to prey on primates (n=81);
- Table 2.2. Large carnivores known or suspected to prey on primates (n=35);
- Table 2.3. Species in four families of small carnivores and one marsupial identified as known or suspected primate predators (n=22);
- Table 2.4. Species of reptiles known or suspected to be primate predators (n=36);
- Table 2.5. Species of sharks alleged to prey on primates (n=2).
- Tables 2.6 through 2.9. Geographic distributions of these predatory species.

TABLE 2.1. Diurnal raptors, owls and other predatory birds known or suspected to prey on primates (n=81).

DIURNAL RAPTORS

Madagascar cuckoo hawk	*Aviceda madagascariensis*
Grey-headed kite	*Leptodon cayanensis*
Double-toothed kite	*Harpagus bidentatus*
Black kite	*Milvus migrans*
Brahminy kite	*Haliastur indus*
White-bellied sea eagle	*Haliaeetus leucogaster*
African fish eagle	*H. vocifer*
Madagascar fish eagle	*H. vociferoides*
Tank eagle	*Ichthyophaga ichthyaetus*
Short-toed eagle	*Circaetus gallicus*
Black-chested snake eagle	*C. pectoralis*
Brown snake eagle	*C. cinereus*
Bateleur	*Terathopius ecaudatus*
Crested serpent eagle	*Spilornis cheela*
Madagascar serpent eagle	*Eutriorchis astur*
African harrier hawk	*Polyboroides typus*
Madagascar harrier hawk	*P. radiatus*
Madagascar goshawk	*Accipiter francesii*
Madagascar sparrow hawk	*A. madagascariensis*
Bi-colored hawk	*A. bicolor*
Henst's goshawk	*A. henstii*
Slate-colored hawk	*Leucopternis schistacea*
White hawk	*L. albicollis*
Common black hawk	*Buteogallus anthracinus*
Great black hawk	*B. urubitinga*
Crowned solitary eagle	*Harpyhaliaetus coronatus*
Black-collared hawk	*Busarellus nigricollis*
Grey hawk	*Buteo nitidus*
Roadside hawk	*B. magnirostris*
Madagascar buzzard	*B. brachypterus*
Guiana crested eagle	*Morphnus guianensis*
Harpy eagle	*Harpia harpyja*
Philippine eagle	*Pithecophaga jefferyi*
Asian black eagle	*Ictinaetus malayensis*
Lesser spotted eagle	*Aquila pomarina*
Tawny eagle	*A. rapax*
Imperial eagle	*A. heliaca*

CONTINUED ... TABLE 2.1. Diurnal raptors, owls and other birds known or suspected to prey on primates (n=81).

Golden eagle	*A. chrysaetos*
Verreaux's eagle	*A. verreauxii*
Wahlberg's eagle	*Hieraaetus wahlbergi*
Bonelli's eagle	*H. fasciatus*
African hawk eagle	*H. spilogaster*
Chestnut-bellied hawk eagle	*H. kienerii*
Black and white hawk eagle	*Spizastur melanoleucus*
Martial eagle	*Polomaetus bellicosus*
Cassin's hawk eagle	*Spizaetus africanus*
Crested hawk eagle	*S. cirrhatus*
Hodgson's hawk eagle	*S. nipalensis*
Black hawk eagle	*S. tyrannus*
Ornate hawk eagle	*S. ornatus*
Isidor's eagle	*S. isidori*
Crowned eagle	*Stephanoaetus coronatus*
Red-throated caracara	*Daptrius americanus*
Common caracara	*Polyborus plancus*
Laughing falcon	*Herpetotheres cachinnans*
Barred forest falcon	*Micrastur ruficollis*
Slaty-backed forest falcon	*M. mirandollei*
Collared forest falcon	*M. semitorquatus*
Madagascar kestrel	*Falco newtoni*
Madagascar banded kestral	*F. zoniventris*

OWLS

Madagascar red owl	*Tyto soumagnei*
Barn owl (Madagascar)	*T. alba affinis*
Barn owl (Neotropics)	*T. a. guatemalae*
Madagascar scops owl	*Otus rutilus*
Great horned owl	*Bubo virginianus*
Northern eagle owl	*B. bubo*
Desert eagle owl	*B. ascalaphus*
Spotted eagle owl	*B. africanus*
Fraser's eagle owl	*B. poensis*
Forest eagle owl	*B. nipalensis*
Shelley's eagle owl	*B. shelleyi*
Verreaux's eagle owl	*B. lacteus*
Brown fish owl	*B. zeylonensis*

CONTINUED ... TABLE 2.1. Diurnal raptors, owls and other birds known or suspected to prey on primates (n=81).

Burrowing owl	*Athene cunicularia*
Madagascar long-eared owl	*Asio madagascariensis*

MISCELLANEOUS PREDATORY BIRDS

Squirrel cuckoo	*Piaya cayana*
Grey-breasted mountain toucan	*Andigena hypoglauca*
Keel-billed toucan	*Ramphastos sulfuratus*
Chestnut-mandibled toucan	*R. swainsonii*
Hook-billed vanga	*Vanga curvirostris*
Jungle crow	*Corvus macrorhynchos*
Pied crow	*C. albus*

TABLE 2.2. Large carnivores known or suspected to prey on primates (n=35).

FELIDS

Lion	*Panthera leo*
Jaguar	*P. onca*
Leopard	*P. pardus*
Tiger	*P. tigris*
Cheetah	*Acinonyx jubatus*
Clouded leopard	*Neofelis nebulosa*
African golden cat	*Felis aurata*
Leopard cat	*F. bengalensis*
Caracal	*F. caracal*
Feral cat	*F. catus*
Jungle cat	*F. chaus*
Puma	*F. concolor*
Ocelot	*F. pardalis*
Rusty-spotted cat	*F. rubignosa*
Serval	*F. serval*
African wildcat	*F. silvestris lybica*
Asiatic golden cat	*F. temmincki*
Oncilla	*F. tigrina*
Fishing cat	*F. viverrina*
Margay	*F. wiedii*
Jaguarundi	*F. yagouroundi*

CANIDS

Side-striped jackal	*Canis adustus*
Golden jackal	*C. aureus*
Blackbacked jackal	*C. mesomelas*
Domestic dog	*C. familiaris*
Coyote	*C. latrans*
Wolf	*C. lupus*
African hunting dog	*Lycaon pictus*
Dhole	*Cuon alpinus*
Raccoon dog	*Nyctereutes procyonoides*
Red fox	*Vulpes vulpes*

CONTINUED ... TABLE 2.2. Large carnivores known or suspected to prey on primates (n=35).

HYAENIDS

Spotted hyena	*Crocuta crocuta*
Striped hyena	*Hyaena hyaena*
Brown hyena	*H. brunnea*

URSIDS

Asian black bear	*Selenarctos thibetanus*

TABLE 2.3. Small carnivores and marsupials known or suspected to prey on primates (n=22).

VIVERRIDS

African linsang	*Poiana richardsoni*
Small spotted genet	*Genetta genetta*
Servaline genet	*G. servalina*
Large spotted genet	*G. tigrina*
Giant genet	*G. victoriae*
Indian civet	*Viverricula indica*
African civet cat	*Civettictis civetta*
African palm civet	*Nandinia binotata*
Sulawesi civet	*Macrogalidia musschenbroekii*
Malagasy civet	*Fossa fossana*
Fossa*	*Cryptoprocta ferox*

HERPESTIDS

Ring-tailed mongoose	*Galidia elegans*
Broad-striped mongoose	*Galidictis* (spp.)
Narrow-striped mongoose	*Mungotictis decemlineata*
Malagasy brown-tailed mongoose	*Salanoia concolor*
Striped-necked mongoose	*Herpestes vitticollis*
Marsh mongoose	*Atilax paludinosus*
Black-legged mongoose	*Bdeogale nigripes*

PROCYONIDS

Coati	*Nasua nasua*
Crab-eating raccoon	*Procyon cancrivorus*

MUSTELIDS

Tayra	*Eira barbara*

DIDELPHIDS

Neotropical opossum	*Didelphis marsupialis*

* The fossa (*Cryptoprocta ferox*) is classified here as a member of the Viverridae in accordance with Corbet and Hill (1991). Other sources classify this species as an herpestid (Nowak 1999). Differences in classification stem from controversy over single versus multiple radiations of carnivores to Madagascar from mainland Africa.

TABLE 2.4. Reptiles known or suspected to prey on primates (n=36).

REPTILES

Common caiman	*Caiman crocodilus*
Indopacific crocodile	*Crocodylus porosus*
Mugger crocodile	*C. palustris*
Nile crocodile	*C. niloticus*
False gharial	*Tomistoma schlegeli*
Tegu	*Tupinambis* (spp.)
African monitor	*Varanus niloticus*
Asian water monitor	*V. salvator*
Komodo dragon	*V. komodoensis*
Reticulated python	*Python reticulatus*
Indian python	*P. molurus*
African python	*P. sebae*
Malagasy boa constrictor	*Acrantophis madagascariensis*
Malagasy tree boa	*Sanzinia madagascariensis*
Rainbow boa	*Epicrates cenchria*
Emerald tree boa	*Corallus canima*
Amazon tree boa	*C. enydris*
Boa constrictor	*Boa constrictor*
Anaconda	*Eunectes murinus*
Malagasy forest night snake	*Ithycyphys miniatus*
Yellow rat snake	*Elaphe quadrivittata*
Malagasy giant hognose snake	*Leioheterodon madagascariensis*
Mussurana	*Clelia clelia*
Boomslang	*Dispholidus typus*
Egyptian cobra	*Naja haje*
Black cobra	*N. nigricollis*
Black mamba	*Dendroaspis polylepsis*
Green mamba	*D. viridis*
Common mamba	*D. angusticeps*
Jameson's mamba	*D. jamesonii*
Puff adder	*Bitis arietans*
Gaboon viper	*B. gabonica*
Neotropical rattlesnake	*Crotalus durissus*
Fer-de-lance	*Bothrops asper*
Jararaca pit viper	*B. jararaca*
Bushmaster	*Lachesis muta*

TABLE 2.5. Sharks known or suspected to prey on primates (n=2).

SHARKS

Wolf shark	*Alopias vulpimus*
Requiem shark	*Carcharhimus gangeticus*

TABLE 2.6. Primate predators – Africa.

DIURNAL RAPTORS, OWLS, AND OTHER PREDATORY BIRDS

Black kite	*Milvus migrans*
African fish eagle	*Haliaeetus vocifer*
Short-toed eagle	*Circaetus gallicus*
Black-chested snake eagle	*C. pectoralis*
Brown snake eagle	*C. cinereus*
Bateleur	*Terathopius ecaudatus*
African harrier hawk	*Polyboroides typus*
Lesser spotted eagle	*Aquila pomarina*
Tawny eagle	*A. rapax*
Imperial eagle	*A. heliaca*
Verreaux's eagle	*A. verreauxii*
Wahlberg's eagle	*Hieraaetus wahlbergi*
Bonelli's eagle	*H. fasciatus*
African hawk eagle	*H. spilogaster*
Martial eagle	*Polomaetus bellicosus*
Cassin's hawk eagle	*Spizaetus africanus*
Crowned eagle	*Stephanoaetus coronatus*
Desert eagle owl	*Bubo ascalaphus*
Spotted eagle owl	*B. africanus*
Fraser's eagle owl	*B. poensis*
Shelley's eagle owl	*B. shelleyi*
Verreaux's eagle owl	*B. lacteus*

FELIDS

Lion	*Panthera leo*
Leopard	*P. pardus*
Cheetah	*Acinonyx jubatus*
African golden cat	*Felis aurata*
Caracal	*F. caracal*
Serval	*F. serval*
African wildcat	*F. silvestris lybica*

CONTINUED ... TABLE 2.6. Primate predators –Africa.

CANIDS

Side-striped jackal	*Canis adustus*
Golden jackal	*C. aureus*
Blackbacked jackal	*C. mesomelas*
African hunting dog	*Lycaon pictus*

HYAENIDS

Spotted hyena	*Crocuta crocuta*
Brown hyena	*Hyaena brunnea*
Striped hyena	*H. hyaena*

VIVERRIDS

African linsang	*Poiana richardsoni*
Small spotted genet	*Genetta genetta*
Servaline genet	*G. servalina*
Large spotted genet	*G. tigrina*
Giant genet	*G. victoriae*
African civet cat	*Civettictis civetta*
African palm civet	*Nandinia binotata*

HERPESTIDS

Marsh mongoose	*Atilax paludinosus*
Black-legged mongoose	*Bdeogale nigripes*

REPTILES

Nile crocodile	*Crocodylus niloticus*
African monitor	*Varanus niloticus*
African python	*Python sebae*
Boomslang	*Dispholidus typus*
Egyptian cobra	*Naja haje*
Black cobra	*N. nigricollis*
Black mamba	*Dendroaspis polylepsis*
Green mamba	*D. viridis*
Common mamba	*D. angusticeps*

CONTINUED … TABLE 2.6. Primate predators – Africa.

Jameson's mamba	*D. jamesonii*
Puff adder	*Bitis arietans*
Gaboon viper	*B. gabonicus*

TABLE 2.7. Primate predators -- Madagascar.

DIURNAL RAPTORS, OWLS, AND OTHER PREDATORY BIRDS

Madagascar cuckoo hawk	*Aviceda madagascariensis*
Black kite	*Milvus migrans*
Madagascar fish eagle	*Haliaeetus vociferoides*
Madagascar serpent eagle	*Eutriorchis astur*
Madagascar harrier hawk	*Polyboroides radiatus*
Madagascar goshawk	*Accipiter francesii*
Madagascar sparrow hawk	*A. madagascariensis*
Henst's goshawk	*A. henstii*
Madagascar buzzard	*Buteo brachypterus*
Madagascar kestrel	*Falco newtoni*
Madagascar banded kestrel	*F. zoniventris*
Madagascar red owl	*Tyto soumagnei*
Barn owl (Madagascar)	*T. alba affinis*
Madagascar scops owl	*Otus rutilus*
Madagascar long-eared owl	*Asio madagascariensis*
Hook-billed vanga	*Vanga curvirostris*
Pied crow	*Corvus albus*

VIVERRIDS

Indian civet	*Viverricula indica*
Malagasy civet	*Fossa fossana*
Fossa	*Cryptoprocta ferox*

HERPESTIDS

Ring-tailed mongoose	*Galidia elegans*
Broad-striped mongoose	*Galidictis* (spp.)
Narrow-striped mongoose	*Mungotictis decemlineata*
Malagasy brown-tailed mongoose	*Salanoia concolor*

CONTINUED ... TABLE 2.7. Primate predators – Madagascar.

REPTILES

Nile crocodile	*Crocodylus niloticus*
Malagasy boa constrictor	*Acrantophis madagascariensis*
Malagasy tree boa	*Sanzinia madagascariensis*
Madagascar forest night snake	*Ithycyphys miniatus*
Malagasy giant hognose snake	*Leioheterodon madagascariensis*

TABLE 2.8. Primate predators -- Asia.

DIURNAL RAPTORS, OWLS, AND OTHER PREDATORY BIRDS

Black kite	*Milvus migrans*
Brahminy kite	*Haliastur indus*
White-bellied sea eagle	*Haliaeetus leucogaster*
Tank eagle	*Ichthyophaga ichthyaetus*
Crested serpent eagle	*Spilornis cheela*
Philippine eagle	*Pithecophaga jefferyi*
Asian black eagle	*Ictinaetus malayensis*
Golden eagle	*Aquila chrysaetos*
Chestnut-bellied hawk eagle	*Hieraaetus kienerii*
Crested hawk eagle	*Spizaetus cirrhatus*
Hodgson's hawk eagle	*S. nipalensis*
Northern eagle owl	*Bubo bubo*
Forest eagle owl	*B. nipalensis*
Brown fish owl	*B. zeylonensis*
Jungle crow	*Corvus macrorhynchos*

FELIDS

Leopard	*Panthera pardus*
Tiger	*P. tigris*
Clouded leopard	*Neofelis nebulosa*
Leopard cat	*Felis bengalensis*
Jungle cat	*F. chaus*
Rusty-spotted cat	*F. rubignosa*
Asiatic golden cat	*F. temmincki*
Fishing cat	*F. viverrina*

CANIDS

Golden jackal	*Canis aureus*
Wolf	*C. lupus*
Dhole	*Cuon alpinus*
Raccoon dog	*Nyctereutes procyonoides*
Red fox	*Vulpes vulpes*

HYAENIDS

Striped hyena	*Hyaena hyaena*

CONTINUED ... TABLE 2.8. Primate predators – Asia.

URSIDS

Asian black bear	*Selenarctos thibetanus*

VIVERRIDS

Indian civet	*Viverricula indica*
Sulawesi civet	*Macrogalidia musschenbroekii*

HERPESTIDS

Striped-necked mongoose	*Herpestes vitticollis*

REPTILES

Indopacific crocodile	*Crocodylus porosus*
Mugger crocodile	*C. palustris*
False gharial	*Tomistoma schlegeli*
Asian water monitor	*Varanus salvator*
Komodo dragon	*V. komodoensis*
Reticulated python	*Python reticulatus*
Indian python	*P. molurus*

TABLE 2.9. Primate predators – Neotropics.

DIURNAL RAPTORS, OWLS, AND OTHER PREDATORY BIRDS

Grey-headed kite	*Leptodon cayanensis*
Double-toothed kite	*Harpagus bidentatus*
Bi-colored hawk	*Accipiter bicolor*
Slate-colored hawk	*Leucopternis schistacea*
White hawk	*L. albicollis*
Common black hawk	*Buteogallus anthracinus*
Great black hawk	*B. urubitinga*
Crowned solitary eagle	*Harpyhaliaetus coronatus*
Black-collared hawk	*Busarellus nigricollis*
Grey hawk	*Buteo nitidus*
Roadside hawk	*B. magnirostris*
Guiana crested eagle	*Morphnus guianensis*
Harpy eagle	*Harpia harpyja*
Black and white hawk eagle	*Spizastur melanoleucus*
Black hawk eagle	*Spizaetus tyrannus*
Ornate hawk eagle	*S. ornatus*
Isidor's eagle	*S. isidori*
Red-throated caracara	*Daptrius americanus*
Common caracara	*Polyborus plancus*
Laughing falcon	*Herpetotheres cachinnans*
Barred forest falcon	*Micrastur ruficollis*
Slaty-backed forest falcon	*M. mirandollei*
Collared forest falcon	*M. semitorquatus*
Barn owl (Neotropics)	*Tyto alba guatemalae*
Great horned owl	*Bubo virginianus*
Burrowing owl	*Athene cunicularia*
Squirrel cuckoo	*Piaya cayana*
Grey-breasted mountain toucan	*Andigena hypoglauca*
Keel-billed toucan	*Ramphastos sulfuratus*
Chestnut-mandibled toucan	*R. swainsonii*

FELIDS

Jaguar	*Panthera onca*
Puma	*Felis concolor*
Ocelot	*F. pardalis*
Oncilla	*F. tigrina*

CONTINUED ... TABLE 2.9. Primate predators – Neotropics.

Margay	*F. wiedii*
Jaguarundi	*F. yagouroundi*

CANIDS

Coyote	*Canis latrans*

PROCYONIDS

Coati	*Nasua nasua*
Crab-eating raccoon	*Procyon cancrivorus*

MUSTELIDS

Tayra	*Eira barbara*

DIDELPHIDS

Neotropical opossum	*Didelphis marsupialis*

REPTILES

Common caiman	*Caiman crocodilus*
Tegu	*Tupinambis* (spp.)
Rainbow boa	*Epicrates cenchria*
Emerald tree boa	*Corallus canima*
Amazon tree boa	*C. enydris*
Boa constrictor	*Boa constrictor*
Anaconda	*Eunectes murinus*
Yellow rat snake	*Elaphe quadrivittata*
Mussurana	*Clelia clelia*
Neotropical rattlesnake	*Crotalus durissus*
Fer-de-lance	*Bothrops asper*
Jararaca pit viper	*B. jararaca*
Bushmaster	*Lachesis muta*

Birds of prey

At least 81 species of diurnal raptors (hawks, eagles, falcons), owls, and other birds are known or alleged to prey on primates. Strong legs and powerful feet equipped with sharp curved talons, in conjunction with a hooked bill, define the birds of prey. For the diurnal birds of prey, sight is the most important of all the senses (Brown and Amadon 1989). Their hooked and curved bills are not tailored to obtaining prey, but are universally used by hawks, eagles, and even vultures, to tear apart prey already killed or scavenged (Tarboton 1989). It is the relative size, curvature and thickness of talons, along with the length of the toes that vary with the type of food consumed; a raptor's feet are dangerous, and their power is exceptional (Brown and Amadon 1989). A blow delivered by the feet in a strike is at least as important as the gripping or piercing of the talons (Kemp 1990).

The size and strength of the talons of some primate-eating raptors are illustrated in Fig.2.1. Raptors that prey on mammals have large tarsi, thick toes and well-curved talons. The talons probably serve as much to provide anchorage for the powerful grip as to be used as daggers for incapacitating prey; the inner and hind toes are the most powerful and work in opposition to each other, applying the main grip to prey (Kemp 1990). Harpy eagles (*Harpia harpyja*) have tarsi that are 2.9 cm thick; their feet span 22.9-25.4 cm, and the massive dagger-like talons are 8.1-8.5 cm long (Voous 1969, Brown 1977). Crowned eagles (*Stephanoaetus coronatus)* have exceptionally thick, powerful legs and short thick toes that end in very strong rigid talons (Brown et al. 1982).

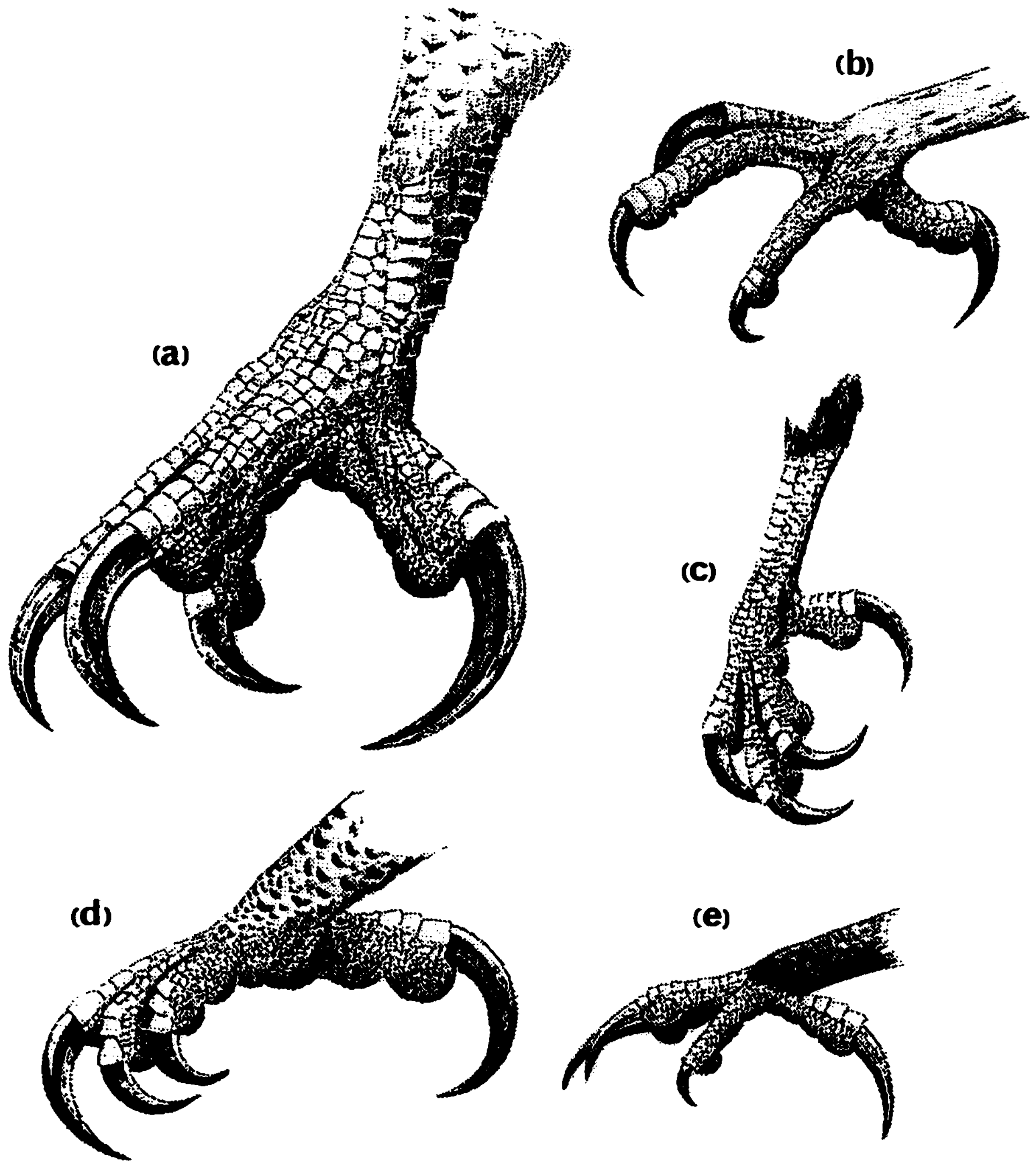


Fig.2.1. Feet and talons of (a) harpy eagle (*Harpia harpyja*), (b) Bonelli's eagle (*Hieraaetus fasciatus*), (c) African fish eagle (*Haliaeetus vocifer*), (d) crowned eagle (*Stephanoaetus coronatus*), (e) Asian black eagle (*Ictinaetus malayensis*). Scale = 50% life size. (Redrawn after Brown 1977.)

There are three large birds of prey that historically have been known as fierce predators of primates: harpy eagles in the Neotropics, crowned eagles in Africa, and Philippine eagles (*Pithecophaga jefferyi*) on the island of Mindanao. Scientific research has upheld and, for the former two species, even expanded upon this reputation. The harpy eagle, nearly the largest and undoubtedly the most powerful eagle in the world (Brown and Amadon 1989), is the premier predator of many Neotropical monkeys (Fowler and Cope 1964, Rettig 1977, 1978, 1995, Izor 1985). Harpy eagles attain speeds of 65-80 km/hr and can exert 2045 kg/m upon impact with their prey, nearly three times the muzzle energy of a bullet from a heavy rifle (Brown 1977). Momentum allows them to continue in flight and carry their victims to nesting or feeding trees. The talons can be driven through the body of a monkey to kill it instantly, or the monkey may be struck with such force that it dies by falling to the ground (Brown 1977).

Heavy eagles that prey on primates within the canopy, such as the harpy, Philippine, and crowned eagle, have short, broad wings and relatively long, graduated tails (Brown and Amadon 1989). Tails are 68.0-85.0% of wing length (Brown 1977). These morphological adaptations allow the eagles to maneuver better in the air and dodge dexterously around trees and other obstacles in thick forest as they target their prey. In some cases, these raptors can lift off almost vertically from the forest floor (Brown and Amadon 1989). The same pattern of wing and tail proportions is repeated in smaller genera of forest-hunting raptors, such as *Accipiter*, *Spizaetus*, and *Micrastur* (Brown and Amadon 1989).

The second largest of the African eagles, the crowned eagle, is the most powerful raptor on the continent and able to kill the largest prey (Brown 1966, Fannin and Webb 1975, Andrews 1990). The combination of short tarsi with exceptionally strong talons (Voous 1969, Brown 1977) has given the crowned eagle a reputation as a "primate specialist" (Gautier-Hion et al. 1983, Skorupa 1989, Cordeiro 1992). Studies of this raptor in Kibale, Uganda, found that 83.7-87.9% of its prey was *Colobus*, *Cercocebus*, and *Cercopithecus* (Skorupa 1989, Struhsaker and Leakey 1990, Leland and Struhsaker 1993). At another research site in Kiwengoma Forest Reserve, Tanzania, blue monkeys (*Cercopithecus mitis*) composed nearly 90.0% of the prey remains at a crowned eagle roost (Msuya 1993). Reliance on primate prey has been credited with the evolution of such adaptive behaviors in the crowned eagle as coordinated hunting of monkeys by breeding pairs (Daneel 1979), soft whistling to attract curious monkeys (Maclatchey 1937, Brown and Amadon 1989), and a protracted breeding cycle which leads to economy in the utilization of prey (Brown 1966). The latter adaptation – biennial rather than annual breeding – is also found in the harpy eagle and may indicate coevolution with prey (Brown 1966). The pressure on prey species, i.e., slow breeding primates, is doubled when a pair of crowned or harpy eagles are feeding a fledgling. Spacing extra food requirements to alternate years gives prey a respite to recover their numbers before the next breeding cycle of the eagles.

The hunting behavior of the crowned eagle consists of silent watchfulness from a perch within the forest, culminating in a swift drop onto prey (Brown et al. 1982). If a monkey is killed on the forest floor, the eagle will fly almost vertically upward and eat the whole carcass or torn pieces of it while perched on a branch (Brown and Amadon 1989). While cercopithecines and colobines are the most commonly-recorded primate prey for crowned eagles, a wide range of primate species are within the limits of this bird, including infant bonobos (*Pan paniscus*) (Badrian and Malenky 1984) and subadult mandrills (*Mandrillus sphinx*) (Jouventin 1975).

The third species of robust, primate-eating raptors, the Philippine eagle, has a huge, narrow bill (which may be an adaptation to enhance its binocular field of vision) and tarsi almost as heavy as the harpy eagle (Brown and Amadon 1989). Pairs of Philippine eagles have been observed hunting together, and estimates for successful capture of monkeys were significantly higher when two birds combined their efforts (Alvarez 1970). While data on the frequency of primates in the diet of Philippine eagles are sparse, three studies have estimated 3.0-6.3% of their diet is crab-eating macaques (*Macaca fascicularis*) (Gonzales 1968, Kennedy 1985, H. Miranda, pers. comm.) -- a range of percentages that is lower than the level of primates in the diets of harpy or crowned eagles.

Forest-hunting raptors are in most cases more threatening to arboreal primates than to terrestrial species. Nonetheless, baboons are crowned eagle prey in Southern Africa (Maclean 1985), and researchers saw a crowned eagle attack a subadult mandrill on the ground, hold on with its claws, and strike repeated blows at the mandrill's head with its beak (Jouventin 1975).

There are many large eagles that hunt by scanning for prey on the ground from a perch or while soaring: Verreaux's eagles (*Aquila verreauxii*) prey on baboons and semi-terrestrial vervets (Vernon 1965, Gargett 1971, 1990). Madagascar buzzards (*Buteo brachypterus*), and Madagascar harrier hawks (*Polyboroides radiatus*) prey on semi-terrestrial ringtailed lemurs (*Lemur catta*) when they descend to the ground (Sauther 1989).

Madagascar harrier hawks also have special morphological adaptations of the legs that allow them to bend and probe into narrow tree cavities and behind tree bark to find resting mouse lemurs (*Microcebus* spp.) during the day (Goodman et al. 1993c). Another Madagascar diurnal raptor, Henst's goshawk (*Accipiter henstii*), preys on nocturnal woolly lemurs (*Avahi laniger*) while they cling to trees during daylight hours (Goodman et al. 1998).

The hunting technique of small rainforest hawks involves sitting motionless and inconspicuous, interspersed with occasional swift and soundless flights from tree to tree (Thiollay 1985). Some species pursue active hunting, such as the Neotropical collared forest falcon (*Micrastur semitorquatus*) which runs along branches, through thickets, and even on the ground in pursuit of prey (Thiollay 1985). This species was seen to make 29 predation attempts on neonate squirrel monkeys (*Saimiri oerstedi*) at Corcovado, Costa Rica; grey hawks (*Buteo nitidus*) made four attempts, roadside hawks (*B. magnirostris*) made five attempts, and chestnut-mandibled toucans (*Ramphastos swainsonii*) made three attempts (Boinski 1987). Successful attacks on neonates were accomplished by the toucans and an ornate hawk eagle (*Spizaetus ornatus*), and a collared forest falcon killed one of the adult female monkeys. Predation on *Saimiri oerstedi* at Corcovado and *S. sciureus* at Manu National Park, Peru, by diurnal raptors was calculated to occur at the rate of one attack every six or seven days (Mitchell et al. 1991). This level of predation pressure by raptors on small Neotropical primates is supported by other studies. Terborgh (1983) recorded one or more raptor attacks at Manu in almost all three-week samples; the attacks were more frequent against *Saimiri* and *Saguinus* than against larger primates, such as *Cebus*. In another study, also at Manu, tamarin groups underwent attacks by raptors about once every one or two weeks (Goldizen 1987). In Brazilian Amazonia, raptors attacked a mixed group of *Saguinus mystax* and *S. fuscicollis* at the rate of once every 8.8 days (Peres 1991). In general, birds of prey launch more successful than unsuccessful attacks (Brown and Amadon 1989); based on the sightings of attacks listed above, predation pressure on Neotropical primates from predatory birds may be higher than records indicate.

Owls usually hunt from perches and at fairly close quarters without the variety of adaptations found in diurnal raptors (Brown 1971a). The soft edges of the owl's feathers are an adaptation for quiet flight (Everett 1977). Verreaux's eagle owl (*Bubo lacteus*), a very large nocturnal bird of Africa, has two hunting patterns: Adults sit singly on an elevated perch with a wide field of vision over open ground. Subadults roam more than adults, actively seeking out prey by gliding from perch to perch (Newman 1970, Pitman and Adamson 1978, Gillard 1979). Although it is the largest of the African owls, Verreaux's eagle owl is not as powerful as the large African eagles (Brown 1971a). Nevertheless, it can catch and kill diurnal prey up to the size of vervet monkeys (*Cercopithecus aethiops*) (Pitman and Adamson 1978, Steyn 1982, Andrews 1990), although nocturnal bushbabies are probably more common in its diet (Brown 1971a).

The Madagascar subspecies of barn owl (*Tyto alba affinis*), the Madagascar red owl (*T. soumagnei*), and the Madagascar long-eared owl (*Asio madagascariensis*) are predators of small, nocturnal prosimians. The barn owl is the most common and widely-distributed nocturnal raptor in Madagascar (Langrand 1990). It has unparalleled acoustic ability and is able to detect, locate, and catch prey in complete darkness (Payne 1971, Goodman et al. 1993c). Mouse lemurs (*Microcebus murinus*) are small, solitary, nocturnal foragers that are particularly vulnerable to barn owl predation (Goodman et al. 1993b). Madagascar long-eared owls, a reclusive endemic species, feed on bats, rodents, and small lemurs (Goodman et al. 1991). At one nest of Madagascar long-eared owls, 50.0% of the prey identified from pellets (regurgitations of indigestible bones) were sportive lemurs (*Lepilemur mustelinus*) (Rasoloarison et al. 1995). At four other sites, mouse lemurs made up 16.7-44.4% of the prey killed by a pair of Madagascar long-eared owls (Goodman et al. 1993a, Rasoloarison et al. 1995). When the combined predation pressure from barn owls and long-eared owls on mouse lemurs at Beza Mahafaly is considered, an estimated predation rate of 25.0% per year may be a conservative calculation (Goodman et al. 1993c).

Felids

Primates are a frequent prey item of many species of wild cats. Normally opportunistic hunters, availability of prey or total prey biomass are the primary criteria in food selection by wild cats (Emmons 1987).

Nearly every feature of a cat's body is related to its ability to detect and catch prey, e.g., adaptations such as camouflaging pelage, heightened senses of sight and hearing, skeletal design to enhance speed and power, and specializations of teeth and jaws (Kitchener 1991). Olfaction, however, is less important to felids for location of prey than other carnivores, such as canids (Guggisberg 1975). The basic sequence of felid predation is search, approach, and immobilization (Kruuk 1986). Hunting strategies of various felid species can be divided between active, mobile scanning of the the home range until potential prey is encountered versus stationary waiting in ambush at a probable locality for prey to approach (Kruuk 1986). Once potential prey has been observed, most cat species approach through a series of crouched stalks or slinking runs between available cover (Ewer 1973). A single, well-directed neck bite which severs the spinal cord is the lethal speciality of all cat species, allowing them to kill prey larger than themselves (Rautenbach and Nel 1978). In addition, felids possess morphological adaptations for leaping and grasping prey with their sharp, retractile claws (Kruuk 1986). Only the cheetah (*Acinonyx jubatus*) has non-retractile claws, along with smaller canines and larger nostrils than other large cat species (Lumpkin 1993).

Leopards (*Panthera pardus*) have a wide geographic range over much of Africa and southern Asia. They are able to exist in almost any habitat, from arid, semi-desert to dense rain forest (Smithers 1968, Hamilton 1986). Hills and riverine habitat are often selected by leopards (Mills and Biggs 1993). The hunting strategy of the leopard is largely a matter of lurking in likely places (e.g., waterholes) and stealthy approach followed by a quick spring and swipe with the paw (Rosevear 1974). When capturing primates, the leopard will grab ahold wherever possible (Turnbull-Kemp 1967). Leopards feed on relatively small prey, such as primates, because they hunt alone and need to carry carcasses into trees to keep them from being pirated by larger cats or pack-hunting canids or hyaenids (Bertram 1982).

Leopards have a wider prey base than the other large cats enabling them to utilize primates of all sizes in their diets (Mills and Biggs 1993). The range of primate species in the diet of leopards is extensive. In Africa they are known to prey on bonobos (*Pan paniscus*) (Badrian and Malenky 1984), chimpanzees (*P. troglodytes*) (Boesch 1991, 1992), western lowland gorillas (*Gorilla g. gorilla*) (Fay et al. 1995), rain forest guenons (*Cercopithecus* spp.) (Hart et al. 1996), vervets (*C. aethiops*) (Isbell 1990a, 1990b), geladas (*Theropithecus gelada*) (Iwamoto et al. 1995), baboons (*Papio* spp.) (Stoltz 1977, Cleave 1995), and drills (*Mandrillus leucophaeus*) (Rosevear 1974). In Asia, leopards prey on langurs (*Presbytis* spp.) (Srivastava et al. 1996), golden snub-nosed monkeys (*Rhinopithecus roxellana*) (Schaller et al. 1985, Schaller et al. 1987), macaques (*Macaca* spp.) (Seidensticker and Suyono 1980), and gibbons (*Hylobates moloch*) (Hoogerwerf 1970).

The proportion of primate prey differs greatly among felid species. Leopards seem to rely heavily on primates throughout many parts of their range. Hoppe-Dominik (1984) provided a review of leopard ecology in the Ivory Coast, where seven species of primates accounted for 16.2% of the prey in the diet of leopards. Based on fecal analysis, Hanuman langurs (*Presbytis entellus*) were found to comprise 27.0% of leopard diets at Kanha, India (Schaller 1967). One of the highest frequencies of primates in a leopard diet

(81.4%) was also from a research site in India (Srivastava et al. 1996). An absence of ungulates in Indonesia's Meru-Betiri Park converted both tigers (*Panthera tigris*) and leopards to reliance on primates as primary prey; primates in tiger and leopard diets totaled 33.3% and 56.9%, respectively (Seidensticker and Suyono 1980). Increased leopard predation caused an escalation in vervet deaths at Amboseli National Park, Kenya, and approximately 45.0% of the population died during a one-year period (Isbell 1990b).

Tigers are solitary, territorial hunters that thrive in dense vegetation where their camouflage stripes hide them from prey (Whitfield 1978). Stripes break up the tiger's silhouette giving it a great advantage during the stalking phase of the hunt (McDougal 1977, Sunquist and Sunquist 1988). Tigers prey on langurs (Thapar 1986, Sunquist and Sunquist 1988), orangutans (*Pongo pygmaeus*) (Rijksen 1978), and macaques (Seidensticker and Suyono 1980).

All felids are solitary hunters except lions (*Panthera leo*) (Kruuk 1986). Schaller (1972) calculated that lions hunted with at least one other pride member in 52.0% of his observations in the Serengeti. However, the number of prey killed per lion per hunt decreases when more than two lions are hunting together (Kruuk 1986). Benefits must accrue to groups of females in maintaining territories and protecting young because the foraging benefits of social hunting for lions are not sufficient to account for the formation of groups (Packer et al. 1990). Lions begin their hunt by randomly searching their environment for prey; the stalk can be of varying length, alternating between crouched movements and freezing in place; if the prey remains unaware of the stalking lion, it will make a final fast dash (Kruuk and Turner 1967). At several African sites, fecal analyses showed <1.0-6.0% of total prey consumed by lions were primates (Kruuk and Turner 1967, Makacha and Schaller 1969, Pienaar 1969, Schaller 1972). Based on nocturnal observations, an estimated >8.0% of the baboon population at Moremi, Botswana was killed annually due to predation by lions and leopards (Busse 1980).

The clouded leopard of Southeast Asia (*Neofelis nebulosa*) is most often sighted in trees but is not strictly arboreal (Rabinowitz 1988). It is intermediate in many morphological criteria between the large cats of the genus *Panthera* and the small cats of the genus *Felis* (Seidensticker 1985). It has a relatively small head with large canines and muzzle, equipment unnecessary to capture squirrels or birds, but that would be beneficial in the successful capture of primates (Seidensticker 1985). It is known to prey on orangutans (Rijksen and Rijksen-Graatsma 1975, Rijksen 1978) and proboscis monkeys (*Nasalis larvatus*) (Boonratana 1994).

Neotropical ocelots (*Felis pardalis*) hunt by slowly walking a nightly path until prey is opportunistically encountered (Emmons 1988). Recorded primate prey from scat analyses includes squirrel monkeys (*Saimiri sciureus*) and tamarins (*Saguinas fuscicollis*) (Emmons 1987). Although they are competent climbers, ocelots in one study were only seen to hunt terrestrially (Emmons 1988). Jaguar (*Panthera onca*), the largest of the Neotropical cats, have a wide food base (Schaller and Vasconcelos 1978). Prey capture is non-selective and opportunistic (Terborgh 1990b). While the jaguar climbs well and is almost as arboreal as the leopard, most hunting is done on the ground (Nowak 1991). It is often found near water and is known to swim across rivers while hunting (Green 1991). At a site in Venezuela where flooding from a new dam had stranded arboreal prey on islands, Peetz et al. (1992) documented a 66.7% decline in a group of red howlers (*Alouatta seniculus*) during a seven-month period as a result of jaguar predation.

Canids and hyaenids

Canids can be defined by their hunting strategy of trailing, running down prey, and attacking it from the rear (Estes 1967). They lack the claws and powerful forelimbs of felids, but compensate with heightened olfactory powers, long legs and deep chests that give them superior endurance to run down prey (Estes 1967). The African hunting dog (*Lycaon pictus*) is a diurnal predator that relies heavily on sight; no concealed stalk is attempted since hunting dogs are usually found only in short grass savannah (Estes and Goddard 1967, Fuller and Kat 1990).

Dholes (*Cuon alpinus*), the wild dogs of Asia, are diurnal and hunt in packs composed of approximately four to ten animals (Hoogerwerf 1970, Rice 1986). Due to lack of research on this species, there is no clear account of diet composition for dholes (Paulraj 1995). Nevertheless, two studies in India and one in Indonesia found primate remains in dhole scats (Johnsingh 1980, Seidensticker and Suyono 1989, Srivastava et al. 1996). Although it has been assumed that dholes, as pack hunters, concentrate on large deer (e.g., chital, *Axis axis*, and sambar, *Cervus unicolor*), 42.0% of dhole kills in the Bandipur Tiger Reserve, India were animals under 25 kg (Johnsingh 1983). .

Jackals and foxes pick up scents and pounce on their prey rather than run it down in packs (Estes 1967, Lloyd 1980). In Asia, successful captures of arboreal capped leaf monkeys (*Trachypithecus pileata*) and semi-terrestrial Hanuman langurs by golden jackals

(*Canis aureus*) hunting in pairs were recorded (Newton 1985, Stanford 1989). All observed encounters between jackals and patas monkeys (*Erythrocebus patas*) in West Africa were aggressive and clearly supported the position that jackals are predators on these primates (Struhsaker and Gartlan 1970). In areas without a full complement of larger carnivores, jackals become major predators of animals the size of primates by hunting cooperatively (Lamprecht 1978, McKenzie 1991).

Hyenas use their powerful teeth and jaws both to kill and to crush the bones of prey (Kruuk 1970). There are records of primates in the diets of all three species of hyenas (*Crocuta crocuta*, *Hyaena hyaena* and *H. brunnea*) (Bourliere 1963, Pienaar 1969, Skinner 1976, Bearder 1977, Stelzner and Strier 1981, Kerbis-Peterhans 1990), but instances of observed predation events on primates are rare. Nevertheless, researchers witnessed the capture and killing of an adult male yellow baboon (*Papio cynocephalus*) by a spotted hyena in Amboseli National Park, Kenya (Stelzner and Strier 1981) and zoo hyenas caught a red colobus (*Colobus badius*) in their enclosure at Abuko Reserve, The Gambia (Starin 1991).

Spotted hyenas live in clans of up to 50 members; three-quarters of their food is obtained by hunting and one-quarter by scavenging (Cooper 1990). Because of the relatively small size of primates in relation to large African ungulates, packs of hyenas cannot depend on animals the size of primates as staple food (Henschel and Tilson 1988). Primates, instead, appeal to the solitary forager, such as a single spotted hyena that is looking for a quick meal (Cooper 1990). The solitary brown hyenas and striped hyenas do not hunt in packs and are basically scavengers (Kruuk 1975, Owens and Owens 1978, Rautenbach and Nel 1978). However, they are known to hunt and kill small mammals opportunistically (Mills 1978, 1989).

The efficiency of cooperative hunting by hyenas and canids is reflected in capture rates (Bertram 1979), e.g., 35% success rate for spotted hyenas and 50-70% for African hunting dogs. Their emphasis is entirely on terrestrial species, which limits primate prey in Africa to savannah dwellers such as baboons, patas monkeys, and vervets.

Damaging effects on wild animal populations by feral domestic dogs (*Canis familiaris*) should not be underestimated (Barnett and Rudd 1983). An evaluation of dogs as predators found that they had killed seven species of primates (Anderson 1986b). In populated parts of India and Sri Lanka, feral dogs more frequently attack and kill langurs than any other carnivore (Oppenheimer 1977).

Ursids

Bishop (1975) is the only source to mention bears as a potential predator of primates. The Asian black bear (*Selenarctos thibetanus*) is the most carnivorous of the Asian bears (Prater 1971), and individuals of the species are known to kill animals as large as adult water buffaloes by breaking their necks (Nowak 1991). The bears of the Himalayan foothills have been credited by locals with killing Hanuman langurs, but there was no empirical evidence (Bishop 1975).

Small carnivores

There are four families of small carnivores known to prey on primates: Viverrids – genets, civets, and the Malagasy fossa (*Cryptoprocta ferox*); herpestids – seven species of mongoose; mustelids – the tayra (*Eira barbara*); procyonids – raccoons and coatis. One species of marsupial in the didelphid family – the Neotropical opossum (*Didelphis marsupialis*) – has been identified as a probable primate predator.

Generally, predators are most dangerous to prey when the prey is moving or sleeping (Moynihan 1976b). Predatory mammals, many of which are nocturnal, are more likely to successfully secure vulnerable sleeping primates than are nocturnal owls because small carnivores hunt by smell in addition to sight and sound (Moynihan 1976b). They also possess forelimbs with strong claws that make them likely to dig at the entrances to sleeping nests and holes. For example, fossa have been seen to dig out hibernating prey such as fat-tailed dwarf lemurs (*Cheirogaleus medius*) (Rasoloarison et al. 1995).

Viverrids, herpestids, and mustelids are generalist carnivores with simple tooth morphology (Andrews 1990), but their attack has been likened to being "bitten by a sewing machine" (Ewer 1973). The elongated bodies of these small carnivores are geared for speed and maneuverability rather than strength of attack. Genets and many civets are nocturnal and highly arboreal, allowing them access to small, canopy-dwelling primates. Genets are thought to favor denser vegetation than other small carnivores (Waser 1980b). The hunting strategy for genets involves slow, cat-like stalking culminating in a sudden pounce (Waser 1980b). The excellent binocular vision of the large-spotted genet (*Genetta tigrina*) enables it to judge distances accurately in the arboreal milieu (Macdonald 1992).

Genets inflicted significant mortality (33.3% over a two-year period) on a population of Senegal bushbabies (*Galago senegalensis*) in South Africa (Martin and Bearder 1979). The African palm civet (*Nandinia binotata*) is omnivorous, consuming fruit along with arboreal mammals; records of primate prey include pottos (*Perodicticus potto*) (Charles-Dominique 1974) and an unsuccessful attack on a mona monkey (*Cercopithecus mona*) (Ewer 1973).

The largest of the viverrids is the endemic fossa of Madagascar, which weighs as much as 20 kg. The fossa has adapted to the role felids play on the continents (Macdonald 1992). It has evolved the sharp retractile claws, strong mandible, carnassial molars, and formidable canines to fill the ecological niche of the absent felids (Macdonald 1984b, Wright et al. 1997). The fossa's agility in the trees has been compared to the clouded leopard of Asia (Wright et al. 1997). Fossa use their front paws to capture prey and immobilize it prior to inflicting a killing bite on the back of the head, a killing technique unlike other viverrids that seize prey directly in their jaws (Albignac 1970, 1984, Eisenberg and Leyhausen 1972). Male and female fossas have been observed working as a team in pursuit of diadem sifakas (*Propithecus diadema*); this has led to speculation that during the breeding season fossas may hunt in pairs (Blakey 1994, J. Powzyk, pers. comm.). According to Rasolonandrasana (1994) lemurs constitute the basis of the fossa's diet. He identified remains of mouse lemurs (*Microcebus* cf. *M. murinus*), Coquerel's dwarf lemurs (*Mirza coquereli*), fat-tailed dwarf lemurs (*Cheirogaleus medius*), fork-marked lemurs (*Phaner furcifer*), sportive lemurs (*Lepilemur mustelinus*), brown lemurs (*Lemur fulvus*), and Verreaux's sifakas (*Propithecus verreauxi*) in fossa scats collected at two study sites. Current research substantiates that fossa exert considerable pressure on the larger lemurs, such as *P. verreauxi* (Rasoloarison et al. 1995). The diet of the fossa also includes Milne-Edward's sifakas (*P. diadema edwardsi*), which weigh 6.5-7.5 kg, and are the biggest prey animal taken by any viverrid (Macdonald 1992, Wright et al. 1997).

The typical mustelid method of killing is a bite on the back of the prey's neck or base of skull, thus severing the spinal cord (Ben-David et al. 1991). However, variations on this standard killing technique have been documented (Powell 1978, Rowe-Rowe 1978) and such versatility allows for a wide range of potential prey (Ben-David et al. 1991). The only mustelid species that is a confirmed predator on primates is the marten-like tayra, a Neotropical arboreal carnivore that often travels in pairs or small groups (Hershkovitz 1969). Tayras exhibit a strong affinity for close-canopy forests, although they den in the ground (Sunquist et al. 1989). Successful predation and unsuccessful attacks by tayras have been observed on *Saguinus nigricollis* (Izawa 1978), *S. oedipus* (Moynihan 1970), *S. mystax* (Ramirez 1989), *S. midas* (Galef et al. 1976), *Leontopithecus rosalia* (Stafford and Ferreira 1995), *Cebus apella* (Hernandez-Camacho and Cooper 1976), *C. albifrons* (Defler 1980), and *Saimiri sciureus* (Galef et al. 1976). In addition, tayras are suspected of preying on infant woolly spider monkeys (*Brachyteles arachnoides*) (Printes et al. 1996).

Mongoose exploit prey by rapid, opportunistic hunting (Waser 1980b). They are agile and terrestrial, preying on small vertebrates (Macdonald 1984b). Four of the seven mongoose species identified as predators on primates are indigenous to Madagascar: narrow-striped mongoose (*Mungotictis decemlineata*), ring-tailed mongoose (*Galidia* *elegans*), Malagasy brown-tailed mongoose (*Salanoia concolor*), and broad-striped mongoose (*Galidictis* spp.). Narrow-striped mongoose have been studied in the wild and were found to hunt mouse lemurs alone or in pairs during the dry season; however, in the wet season they forage in bands and reputedly cooperate in the pursuit of *Microcebus* (Macdonald 1992). Ring-tailed mongoose are more arboreal than other herpestids and have been seen climbing and descending vertical trunks only 4 cm in diameter (Nowak 1991). Predation by ring-tailed mongoose on brown mouse lemurs (*M. rufus*) and greater dwarf lemurs (*Cheirogaleus major*) has been observed (Wright and Martin 1995, Wright et al. 1998). The Malagasy brown-tailed mongoose is said to resemble the ring-tailed mongoose in morphology but to have a diet very similar to the narrow-striped mongoose (Albignac 1984).

Omnivorous Neotropical opossums (*Didelphis marsupialis*) are the only marsupials suspected to prey on primates (Boinski 1992). They are known to be entirely opportunistic, taking any prey they encounter and can kill (Moynihan 1976b). Although primarily terrestrial, they are competent climbers and can be found feeding at heights of 25 m (Macdonald 1984b).

Procyonids identified as potential primate predators are crab-eating raccoons (*Procyon cancrivorus*) and coatis (*Nasua nasua*). Their predation on primates is suspected to be limited to callitrichids and squirrel monkeys (Ferrari 1988, Boinski 1992). Crab-eating raccoons replace the common raccoon (*Procyon lotor*) in the Neotropics, but are very similar in morphology except for a longer tail (Macdonald 1984b). They are nocturnal, generalized omnivores, but little else is known of their ecology other than they are often found near streams, lagoons, and lakes (Eisenberg 1989). Coatis are similar in form and behavior to Old World viverrids (Hershkovitz 1969). They are diurnal, highly social carnivores (social bonds between adult females and their young are much like primates) that are very tolerant of habitat type, exploiting everything from dry, deciduous forest to tropical evergreen forest (Eisenberg 1989). Coatis have strong forelimbs and long claws for excavating food in leaf litter and rotten logs; they are also equipped for an arboreal lifestyle with squirrel-like retrovertible hind legs to descend trees head first and a long, semi-prehensile tail (Macdonald 1984b, Nowak 1991). In addition, their long, mobile snouts are well adapted for investigating crevices and holes (Nowak 1991). Males tend to take up a solitary existence and turn their attention toward larger vertebrate prey (Bisbal 1986).

Reptiles

Crocodiles are master predators on a wide tropical food base. No set hunting strategy exists for crocodiles, although stealth, surprise and a sudden final burst of speed are always involved (Cott 1961). Besides the strength of a lone individual, which can reach 8 m in length (J. Losos, pers. comm.), Nile crocodiles (*Crocodylus niloticus*) often hunt cooperatively and may even divide prey among group members (Pooley and Gans 1976). For mammalian prey as large as primates, adult crocodiles will lurk offshore near game trails and watering places; upon sighting the prey, the crocodile quietly submerges, waiting to make a fatal upward rush (Alderton 1991).

To cross the river at the Abuko Nature Reserve in The Gambia, red colobus (*Colobus badius*) frequently used a narrow land bridge where camouflaged crocodiles would lie in the grasses (Starin 1991). Two juvenile red colobus and an adult vervet (*Cercopithecus aethiops*) were captured by the crocodiles.

Remains of baboons (*Papio ursinus*) and *Cercopithecus* spp. were found in Nile crocodiles in southern Africa (Cott 1961). On two occasions crocodiles seemed to be stalking silverback western lowland gorillas (*Gorilla g. gorilla*) in the Republic of Congo (C. Olejniczak, pers. comm.). In both cases, the male gorillas hastily left the area after becoming aware of the crocodile's presence. In Indonesia, false gharials (*Tomistoma schlegeli*), previously assumed to eat only fish (Pooley 1989), have been observed preying on crab-eating macaques (*Macaca fascicularis)* and proboscis monkeys (*Nasalis larvatus)* as the monkeys swam across rivers (Galdikas and Yeager 1984, Galdikas 1985, Yeager 1991).

Asian water monitors (*Varanus salvator*) measure approximately 1.5-2.0 m in length. They have formidable claws and sharp teeth, along with a well-developed sense of smell and keen eyesight; in addition they are good swimmers, run at high speed on land, and are agile arboreally (Hoogerwerf 1970). The largest of the monitors, the Komodo dragon (*V. komodoensis*), is terrestrial and feeds mostly on mammals, including monkeys (Pfeffer 1989). The hunting strategy of all of the monitor lizards is very active in comparison to other reptiles that prey on primates. Monitor lizards pick up scent trails with their long forked tongues and follow them to prey (Pfeffer 1989). So few studies have dealt with predator/prey interactions of monitor lizards that it is impossible to assess what impact they may have on primates.

There is also a paucity of field studies on tropical snakes (Murphy and Henderson 1997). While few data are available on the interactions between primates and these predators, there are numerous observations published in the scientific literature documenting predation by snakes. To cite a few examples, African pythons (*Python sebae*) have been observed swallowing baboons (Isemonger 1962, Pienaar 1969); anacondas (*Eunectes murinus*) prey on *Saguinus mystax* (Heymann 1987); *Boa constrictor* is a predator of *Cebus capucinus* (Chapman 1986); Richard (1978) reported a Malagasy colubrid, the forest night snake (*Ithycyphus miniatus*), strangling an adult gray mouse lemur (*Microcebus murinus*); Rakotondravony et al. (1998) recounted a Malagasy tree boa (*Sanzinia madagascariensis*) suffocating and swallowing a bamboo lemur (*Hapalemur griseus*) in the littoral forest of eastern Madagascar.

The so-called giant snakes, pythons, boas, and anacondas, rely on a combination of sensory inputs to locate food, including vision, vibration, heat and odor (Murphy and Henderson 1997). Because they eat mostly active animals, they hunt mainly by "sit and wait" ambush (Mattison 1995). When prey are encountered, they usually retract the head and neck, then rapidly strike, immediately immobilizing the victim by constriction, followed by swallowing (Greene 1997). One boa constrictor under study in Panama entered a different medium-sized mammal burrow every three or four days, waiting up to 96 hours for prey to approach within striking distance (Montgomery and Rand 1978).

Giant snakes eat a wide variety of vertebrates and, generally, this leads them to be very opportunistic in their choice of prey, taking advantage of almost any potential prey species of an appropriate size (Murphy and Henderson 1997). Adults of the family Boidae -- Asian and African pythons (*Python molurus, P. reticulatus*, and *P. sebae*) and the anacondas and boas of the Neotropics -- are restricted to terrestrial or aquatic habitats because their heavy weight precludes arboreality (Grzimek 1975). Pythons, however, have a wider variety of large terrestrial mammals, such as primates, to choose from than do anacondas and boas since fewer large, ground-dwelling species have evolved in the Neotropics (Murphy and Henderson 1997). Thus, the range of species and absolute numbers of individual primates and other medium to large mammals in the diets of Asian and African pythons can be expected to be greater than those found in the diets of the Neotropical boids. A study of African pythons in The Gambia found that the density of individuals over 2 m in length (i.e., adults) was approximately 20-25 snakes in a 33.5 ha area (Starin and Burghart 1992). The researchers surmised that pythons at this density have considerable impact on small and medium–sized mammals.

Vipers and pit vipers (family Viperidae), cobras and mambas (family Elapidae), and mussuranas and rat snakes (family Colubridae) have different feeding patterns than the large constricting boid snakes because many inject venom, an adaptive strategy which allows them to subdue and ingest very large prey (Greene 1997). After cobras and colubrids strike, they retain an initial grip until struggling ceases; most vipers, however, bite rapidly, release, and then relocate prey after it dies. Poisonous snakes were a significant source of mortality to sleeping rhesus macaques (*Macaca mulatta*) at a research site in India (I. Malik, pers. comm.).

Neotropical bushmasters (*Lachesis muta*) are the largest of the pit vipers and suspected to prey on tamarins (Bartecki and Heymann 1987). This species also uses a sit-and-wait hunting strategy; one female bushmaster traveled just 50 m in 35 days, catching only one prey item during that time (Greene and Santana 1983).

Sharks

Rhesus macaques have colonized the mangrove swamps in the Sunderbans, West Bengal, India (Mukherjee and Gupta 1965). Besides Indian pythons (*Python molurus*) and estuarine crocodiles (*Crocodilus porosus*), wolf sharks (also known as common thresher sharks) (*Alopias vulpinus*) and requiem sharks (*Carcharhinus gangeticus*) prey on the macaques when the monkeys swim across estuaries at ebb tide. Wolf sharks are approximately 6.1 m, 3 m of which is an elongated tail used to stun prey (Lineaweaver and Backus 1970, Ellis 1996). Individuals are usually found offshore but not in exceedingly deep waters (Ellis 1996). Requiem sharks are found in tropical and temperate seas and reach a maximum length of 4 m (Stafford-Deitsch 1987). Little is known about the natural history of requiem sharks or other species in the family Carcharhinidae (Ellis 1996).

Primates preying on other primates

Chimpanzees, orangutans, baboons, blue monkeys, capuchin monkeys (*Cebus* spp.), lemurs (*Lemur fulvus rufus*), and cheirogaleidids (*Mirza coquereli*) have been observed hunting and eating smaller primates. Information on primates eating primates is summarized in Appendix 2.

Certain instances of primates preying on other primates are relatively well-studied, particularly chimpanzee predation (Uehara et al. 1992, Stanford et al. 1994a, Stanford 1995b, Stanford and Wrangham 1998). At Gombe National Park in Tanzania, chimpanzee predation on red colobus 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. 1994a, p. 221). This annual harvest rate is controversial when compared to Goodman et al.'s (1993c) estimation of 25.0% estimated predation rate on *Microcebus*, which has a higher reproduction capacity than anthropoids. Additionally, the extrapolation of Gombe chimpanzee kill rates on red colubus to all chimpanzee populations is questionable. Boesch (1994c) believed that human presence had a much stronger impact on chimpanzees hunting red colobus in Gombe than in the Tai Forest, Ivory Coast. Yet, Boesch and Boesch (1989) identified red colobus as the most significant prey item for chimpanzees in the Tai Forest.

The study of primate predators and prey is an intriguing contribution to both primatology and paleoanthropology; however, it is outside the scope of this thesis. The situation is relatively rare and represents a small number of species, so little can be inferred from it regarding broad predator-prey interactions. Data from questionnaires or from the literature concerning predation by primates on other primates were not included in any analyses in subsequent chapters.

Human predation on primates

The latter half of the twentieth century has seen primates killed for sport, trophies, and during capture for the pet trade and medical research. The most current crisis is the escalating "bush meat" trade in Africa. In the past decade, logging roads have opened up rainforests in West and Central Africa to commercial hunters who kill bush meat (primarily antelopes and primates) for urban markets. Some estimates suggest that several thousand gorillas (*Gorilla g. gorilla*), chimpanzees (*Pan troglodytes*), and bonobos (*P. paniscus*) are killed annually in West and Central Africa to supply this lucrative market (Redmond 1998).

In addition, the greatest insidious threat to the survival of primates is the destruction of habitat in the tropics and subtropics through uncontrolled burning and cutting of forests (Mittermeier and Coimbra-Filho 1977).

One facet of human predation that is closely related to the study presented here is subsistence hunting of primates by indigenes, a situation which may approximate the predation levels with which non-human primates and hominids evolved. Predation by indigenous hunter-gatherers is a major source of primate mortality in West and Central Africa and in Amazonian South America (Mittermeier 1987, Mittermeier and Cheney 1987, Alvard 1994). The frequency of occurrence of primates killed by indigenous hunters near Manu National Park, Peru, illustrates that humans with simple weapons can be formidable predators on other primates. For example, of 81 animals killed with bows and arrows by the Yomiwato, 48 (59.2%) were primates (Alvard and Kaplan 1991). The Waorani of eastern Ecuador preferentially target large primates; in 867 days of hunting, they killed 562 woolly monkeys (*Lagothrix lagotricha*) and 246 red howlers (*Alouatta seniculus*) (Yost and Kelley 1983).

Traditional subsistence hunting of primates is obviously an increasing rarity throughout the world (Gardner 1972, Sinha 1972, Hart 1978), while commercial exploitation of primates in non-traditional ways is on the rise. Both subsistence and commercial exploitation of primates by humans are complex issues that require intensive examination and are not addressed within this thesis.

Fossil record

Fossil evidence supporting theories of long term coevolution between primates and their predators is sparse. Nevertheless, some discoveries tend to generate speculation. For example, predation on *Notharctus*, a prosimian-like Eocene fossil, was reconstructed based on the size and shape of skull puncture marks which matched the teeth of *Vulpavus*, an arboreal mammalian predator (Alexander 1992).

Gebo and Simons (1984) measured puncture marks on Fayum Oligocene fossil primates. Due to tooth structure, they concluded that primitive mammalian carnivores, the creodonts, preyed and/or scavenged on these primates. However, based upon their assumption that predation on living primates is a rare event, the authors concluded that it was also rare in the Oligocene, although 9.0% of the fossils they examined showed evidence of predation.

On the basis of the discovery of a skull evidencing bitemarks, *Metailurus parvulus*, a fossil felid the size of a modern leopard, was identified as the probable predator of *Mesopithecus*, an Upper Miocene primate (Zapfe 1981).

Fossil bones of early hominid origin were found with baboon remains in South African cave excavations at Swartkrans, Kromdraii and Sterkfontein (Brain 1970, 1978, Cavallo 1991). Brain (1981) offered two hypotheses to explain the preponderance of australopithecine and cercopithecine remains. Either a specialized primate predator, besides leopards and hyenas existed at the sites, or fossil primates and early hominids slept in caves providing an excellent opportunity for leopards to kill them and drag the carcasses farther into the caves for feeding. The Mt. Suswa lava caves in Kenya provide a current analogy to the paleontological record in South Africa and lend credibility to the second hypothesis. Mt. Suswa is a favorite sleeping site for baboons, and leopards in the area subsist almost entirely on these primates (Coryndon 1964, Simons 1966).

CHAPTER III.

OBSERVED PREDATION EVENTS

"Spying from some high-lying place, [the leopard] *picks out a half-grown baboon which has wandered from the troop, and with all the cunning of its race it chooses an ambush that will bring the baboon within reach of its merciless claws. No matter how acute the baboon's power of vision, the mantle of invisibility which the leopard seems to possess plays the fool with even that astonishing keen-sightedness."* (Marais 1939, p.35-36)

INTRODUCTION

Variations on the statement: "Predation is rarely observed..." (Cheney and Wrangham 1987, p.227, Hall 1966, Altmann 1974, Hausfater and Hrdy 1984, Chapman 1986, Stanford 1989, Isbell 1990a, Srivastava 1991, Peetz et al.1992, Hrdy et al. 1995, Nunes et al. 1998) are frequently employed as a caveat when the topic of primates as prey is under discussion. It is not an exaggeration to say that the statement has come to be accepted as axiomatic within the primatology community and is sometimes used to convey that the evolutionary consequences of predation on primates are as incalculable as the unknown magnitude of predation. Yet, a *systematic count* of observed predations on primate species has never been attempted.

It is not my intention here to define at what level primate predation can be judged as "rare" or "common," since these are relative terms, or to make a statistical statement of significant difference between occurrences of predation and other phenomena in primate life histories that have been said to be rarely observed, such as birth or infanticide (Jolly 1972, Hrdy et al. 1995). My intention is to examine and document the prevalence of predation on primates found in the published literature.

Approaching the subject of predation on primates from an objective viewpoint, I found it evident that a divergence of views concerning the rarity of predation exists between primate researchers and their counterparts studying predatory species. The evidence for primates in the diets of many predators is indisputable to researchers who study predatory animals, but my specific goal in this chapter is to calculate the total published *observations* of predation that can be found within all the evidence of predation.

An extensive assortment of articles in the primate scientific literature, along with general biological and natural history journals, contain observations of predation on primates. (See Appendix 3 for sources containing data used in this chapter.)

Some primate researchers have made an attempt to document thoroughly the circumstances surrounding an attempted or successful killing of a primate by a predator, including the behavioral repertoire of both predator and prey (for instance, Busse 1980, Boinski 1987, Starin 1991). Anecdotal descriptions of predatory events have even appeared as short reports in scientific journals (Stelzner and Strier 1981, Eason 1989, Peres 1990, Sherman 1991, Julliot 1994). However, most field researchers are in the process of studying some other aspect of primate ecology or behavior when the unexpected drama of predation unfolds. Given the instantaneous reaction time necessary to process this phenomenon, most records of predation are brief anecdotal asides to the main body of the published research.

The wider scientific literature encompassing field research on mammalian carnivores, birds of prey, and the large predatory reptiles contains both quantitative and descriptive discussions of primates as prey. Quantitative data are presented through sampling methodologies such as the contents of stomachs, feces, or regurgitations (e.g., Kruuk and Turner 1967, Emmons 1987, Rasoloarison et al. 1995), or analyses of nest and den remains (e.g., Skinner 1976, Rettig 1978) and prey carcassses (e.g., Schaller 1967, 1972).

Such sampling methods provide excellent data on numbers of primates eaten by predators. Nevertheless, these are inferred data. Although some species of predators, such as cheetah, falcons, and hawks never scavenge food (Eaton 1974, Brown and Amadon 1989), other predators -- lions, as an example -- may occasionally scavenge or appropriate another predator's kill (Schaller 1972). One could not exclude the possibility that the prey item had died of disease, accident or intraspecific aggression and subsequently been eaten by the predator.

To prevent any ambiguity over the process by which a primate died – whether by "natural" causes or through predation – in this chapter I have considered only those reports clearly describing witnessed predation events. From these I have compiled a data set including over five hundred published, direct observations from field researchers and naturalists so I could document the prevalence of this phenomenon.

Compiling qualitative reports to examine a subject that has not been analyzed quantitatively has scientific merit because, while a single anecdotal account may be of limited significance, multiple records warrant deeper investigation (Daly and Wilson 1988, Whiten and Byrne 1988, Byrne and Whiten 1990). Although care must be taken as to how these data are interpreted, the process of collecting, cataloging, and extracting a meaningful pattern from isolated observations is a legitimate approach to the study of rare phenomena (Whiten and Byrne 1988). A branch of statistics – meta-analysis – involves the same approach, i.e., synthesizing the results from independent studies for the purpose of integrating the findings (Taylor Halvorsen 1986).

METHODS

From a bibliography of approximately 900 citations, dated 1895-1999 (all of which discuss some element of predation), articles were scrutinized for *direct* observation of primates attacked or killed by predators. Although no limits were set on the time period of references extracted during this literature search, 91.3% of the articles were published between 1960-1998.

Three criteria were used to determine instances of observed predation events involving primates.

- *Criterion 1.* An eyewitness account of the killing of a primate by a predatory species.
- *Criterion 2.* An eyewitness account of a predator carrying a recently-killed primate and/or consuming the carcass of a recently-killed primate.
- *Criterion 3.* An eyewitness account of an unsuccessful attack on a primate by a predator.

Predation events meeting the three criteria were collated by region (Africa, Madagascar, Asia, and the Neotropics), by predator categories (felids, raptors, canids/hyaenids, small carnivores, reptiles, or unidentified predators), and by family or subfamily of the species of primate prey.

RESULTS

One hundred eighty-three sources (articles from professional scientific journals, n=91; natural history journals, n=18; authored books, n=34; chapters in edited volumes, n=26; dissertations, n=13; reports, n=1) contained 583 references to eyewitness accounts of predation (see Table 3.1). *Criterion 1* (eyewitness to a predatory act) was recorded in 229 instances (from 96 sources). There were 79 observations (from 43 sources) meeting *Criterion 2* (eyewitness to predator with fresh carcass). *Criterion 3* (eyewitness to unsuccessful predation) accounted for the remaining 275 observations (from 92 sources).

Considerable numbers of predations occurred in all geographic areas: 47.3% (n=276) of the observed predations occurred in Africa (47.0%, n=86, of the citations); 9.4% (n=55) occurred in Madagascar (7.7%, n=14, of the citations); 16.5% (n=96) occurred in Asia (25.1%, n=46, of the citations); 26.8% (n=156) occurred in the Neotropics (20.8%, n=38, of the citations).

In Table 3.2, I categorized the predation sightings by predator taxa. Felids accounted for 24.2% of all witnessed predations; raptors and other predatory birds were responsible for 46.3%; species in the dog and hyena families, small carnivores, and

TABLE 3.1. Summation of observed and published predation events.

REGION AND PREDATOR	EYEWITNESS ACCOUNT OF PREDATION ON PRIMATE (No. of Published Sources)		PREDATOR IN POSSESSION OF CARCASS OR CONSUMING RECENTLY-KILLED PRIMATE (No. of Published Sources)		EYEWITNESS ACCOUNT OF UNSUCCESSFUL ATTACK ON PRIMATE (No. of Published Sources)		TOTAL PUBLISHED ACCOUNTS OF PREDATION (No. of Published Sources)	
AFRICA								
Felid	42	(23)	33	(13)	30	(16)	105	(52)
Raptor	36	(22)	17	(7)	46	(22)	99	(51)
Canid/Hyaenid	5	(5)	1	(1)	22	(10)	28	(16)
Small Carnivore	1	(1)	0		4	(2)	5	(3)
Reptile	8	(5)	0		4	(3)	12	(8)
Unidentified Predator	26	(2)	0		1	(1)	27	(3)
TOTAL AFRICA	***118***	***(58)***	***51***	***(21)***	***107***	***(54)***	***276***	***(133)***
MADAGASCAR								
Felid	0		0		0		0	
Raptor	10	(3)	6	(3)	16	(4)	32	(10)
Canid/Hyaenid	1	(1)	0		0		1	(1)
Small Carnivore	12	(4)	0		4	(4)	16	(8)
Reptile	4	(4)	2	(1)	0		6	(5)
TOTAL MADAGASCAR	***27***	***(12)***	***8***	***(4)***	***20***	***(8)***	***55***	***(24)***

CONTINUED … TABLE 3.1. Summation of observed and published predation events.

REGION AND PREDATOR	EYEWITNESS ACCOUNT OF PREDATION ON PRIMATE (No. of Published Sources)		PREDATOR IN POSSESSION OF CARCASS OR CONSUMING RECENTLY-KILLED PRIMATE (No. of Published Sources)		EYEWITNESS ACCOUNT OF UNSUCCESSFUL ATTACK ON PRIMATE (No. of Published Sources)		TOTAL PUBLISHED ACCOUNTS OF PREDATION (No. of Published Sources)	
ASIA								
Felid	13	(11)	5	(4)	7	(5)	25	(20)
Raptor	2	(2)	2	(2)	9	(7)	13	(11)
Canid/Hyaenid	26	(11)	1	(1)	13	(6)	40	(18)
Small Carnivore	0		0		0		0	
Reptile	4	(4)	3	(3)	0		7	(7)
Unidentified Predator	11	(1)	0		0		11	(1)
TOTAL ASIA	***56***	***(29)***	***11***	***(10)***	***29***	***(18)***	***96***	***(57)***
NEOTROPICS								
Felid	4	(4)	1	(1)	6	(4)	11	(9)
Raptor	17	(10)	6	(6)	103	(14)	126	(30)
Canid/Hyaenid	0		0		0		0	
Small Carnivore	0		1	(1)	10	(7)	11	(8)
Reptile	3	(2)	1	(1)	0		4	(3)
Unidentified Predator	4	(1)	0		0		4	(1)
TOTAL NEOTROPICS	***28***	***(17)***	***9***	***(9)***	***119***	***(25)***	***156***	***(51)***
GRAND TOTAL	***229***	***(116)***	***79***	***(44)***	***275***	***(105)***	***583***	***(265)***

TABLE 3.2. Published accounts of observed predation on primates categorized by predator taxa.

PREDATOR TAXA	PREDATION EVENTS (N=583)	NUMBER OF SOURCES	PREDATION EVENTS (%)
Felids	141	64	24.2
Diurnal raptors, owls and other predatory birds	270	83	46.3
Canids and hyaenids	69	34	11.8
Small carnivores	32	16	5.5
Reptiles	29	20	5.0
Unidentified predators	42	3	7.2

reptiles accounted for 11.8%, 5.5%, and 5.0% respectively. In 7.2% of the cases, the predator was not identified by the author.

Data were available for ten families of non-human primates (Fig.3.1). The subfamily Cercopithecinae represented 45.7% (n=254) of documented predations; references to sightings of cercopithecine predation were found in 45.9% of the articles. Next in magnitude was the family Cebidae (21.8%, n=121, found in 12.0% of articles), followed by Colobinae (13.1%, n=73, 23.5% of articles), Callitrichidae (5.6%, n=31, 8.7% of articles), Cheirogaleidae (5.2%, n=29, 5.5% of articles), Lemuridae (3.2%, n=18, 2.7% of articles), Lorisidae (2.0%, n=11, 3.3% of articles), Pongidae (1.6%, n=9, 3.8% of articles), Indriidae (1.3%, n=7, 2.2% of articles), Hylobatidae (0.4%, n=2, 1.1% of articles), and Tarsiidae (0.2%, n=1, 0.5% of articles).

DISCUSSION

Instances of predation on primates have been recorded as anecdotal observations in numerous research journals. Predators include: diurnal raptors, owls, and other predatory birds (such as toucans), small and large felids, wild canids (e.g., jackals and dholes, as well as feral dogs), other carnivorous mammals (e.g., hyenas, genets, civets, fossa, mongoose, and tayra), crocodiles, and large snakes.

That predation on primates is a rarely-observed event with unknown implications on primate evolution is an assumption frequently expressed within the primate research community (see Cheney and Wrangham 1987). The literature search I describe in this

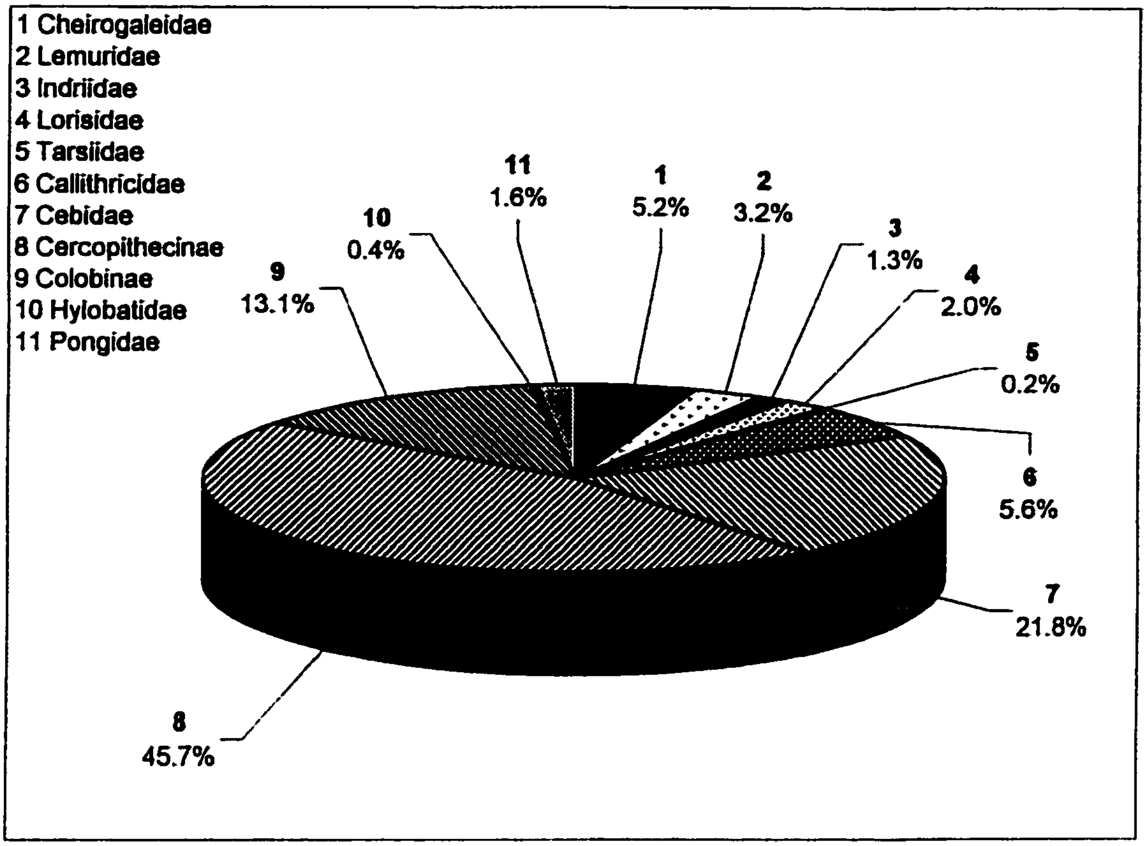


Fig.3.1. Percentage of observed predations per primate family or subfamily.

chapter was undertaken to test this popular assumption by assessing the actual numbers of witnessed predations on primates.

Two hundred and twenty-nine eyewitness accounts (from 96 sources) were found describing the deaths of primates due to predation. In addition, there were 79 published accounts (from 43 sources) of predators seen in possession of a fresh carcass or consuming a recently-killed primate. A further 275 published descriptions (from 92 sources) concerned unsuccessful attacks on primates by various predators. In total, 583 successful and unsuccessful predations (published in 183 sources) have been witnessed by researchers and naturalists.

The more numerous instances involving Cercopithecinae may be due in large part to the quantity of field research carried out on three genera -- *Macaca*, *Papio*, and *Cercopithecus* -- rather than their greater susceptibility to predation. The paucity of field studies on tarsiers is probably reflected in the lone instance of observed predation for this family. The emphasis on certain species is not problematic since I compiled this data set only to assess the extent of published observations of predation.

Two reviews of predation contributed 12.0% (n=70) to the total of observed predation events. One review was based on a questionnaire sent to field researchers and reported 42 predations that were not published in the primary literature (Cheney and Wrangham 1987). The other review was based on written interviews with researchers who had carried out fieldwork in Madagascar and reported 28 previously-unpublished predation events (Goodman et al. 1993c). Instances of predation reported in these two reviews were cross-checked against the primary literature to prevent redundancy.

My literature search was not a complete compilation of all observed predation events. For instance, birding journals published locally in Africa and Asia may contain further references to primates as raptor prey, or reports by national park biologists in South Africa prior to 1960 may mention sightings of carnivore predation. To review this literature thoroughly would have been beyond the scope of my thesis. In addition, new field research in Madagascar on owls and indigenous viverrids is forthcoming (S.

Goodman, pers. comm.). Furthermore, while salient articles in French, Spanish, and Japanese were translated, and several articles in Dutch, Afrikaans, and Portuguese were scanned for instances of observed predation, I did not attempt a thorough review of any but English-language literature. However, I feel confident that my review of English-language literature was exhaustive and located most observations of primate predation.

Eyewitness Sightings: An Overview

A comprehensive review of all the observed predation events would be of limited value in this chapter. I do, however, want to highlight important or unusual sightings, such as the earliest published record I encountered describing predation on primates: This short report (Channer 1895) describes the capture and strangulation of a langur (presumably *Presbytis entellus*) by an Indian python (*Python molurus*).

Forty-six percent of published eyewitness accounts of primate predation (from 82 sources) relate to raptor kills. In a "typical" attack by a crowned eagle (*Stephanoaetus coronatus*), the eagle launched itself 150 m away from feeding vervets; using tree cover to make an undetected approach, it suddenly burst skyward from the canopy with a monkey grasped in its talons (Steyn 1982). In another instance, a crowned eagle snatched a colobus monkey from a tree just 1.5 m above an observer's head, driving its talons straight through the monkey's cranium in the process (Clifton 1977). A harpy eagle (*Harpia harpyja*) attack on an adult male red howler monkey (*Alouatta seniculus*) was similarly dramatic; the eagle soared low over the canopy and hit its victim from the back with powerful talons while the monkey was participating in a dawn chorus of calls. (Peres 1990).

Researchers were only 10 m away when a lionness (*Panthera leo*) leaped from cover in full daylight and seized an adult female baboon (*Papio cynocephalus*) from a focal troop in the Tana River National Primate Reserve, Kenya (Condit and Smith 1994). Another investigator photographed an entire sequence of a tiger (*Panthera tigris*) locating her prey, then stalking, capturing and killing a Hanuman langur (Thapar 1986).

Two attacks by golden jackals (*Canis aureus*) on capped langurs (*Presbytis pileata*) were witnessed during 1400 hours of field observation in Bangladesh (Stanford 1989). Further, several unsuccessful attempts on adult *P. entellus* by golden jackals, in addition to a successful attack on an infant langur, were seen at a research site in India (Newton 1985).

Investigators in Amboseli National Park, Kenya witnessed attacks on, or consumption of, both baboons and vervets by leopards (*Panthera pardus*), blackbacked jackals (*Canis mesomelas*), lions, and tawny eagles (*Aquila rapax*) (Altmann and Altmann 1970). A review article, based on interviews with field researchers, reported 28 previously-unpublished observed predations on Madagascar primates by narrow-striped mongoose (*Mungotictis decemlineata*), ring-tailed mongoose (*Galidia elegans*), Indian civets (*Viverricula indica*), fossa (*Cryptoprocta ferox*), domestic dogs (*Canis familiaris*), two species of snakes, and three birds of prey (Goodman et al. 1993c).

Comparing Catastrophic Phenomena: Infanticide and Predation

For perspective, I compared the scale of eyewitness sightings of predation to published cases of infanticide -- another catastrophic phenomenon recorded in studies of primate species. Infanticide (the killing of unrelated offspring by males to bring females into estrus) is a rare and extraordinary occurrence, also, but – unlike predation on primates – it has attained wide credibility within both the scientific community and the general public (Sussman et al. 1995). The sexual selection hypothesis (Hrdy 1974, 1977a, 1979) suggests that males increase their inclusive fitness through the destruction of other males' progeny. Based on this hypothesis, infanticide has been embraced as an evolutionarily adaptive strategy. However, only 48 eyewitness accounts of infant killing have been published (Bartlett et al. 1994). (N.B. Their literature search extended only to 1990). Furthermore, nearly half (n=21) of the infanticidal events recorded in the literature occurred in just one species, *Presbytis entellus*, and more than 50.0% of the 48 eyewitness accounts took place at a single research site in India (Sussman et al. 1995).

The literature search carried out for this chapter uncovered in excess of twelve times the number of eyewitness accounts of predation on primates as have been published concerning infanticide. Furthermore, unlike infanticide, observed predation events have been reported for all regions of the world and for ten non-human primate families.

It has been alleged that witnessed cases of predation on wild primates are unusual occurrences and documentation of them is less frequently found in the literature than observed cases of infanticide: "Forty-eight observed cases of infanticide is far greater than the number of witnessed cases of predation upon primates that made it into the professional literature" (Hrdy et al. 1995, p.152). The information presented in this chapter provides quantification of observed primate predation events and serves to answer this allegation with empirical data.

SUMMARY

- Predation events involving primates as prey are documented in the scientific and natural history literature. Information from branches of biology that study predators of primates can be used to increase our knowledge of primate predation.
- In 183 sources containing sightings of predation, I found 308 observations of successful and 275 cases of unsuccessful predation on primates.
- Eyewitness accounts of predation were documented throughout the range of extant primate species -- Africa, Madagascar, Asia, and the Neotropics.
- Predation was documented in ten non-human primate families; the subfamily Cercopithecinae accounted for the highest percentage (46%) of the 583 observed predations.
- Whether or not research protocols can be developed to quantify predation events under controlled circumstances, direct observation by researchers substantiates that predation is a constant risk in the daily lives of primates (Terborgh 1983, Dunbar 1988).

CHAPTER IV.

QUANTITATIVE ANALYSES OF PREDATION

"...I witnessed a python catching a half-grown baboon. I was attracted to the scene by the noise of the baboon troop and arrived shortly after the snake had wrapped its coils round its prey. The other members of the troop crowded round the scene of the tragedy, the more adventurous amongst them occasionally darting forward and nipping the coils of the snake in a hopeless effort to frighten it and make it discard its catch." Isemonger 1962, p. 12)

INTRODUCTION

The dichotomy within the primatology community regarding the subject of predation on primates is entrenched. Opinions range from a belief that the role of predation has been minimal (Raemakers and Chivers 1980, Wrangham 1980) to theories that predation has been a powerful force in shaping social patterns (van Shaik 1983, Terborgh and Janson 1986, Dunbar 1988). To that end, I have collected and analyzed a set of data that can serve as a basis for objective review of this topic.

The previous chapter dealt exclusively with instances of *observed* predation events. In the present chapter, I address and analyze a wider range of data. These data are drawn from both published and unpublished sources (viz., scientific journals and questionnaires); they are drawn from the fieldwork of primate researchers, ornithologists, herpetologists, and mammalogists. Data are derived from both the observed predation events analyzed in Chapter III and studies on predation that have produced quantitative results. The latter are confined – not exclusively, but nearly so – to research on the predators of primates and offer information on the entire spectrum of prey in the diet of many of the 176 predator species identified in Appendix 1. Along with other food items, primate remains – ranging from *Microcebus* to *Gorilla* – are found in predator scats, pellets, nests, and dens.

Predator-prey relationships can best be studied from the perspective of the predator (Busse 1980). Observation of only one group of one species (the typical parameters of primate research) provides limited data and often skews 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 (Busse 1980). For example, the range of an African forest guenon, such as the blue monkey (*Cercopithecus mitis*), is approximately 0.05 km^2 (Aldrich-Blake 1970b); redfronted lemurs (*Lemur fulvus rufus*) in Madagascar have a home range of about 0.01 km^2 (Sussman 1974); a chacma baboon (*Papio ursinus*) troop may range 2.1-33.7 km^2 (Wolfheim 1983).

Within the range of the typical leopard (*Panthera pardus*), there may be many populations of one primate species, as well as many populations of sympatric primate species, and the leopard may be preying on all of them. Home ranges for predatory species are large: Leopard home ranges have been estimated to be as small as 6-13 km^2 or as large as 400 km^2 (Seidensticker 1991), and one male leopard in the Kalahari Desert had a home range of 800 km^2 (Bothma and Le Riche 1984); tigers (*P. tigris*) defend a territory of 33 km^2 (Rabinowitz 1991); jaguars (*P. onca*) hunt over an area of approximately 50 km^2 (Schaller and Vasconcelos 1978); a pack of African hunting dogs (*Lycaon pictus*) will range over 650 km^2 (Fuller and Kat 1990); spotted hyena (*Crocuta crocuta*) clans occupy a territory of 10-40 km^2 (Kruuk 1975); a harpy eagle pair may possess a 100-200 km^2 territory (Collar 1989); Philippine eagle pairs (*Pithecophaga jefferyi*) have a home range of 25-50 km^2 (Kennedy 1977); the total home range of a pair of crowned eagles (*Stephanoaetus coronatus*) is approximately 10-13 km^2.

Even a relatively small carnivore, such as a fossa (*Cryptoprocta ferox*), is estimated to hold a home range of 4-5 km^2 (Wright et al. 1977). Researchers tracked one individual fossa in the rain forest of southeastern Madagascar which was making regular rounds of four Milne-Edward's sifaka (*Propithecus diadema edwardsi*) social groups, each separated by at least one km (Wright et al. 1997). They concluded that this fossa's home range was large enough to encompass four sifaka groups and that it took one year for the fossa to cycle through the four sifaka territories.

Lions (*Panthera leo*) move in and out of the Mahale Mountains National Park, Tanzania where there is substantive evidence of chimpanzees (*Pan troglodytes*) in their diet (Tsukahara 1993). While Tsukahara speculated that predation on chimpanzees could be heavy if the lions would permanently stay, it may be that the Mahale Mountains are simply one portion of the lions' home range through which they periodically cycle.

The difference between data gathered from primate and predator researchers can be dramatic. This was apparent from questionnaires sent out to the two different research communities. Only 19 primatologists out of 227 questionnaire respondents had knowledge of more than two predations on their study populations. Contrast this with the responses from predator researchers; known or observed kills by the predator they were studying averaged 20 primates, and one researcher had gathered information on 350 primate kills by leopards (D. Jenny, pers. comm.).

METHODS

Data on predation were gathered from questionnaires and scientific literature. Three comprehensive questionnaires were formulated to quantify field researchers' observations (see Appendix 4 for samples) and distributed worldwide to different subsets of researchers. Questionnaire One was distributed to 1928 primate field researchers; Questionnaire Two was disseminated to 236 researchers who study predators; Questionnaire Three was sent to 62 government wildlife departments, national parks, and naturalists in Africa, Madagascar, Asia, and the Neotropics. In addition, Questionnaire One was posted on Primate Talk, the e-mail network for primatologists and reproduced in *Laboratory Primate Newsletter*. Rate of response to the questionnaires was excellent: Questionnaire One = 227 respondents (11.8%), Questionnaire Two = 43 respondents (18.2%), Questionnaire Three = 7 respondents (11.3%). (Appendix 5 acknowledges the important contribution of questionnaire respondents.)

To supplement the information from questionnaires, I undertook a literature search to find quantitative and qualitative descriptions of primates as prey that have been published in primatology, ornithology, herpetology, mammalogy, general biology and ecology journals. (The observed predation events discussed in Chapter III are also included in the data set I assembled.) In addition, I searched out published and unpublished reports on predation authored by national park biologists, surveys of predator species by conservation organizations, and manuscripts of papers presented at symposia.

Data from the above sources were entered on Microsoft Excel 4.0 for Windows (Microsoft Corporation, Seattle, Washington) spreadsheets. Primate data were categorized as follows: geographic range (Africa, Madagascar, Asia, and Neotropics), weight, a size variable of two categories (small=<2 kg and large=>2 kg), stratum occupied (arboreal or terrestrial), daily activity cycle (diurnal or nocturnal). For each primate prey, the data on its predator were categorized by taxa (felids, raptors, canids/hyaenids, small carnivores, reptiles, or unknown), geographic range, weight, stratum occupied (aerial, arboreal, terrestrial, or aquatic), daily activity cycle (diurnal or nocturnal).

Numbers of known or observed predations, unsuccessful attacks, and suspected predations were recorded, along with both the age (infant, subadult, or adult) and gender of primate prey if available. While the parameters of the three categories of predation were at the discretion of the questionnaire respondent (or journal author), there seems to be general agreement throughout the literature on their definitions:

- Known predations are confirmed by sightings of kills, predators in possession of a primate, or quantified data such as stomach contents, fecal or regurgitation analyses, and prey remains.
- Unsuccessful attacks are defined as the pursuit of a prey animal at a run (or stoop for birds of prey) or any approach toward prey in which there is an attempt by the predator to conceal itself during stalking (van Orsdol 1984).

- Suspected predations are defined as the disappearance of an animal within 24 hours of having been observed in a healthy condition and not found to have transferred to another troop (Isbell 1990b). To err on the conservative side, some primatologists eliminated from the category of suspected predations any study animals in an age group or gender which *could* transfer to another primate group (Busse 1980, Isbell 1990b, Wright 1995).

After an initial look at the sheer magnitude of recorded predation in the four geographic regions, I eliminated the data on suspected predations from further analysis. I based this decision on a simple rationale: There was an inherent margin of error built into the "suspected" classification. Even with the most conservative approach to gauging suspected predation, it would be problematic to combine these data with those gathered from eyewitness observations and/or results from controlled studies.

At this point in the analysis, I also combined the data from the remaining two classifications -- unsuccessful attacks and known predations – since these categories were empirical in nature.

Where available, frequencies of occurrence (primates as a percentage of all prey consumed) and estimated predation rates (percentage of the primate population removed annually by a predator or predators) were entered. (If a range of percentages was given by a questionnaire respondent or journal author for these two categories, I calculated the mean and entered it in the data set.)

In 69 instances the estimated predation rate (EPR) was provided by the respondent or author; in a further 23 cases I calculated the estimated predation rate from information provided. (Appendix 6 gives an example of my methodology.)

Each frequency of occurrence was identified by the sampling method used to arrive at the percentage of primates in the predator's diet (e.g., stomach contents, fecal or regurgitation sampling, nest or den remains, analyses of prey carcasses, and direct observation of kills). Since all of these measure the percentage of primates in comparison to all prey killed, I combined the six methodologies in the analysis.

Absolute frequency of prey is the amount of samples examined that contain a specific prey item in relation to the total number of all samples; *relative* frequency is the proportion of a specific food in relation to the total number of all the foods (Hoppe-Dominik 1984). If both absolute and relative frequency of prey were provided, I entered the figure representing relative frequency since it gives the minimum number of prey individuals.

Combining data from various sources is commonly carried out in a branch of statistics called meta-analysis (Taylor Halvorsen 1986). Because the broad overview of data collected in this study is the 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 and Rohlf 1981, Mansfield 1986). It was my intent to collect raw data and use descriptive statistics throughout to summarize the data. It was not my intent to show that there are statistically significant differences between predation by different categories of predators or between geographic regions, simply to give the frequencies of predation events as gathered from questionnaires and the literature. Frequency distributions were used for the comparison of variables; summaries, based on percentages, were employed to interpret specific issues.

Every effort was made to keep the data from containing redundancies. I employed cross-referencing procedures to:

- Prevent redundancy between questionnaires and articles or books by the same researcher. (If, for example, observed predations were provided on the questionnaire returned by a researcher, I checked publications written by the same author to avoid duplication. Of course, additional data were entered from published sources by an author who did *not* duplicate information on a questionnaire);
- Avoid redundant data from more than one published source authored by the same researcher;
- Prevent duplication of data when review articles contained the same data as the primary literature.

After comparing data from questionnaires and the literature (see Appendix 7 for detailed discussion), it was evident that these were compatible and could be combined into one large data set.

Taxonomy and life history information for primates and predatory species were taken from Bueler (1973), Ewer (1973), Grzimek (1975), Guggisberg (1975), Kingdon (1977), Eisenberg (1981), Brown et al. (1982), Macdonald (1984a, 1984b, 1992), Fleagle (1988), Brown and Amadon (1989), Ross (1989), Alderton (1991), Corbet and Hill

(1991), Howard and Moore (1991), Kitchener (1991), Nowak (1991), and Frank and Ramus (1995).

RESULTS

Magnitude of Recorded Predation

Fig.4.1 is an overall representation of 3592 instances of predation cited in questionnaires and literature, classified by predator category and geographic range. Table 4.1 separates the 3592 predation incidents into unsuccessful attacks (n=679, 18.9%), known predations (n=2229, 62.1%), and suspected predations (n=684, 19.0%). (See Appendix 8 for analyses and graphical representations of the number of predation events

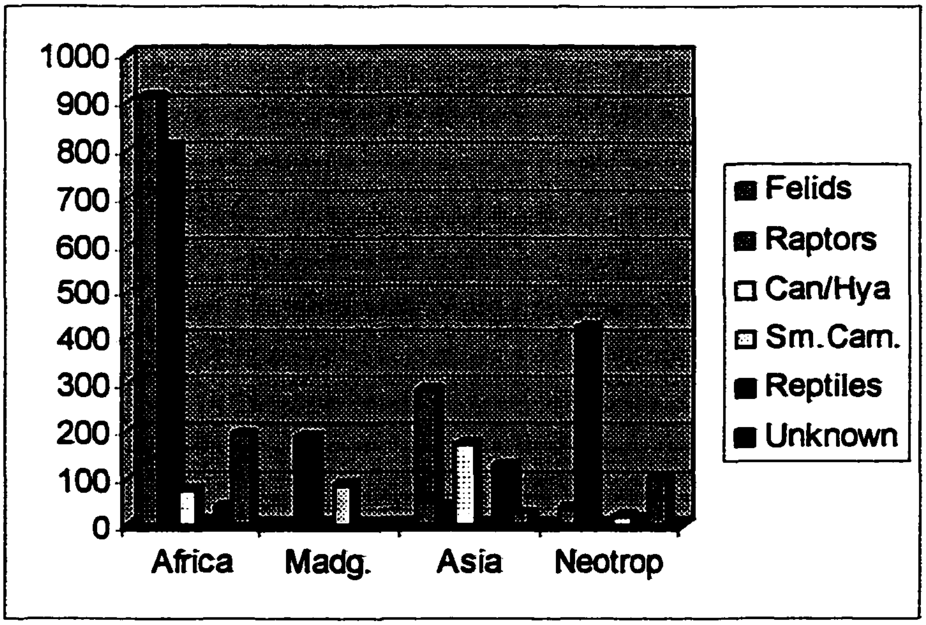


Fig.4.1. Overall magnitude of recorded predation on primates.

TABLE 4.1. Summation of recorded predations from questionnaires and literature.

REGION AND PREDATOR	UNSUCCESSFUL ATTACKS (No. of Sources)		KNOWN PREDATIONS (No. of Sources)		SUSPECTED PREDATIONS (No. of Sources)	
AFRICA						
Felid	66	(23)	725	(68)	123	(19)
Raptor	199	(30)	573	(61)	36	(12)
Canid/Hyaenid	26	(14)	40	(18)	10	(4)
Small Carnivore	4	(2)	9	(3)	0	
Reptile	4	(3)	36	(15)	3	(2)
Unknown	5	(3)	37	(7)	149	(10)
Total Africa	***304***	***(75)***	***1420***	***(172)***	***321***	***(47)***
MADAGASCAR						
Felid	0		3	(2)	1	(1)
Raptor	18	(5)	158	(14)	10	(4)
Canid/Hyaenid	0		3	(3)	0	
Small Carnivore	5	(5)	63	(15)	17	(6)
Reptile	0		6	(4)	0	
Unknown	0		0		2	(2)
Total Madagascar	***23***	***(10)***	***233***	***(38)***	***30***	***(13)***
ASIA						
Felid	8	(7)	254	(36)	27	(8)
Raptor	13	(11)	26	(10)	4	(4)
Canid/Hyaenid	13	(6)	58	(24)	100	(16)
Small Carnivore	0		0		0	
Reptile	2	(1)	41	(15)	83	(4)
Unknown	0		10	(1)	19	(4)
Total Asia	***36***	***(25)***	***389***	***(86)***	***233***	***(36)***
NEOTROPICS						
Felid	10	(6)	20	(12)	6	(3)
Raptor	263	(20)	146	(20)	15	(8)
Canid/Hyaenid	1	(1)	1	(1)	1	(1)
Small Carnivore	15	(9)	3	(2)	2	(2)
Reptile	11	(3)	7	(6)	1	(1)
Unknown	16	(1)	10	(2)	75	(13)
Total Neotropics	***316***	***(40)***	***187***	***(43)***	***100***	***(28)***
GRAND TOTAL	**679**	**(150)**	**2229**	**(339)**	**684**	**(124)**

as a function of the number of sources from which they were collected.) Felids and raptors preying on primates accounted for the most predations (40.7% and 34.6%, respectively), followed by unknown predators (9.0%), canids and hyaenids (7.0%), reptiles (5.4%), and small carnivores (3.3%).

Figs.4.2-4.5 are corollaries to the information in Table 4.1, comparing predation by various predator species in different geographic regions. Fig.4.2, representing predations in Africa, shows felids and raptors constituting the majority of the recorded predation instances on primates. Suspected predations (versus known or unsuccessful) are high for felids (n=123) and in the "unknown predator" category (n=149). Raptors have the highest number of unsuccessful predation attempts (n=199). This figure is borne out by observations of unsuccessful attacks on diana monkeys (*Cercopithecus diana*) several times per day by crowned eagles (*Stephanoaetus coronatus*) (Zuberbuhler et al. 1997).

The corresponding information for Madagascar (Fig.4.3) shows a distinct emphasis on raptor and small carnivore predation. Madagascar is the only region in which small carnivores (specifically the fossa, *Cryptoprocta ferox*) are important as primate predators. Six other species of small carnivores prey on Madagascar primate fauna: 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.). Since there are no indigenous wild cats on the island, the few instances of felid predation are due to feral cats (*Felis catus*) (see Sauther 1989). Nocturnal raptors, the Malagasy

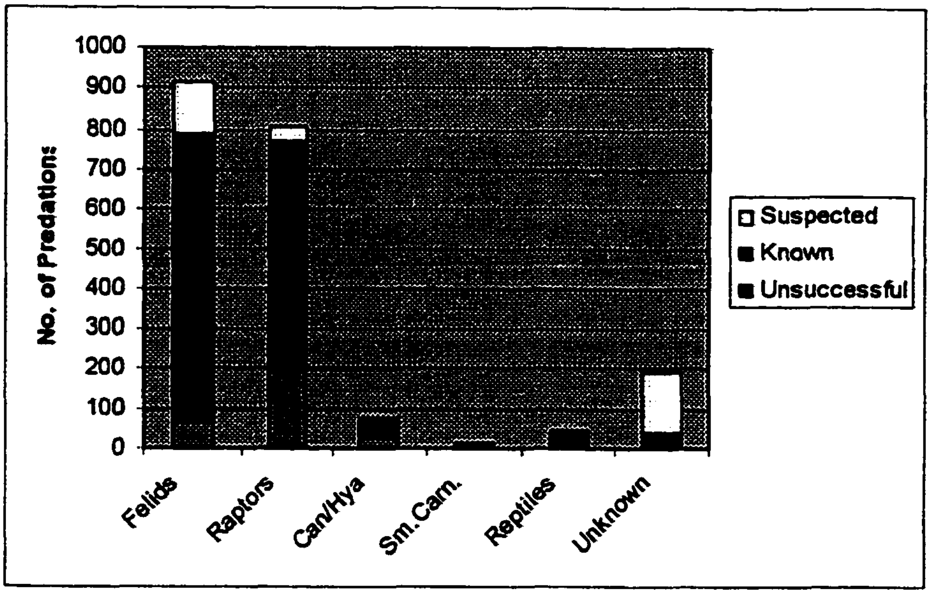


Fig.4.2. Region: Africa -- comparison of recorded unsuccessful attacks, known predations, and suspected predations.

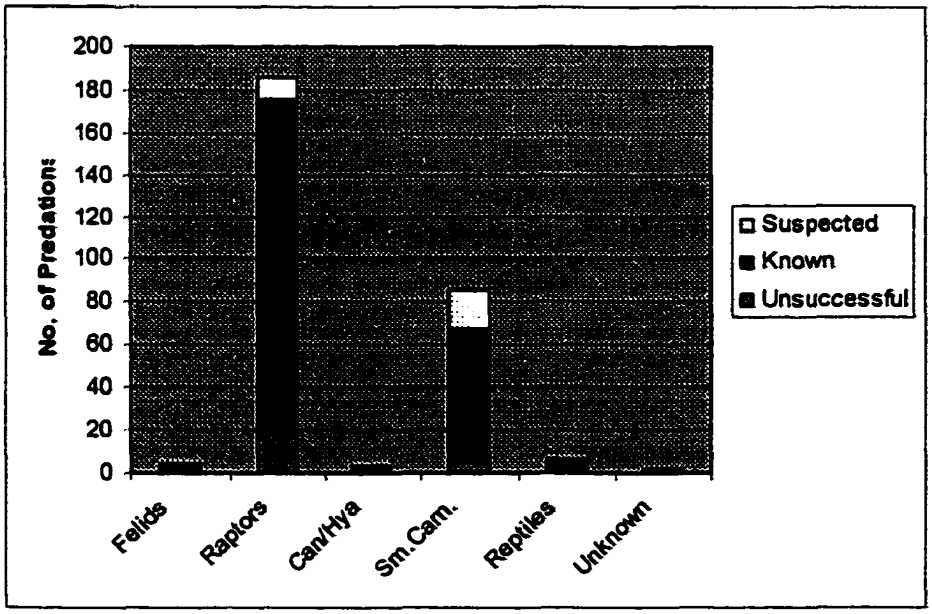


Fig.4.3. Region: Madagascar -- comparison of recorded unsuccessful attacks, known predations, and suspected predations.

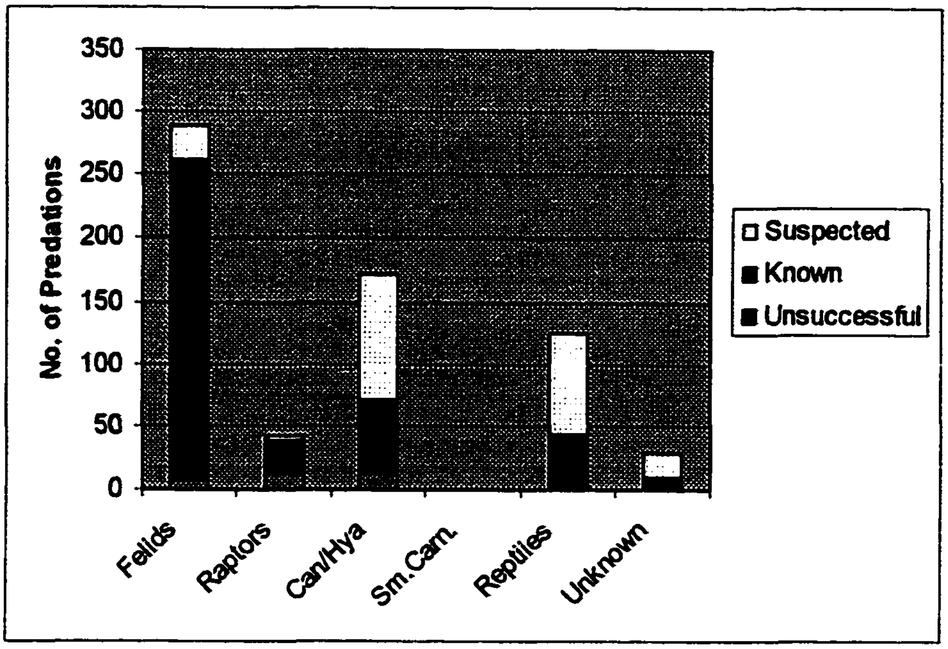


Fig.4.4. Region: Asia -- comparison of recorded unsuccessful attacks, known predations, and suspected predations.

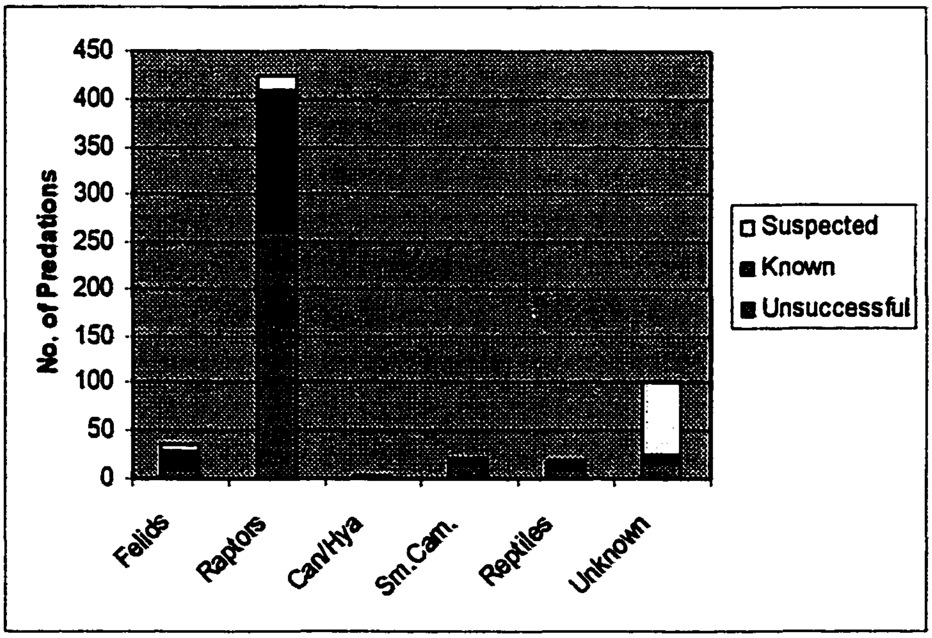


Fig.4.5. Region: Neotropics -- comparison of recorded unsuccessful attacks, known predations, and suspected predations.

owls, are frequent predators on primates (Goodman et al. 1991, Goodman and Langrand 1993, Goodman et al. 1993a, 1993b).

Asia is unlike the previous two regions in several respects (Fig.4.4). Asian canids figure prominently in both suspected and known categories due to golden jackal (*Canis aureus*) and dhole (*Cuon alpinus*) predation on primates (Johnsingh 1980, Newton 1985, Stanford 1989). Recorded raptor predations for Asia are minimal compared with other regions.

Fig.4.5, the Neotropics, shows a paucity of recorded felid predation even though two large felid 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*) are indigenous carnivores suspected or known to prey on primates. The high level of unsuccessful raptor predation in the Neotropics is attributable to recorded attacks by hawks, falcons, and toucans on very young squirrel monkeys and callitrichids. Terborgh (1983), Boinski (1987), Goldizen (1987), Mitchell et al. (1991) reported fairly constant and predictable attacks by raptors on small, arboreal, diurnal primates (see Chapter II for a full discussion).

Which primates get eaten?

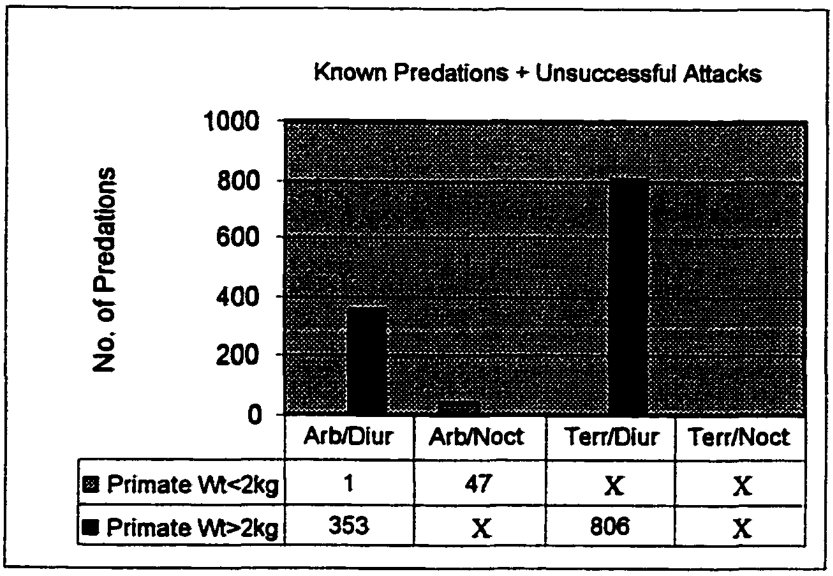
In the previous section, results concerning the sheer magnitude of recorded predation were presented graphically. In the next stage of data analysis, I attempt to isolate the variables that determine which primate species are preyed upon. In Figs.4.6

through 4.9, I examine all possible combinations of primate body weight, strata, and activity cycles in each of the four geographic regions.

I examine the data to see whether there are primates under or over 2 kg, nocturnal or diurnal, arboreal or terrestrial that are exempt from predation or are preyed upon at very low levels. Figs.4.6-4.9 indicate that neither weight, stratum, activity cycle, nor region were variables that protected primates from predators. Although the rates of predation are unknown, primates are preyed upon if they are small or large, nocturnal or diurnal, arboreal or terrestrial.

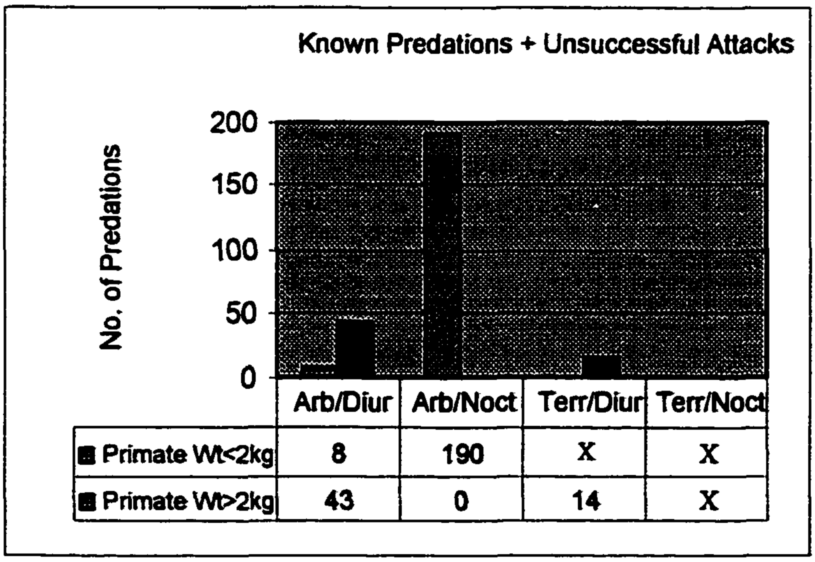
Fig.4.6 compares predation levels between two weight categories of African primates (< and >2 kg) within the four possible combinations of strata and activity cycles. There are no arboreal, nocturnal primates weighing more than 2 kg; no terrestrial, diurnal primates weighing less than 2 kg; no terrestrial, nocturnal primates over or under 2 kg. Predation *was* recorded in the remaining categories in Fig.4.6. The single data point representing small, arboreal, diurnal primates refers to predation on *Miopithecus*, the only African primate species in this category. Three categories – arboreal, diurnal primates over 2 kg (guenons, some mangabeys, and *Colobus* spp.), arboreal, nocturnal primates under 2 kg (galagos and lorisids), and terrestrial, diurnal primates over 2 kg (apes and *Papio*) – account for nearly all the predation.

Madagascar prosimians (Fig.4.7) fill five different ecological niches. Arboreal, diurnal primates weighing less than 2 kg is a category filled only by bamboo lemurs (*Hapalemur* spp.); those over 2 kg include *Propithecus*, *Indri*, *Lemur*, and *Varecia*. The



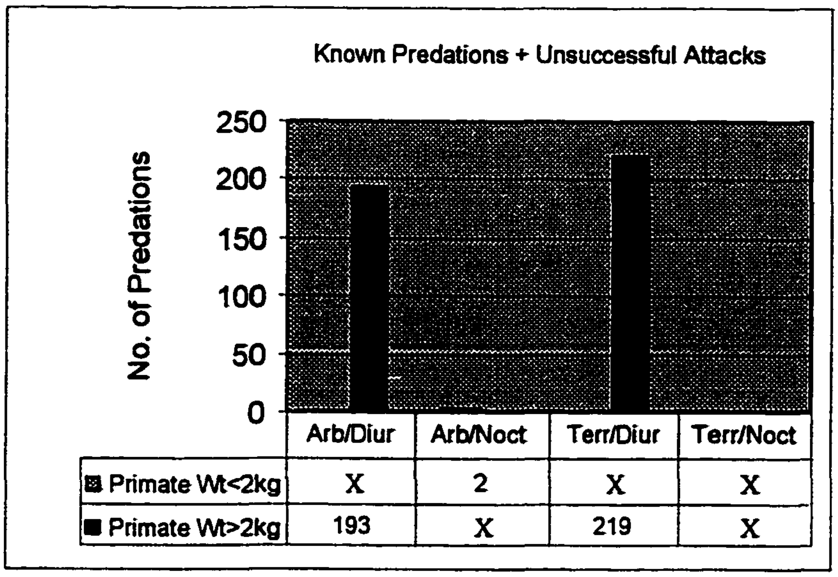
	Arb/Diur	Arb/Noct	Terr/Diur	Terr/Noct
▨ Primate Wt<2kg	1	47	X	X
■ Primate Wt>2kg	353	X	806	X

Fig.4.6. Region: Africa -- comparison of recorded predation on primates weighing < and >2 kg that inhabit different ecological niches. (X's stand for categories not occupied by primate species.)



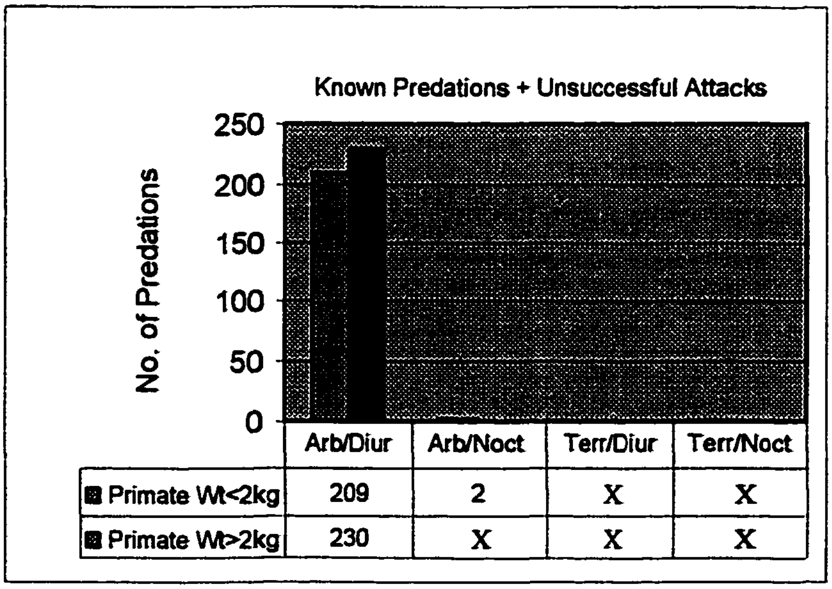
	Arb/Diur	Arb/Noct	Terr/Diur	Terr/Noct
▨ Primate Wt<2kg	8	190	X	X
■ Primate Wt>2kg	43	0	14	X

Fig.4.7. Region: Madagascar -- comparison of recorded predation on primates weighing < and >2 kg that inhabit different ecological niches. (X's stand for categories not occupied by primate species.)



	Arb/Diur	Arb/Noct	Terr/Diur	Terr/Noct
▨ Primate Wt<2kg	X	2	X	X
■ Primate Wt>2kg	193	X	219	X

Fig.4.8. Region: Asia -- comparison of recorded predation on primates weighing < and >2 kg that inhabit different ecological niches. (X's stand for categories not occupied by primate species.)



	Arb/Diur	Arb/Noct	Terr/Diur	Terr/Noct
▨ Primate Wt<2kg	209	2	X	X
■ Primate Wt>2kg	230	X	X	X

Fig.4.9. Region: Neotropics -- comparison of recorded predation on primates weighing < and >2 kg that inhabit different ecological niches. (X's stand for categories not occupied by primate species.)

arboreal, nocturnal category less than 2 kg in weight is filled by the Cheirogaleidae. The terrestrial, diurnal, over 2 kg category is filled by *Lemur catta. Daubentonia* is the singular primate in Madgascar that is arboreal, nocturnal, and weighs more than 2 kg. Except for *Daubentonia*, predation has been recorded for all other families of Malagasy primates.

Asian primates (Fig.4.8) occupy three ecological niches: arboreal, diurnal primates over 2 kg (*Pongo*, *Presbytis*, *Trachypithecus*, *Nasalis*, etc.); arboreal, nocturnal under 2 kg (*Tarsius*, *Nycticebus*, *Loris*); terrestrial, diurnal primates over 2 kg (*Macaca*). Little data on predation are available for small, nocturnal Asian primates. Only three ecological field studies have been carried out on tarsiers (Niemitz 1972, Fogden 1974, MacKinnon and MacKinnon 1980), one field study on slow loris (*Nycticebus coucang*) (Wiens and Zitzmann 1999), and one on slender loris (*Loris tardigradus*) (Nekaris 2000).

Considerable predation is recorded for small and large arboreal, diurnal Neotropical primates, i.e., Callitrichidae and Cebidae (Fig.4.9). The only species that is arboreal and nocturnal in the New World is *Aotus*, for which a small number of predations have been recorded from two studies (Wright 1985, Brooks, in press). There are no Neotropical primates filling other ecological niches.

Which species prey on primates?

Figs.4.6 through 4.9 portray the instances of predation that have been reported in all regions, weight categories, activity cycles and strata in which primates exist. Figs.4.10

through 4.13 identify the predators that prey on primates in the four most common ecological niches.

Fig.4.10 combines recorded predations on all arboreal, diurnal primates under 2 kg in weight. Three-quarters of the predation is attributable to diurnal raptors and other diurnal predatory birds such as toucans, crows, vangas, and cuckoos. Small arboreal primates are particularly vulnerable to raptors. Being entirely terrestrial, canids and hyaenids do not have easy access to these primates. Species of felids and small carnivores, often scansorial or fully arboreal, together account for 11.0% of the reported predation. Reptiles account for only 3.0%, even though many small species of snakes are arboreal as well as younger individuals (<2 m) of *Python* and *Boa*.

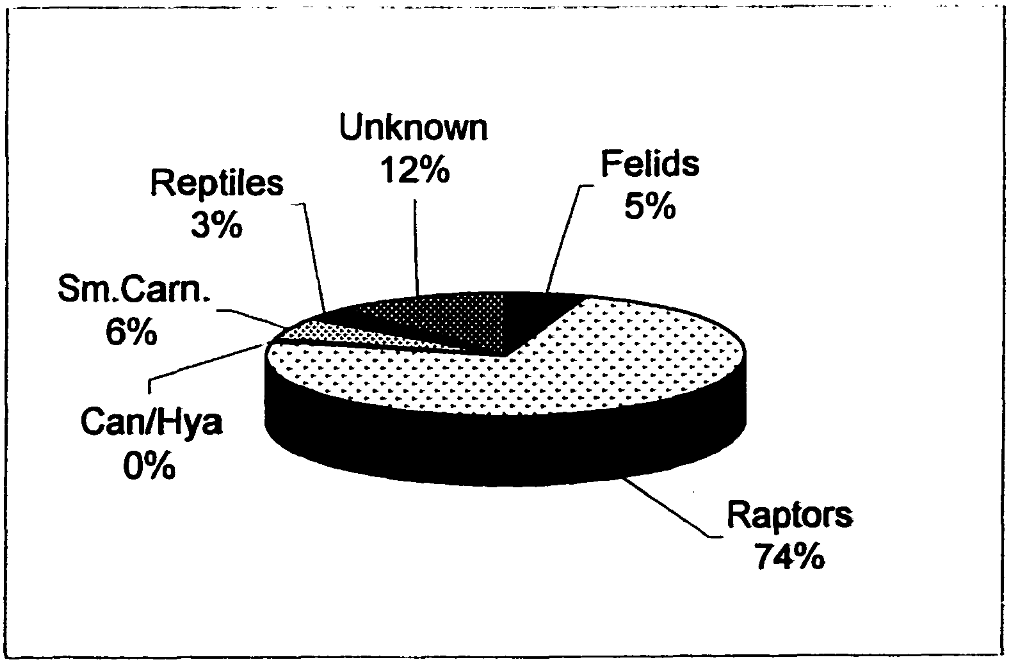


Fig.4.10. Predators of arboreal, diurnal primates <2 kg.

Arboreal, nocturnal primates weighing under 2 kg have a similar division of predatory species (Fig.4.11). Birds of prey account for 75.0% of all recorded predation, but these are mostly owl species preying on primates rather than diurnal raptors. Small carnivores (arboreal, nocturnal genets, for example) also figure prominently as predators of this primate category. Felids, canids, hyaenids, and reptiles account for only 6.0% of the total predation.

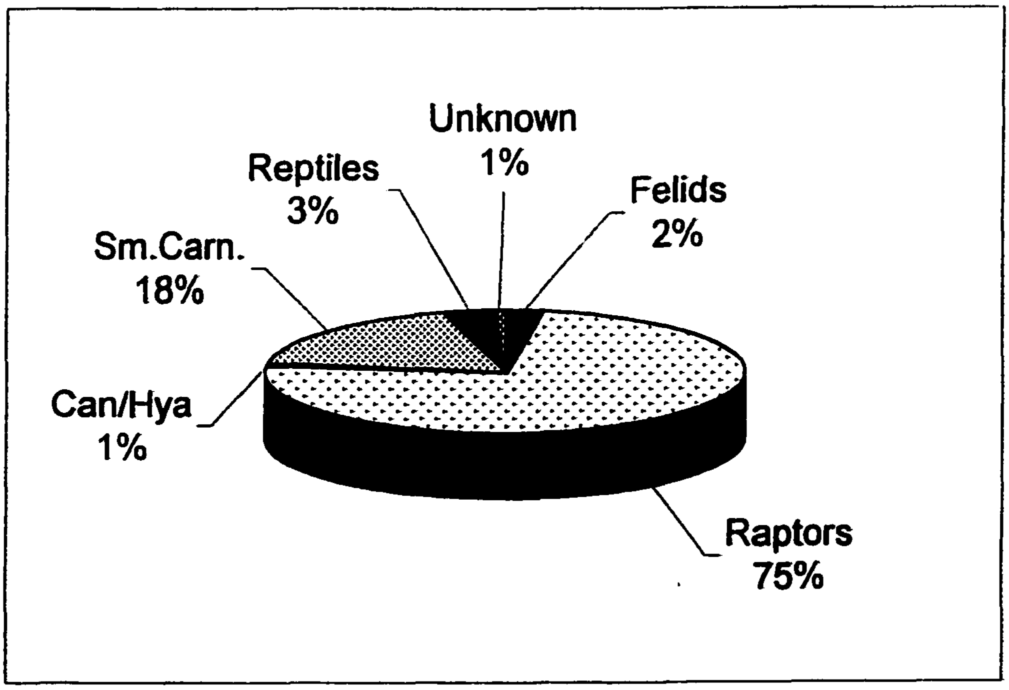


Fig.4.11. Predators of arboreal, nocturnal primates <2 kg.

Fig.4.12 charts the predators on arboreal, diurnal primates weighing more than 2 kg. Again, raptors are the dominant predators (59.0%). However, felids are more apparent in this category, most likely due to their preference for larger prey. Canids and hyaenids and reptiles represent small components of the predation on these primates. Small carnivores (other than the scansorial fossa in Madagascar) are outweighed by many of these larger arboreal primates.

Fig.4.13 provides the percentages of predators on terrestrial, diurnal primates over 2 kg in weight. In this category, felids compose nearly one-half of recorded predations. Raptors still figure heavily, carrying out one-third of the predatory activity. Small carnivores have been eliminated as predators, either by increased primate weight or their

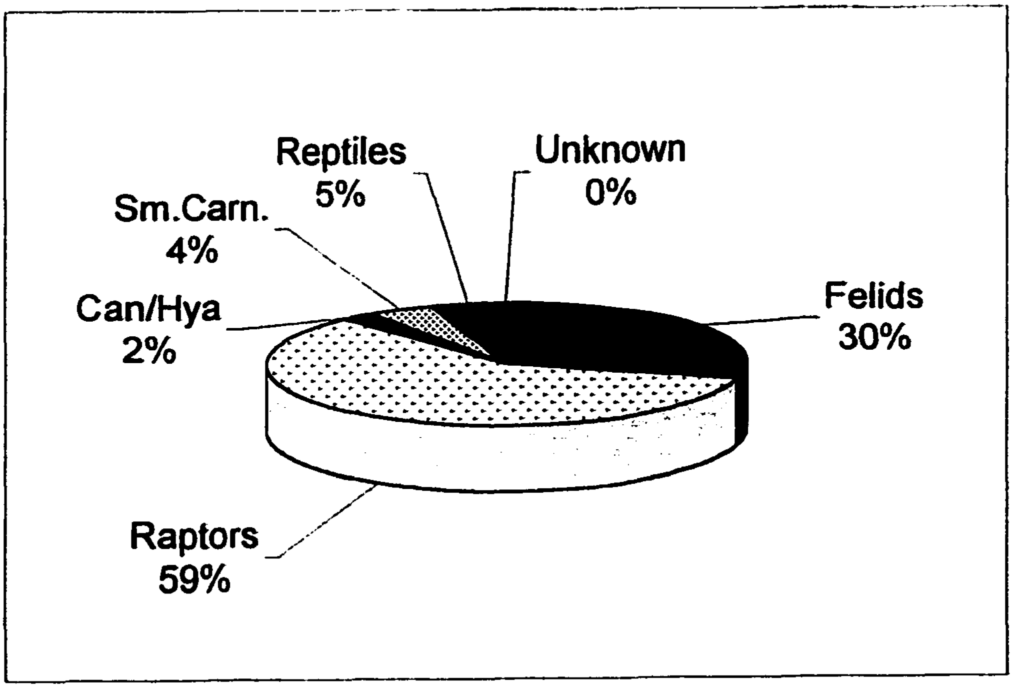


Fig.4.12. Predators of arboreal, diurnal primates >2 kg.

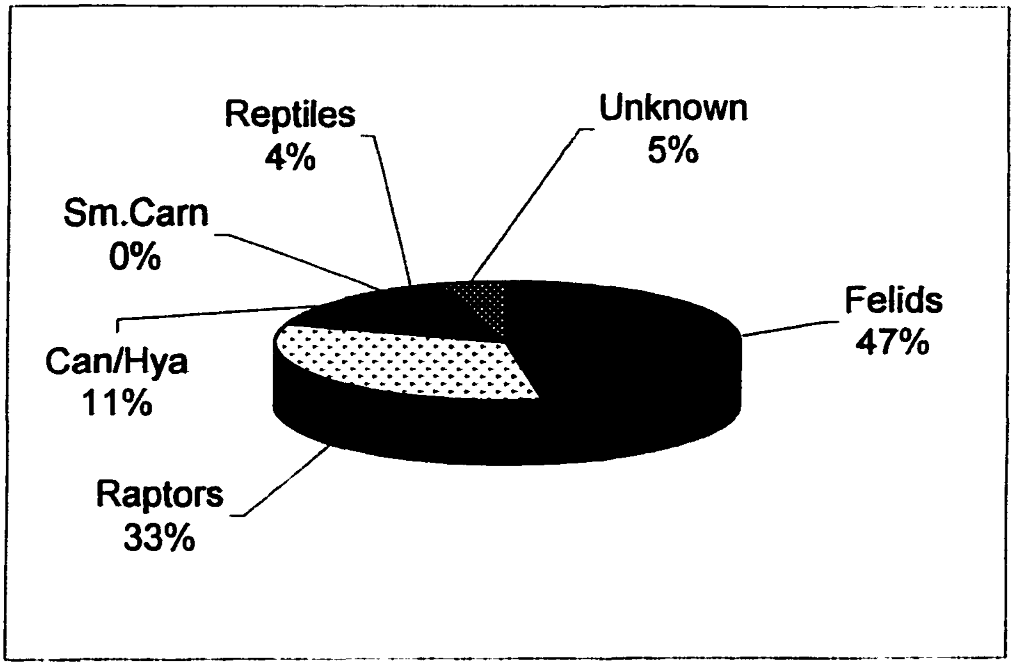
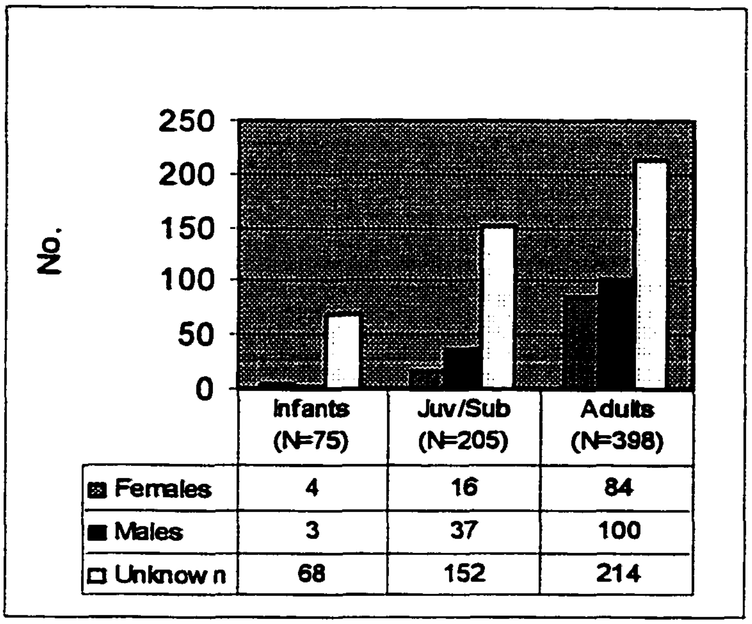


Fig.4.13. Predators of terrestrial, diurnal primates >2 kg.

inability to kill outside the arboreal milieu. Canids and hyaenids play a considerable role (11.0%) due to their terrestrial lifestyles.

Age and Sex of Primate Prey

In the questionnaires sent to researchers, I inquired about the age and sex of primate prey. While these specifics were not universally available, Fig.4.14 presents data I received. In 244 cases both the age and the sex of the primate victim were known, while in 678 instances of predation, only the age could be identified. In this sample (based on questionnaires alone), most predation events involved adult animals (n=398). Lesser



	Infants (N=75)	Juv/Sub (N=205)	Adults (N=398)
▨ Females	4	16	84
■ Males	3	37	100
☐ Unknown	68	152	214

Fig.4.14. Age and sex of recorded primate prey.

numbers of juvenile/subadults (n=205) or infants (n=75) were observed being preyed upon in these studies, although often infants were noted to have high mortality due to a variety of causes, including predation. Male primates in the juvenile/subadult and adult divisions (n=137) underwent higher predation levels than females (n=90). There were too few infant predations in which gender was noted (n=7) to allow for any conclusions.

Estimated Predation Rate (EPR)

Table 4.2 lists the estimated predation rates (the percentage of the primate population that is eliminated annually through predation) available from 40 questionnaire respondents and 15 literature sources. Sufficient mandatory information was available in

TABLE 4.2. Estimated predation rates from questionnaires and literature.

PRIMATE FAMILES AND SUBFAMILIES	ESTIMATED PREDATION RATE (%)		SOURCE
Cheirogaleidae			
Microcebus murinus	25.0		Goodman et al. 1993c
Indriidae			
Propithecus diadema edwardsi	6.5	*	Wright et al. 1997
P. verreauxi	5.7	*	Rasoloarison et al. 1995
Indri Indri	2.0		J. Powzyk (questionnaire)
I. indri	14.0	*	J. Powzyk (questionnaire)
Daubentoniidae			
Daubentonia madagascariensis	0		E. Sterling (questionnaire)
Lorisidae			
Galago senegalensis	8.6	*	Martin & Bearder 1979
G. senegalensis	15.0		Cheney & Wrangham 1987 (see Table 19-1, Bearder and Martin)
Callitrichidae			
Saguinus fuscicollis	15.0		Cheney & Wrangham 1987 (see Table 19-1, Terborgh)
S. imperator	15.0		Cheney & Wrangham 1987 (see Table 19-1, Terborgh)
Cebidae			
Callicebus moloch	4.5		Cheney & Wrangham 1987 (see Table 19-1, Wright)
Saimiri boliviensis	1.0		R. Fontaine (questionnaire)
S. oerstedii	7.7	*	S. Boinski (questionnaire)
S. oerstedii	3.6	*	Boinski 1992
S. sciureus	2.5		Cheney & Wrangham 1987 (see Table 19-1, Bailey)
Alouatta seniculus	83.0	*	M. Norconk (questionnaire)

* Estimated predation rate calculated by D. Hart.

CONTINUED ... TABLE 4.2. Estimated predation rates from questionnaires and literature.

PRIMATE FAMILES AND SUBFAMILIES	ESTIMATED PREDATION RATE (%)		SOURCE
A. seniculus	0.5		C. Crockett (questionnaire)
Cebus apella	15.0	*	K. Izawa (questionnaire)
C. apella	13.0		Cheney & Wrangham 1987 (see Table 19-1, Terborgh)
C. capucinus	10.0		L. Rose (questionnaire)
C. nigrivittatus	3.0		Cheney & Wrangham 1987 (see Table 19-1, Robinson)
Brachyteles arachnoides	0		F. Mendes (questionnaire)
Lagothrix lagotricha	3.0		P. Stevenson (questionnaire)
Cercopithecinae			
Cercocebus spp.	3.0		Struhsaker & Leakey 1990
Cercocebus spp.	1.0		Aldrich-Blake 1970b
C. albigena	18.0	*	P. Waser (questionnaire)
C. galeritus	1.6		M. Kinnaird (questionnaire)
Cercopithecus spp.	11.8	*	Gautier-Hion et al. 1983
Cercopithecus spp.	1.0		Aldrich-Blake 1970b
C. aethiops	45.0		Isbell 1990b
C. aethiops	11.0		Isbell 1990b
C. aethiops	7.2	*	Baldellou & Henzi 1992
C. aethiops	6.0		Cheney & Wrangham 1987 (see Table 19-1, Whitten)
C. aethiops	15.0		Cheney & Wrangham 1987 (see Table 19-1, Cheney et al.)
C. ascanius	0.3		Struhsaker & Leakey 1990
C. ascanius	2.0		Cheney & Wrangham 1987 (see Table 19-1, Butynski)
C. ascanius	10.0		Cheney & Wrangham 1987 (see Table 19-1, Cords)
C. cephus	10.0		Cheney & Wrangham 1987 (see Table 19-1, Gautier-Hion, Quris & Gautier)
C. mitis	4.0		M. Lawes (questionnaire)

***Estimated predation rate calculated by D. Hart.**

CONTINUED ... TABLE 4.2. Estimated predation rates from questionnaires and literature.

PRIMATE FAMILES AND SUBFAMILIES	ESTIMATED PREDATION RATE (%)		SOURCE
C. mitis	2.0		T. Butynski (questionnaire)
C. mitis	2.0		M. Beeson (questionnaire)
C. mitis	1.2		Struhsaker & Leakey 1990
C. mitis	10.0		Cheney & Wrangham 1987 (see Table 19-1, Butynski)
Erythrocebus patas	4.0		J. Chism (questionnaire)
E. patas	11.0		Cheney & Wrangham 1987 (see Table 19-1, Cords)
Papio anubis	2.5		T. Sambrook (questionnaire)
P. anubis	2.0		R. Sapolsky (questionnaire)
P. anubis	0.8	*	B. Smuts (questionnaire)
P. anubis	3.0		Cheney & Wrangham 1987 (see Table 19-1, Sapolsky)
P. anubis	0.5		B. Bertram (questionnaire)
P. cynocephalus	0		S. Pochron (questionnaire)
P. cynocephalus	14.7	*	V. Condit (questionnaire)
P. cynocephalus	5.3	*	V. Condit (questionnaire)
P. cynocephalus	9.3	*	V. Condit (questionnaire)
P. cynocephalus	3.8	*	V. Condit (questionnaire)
P. cynocephalus	6.0		Cheney & Wrangham 1987 (see Table 19-1, J. Altmann, S. Altmann & Hausfater)
P. cynocephalus	4.0		Cheney & Wrangham 1987 (see Table 19-1, Rhine & Norton)
P. cynocephalus	1.0		T. Williamson (questionnaire)
P. ursinus	0		Anonymous (questionnaire)
P. ursinus	8.0		Busse 1980
P. ursinus	0		P. Henzi (questionnaire)
P. ursinus	9.0		Cheney & Wrangham 1987 (see Table 19-1, Busse & Smith)
P. ursinus	6.0	*	Bulger & Hamilton 1987

*Estimated predation rate calculated by D. Hart.

CONTINUED ... TABLE 4.2. Estimated predation rates from questionnaires and literature.

PRIMATE FAMILES AND SUBFAMILIES	ESTIMATED PREDATION RATE (%)		SOURCE
Theropithecus gelada	0.5	*	R. Dunbar (questionnaire)
Macaca fascicularis	3.0		J. Fellowes (questionnaire)
M. fascicularis	10.0		Cheney & Wrangham 1987 (see Table 19-1, van Schaik & van Noordwijk)
M. fuscata	5.0		S. Azuma (questionnaire)
M. mulatta	1.2	*	D. Lindburg (questionnaire)
M. mulatta	3.0		J. Fellowes (questionnaire)
M. nigra	0.5		B. O'Brien & M. Kinnaird (questionnaire)
M. radiata	3.0		P. Simonds (questionnaire)
M. sinica	0.5		Cheney & Wrangham 1987 (see Table 19-1, Dittus)
M. sinica	1.0		J. Eisenberg (questionnaire)
M. thibetana	3.3		J. Li (questionnaire)
Colobinae			
Colobus spp.	1.0		Alrdrich-Blake 1970b
C. badius	15.3	*	E. Starin (questionnaire)
C. badius	0		Struhsaker & Leakey 1990
C. badius	1.5		Cheney & Wrangham 1987 (see Table 19-1, Skorupa)
C. guereza	0.7		Struhsaker & Leakey 1990
Presbytis entellus	7.5		J. Moore (questionnaire)
P. entellus	0.5		Cheney & Wrangham 1987 (see Table 19-1, Vogel)
P. entellus	1.0		Cheney & Wrangham 1987 (see Table 19-1, Moore)
P. entellus	10.0		Cheney & Wrangham 1987 (see Table 19-1, Moore)
P. entellus	1.0		J. Eisenberg (questionnaire)
Presbytis johnii	3.5	*	Paulraj 1995
P. melalophus	0		E. Bennett (questionnaire)
P. senex	1.0		J. Eisenberg (questionnaire)

***Estimated predation rate calculated by D. Hart.**

CONTINUED ... TABLE 4.2. Estimated predation rates from questionnaires and literature.

PRIMATE FAMILES AND SUBFAMILIES	ESTIMATED PREDATION RATE (%)		SOURCE
Hylobatidae			
Hylobates lar	5.0		W. Brockelman (questionnaire)
Pongidae			
Pongo pygmaeus	0		C. van Schaik (questionnaire)
Pan troglodytes	0		R. Wrangham (questionnaire)
P. troglodytes	5.5		C. Boesch (questionnaire)
P. troglodytes	6.3	*	Tsukahara 1993

*Estimated predation rate calculated by D. Hart.

22 questionnaires or journal articles for me to calculate an EPR. (See Appendix 6 for an example of the methodology used.) EPR's ranged from zero to 83.0%.

In Table 4.3, I compare 86 of these 92 EPR's by primate ecological niche. Two of the EPR's from Table 4.2 were rejected as aberrant situations: (1) A predation rate of 83.0% estimated for a troop of *Alouatta seniculus* stranded with a jaguar on an island formed by a dam project (Peetz et al 1992), and (2) a 45.0% EPR attributed to a drastic increase in leopard predation on vervets (*Cercopithecus aethiops)* in Amboseli National Park during a single year (Isbell 1990b). I rejected another four EPR's due to insufficient information regarding the identification of the primate prey.

According to the data in Table 4.3, the annual rate of predation on small, arboreal, nocturnal primates may be higher than for species in other ecological niches. However, the sample sizes are very small for three of the categories and relatively large for the other two. In an attempt to measure whether this high EPR for small nocturnal primates had legitimacy, I calculated the total number of predators that had been identified as preying on each category of primates. The aye-aye (*Daubentonia madagascariensis*) is the only species of primate that is nocturnal, arboreal, and weighs over 2 kg; a questionnaire respondent assigned a 0% EPR to her study individuals and identified no known predators (Sterling, pers. comm.). Excluding the aye-aye, Table 4.4 presents what would appear to be a fairly uniform distribution of predator species for the other four classifications of primates. If concern over the small sample sizes is dismissed, there seems to be evidence that small, nocturnal primates may be more prone to predation than diurnal, terrestrial, or larger primates that have approximately the same overall number of predators.

TABLE 4.3. Estimated predation rates for categories of primates.

PRIMATES <2 KG ARBOREAL DIURNAL (N = 7)	PRIMATES <2 KG ARBOREAL NOCTURNAL (N = 3)	PRIMATES >2 KG ARBOREAL NOCTURNAL (N=1)	PRIMATES >2 KG ARBOREAL DIURNAL (N = 31)	PRIMATES >2 KG TERRESTRIAL DIURNAL (N = 44)
Mean EPR = 7.0%	Mean EPR = 16.2%	Mean EPR = 0%	Mean EPR = 5.2%	Mean EPR = 4.4%
Median EPR = 4.5%	Median EPR = 15.0%	Median EPR = 0%	Median EPR = 3.0%	Median EPR = 3.2%
Range = 1.0-15.0%	Range = 8.6-25.0%	Range = 0%	Range = 0-18.0%	Range = 0-15.0%

TABLE 4.4. Number of predator species preying on primates < and >2 kg.

PRIMATES <2 KG ARBOREAL DIURNAL		PRIMATES <2 KG ARBOREAL NOCTURNAL		PRIMATES >2 KG ARBOREAL NOCTURNAL		PRIMATES >2 KG ARBOREAL DIURNAL		PRIMATES >2 KG TERRESTRIAL DIURNAL	
PREDATOR SPECIES (N = 33)		PREDATOR SPECIES (N = 28)		PREDATOR SPECIES (N=0)		PREDATOR SPECIES (N = 34)		PREDATOR SPECIES (N = 43)	
Felid	3	Felid	2	Felid	0	Felid	7	Felid	9
Raptor	16	Raptor	17	Raptor	0	Raptor	12	Raptor	15
Canid/ Hyaenid	1	Canid/ Hyaenid	1	Canid/ Hyaenid	0	Canid/ Hyaenid	5	Canid/ Hyaenid	11
Sm.Car-nivore	7	Sm.Car-nivore	2	Sm.Car-nivore	0	Sm.Car-nivore	3	Sm.Car-nivore	1
Reptile	6	Reptile	6	Reptile	0	Reptile	7	Reptile	7

Frequencies of Occurrence

Frequency of occurrence is defined as the number of individual prey animals of one taxon relative to all prey eaten (Rabinowitz and Nottingham 1986). Expressed as a percentage of all food intake by a predator, frequencies of occurrence can be attained by six different methodologies. (Table 4.5 lists these techniques, along with the number of studies in my data set that used each sampling method.) The most commonly used methods (fecal sampling, pellet/regurgitation sampling, analysis of nest or den remains, and analysis of prey carcasses) provide information on food ingested over an extended period of time and are non-invasive -- unlike analysis of stomach contents which traditionally has involved dissection of the predator (Cott 1961, Bothma 1966, Biquand et al. 1994, Shine et al. 1998). Direct observation of kills will provide indisputable confirmation of predation, rather than scavenging, but it requires both perseverance and luck, and yields more limited information since only one meal at a time can be identified.

TABLE 4.5. Frequency of occurrence sampling methodologies.

TYPE OF SAMPLING	NUMBER OF STUDIES
Stomach contents	6
Fecal sampling	82
Pellets and regurgitations	23
Nest and den remains	64
Analysis of prey carcasses	33
Direct observation of kills	5

Another drawback to direct observation is that prey are often alerted to the predator or made more vigilant by the presence of human observers (Caro and Fitzgibbon 1992, Isbell and Young 1993).

The sampling of feces, regurgitations, nest or den remains, and prey carcasses provide the minimum number of individuals (MNI) of one taxon through a tedious cleaning and reconstruction process. Indigestible hard tissue expelled in feces or regurgitations (called "pellets" in owls, these regurgitations occur very regularly every two or three days) is dried, washed, and broken up in a sieve (Lockie 1959, Vernon 1972). Components are identified using comparative osteological collections; paired bones of any taxon are separated and the largest number of elements from either the left or right side are considered the minimum number of individuals among prey items (Goodman and Thorstrom 1998). Hairs or fur from the prey are also identifiable through a process of electron microscope study (Rajaram and Menon 1986) or comparison with museum collections of animal hair (Johnsingh 1980).

Nest and den remains yield excellent data for compilation of predator diets. Several nesting cycles result in large build-ups of prey bones below raptor nests (Brown 1966, Gargett 1971, Rettig 1978). Ideally, these remains are combined with other prey remains from within the nest and from under feeding perches (Boshoff and Palmer 1980, Boshoff et al. 1990). The larger the collection of nest and den remains, the greater the accuracy of dietary content; the length of time the site has been used does not adversely affect the data if care is taken to ascertain that only one species of predator has been in residence.

Frequencies of occurrence were provided from 103 studies on 34 species, plus unidentified felids and one completely unidentified predator. The range of percentages of primates in a predator's diet is wide. At the high end of the continuum, a study of forest-hunting crowned eagles found that 87.9% of their nest remains consisted of primates. At the low end, a study of open-country Verreaux's eagles (*Aquila verreauxii*) identified only 0.03% of primates in the diet of that predator at the time of the research. In Table 4.6, I list the frequency of occurrence ranges, means, and medians for each predator species in which field studies have used sampling techniques to achieve components of the diet. The four highest mean and median frequencies of occurrence were all found in birds of prey: Harpy eagles (*Harpia harpyja*) mean = 48.1%, median =50.0% (n=5); Madagascar long-eared owls (*Asio madagascariensis*) mean = 33.5%, median = 20.5% (n=5); Henst's goshawks (*Accipiter henstii*) mean = 28.3%, median = 28.3% (n=2);Guiana crested eagles (*Morphnus guianensis*) mean = 25.0%, median = 25.0%, (n=1). All three accipitrid taxa (harpy eagles, Henst's goshawks, and Guiana crested eagles) are classic forest-hunting birds with the short wings, long tails, and powerful legs described in Chapter II.

Fig.4.15 is a scatterplot showing frequency of occurrence percentages divided into predator categories. More data exist on felid and raptor diets containing primates than for other predators. But, since much published research is available regarding the total range of hyena and wild canid prey (largely ungulate species), it is legitimate to compare them with felids and raptors in this figure. Reptile and small carnivore species inhabiting the same geographic ranges as primates have *not* been the focus of many studies that have generated information on diet composition (reptiles, n=5; small carnivores, n=4). Taking

TABLE 4.6. Frequencies of occurrence: Percentage of primates in the diets of predators.

PREDATOR	NUMBER OF STUDIES	FREQUENCY OF OCCURRENCE		
		Range %	Mean %	Median %
FELIDS				
Leopard (*Panthera pardus*)	30	0.4 – 81.4	15.2	10.0
Lion (*P. leo*)	2	0.3 – 6.0	3.2	3.2
Tiger (*P. tigris*)	6	1.0 – 33.0	7.7	3.6
Jaguar (*P. onca*)	1	2.5	2.5	2.5
Cheetah (*Acinonyx jubatus*)	1	0.5	0.5	0.5
Puma (*Felis concolor*)	1	4.5	4.5	4.5
Ocelot (*F. pardalis*)	1	1.8	1.8	1.8
African golden cat (*F. aurata*)	1	3.0	3.0	3.0
Felid (spp.)	2	1.1-6.5	2.1	1.9
RAPTORS				
Madagascar buzzard (*Buteo brachypterus*)	1	15.4	15.4	15.4
African hawk eagle (*Hieraaetus spilogaster*)	1	6.7	6.7	6.7
Harpy eagle (*Harpia harpyja*)	3	31.6 – 63.6	48.1	50.0
Philippine eagle (*Pithecophaga jefferyi*)	3	3.0 – 6.3	4.4	4.0
Verreaux's eagle (*Aquila verreauxii*)	3	0.03 – 41.6	9.2	2.0
Tawny eagle (*A. rapax*)	1	0.5	0.5	0.5
Martial eagle (*Polomaetus bellicosus*)	2	2.5 – 5.6	4.1	4.1
Crowned eagle (*Stephanoaetus coronatus*)	12	2.1 – 87.9	16.3	8.9
Bateleur (*Terathopius ecaudatus*)	2	1.9 – 6.3	4.1	4.1
Guiana crested eagle (*Morphnus guianensis*)	1	25.0	25.0	25.0
Henst's goshawk (*Accipiter henstii*)	1	25.0 – 31.5	28.3	28.3
Verreaux's eagle owl (*Bubo lacteus*)	1	1.7	1.7	1.7

CONTINUED … TABLE 4.6. Frequencies of occurrence: Percentage of primates in the diets of predators.

PREDATOR	NUMBER OF STUDIES	FREQUENCY OF OCCURRENCE		
		Range %	Mean %	Median %
Barn owl (*Tyto alba affinis*)	3	0.2 – 12.3	3.0	0.7
Madagascar red owl (*T. soumagnei*)	1	2.6 – 11.1	6.9	6.9
Madagascar long-eared owl (*Asio madagascariensis*)	3	9.0 – 66.7	33.5	20.5
CANIDS/HYAENIDS				
Dhole (*Cuon alpinus*)	3	1.1 – 25.0	9.2	1.5
Golden jackal (*Canis aureus*)	1	0.7	0.7	0.7
Wolf (*C. lupus*)	1	2.0	2.0	2.0
Spotted hyena (*Crocuta crocuta*)	3	0.5 – 13.6	4.5	1.9
Brown hyena (*Hyaena brunnea*)	2	2.4 – 20.0	9.6	8.0
SMALL CARNIVORES				
Fossa (*Cryptoprocta ferox*)	3	5.4 – 54.0	25.1	15.8
Small spotted genet (*Genetta genetta*)	1	1.0	1.0	1.0
REPTILES				
Nile crocodile (*Crocodylus niloticus*)	2	0.8 – 17.8	6.5	0.8
Reticulated python (*Python reticulatus*)	1	6.2	6.2	6.2
Indian python (*P. molurus*)	1	2.0	2.0	2.0
African python (*P. sebae*)	1	4.0	4.0	4.0
UNKNOWN				
Unknown predator	1	1.1	1.1	1.1

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, *Cryptoprocta ferox*) are above the 90th percentile. This level of consumption represents an indisputable emphasis on securing primates.

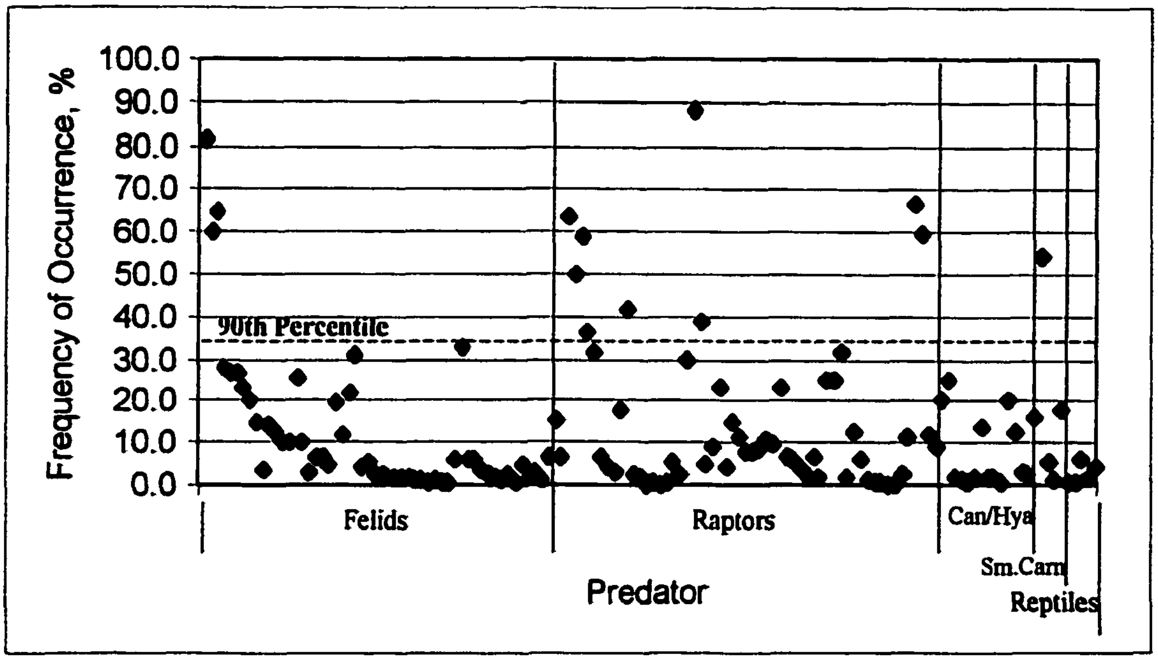


Fig.4.15. Frequency of occurrence of primates in predator diets. Each point represents a datum from a field study on a species of felid, raptor, canid/hyaenid, small carnivore, or reptile. Each datum is a percentage of primates found in the diet of a single predator. (*Median values: Felids, 5.2%, n=53; raptors, 7.6%, n=59; canids/hyaenids, 2.0%, n=13; small carnivores, 10.6%, n=4; reptiles, 3.0%, n=6.)*

DISCUSSION

Measuring the magnitude of predation has been deemed an important task to clarify aspects of primate ecology (Terborgh and Janson 1986). The identification of almost 3600 primate mortalities and unsuccessful predation attempts establishes a baseline for understanding the implications of predation on primates and serves the important purpose of countering erroneous assumptions. Even proponents of hypotheses citing major consequences to primate sociality from the perceived risk of predation have assumed that "mortality due to predation appears to be negligible" (Dunbar 1988, p.53).

The importance of Figs.4.6 through 4.9 is the lack of gaps in the data. I found limited data on *rates* of predation (see section below on estimated predation rates), but Figs.4.6-4.9 indicate that some level of predation has been reported for nearly every group of primates that exist – small and large, nocturnal and diurnal, arboreal and terrestrial. The data in these figures are in conflict with the following assumptions in the literature: Arboreal primates are less at risk from predators than terrestrial because they have only raptors with which to contend (DeVore and Hall 1965); species that inhabit open country are more exposed to predation than those in forested habitat because they cannot easily reach the safety of trees (Gartlan and Brain 1968); small primates are more vulnerable to predation than larger ones because small-sized predators increase the number of animals capable of preying on them (Struhsaker 1967b, Terborgh 1983); no gorilla or chimpanzee has been seriously hurt by a predator (Bourliere 1979); there are no Asian raptors large enough to prey on any but the smallest primates (Whitten 1980, Bennett 1983, Bennett and Davies 1994).

Felids and raptors in Africa accounted for the highest frequencies of predation on primates, 45.2% of all recorded predations (see Table 4.1). That nearly half of all predation data can be attributed to African felids and raptors is most likely an artifact of the greater quantity of questionnaire returns and of scientific articles based on field research on that continent. For example, one researcher in the Tai Forest, Ivory Coast contributed approximately 10.0% of the total predations (n=350) (D. Jenny, pers. comm.). Tracking seven leopards over a 100 km^2 area, Jenny used fecal analysis, carcass remains, and direct observation of kills to identify prey. Nine species of primates were preyed on by leopards during his two-year study: *Pan troglodytes, Colobus badius, C. polykomos, C. verus, Cercopithecus diana, C. petaurista, C. campbelli, Cercocebus torquatus*, and *C. atys*.

The magnitude of predation on primates may be underestimated unless a significant amount of predator research is available, as it is for African felids and raptors. Instances of Asian raptor predation in the data are minimal. One reason may be a sheer lack of field studies on South and Southeast Asian raptors. (Other than the Philippine eagle, I found no literature on the diets of raptor species known to prey on primates.) When a similar body of field research becomes available for other regions and other predators, African felids and raptors may no longer dominate primate predation.

With regard to currently available data on other primate predators, canids and hyaenids are not heavily represented in any region, and since domestic/feral dogs are included in this category, the actual level of predation by wild jackals, dholes, wolves, fox, and other canids (plus three species of hyenas) appears to be relatively low throughout primate geographic ranges. However, several studies have recently identified canid species that have not heretofore been considered primate predators. N. Itoigawa (pers.comm.) cited evidence of 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 as 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 carnivores has been dramatic over the last twenty-five years, but in the early 1970's, both wolves and Asian black bears (*Selenarctos thibetanus*) in Nepal were alleged to prey on *Presbytis entellus* (Bishop 1975).

Reptiles are recorded in low numbers of unsuccessful attacks (2.5%), known predations (4.0%), and suspected predations (12.7%). It is my opinion, based on discussions with herpetologists, that these low percentages are attributable to a lack of reptile fieldwork in Africa, Madagascar, Asia and the Neotropics. The smaller arboreal snakes, such as tree boas (*Corallus* spp.) in the Neotropics, have not been studied *in situ* so future fieldwork may change this picture. The first quantitative study of large tropical snake diets was published less than two years ago (Shine et al. 1998). Specimens of *Python reticulatus*, a giant snake (females routinely reach 7 m) that most authorities credit with being the longest and second-heaviest in the world (Pope 1980), were examined for stomach contents within the context of commercial exploitation for the skin trade. Larger prey were more identifiable in the hindgut than smaller species (Shine et al. 1998). Of the 417 identifiable remains of food in the python alimentary tracts, 3.4% consisted of primates (n=14) of the following species: *Macaca fascicularis* (4930 g), *Presbytis melalophos* (6543 g), and *Trachypithecus cristata* (6608 g). Giant snakes also consume small, nocturnal, arboreal primates (Wiens and Zitzmann 1999). During a study of slow loris (*Nycticebus coucang*, 880 g) in Indonesia, weak signals from a radio-collared focal animal were traced to a patch of dense ferns on the forest floor. When these signals continued over a three-day period from such an unlikely location for an arboreal primate, the authors investigated and found a reticulated python (Wiens and Zitzmann 1999). They confirmed that the signals were being emitted from the interior of the python which had, undoubtedly, swallowed the loris. Using this unexpected opportunity, they radio-tracked the python for a week longer until it excreted the radio collar. However, there was no trace of the slow loris in the feces. This report illustrates that predations involving small primates are nearly impossible to observe indirectly; the predator/prey connection is revealed only if researchers are on the scene.

Predation by small carnivores comprised only 3.3% of the total for all regions in Table 4.1. This is a very low percentage considering that four families of carnivores – viverrid (four genets, six civets, and the fossa), herpestid (seven species of mongoose), procyonid (coati, *Nasua nasua*, and crab-eating raccoon, *Procyon cancrivorus*), mustelid (tayra, *Eira barbara*) -- and one family of marsupials (Neotropical opossum, *Didelphis marsupialis*) have been reported to prey on primates. More than half the predatory data included in the small carnivore category refer to the fossa of Madagascar, which is the only species of small carnivore that has been the subject of repeated studies with the object of understanding the relationship between it and its primate prey (Rasolonandrasana 1994, Rasoloarison et al. 1995, Goodman et al. 1997, Wright et al. 1997). A single study on galagos and their predators, large-spotted genets (*Genetta tigrina*), resulted in data on primate mortality by another small carnivore (Martin and Bearder 1979).

Viverrids and herpestids are formidable Old World predators. Their counterpart in the Neotropics, the tayra, is suspected by many researchers to be a major predator of arboreal New World monkeys (Galef et al. 1976, Defler 1980, Ramirez 1989, Stafford and Ferreira 1995).

Age and sex of primate prey

The effect predation has on the demographics of a primate group depends not only on levels of mortality but on total population size, age, and sex of prey animals (Cheney and Wrangham 1987). Theoretically, predation would exert the strongest pressure demographically when three factors are present simultaneously: small population, high predation rate, and mortality of reproductive age females (Cheney and Wrangham 1987). Infants are often assumed to be the focus of predatory activity, but it is unlikely that younger age classes are the primary target of all predators, particularly if opportunistic hunting is taking place (Emmons 1987, Peetz et al. 1992), or if adult males become conspicuous and, therefore, more vulnerable while defending the group (Boesch and Boesch 1989, Struhsaker and Leakey 1990).

Although Fig.4.14 shows limited predation on infants, this conclusion is not supported by other published data. For example, one investigator saw 41 attempts by hawks and toucans to remove neonates from female *Saimiri oerstedi* (Boinski 1987). Another group of researchers recorded >0.011 attacks per hour on *S. sciureus* by hawks and toucans, mostly directed at mothers and newborn infants (Mitchell et al. 1991). Estimated rates of predation on immature primates (infant and juvenile age classes) in comparison to adults have been collected; the predation rate was 3-17 times higher for immatures than adults in species of cercopithecines and 3-6 times higher in cebids (Janson and van Schaik 1993). *Saguinus oedipus* in Panama lost 50.0% of its offspring to raptors (Dawson and Dukelow 1976); the same mortality rate for infant *S. fuscicollis* and *S. imperator* under the age of one year was observed in Peru (Wright 1984). An estimated 57.0% of infant vervets in Amboseli do not survive their first year; 70.0% of this mortality is due to predation (Cheney et al. 1988). High infant mortality also has been calculated for baboons (Rowell 1969), macaques (Dittus 1975), and chimpanzees (Teleki et al. 1976), but the portion that can be attributed to predation is unknown.

Some data reveal that predators may not target any particular age or sex of primate prey. Fossa are "equal opportunity" predators according to Wright et al. (1998). Deaths due to fossa predation in three groups of Milne-Edward's sifakas (*Propithecus diadema edwardsi*) were spread over all age and sex classes.

Estimated Predation Rates

Estimated predation rate per year (i.e., the percentage of the primate population killed annually by predators) is a valuable insight into the effect predation has on a primate group. Removal of infants may be high in some populations (as discussed above), but EPR calculations measure the effect of predator mortality on all components of the population, including the reproductively-active segments.

The estimated predation rate for *Microcebus murinus* is 25.0% (Goodman et al. 1993c). This rate is based on predation by two genera of owls and does not include predation by diurnal raptors, snakes or small carnivores. High reproductive potential for *M. murinus* adjusts what would seem to be an intolerable level of predation (Goodman et al. 1993c, Hill and Dunbar 1998). Unlike other primate species, female *Microcebus* have an average of two infants twice per year (Martin 1972). The mouse lemur is able to sustain a predation rate of 25.0% because the species, for a primate, has a high reproductive capacity (Martin 1972, Goodman et al. 1993c).

A higher rate of predation for small, arboreal, nocturnal primates (Table 4.3) is partially reflective of the 25.0% EPR calculated for mouse lemurs and may not be an indication of more than this one high EPR. In addition, the sample sizes are very small for three of the categories and relatively large for the other two. However, high reproductive potential is inherent in *Microcebus* (Martin 1972, Goodman et al. 1993c), and the genus may have evolved the ability to sustain predation pressure from a wide variety of nocturnal and diurnal predators of many sizes. Alternatively, the high rate for mouse lemurs may reflect the thorough study of Madagascar owls (Goodman et al. 1991, Goodman and Langrand 1993, Goodman et al. 1993a, 1993b); similar studies of owls in the ranges of other small primates may yield comparable rates.

Frequency of Occurrence

A standard tool for basic data collection on predators involves compiling the frequency of occurrence of prey species in the diet of the predator. Boshoff et al. (1994) give an excellent explanation of how this tool provides 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.

Frequencies of occurrence of primates in predator diets are based on conservative estimates for several reasons. Biases against finding the remains of arboreal, young, small or nocturnally-active prey are great (Muckenhirn 1972, Rice 1986, Thapar 1986). Smaller species, such as primates, are always 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 (Foster and Kearney 1967, Pienaar 1969, Schaller 1972, Eloff 1973, Floyd et al. 1978, Bothma and Le Riche 1986). Observing the kill of a secretive, nocturnal predator, such as the leopard, is particularly problematic. Even though an estimated 45.0% of the vervet population fell victim to leopards during one year at Amboseli, no vervets were killed within sight of researchers (Isbell 1990b, 1994b). In addition, the chance that skeletal remains pass through the digestive tract of a leopard in recognizable form are greater for large prey animals than for smaller ones (Muckenhirn 1972).

Even when the largest primates, gorillas, 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 the primary predator, scavengers, and insects (Tutin and Benirschke 1991). A similar amount of time was noted for disappearance of a chimpanzee carcass after leopard predation in the Tai Forest, Ivory Coast (Boesch 1991). Fecal samples 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).

When all data on frequencies of occurrence presented in Table 4.6 are combined into predator categories, i.e., to give the mean and median frequency of occurrence per *predator group*, felids, raptors, and small carnivores appear to have considerably higher consumption rates of primates than do canids, hyenas, or reptiles (Table 4.7).

TABLE 4.7. Frequencies of occurrence categorized by predator taxa.

PREDATOR CATEGORY	FREQUENCY OF OCCURRENCE	
	Mean %	Median %
Felids (n=53)	12.1	5.2
Raptors (n=59)	15.5	7.6
Canids/Hyaenids (n=13)	6.6	2.0
Small Carnivores (n=4)	19.1	10.6
Reptiles (n=6)	5.3	3.0

Any comparison between felids and raptors and other predator categories is likely skewed by the disparity in the number of studies producing data and may not represent a true picture of the difference in levels of primates being taken. It should be noted that the number of data points on which the means and percentiles for individual species are based vary a great deal, also. For example, there are 37 data points from 12 studies of crowned eagles (*Stephanoaetus coronatus*) and only one data point from one study for Madagascar buzzards (*Buteo brachypterus*), African hawk eagles (*Hieraaetus spilogaster*), Guiana crested eagles (*Morphnus guianensis*), tawny eagles (*Aquila rapax*), and Verreaux's eagle owls (*Bubo lacteus*).

Nevertheless, information based on frequency of occurrence data underscores recommendations that progress in understanding the importance of predation on primates will come from the study of the predators themselves (Anderson 1986a, Cheney and Wrangham 1987, Isbell 1994a, and Boinski and Chapman 1995).

Frequencies of occurrence of primates in diets of *individual* predator species (based on data in Table 4.6) are discussed in detail in Chapter V.

SUMMARY

- Known primate deaths, unsuccessful attacks, and suspected predations were tabulated. Data on almost 3600 separate instances of predation were available from questionnaires and the scientific and natural history literature.
- Diurnal raptors, owls, and other birds were the top predators on primates (40.7% of the total, n=1460), followed by felids (34.6%, n=1243), canids and hyaenids (7.0%, n=253), reptiles (5.4%, n=194), and small carnivores (3.3%, n=118). Further fieldwork is necessary to corroborate these findings since many predator species have not been studied *in situ*.
- No region, weight, activity cycle or stratum could be identified in which primates were free of predation.
- The limited data available from questionnaires indicate that adult primates are more often prey than other age groups and that males are more often prey than females.

However, infant mortality is identified in many sources as being very high, and a good portion of this mortality may be due to predation.

- Estimated typical predation rates varied from 0-25.0%. Limited evidence pointed to small, nocturnal, arboreal primates having higher predation rates than larger, diurnal, or terrestrial species.
- The frequencies of occurrence of primates in the diets of predators ranged from 0.03%-87.9%; raptors and felids had the highest percentages of primates in their diets.

CHAPTER V.

PRIMATE SPECIALISTS

"That the crowned eagle in the Congo forest is primarily a monkey-eater, the examinations of crop and stomach in eight cases clearly show. Five of them had been eating monkeys, of the genera Colobus *and* Cercopithecus*; in four cases these remains were noted as of young monkeys, but in at least one case, a full-grown* Cercopithecus *had been devoured, one foot and a tibia being contained in the crop and stomach of a female eagle."* (Chapin 1932, p.583)

INTRODUCTION

My intent in this chapter is to narrow the focus of primate predation down to those species that may warrant the term *primate specialist*. I selected this label to help designate predators that depend on primates as food sources and may have coevolved with their primate prey.

Anecdotal references to certain predators, in particular leopards (*Panthera pardus*), several eagle species, the fossa of Madagascar (*Cryptoprocta ferox*), pythons in Africa, and crocodiles in Java, indicate there are historical and legendary beliefs about the preference certain predators have for primates above all other food. Nineteenth-century naturalists referred to the fossa as "the scourge of lemurs" (R. Orenstein, pers. comm.), and it was stated unequivocally that baboons and snakes are natural enemies, evidenced by the way African pythons (*Python sebae*) employ cover of darkness to snatch stray youngsters from baboon sleeping sites (Isemonger 1962).

In 1933, several residents of Java fell victim to an Indopacific crocodile (*Crocodylus porosus*). The local administrator wrote to Jakarta requesting permission to trap eight proboscis monkeys (*Nasalis larvatus*) as bait to capture the man-eater, based on the Javan belief that these primates were the crocodiles' most favored prey (Hoogerwerf 1970).

Crowned eagles (*Stephanoaetus coronatus*) have been labeled "leopards of the air," thereby implicating both leopards *and* crowned eagles as rapacious hunters of rainforest monkeys (Chapin 1925). The Usambara of the former Belgian Congo called the crowned eagle *Kumbakima*, "the monkey beater" (Brown 1953). The Philippine eagle's scientific nomenclature (*Pithecophaga jefferyi* Grant1896) emphasizes predation on monkeys -- *Pithecophaga* is derived from the Greek words *pithekos*, meaning monkey, and *phagein*, eater. Its common name was officially changed from "monkey-eating eagle" to "Philippine eagle" in 1978 by President Ferdinand Marcos as a public relations move, since the "monkey-eating" appellation was seen as denigration of the noble bird (Kennedy 1981).

Of course, historical references may not be entirely accurate. For instance, the Philippine eagle relies more on a diet of colugos, also known as flying lemurs (*Cynocephalus volans*), than on monkeys (Kennedy 1977, 1981, 1985). Crowned eagles inhabiting treeless savannah environments, instead of dense rainforest, hunt fewer monkeys and turn to rock hyrax (*Procavia capensis*) as preferred prey (Jarvis et al. 1980). New studies show that fossa may substitute large numbers of *Microgale cowani*, a small Malagasy insectivore in the tenrec family, for lemur prey in certain biomes (Goodman et al. 1997).

There are also disagreements among authors of earlier articles. According to one investigator, leopards were routinely live-trapped and reintroduced in baboon-infested areas to eliminate the burgeoning baboon populations in a certain parts of Kenya (Wright 1960). Other authors refer to the exaggerated mythology surrounding leopard predation on baboons (Hall 1966, Norton et al. 1986, Hamilton 1981).

There may be predators that rely on primates only because primates are the most available prey to access. This is likely the situation for the barn owl in Madagascar (*Tyto alba affinis*) which is a major predator of mouse lemurs (*Microcebus* spp.) in undisturbed habitats (Goodman and Langrand 1993). But barn owls (unlike the endemic owls of Madagascar) are able to colonize disturbed areas near human settlements (Goodman and Thorstrom 1998). When barn owl diets are measured in newly-colonized territory – where introduced species, such as *Rattus rattus*, abound as human commensals – there is a demonstrable shift from small nocturnal prosimians to the introduced exotics. This switch to commensals is not the case with the Madagascar red owl (*Tyto soumagnei*) (Goodman and Thorstrom 1998). Another endemic, the Madagascar long-eared owl (*Asio madagascariensis*), will also feed on introduced rodents (Goodman et al. 1991, Goodman and Langrand 1993, Goodman et al. 1993a).

I propose that primate specialists be divided into two categories: dedicated and opportunistic. The former is defined as specifically choosing primate prey; the latter as killing relatively large numbers of primates but doing so in an opportunistic manner and substituting any other favored prey, when available, to the exclusion of primates.

METHODS

Percentages of primates in predators' diets (frequency of occurrence) were available from questionnaires and the literature for 34 species (see Table 4.6), including eight felids, eleven diurnal raptors, four owls, three canids, two hyenas, two viverrids, one crocodile, and three snakes. Numbers of known successful and unsuccessful predations were tabulated for the same 34 species from questionnaires and the literature. Initially, I plotted these two measurements on a log scale to determine which of the 34 predator species fell into each of four possible sectors: 1) low predation level and low frequency of occurrence, 2) high predation level and low frequency of occurrence, 3) low predation level and high frequency of occurrence, 4) high predation level and high frequency of occurrence. To achieve a more precise definition of primate specialists, I calculated and plotted the median for both numbers of predations and frequencies of occurrence. I chose the median value, instead of the mean, to give the best measure of central tendency, since the data for frequencies of occurrence were highly skewed. I identified primate specialists as those species falling above the median; species falling above the 80th percentile were designated as dedicated primate specialists.

In addition, I supplemented this plot with qualitative data on the number of primate families or subfamilies preyed upon by each primate specialist and the range of data from field studies that had yielded information on the primate component of each primate specialist's diet.

RESULTS

I used the number of predations and the frequencies of occurrence in predator diets to determine species that could be designated as primate specialists. In Fig.5.1, I plotted the number of primate predations for 34 predators as a function of the median frequency of occurrence. Eleven species could be immediately identified as primate specialists due to their position on the graph in the high predation level-high frequency of occurrence sector. Leopard (point #1 on graph), Madagascar buzzard (9), harpy eagle (11), Philippine eagle (12), crowned eagle (16), bateleur (17), Henst's goshawk (19), Madagascar long-eared owl (23), fossa (29), reticulated python (32), and African python (34) fell above the median (frequency of occurrence, x=3.8; number of predations, y=13). Four species – leopard (1), harpy eagle (11), crowned eagle (16), and fossa (29) -- fell above the 80th percentile (frequency of occurrence, x=9; number of predations, y=48). One species, the harpy eagle (11), fell above the 90th percentile (frequency of occurrence, x=19; number of predations, y=90).

When literature and questionnaire data were surveyed as a qualitative check on primate specialist species identified in Fig.5.1, results were mixed. In Table 5.1, I compare the primate families and subfamilies recorded as prey of primate specialists to see the *breadth* of their reliance on primate prey. Leopards preyed on the full spectrum of primate families available (excluding tarsiers) within their geographic range. Three of the Malagasy primate specialists, the Madagascar buzzard (*Buteo brachypterus*), Henst's goshawk (*Accipiter henstii*), and fossa have been recorded preying on all available prosimian families (excluding *Daubentonia*); the fourth Malagasy predator, the Madagascar long-eared owl (*Asio madagascariensis*), weighs only 305 g and is limited to

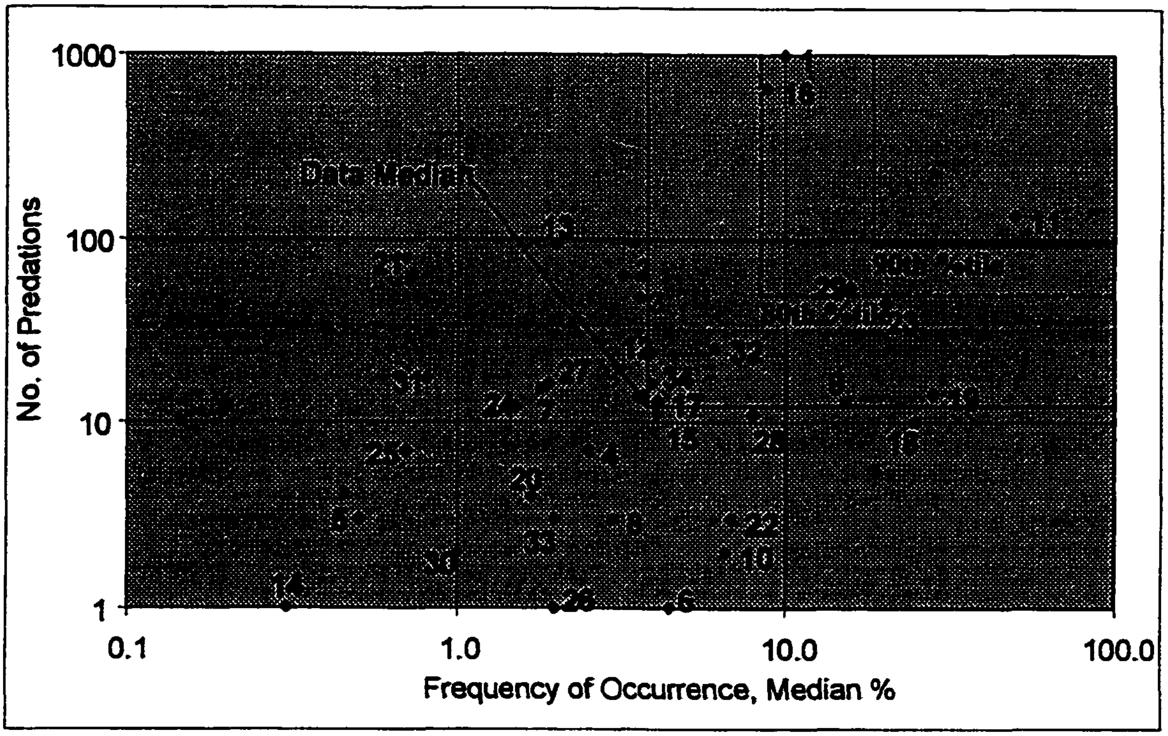


Fig.5.1. Number of predations as a function of percentage of primates in predator diets (frequency of occurrence). (Identification code: *Felids* – 1,leopard; 2, lion; 3, tiger; 4, jaguar; 5, cheetah; 6, puma; 7, ocelot; 8, African golden cat. *Raptors* – 9, Madagascar buzzard; 10, African hawk eagle; 11, harpy eagle; 12, Philippine eagle; 13, Verreaux's eagle; 14, tawny eagle; 15, martial eagle; 16, crowned eagle; 17, bateleur; 18, Guiana crested eagle; 19, Henst's goshawk; 20, Verreaux's eagle owl; 21, barn owl; 22, Madagascar red owl; 23, Madagascar long-eared owl. *Canids/Hyaenids* – 24, dhole; 25, golden jackal; 26, wolf; 27, spotted hyena; 28, brown hyena. *Small Carnivores* – 29, fossa; 30, small spotted genet. *Reptiles* – 31, Nile crocodile; 32, reticulated python; 33, Indian python; 34, African python.)

smaller primates in the cheirogaleid and lemurid families. Likewise, the crowned eagle would be too small at 3640 g to include chimpanzees or gorillas in its diet, although it is capable of killing adult male *Colobus guereza* that weigh in excess of 10000 g (Skorupa 1989) and subadult mandrills (*Mandrillus sphinx*) (Jouventin 1975). The Philippine eagle is basically limited to *Macaca fasicularis* as primate prey since the other two indigenous

TABLE 5.1. Primate specialists.

PREDATOR SPECIES	FREQUENCY OF OCCURRENCE		RECORDED PREDATIONS (No. of Sources)		PRIMATE PREY: FAMILY OR SUBFAMILY	NUMBER OF DATA POINTS MEASURING % OF PRIMATES IN PREDATOR'S DIET
	Mean (%)	Median (%)				
DEDICATED PRIMATE SPECIALISTS						
Leopard (*Panthera pardus*)	15.2	10.0	994	(85)	Lorisidae Cercopithecinae Colobinae Hylobatidae Pongidae	37
Harpy eagle (*Harpia harpyja*)	48.1	50.0	135	(15)	Cebidae	5
Crowned eagle (*Stephanoaetus coronatus*)	16.3	8.9	659	(58)	Lorisidae Cercopithecinae Colobinae	19
Fossa (*Cryptoprocta ferox*)	25.1	15.8	49	(12)	Cheirogaleidae Lemuridae Indriidae	3

CONTINUED … TABLE 5.1. Primate specialists.

PREDATOR SPECIES	FREQUENCY OF OCCURRENCE		RECORDED PREDATIONS (No. of Sources)		PRIMATE PREY: FAMILY OR SUBFAMILY	NUMBER OF DATA POINTS MEASURING % OF PRIMATES IN PREDATOR'S DIET
	MEAN (%)	MEDIAN (%)				
OPPORTUNISTIC PRIMATE SPECIALISTS						
Madagascar buzzard (*Buteo brachypterus*)	15.4	15.4	13	(3)	Cheirogaleidae Lemuridae Indriidae	1
Philippine eagle (*Pithecophaga jefferyi*)	4.4	4.0	24	(4)	Cercopithecinae	3
Bateleur (*Terathopius ecaudatus*)	4.1	4.1	13	(3)	Lorisidae Cercopithecinae	2
Henst's goshawk (*Accipiter henstii*)	28.3	28.3	14	(2)	Cheirogaleidae Lemuridae Indriidae	2
Madagascar long-eared owl (*Asio madagascariensis*)	33.5	20.5	46	(3)	Cheirogaleidae Lemuridae	5
Reticulated python (*Python reticulatus*)	6.2	6.2	25	(8)	Lorisidae Cercopithecinae Colobinae Hylobatidae	1
African python (*P. sebae*)	4.0	4.0	16	(6)	Cercopithecinae Colobinae	1

primates on the islands are nocturnal. The rest of the primate specialist species in Table 5.1 have not been observed exploiting the full range of primates available to them.

One field study may produce several frequencies of occurrence, i.e., data points separated by time or location. Therefore, I tabulated the number of data points generated in field studies producing frequency of occurrence information to check on the *depth* of the data.

DISCUSSION

The morphological, behavioral and ecological parameters of certain predators make them particularly suited for preying on primates. Morphological characteristics include talon length and tarsus strength in raptors, canine length in carnivores, and mouth gape extension in snakes; behavioral repertoires include team hunting in eagles, raptor flight patterns in rainforest canopy, and nocturnality in many felids, canids, hyaenids, and small carnivores; ecological parameters include use of heavy forest, open savannah, or riparian habitats and biennial breeding in large eagles.

Coevolution between predator and prey is a case of "the deer flees, the wolf pursues" (Janzen 1980, Bakker 1983). Major destabilizations in predator-prey coexistence come about from evolution of the prey *followed* by predator counter-adaptations (Roughgarden 1983). Thus, coevolution between predators and their primate prey is most visible from the behavioral and morphological adaptations in primates that are traceable to specific predators. For example, primate polyspecific associations are limited to geographic regions inhabited by monkey-eating raptors (e.g., harpy eagles of the Neotropics and crowned eagles of Central and West Africa) that provided a strong incentive for aggregation (Gautier-Hion et al. 1983, Terborgh 1990a). Harpy eagles have exerted strong selective pressure on many Neotropical primate species, manifested in both behavior (crypticity and group living) and morphology (increased size) (Terborgh 1983, Peres 1990).

Coevolution seems to have occurred between present-day lemurs in Madagascar and an extinct Holocene eagle, *Stephanoaetus mahery*, which is a congener with the extant crowned eagle (*S. coronatus*) of sub-Saharan Africa. Goodman (1994a) has described the subfossil of this immensely powerful raptor which may have specialized in capturing large, diurnal members of Lemuridae and Indriidae. There are strong stereotypic responses to birds of prey given by *Lemur catta* and *Propithecus verreauxi* (Sauther 1989, Macedonia 1990a, 1990b), but the diurnal hawks currently inhabiting Madagascar that evoke anti-predation behavior in these lemurs are black kites (*Milvus migrans)*, Madagascar harrier hawks (*Polyboroides radiatus)*, and Madagascar buzzards (*Buteo brachypterus)*. They are relatively small compared to the subfossil raptor and would have extreme difficulty in subduing and killing an adult lemur (Goodman 1994b). The long hind talons of the subfossil eagle are equal in size and massiveness -- and the tarsometatarsus is larger -- than modern specimens of *Stephanoaetus coronatus* (Goodman 1994a). *S. mahery* would have been a formidable predator of lemurs, just as *S. coronatus* is the premier threat to African forest monkeys today.

An "intermediate" social form (i.e., not the small family groupings of nocturnal lemurs or the large multi-male groups of *Lemur catta*) has been observed in the diurnal bamboo lemur (*Hapelemur griseus*). These groupings may be an adaptation specifically to guard against the ring-tailed mongoose (*Galidia elegans)* or other small Malagasy carnivores (Hladik 1979).

Consistently high predation rates on primates give indications of long term predator-prey relationships and also can be used to infer coevolution. Studies of leopard predation on vervets (*Cercopithecus aethiops*) at Amboseli have found estimated predation rates (i.e., the percentage removed yearly from a population by predators) are 11.0-15.0% (Cheney and Wrangham 1987, Isbell 1990a, 1990b). Owl predation on mouse lemurs (*Microcebus murinus*) (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 to illustrate that certain predators preferentially kill primates for food. The estimated predation rates for crowned eagle exploitation of cercopithecines and colobines in the Kibale Forest are only 0.3-3.0%, depending on the species of primate (Struhsaker and Leakey 1990).

The frequency of occurrence of primates in the diet of a predator is a more precise measure of the predator-prey relationship since estimated predation rates can be 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, 1971b, Seidensticker and 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. While primates may compose as much as 87.9% of a crowned eagle's diet in forested areas of Central Africa (Msuya 1993), the percentage drops to 2.1-38.9% on the savannah of East Africa (Brown 1953, 1982) where far fewer sympatric primate species exist. As an example of human influence on levels of primate predation, investigators discovered that *Trachypithecus cristata* and *Macaca fascicularis* were the predominant food of large predators in Meru-Betiri Reserve, Indonesia (Seidensticker and Suyono 1980). The situation in Meru-Betiri is quite different from other areas of Asia where leopard, tiger (*Panthera tigris*), and dhole (*Cuon alpinus*) have been studied concurrently (see Johnsingh 1980, 1983, Rice 1986) because small ungulates have been extirpated by humans. In Meru-Betiri, primates are the substitute for a range of other prey normally available to large Asian carnivores.

Temporary ecological shifts on the part of a predator (e.g., leopards moving into a new range or an increase in the number of leopards using the same territory) sometimes results in increased predation on primates rather than increased predation on many different prey species (Isbell 1990a, 1990b). When the estimated predation rate on primates rises as more predators enter the ecosystem, but the composition of prey biomass (i.e., the relative percentage of primates compared to the total weight of all prey species) stays the same, it can be assumed that primates are preferential prey items.

There is wide variation in the number of studies and data points on frequencies of occurrence of primates in predator diets. I have analyzed predator species for which there are small numbers of studies and data points showing high percentages of primates in their diets along with predators for which there are ample data. Leopards have been the subject of 30 field studies yielding 37 frequencies of occurrence, and crowned eagles have been the subject of 12 field studies yielding 19 frequencies of occurrence. The number of studies carried out on the remaining nine predators ranged from one to three;

the number of data points produced by the studies ranged from one to five, with a mean of 2.6 frequencies of occurrence.

Leopards, harpy eagles, crowned eagles, and fossa emerged from the data analysis as dedicated primate specialists. These predators may be selective in their choice of prey and concentrate on primates. The first three species come as no surprise given the published research (cf. Chapter II).

Fossa, the alleged "scourge of lemurs," may be *exactly* that. Although studies on this cat-like viverrid are few in number as yet (Rasolonandrasana 1994, Rasoloarison et al. 1995, Wright et al. 1997), all have concluded that fossa exert considerable pressure on the larger species of lemurs. Calculations based on known kills estimate that fossa remove nearly one-third of the yearly population growth of *Propithecus verreauxi* in the Kirindy Forest (Rasolonandrasana 1994, Rasoloarison et al. 1995, Ganzhorn and Kappeler 1996).

There are several species listed on Table 5.1 that have not garnered a reputation as primate predators. Goodman et al. (1991) documented the first case of predation on *Microcebus* by a nocturnal bird of prey only within the past decade. It was by pure chance, as explained by these authors, that a nest of Madagascar long-eared owls (*Asio madagascariensis*) was found which yielded pellets containing primate remains.

A five-year study of red colobus (*Colobus badius*) in Abuko Nature Reserve, The Gambia found that predation by reptiles (*Python sebae* and *Crocodylus niloticus*, in particular) was a major proximate cause of mortality in adult monkeys (Starin 1991). Based on direct observation of kills and the examination of carcasses, 40.0% of known deaths were attributable to reptiles. In addition, 13 red colobus that disappeared were suspected to have been python victims since this form of predation leaves no evidence unless the event is witnessed or the snake's stomach contents are examined.

New information on lions (*Panthera leo*) in the Mahale Mountains indicates that this felid could be a major predator of primates (Tsukahara 1993). The Mahale chimpanzee population has been the subject of long-term demographic research (Nishida et al. 1990). Until an analysis confirmed the presence of chimpanzee hair in lion feces (Inagaki and Tsukahara 1991, 1993), predation as a mortality factor on chimps was assumed to be negligible. This assumption has been challenged by evidence of chimpanzee hair, bones, and teeth in four out of eleven samples of lion feces collected over widely-spaced periods of time. Predation by lions may constitute an important selective pressure on chimpanzees in Mahale (Tsukahara 1993).

In another instance involving lion predation, a questionnaire respondent reported two lionesses at Mana Pools National Park, Zimbabwe selectively preying on baboons (T. Williamson, pers. comm.). While other members of their pride did not exhibit a predilection for primates, two females began preying on baboons as juveniles and have continued the practice into adulthood. Six sightings of baboon kills by the two lionesses have been recorded in a four-year period.

Tigers are usually assumed to take only very large prey. Nevertheless, langurs (*Presbytis entellus*) are one of the major prey species of tigers in the forest of Ranthambhore, India, where they fall prey when caught on the ground (Thapar 1986). During Thapar's study, he discovered remains of four fresh tiger kills containing remnants of langurs, observed an unsuccessful attack by a tiger on a group of langurs, and photographed a kill sequence from the tiger's first awareness of the langur until the consumption of the carcass. Although langurs were a regular part of the tigers' diets in the Ranthambhore study, finding langur carcasses is rare because a 12-19 kg monkey is consumed completely at one feeding (Thapar 1986). Fecal samples gathered in Royal Chitwan National Park, Nepal confirmed the inclusion of langurs in the tiger's diet (Sunquist and Sunquist 1988), and at Kanha, India, langurs and rhesus monkeys are commonly captured by tigers (Schaller 1967).

New findings on the diets of tigers, lions, Malagasy owls, pythons, and the fossa indicate that far more predators could be *relying* on primates as a prey base than has so far been thought.

SUMMARY

- I propose a new category, termed *primate specialist*, to describe predator species for which there is evidence of high levels of predation on primates.
- Eleven primate specialists could be determined based on the level of recorded predations as a function of the percentage of primates in the predator's diet.
- I have tentatively identified four of these primate specialists -- one felid, two raptors, and a viverrid -- as "dedicated" predators by both quantitative and qualitative measurements.
- Seven predator species (four diurnal raptors, one owl, and two snakes) may best be identified as "opportunistic" primate specialists since studies have shown that other available prey is easily substituted for primates in their diets.
- Recent research indicates that, when more quantitative data are available, the total number of species that could be classified as primate specialists may increase.

CHAPTER VI.

THE EFFECTS OF BODY SIZE ON PREDATION

"King of the raptorine birds, the Harpy eagle is a flying wolf. From the topmost branch of some dead forest giant it surveys the forest below for signs of movement. Then, like a bolt from the blue, it swoops with unerring accuracy upon a sleeping sloth or a leaping monkey and bears off its prey in triumph." (Hanif 1970, p. 24)

INTRODUCTION

Body size is a basic aspect of primate adaptations (Fleagle 1988). Protoprimates from the Paleocene are hypothesized to have been small, arboreal, nocturnal insectivores resembling present-day tree shrews (Conroy 1990). As primates evolved, body size increased along with other adaptations such as terrestriality, diurnality, frugivory/folivory, and complex social structure. Size has been associated with locomotion, behavior, diet and other aspects of ecology. It may also be valuable to look at relative body weights of predators and primates for insight into size as an adaptation to minimize predation, an approach proven useful in the study of invertebrate and mammalian predator-prey associations (Rosenzweig 1966, Paine 1976).

Generally size is credited with being a compelling arbiter of the sheer number of potential predators, with smaller primates more susceptible to predation than larger ones (Struhsaker 1967b, Terborgh 1983). It was found that body size was negatively correlated with available estimated predation rates (Cheney and Wrangham 1987, Isbell 1994a), but this pattern has been examined for only a few species. In this chapter, I present an overview of the effects of body size on predation through two analyses: (a) I compare the body weights of all primates with the body weights of their known or alleged predators and discuss whether or not this comparison supports the hypothesis that increased body size is an evolutionary response to predation, and (b) I compare the body weights of primates and predators from recorded predation events and discuss their relationship.

METHODS

Adult body weights were gathered for 161 primate species (Macdonald 1984a, Fleagle 1988, Willis 1995) and from a variety of sources for 100 known or alleged predators (Fowler and Cope 1964, Voous 1969, 1988, Guggisberg 1975, Grzimek 1975, Brown *et al.* 1982, Terborgh 1983, Macdonald 1984a, 1984b, Brown and Amadon 1989, Pfeffer 1989, Dunning 1993, and D. Payne, pers. comm.). These weights are provided in Tables 6.1 and 6.2. In species of predatory animals exhibiting sexual dimorphism, the heavier sex was used to compute weights. Accordingly, adult male weights were used with the exception of hyenas, raptors, some viverrids, and the large pythons, taxa in which females may be significantly larger.

Descriptive statistics and histograms of weights were used to compare all primates with all their predator species for which weights were available. More specifically, the tenth, twenty-fifth, fiftieth, seventy-fifth and ninetieth percentiles of primate weights were calculated, and the number of predator species falling above those values was counted.

TABLE 6.1. Adult body weights of 161 primate species.

SPECIES	BODY WEIGHT (g)	SPECIES	BODY WEIGHT (g)
Microcebus murinus	70	*Nycticebus coucang*	920
M. rufus	60	*N. pygmaeus*	300
Mirza coquereli	330	*Tarsius syrichta*	122
Cheirogaleus major	450	*T. bancanus*	123
C. medius	300	*T. spectrum*	140
Phaner furcifer	400	*Pithecia pithecia*	1800
Allocebus trichotis	100	*P. monachus*	2800
Lemur catta	2670	*Chiropotes satanas*	2980
L. fulvus	2500	*C. albinasus*	3125
L. mongoz	2025	*Cacajao calvus*	3450
L. macaco	2401	*C. melanocephalus*	2800
L. rubriventer	2350	*Aotus trivirgatus*	1220
L. coronatus	2000	*Callicebus torquatus*	1490
Varecia variegata	3800	*C. moloch*	1070
Hapalemur griseus	880	*C. personatus*	1700
H. simus	2500	*Cebus apella*	3300
H. aureus	1200	*C. albifrons*	3260
Lepilemur mustelinus	1000	*C. capucinus*	3700
Avahi laniger	920	*C. nigrivittatus*	3500
Propithecus verreauxi	3780	*Saimiri sciureus*	960
P. diadema	6500	*S. oerstedii*	750
Indri indri	10000	*Alouatta seniculus*	7880
Daubentonia madagascariensis	2800	*A. palliata*	11590
Otolemur crassicaudatus	1151	*A. villosa*	12000
O. garnettii	760	*A. caraya*	8280
Galago senegalensis	215	*Lagothrix lagothricha*	8700
Euoticus elegantulus	274	*Brachyteles arachnoides*	15000
E. matschiei	210	*Ateles paniscus*	9000
Galagoides demidovii	70	*A. geoffroyi*	7730
G. thomasi	110	*A. belzebuth*	5902
G. zanzabaricus	150	*Callimico goeldii*	630
G. alleni	295	*Saguinus nigricollis*	465
Perodicticus potto	1150	*S. fuscicollis*	462
Arctocebus calabarensis	265	*S. mystax*	580
Loris tardigradus	275	*S. labiatus*	580

CONTINUED ... TABLE 6.1. Adult body weights of 161 primate species.

SPECIES	BODY WEIGHT (g)	SPECIES	BODY WEIGHT (g)
S. imperator	400	*C. lhoesti*	6500
S. midas	570	*C. neglectus*	6320
S. inustus	740	*C. mona*	6000
S. oedipus	490	*C. wolfi*	5000
S. leucopus	490	*C. diana*	4994
Leontopithecus rosalia	500	*C. petaurista*	8172
L. chrysomelas	550	*C. campbelli*	4086
L. chrysopygus	550	*C. aethiops*	5370
Callithrix jacchus	310	*Allenopithecus nigroviridis*	6900
C. penicilata	340	*Miopithecus talapoin*	1380
Cebuella pygmaea	135	*Erythrocebus patas*	11100
Macaca nemestrina	10210	*Colobus guereza*	10100
M. sylvanus	12939	*C. polykomos*	10000
M. sinica	5448	*C. satana*	9000
M. radiata	6280	*C. badius*	8240
M. assamensis	9060	*C. angolensis*	11350
M. fascicularis	4930	*Procolobus verus*	4280
M. mulatta	7730	*Trachypithecus cristata*	6608
M. fuscata	13166	*T. francoisi*	7350
M. arctoides	9060	*T. geei*	10850
M. silenus	6810	*T. obscura*	7903
M. nigra	9988	*T. phayrei*	7710
M. thibetana	11800	*T. pileata*	12750
Cercocebus albigena	8980	*Presbytis entellus*	19100
C. torquatus	10625	*P. senex*	6860
C. galeritus	9988	*P. johnii*	11500
Papio hamadryas	21300	*P. rubicunda*	6339
P. anubis	25100	*P. melalophos*	6543
P. cynocephalus	22800	*P. comata*	6800
P. ursinus	31200	*P. frontata*	5570
Mandrillus sphinx	26900	*P. hosei*	6178
M. leucophaeus	20000	*P. femoralus*	6261
Theropithecus gelada	19000	*P. potenziani*	6407
Cercopithecus mitis	7264	*P. thomasi*	6766
C. nictitans	6500	*Rhinopithecus avunculus*	8000
C. ascanius	4170	*R. roxellana*	17930
C. cephus	4000	*Nasalis larvatus*	20370
C. pogonias	4500	*Simias concolor*	8750

CONTINUED ... TABLE 6.1. Adult body weights of 161 primate species.

SPECIES	BODY WEIGHT (g)	SPECIES	BODY WEIGHT (g)
Pygathrix nemaeus	10900	*H. muelleri*	5760
Hylobates syndactylus	10900	*Pongo pygmaeus*	81000
H. concolor	6300	*Pan troglodytes*	43000
H. hoolock	6930	*P. paniscus*	45000
H. klossii	5670	*Gorilla g. beringei*	159200
H. lar	5700	*G. g. graueri*	175200
H. moloch	5700	*G. g. gorilla*	169500
H. agilis	5830		

TABLE 6.2. Adult body weights of 100 predator species.

SPECIES	BODY WEIGHT (g)	SPECIES	BODY WEIGHT (g)
DIRUNAL RAPTORS, OWLS, AND OTHER PREDATORY BIRDS			
Leptodon cayanensis	540	*A. verreauxii*	4600
Milvus migrans	827	*Hieraaetus wahlbergi*	1000
Haliaeetus vocifer	3400	*H. fasciatus*	2500
Ichtyophaga ichthyaetus	2480	*Spizastur melanoleucus*	850
Circaetus gallicus	1703	*Polomaetus bellicosus*	4230
C. cinereus	2048	*Spizaetus cirrhatus*	1810
Terathopius ecaudatus	2950	*S. tyrannus*	1025
Spilornis cheela	1237	*S. ornatus*	1421
Polyboroides typus	950	*Stephanoaetus coronatus*	3640
Accipiter bicolor	436	*Daptrius americanus*	586
A. henstii	1150	*Micrastur ruficollis*	196
Leucopternis shistacea	1000	*M. semitorquatus*	900
L. albicollis	650	*Tyto alba affinis*	334
Buteogallus urubitinga	1068	*Bubo poensis*	746
Buteo nitidus	460	*B. lacteus*	2625
B. magnirostris	269	*Athene cunicularia*	159
Morphnus guianensis	1750	*Asio madagascariensis*	305
Harpia harpyja	7600	*Piaya cayana*	108
Pithecophaga jefferyi	7000	*Ramphastos sulfuratus*	339
Aquila rapax	2500	*R. swainsonii*	660
A. heliaca	3395	*Vanga curvirostris*	72
A. chrysaetos	4913	*Corvus macrorhynchos*	582
FELIDS			
Panthera leo	190960	*F. catus*	4500
P. onca	102000	*F. chaus*	9000
P. pardus	70000	*F. concolor*	100000
P. tigris	190000	*F. pardalis*	15800
Acinonyx jubatus	72000	*F. serval*	18000
Neofelis nebulosa	21900	*F. temmincki*	11000
Felis aurata	15000	*F. viverrina*	14000
F. caracal	18000	*F. yagouroundi*	9000

CONTINUED ... TABLE 6.2. Adult body weights of 100 predator species.

CANIDS			
Canis adustus	15000	*C. lupus arabs*	20000
C. aureus	11000	*Lycaon pictus*	27000
C. mesomelas	13500	*Cuon alpinus*	17000
C. familiaris	17000	*Nyctereutes procyonoides*	7500
C. latrans	13620	*Vulpes vulpes*	5200
HYAENIDS			
Crocuta crocuta	80000	*H. hyaena*	40000
Hyaena brunnea	50000		
VIVERRIDS			
Genetta genetta	3000	*Nandinia binotata*	3000
G. tigrina	2300	*Cryptoprocta ferox*	20000
Viverricula indica	4000		
HERPESTIDS			
Galidia elegans	900	*Atilax paludinosus*	3500
Mungotictis decemlineata	800	*Bdeogale nigripes*	3000
MUSTELIDS			
Eira barbara	6000		
REPTILES			
Caiman crocodilus	90800	*P. sebae*	70000
Crocodylus palustris	227000	*Acrantophis madagascariensis*	18160
C. niloticus	199760	*Corallus canima*	1816
Tomistoma schlegeli	181600	*Boa constrictor*	60000
Varanus salvator	45400	*Eunectes murinus*	150000
V. komodoensis	136200	*Leioheterodon madagascariensis*	1362
Python reticulatus	100000	*Bitis arietans*	6810
P. molurus	100000	*Bothrops asper*	2724

Data sets from questionnnaires and the literature contained 1858 entries of recorded predation events containing both the weight of the predator and the weight of the primate prey. Adult body weights were analyzed for (a) the range and mean of primate weights taken by five categories of predators, and (b) the range and mean of primate weights taken by predator species classified as primate specialists in Chapter V. Regression analyses were conducted to compare primate prey weights to predator weights in recorded predation events.

RESULTS

Comparing the weight distribution of all primates and their non-primate predators (Fig.6.1) reveals considerable overlap in weight categories between predatory animals and the primates they consume. However, this overlap varies by predator type.

Most species of primates outweigh most birds of prey (Fig.6.2). Table 6.3 shows that the 50th percentile of primate weights (5.45 kg) is greater than all but two raptor species; 57.0% of the birds fall in the 25th-50th percentile range, but only 5.0% of the raptors exceed the 50th, and none exceed the 75th.

Unlike avian predators, most mammalian carnivores listed in Table 6.2 outweigh the majority of primate species (Fig.6.3a). However, the weight of mammalian predators varies considerably by group.

The weights of small carnivores – viverrids, herpestids, and the only mustelid known to prey on primates, the tayra (*Eira barbara*) -- are lower than many primates (Fig.6.3b). The single species in this category outweighing many primates is the fossa (*Cryptoprocta ferox*), which fills the ecological niche of felids in Madagascar and was previously misclassified as one (Macdonald 1984b). By virtue of its cat-like claws, teeth, and mandible, the fossa is equipped to kill mammals nearly its own size (Wright et al. 1997). With the exception of the fossa, the percentile relationships listed in Table 6.3 are similar for small carnivores and raptors.

Felids, as a group, tend to have higher body weights than their primate prey (Fig.6.3b). I combined canid and hyaenid body weights due to similarities in ecological niche and social behavior, although taxonomically hyenas are more closely related to

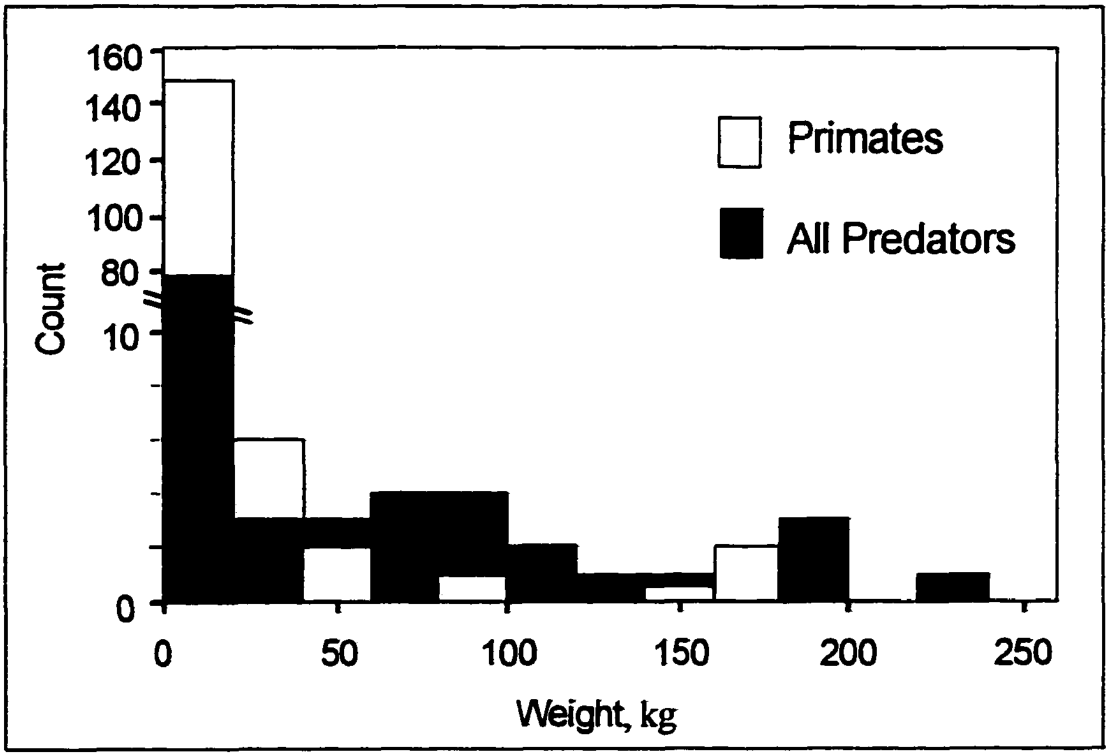


Fig.6.1. Distribution by weight of all primates and all animals that prey upon them.

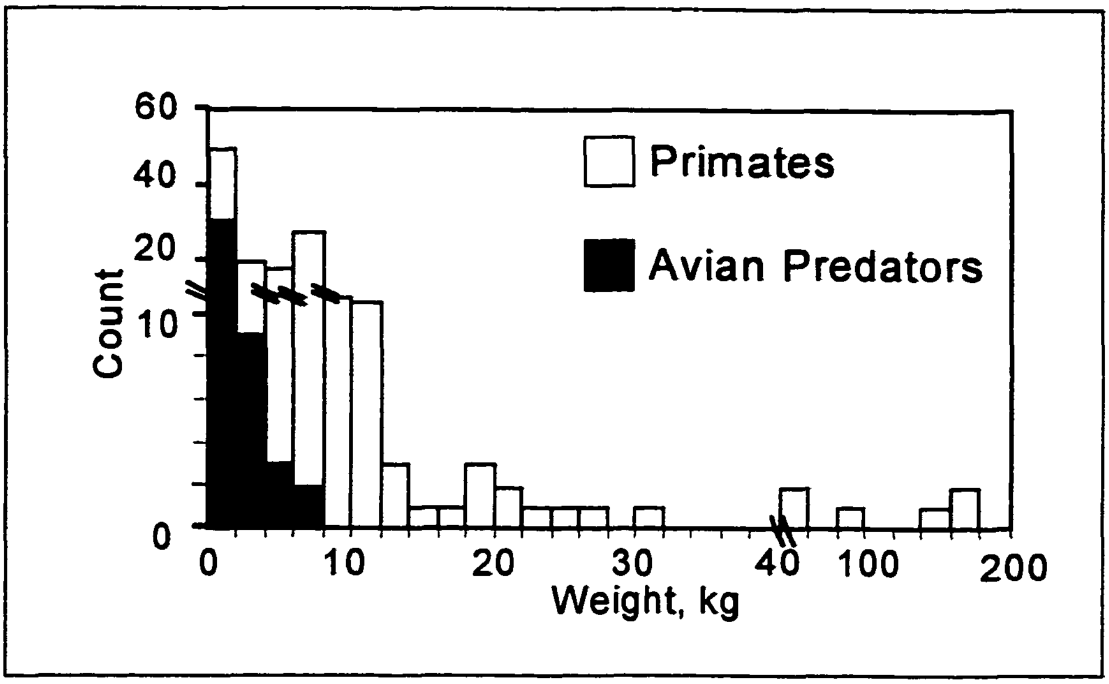


Fig.6.2. Distribution by weight of all primates and birds that prey upon them.

TABLE 6.3. Numbers and percentages of predators weighing more than the 10th, 25th, 50th, 75th, and 90th percentile of primate weights.

PREDATORS	**PRIMATES**				
Percentile ***(Weight)***	**10th** ***(0.30 kg)***	**25th** ***(0.92 kg)***	**50th** ***(5.45 kg)***	**75th** ***(8.98 kg)***	**90th** ***(15.00 kg)***
Raptors	39 (89%)	25 (57%)	2 (5%)	0 (0%)	0 (0%)
Felids	16 (100%)	16 (100%)	15 (94%)	15 (94%)	11 (69%)
Canids/hyaenids	13 (100%)	13 (100%)	12 (92%)	11 (85%)	8 (62%)
Small carnivores	10 (100%)	8 (80%)	2 (20%)	1 (10%)	1 (10%)
Reptiles	16 (100%)	16 (100%)	13 (81%)	12 (75%)	12 (75%)

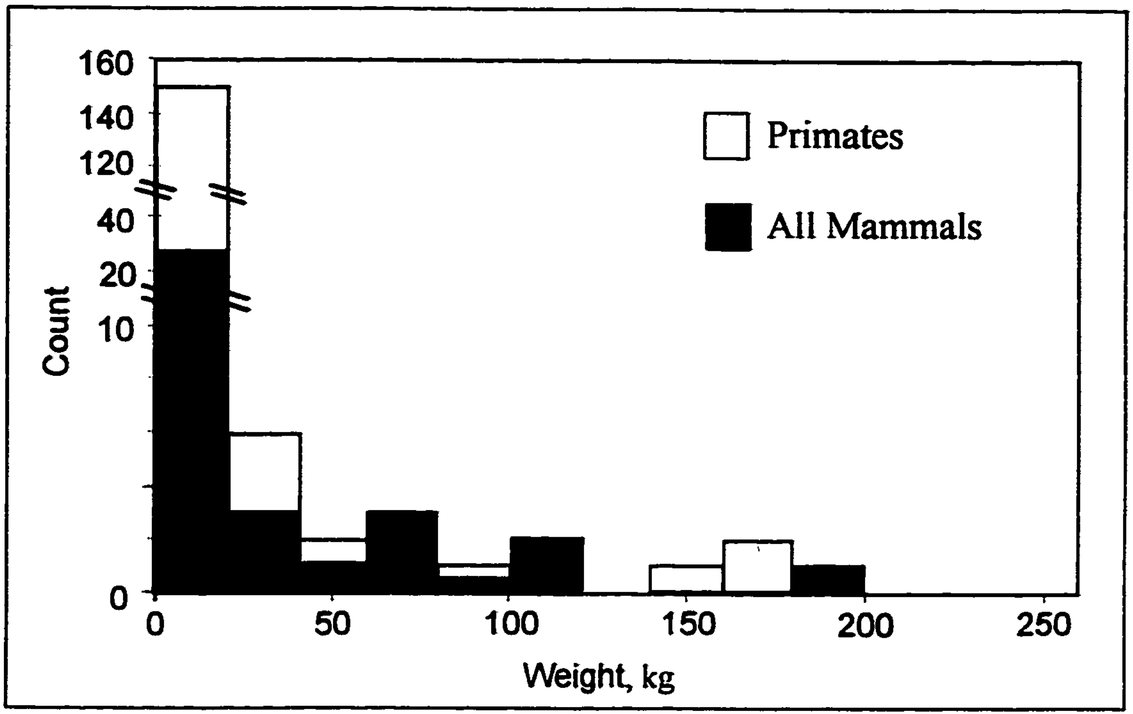


Fig.6.3a. Distribution by weight of all primates and mammals that prey upon them.

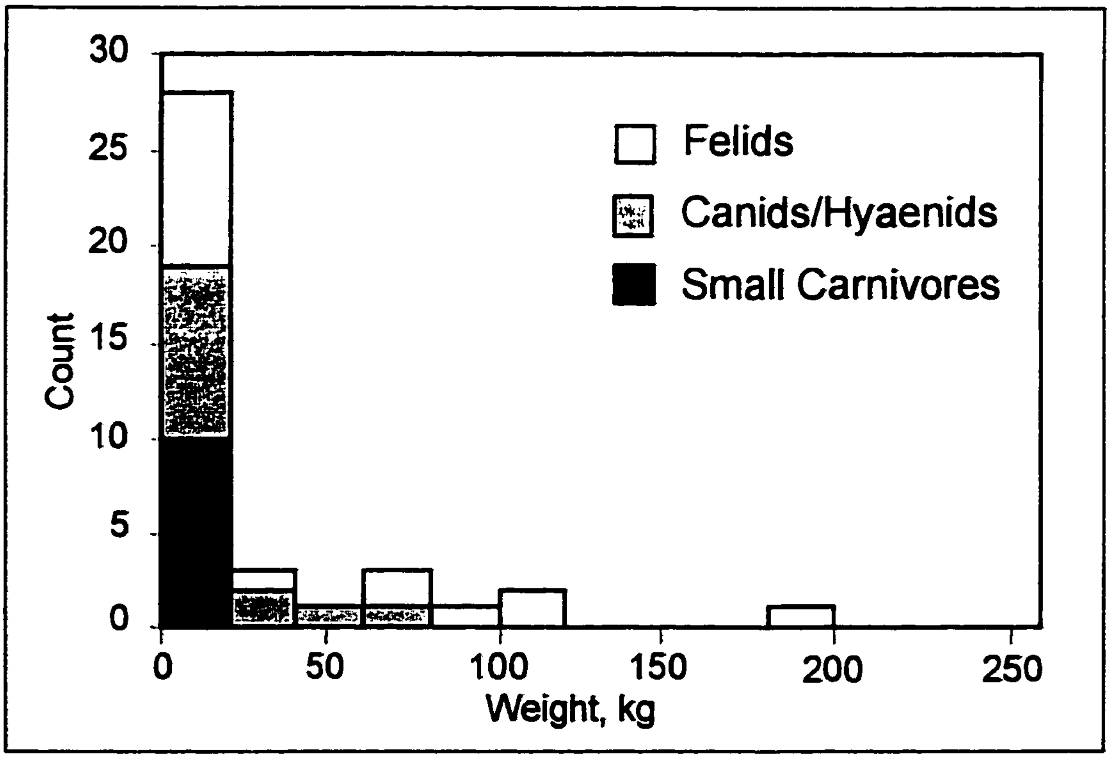


Fig.6.3b. Distribution by weight of mammals that prey upon primates; the counts of three categories of mammals are stacked to show their representation in the general mammalian class.

viverrids (Kruuk 1972a). The distribution of weights for wild dogs and hyenas (Fig.6.3b) is similar to felids, although no species of canid or hyaenid exceeds 100 kg. Table 6.3 indicates that 85% of canid/hyaenid predators are larger than all but the top 10.0% of primates.

The distribution of reptile weights (Figs.6.4a and 6.4b) is also similar to felids in the sense that reptilian predators include extremely large animals. Quantitative summaries presented in Table 6.3 show similar patterns for reptile, felid, and canid/hyaenid weight relationships to primates.

In Fig.6.5, I turn to an analysis of recorded predation events from the questionnaire and literature data sets. Of the five predator categories analyzed, felids have the widest range and highest mean size of primate prey, followed by canids/hyaenids, and reptiles. Raptors and small carnivores had the lowest mean prey weights. Table 6.4 lists the minimum, maximum, and mean sizes of primate prey. All categories of predators took primates under 600 g, but small carnivores had a *maximum* prey size 2.7-3.7 times smaller than canids/hyaenids, raptors, and reptiles, and 15.1 times smaller than felids.

Fig.6.6 deals only with the eleven predator species classified in Chapter V as primate specialists. Again, the only felid in this classification, the leopard (*Panthera pardus*), has the widest range and highest mean size of primate prey. According to these recorded predations, seven of the primate specialists -- six raptors and the fossa -- are limited to primate prey weighing under 8000 g. The crowned eagle (*Stephanoaetus coronatus*) is noteworthy in its unusual ability to take prey many times its own weight.

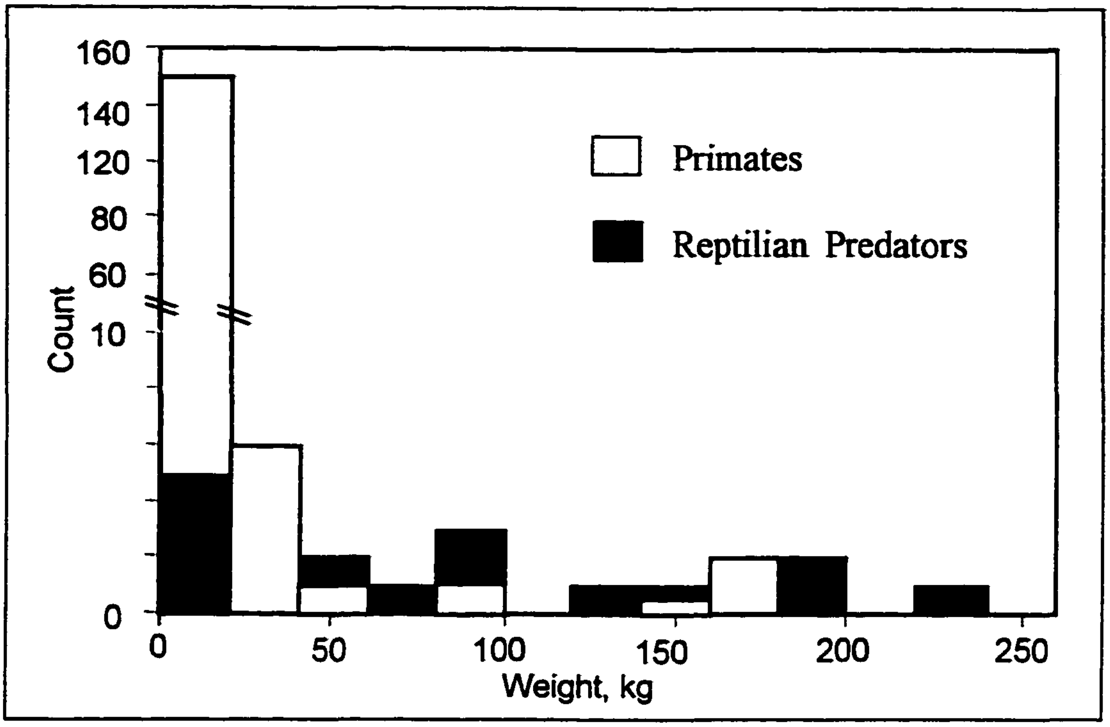


Fig.6.4a. Distribution by weight of all primates and reptiles that prey upon them.

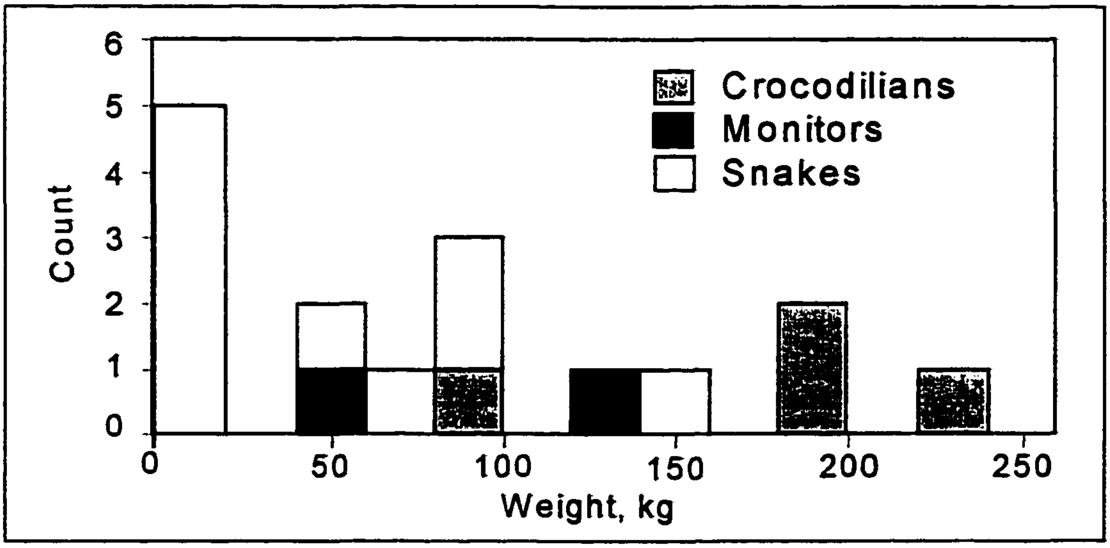


Fig.6.4b. Distribution by weight of reptiles that prey upon primates; the counts of three categories of reptiles are stacked to show their representation in the general reptilian class.

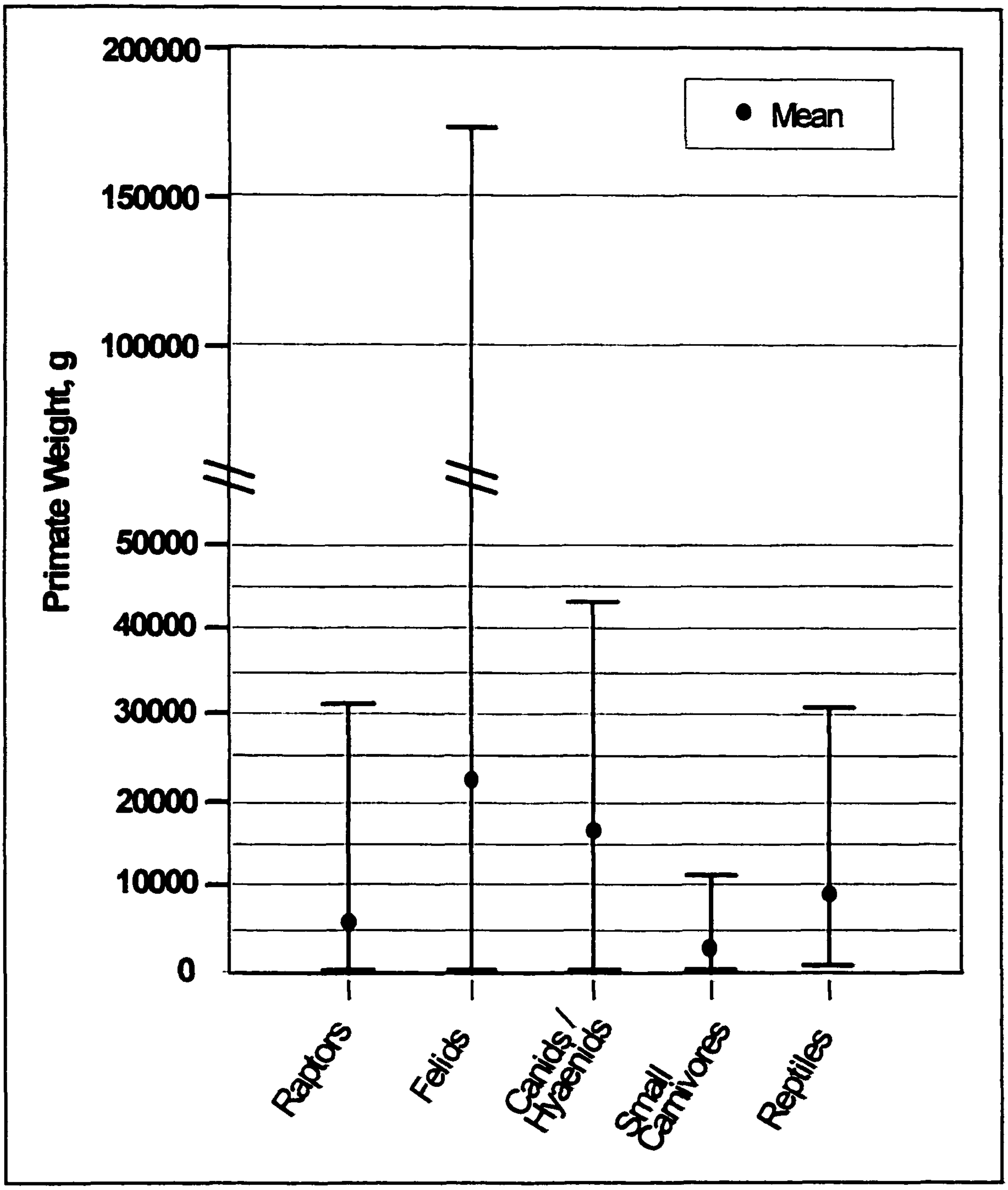


Fig.6.5. Range and mean size of primate prey for five categories of predators.

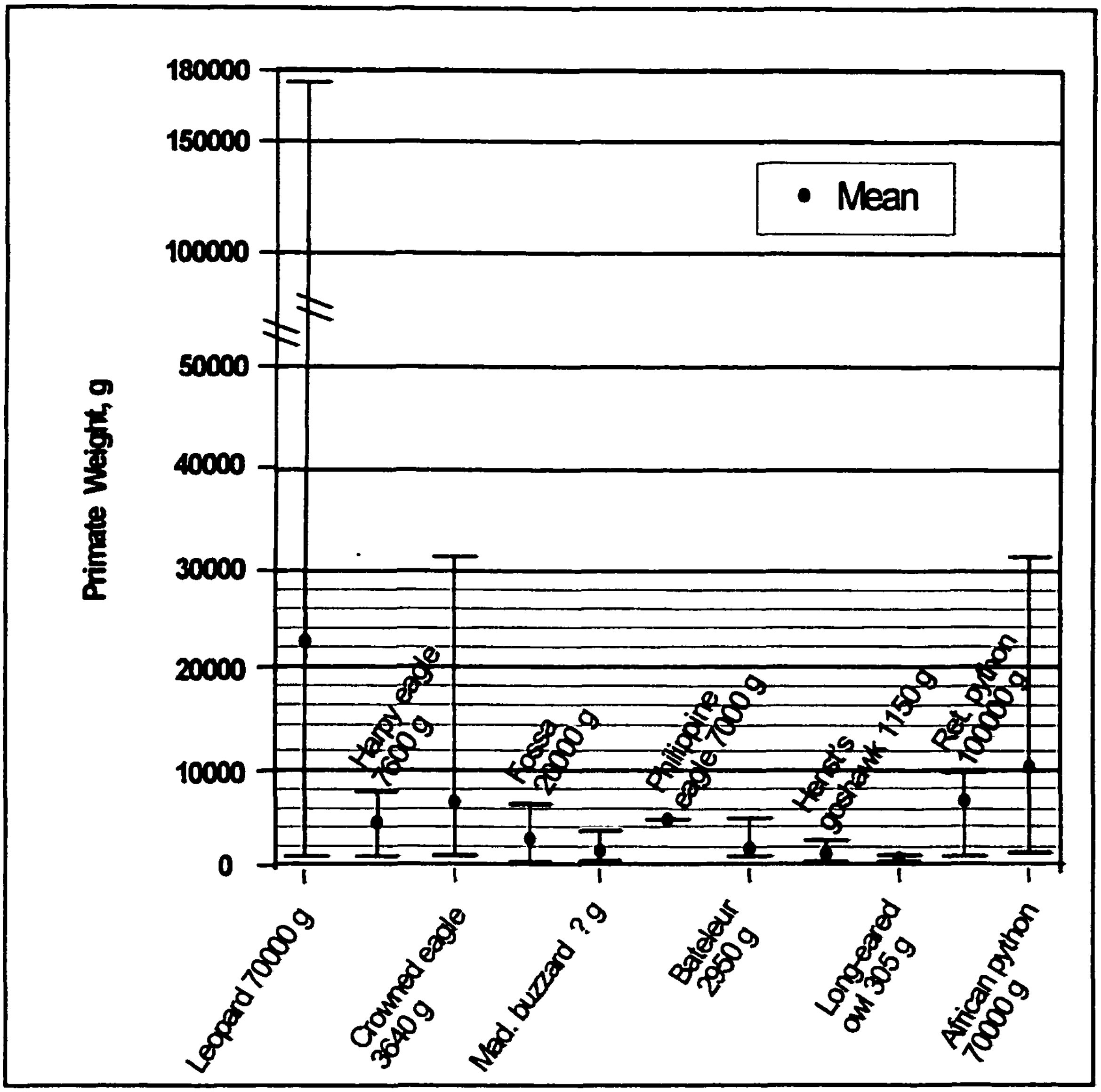


Fig. 6.6. Range and mean size of primate prey for predator species classified as primate specialists.

TABLE 6.4. Range and mean primate prey weights for five categories of predators.

PREDATOR TAXA	MINIMUM WEIGHT OF PRIMATE PREY (g)	MAXIMUM WEIGHT OF PRIMATE PREY (g)	MEAN WEIGHT OF PRIMATE PREY (g)
Raptors	60	31200	5310
Felids	140	175200	22434
Canids/hyaenids	60	43000	16653
Small carnivores	60	11590	2274
Reptiles	580	31200	9170

TABLE 6.5. Range and mean size of primate prey for predator species classified as primate specialists.

PRIMATE SPECIALIST SPECIES	MINIMUM WEIGHT OF PRIMATE PREY (g)	MAXIMUM WEIGHT OF PRIMATE PREY (g)	MEAN WEIGHT OF PRIMATE PREY (g)
Leopard (*Panthera pardus*)	1150	175200	22227
Harpy eagle (*Harpia harpyja*)	960	7880	4193
Crowned eagle (*Stephanoaetus coronatus*)	1150	31200	6445
Fossa (*Cryptoprocta ferox*)	70	6500	2865
Madagascar buzzard (*Buteo brachypterus*)	300	3800	1455
Philippine eagle (*Pithecophaga jefferyi*)	4930	4930	4930
Bateleur (*Terathopius ecaudatus*)	1151	5370	1800
Henst's goshawk (*Accipiter henstii*)	70	2500	1030
Madagascar long-eared owl (*Asio madagascariensis*)	60	1000	256
Reticulated python (*Python reticulatus*)	920	9988	6470
African python (*Python sebae*)	1380	31200	10069

The reticulated python (*Python reticulatus*) is the largest of the primate specialists, weighing 100000 g, but the maximum recorded prey size taken is considerably below the crowned eagle, African python (*P. sebae*), and the leopard. Table 6.5 provides the ranges and means of primate weights taken by individual species of primate specialists.

Fig.6.7, a regression analysis showing the relationship between the weights of all recorded primate prey and their predators, illustrates the low predictability between predator weight and primate prey weight (r^2=0.1356, f=0). Low predictability is supported by Figs.6.8-6.12, regression analyses for five categories of predators and their primate prey. Predator weight is not a good predictor of primate weight for raptors (r^2=0.1721, f=0), felids (r^2=0.0008, f=0), canids/hyaenids (r^2=0.3546, f=0), small carnivores (r^2=0.0875, f=0), or reptiles (r^2=0.2326, f=0).

DISCUSSION

Habitat is a critical consideration for this discussion of body weights in primates and their predators. One theory contends that terrestrial primates are more subject to predation than arboreal species because not only are terrestrial species at risk from raptors, snakes, arboreal carnivores, and large terrestrial carnivores, but that they are also far from trees where they might run for safety (Crook and Gartlan 1966, Dunbar 1988). This theory has been challenged because (a) arboreal primates seem to be more vulnerable to raptors, but less vulnerable to carnivores, than terrestrial species (Cheney and Wrangham 1987), and (b) the vulnerability of small, arboreal primates is exacerbated

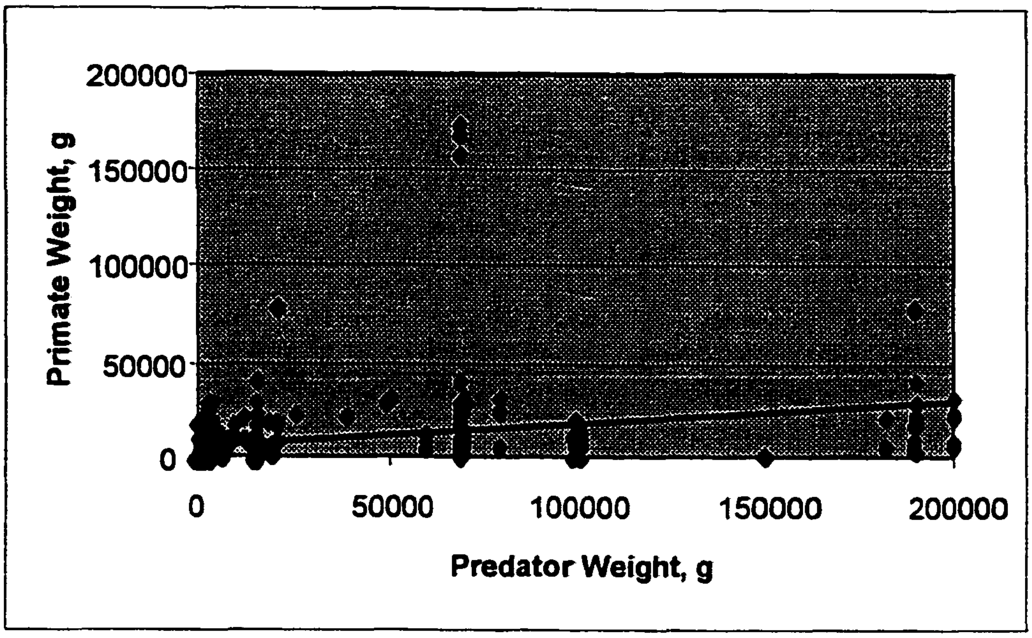


Fig.6.7. Regression line shows straight line fit between primate prey weights and all predator weights for recorded predation events (n=1858) (r^2=0.1356).

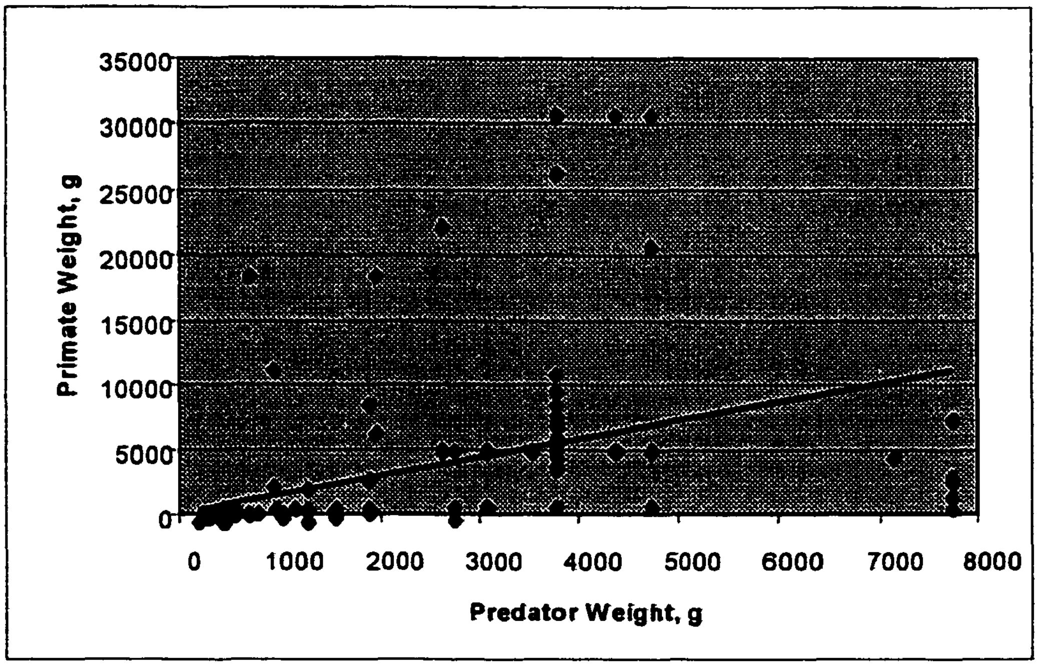


Fig.6.8. Regression line shows straight line fit between primate prey weights and raptor weights for recorded predation events (n=832) (r^2=0.1721).

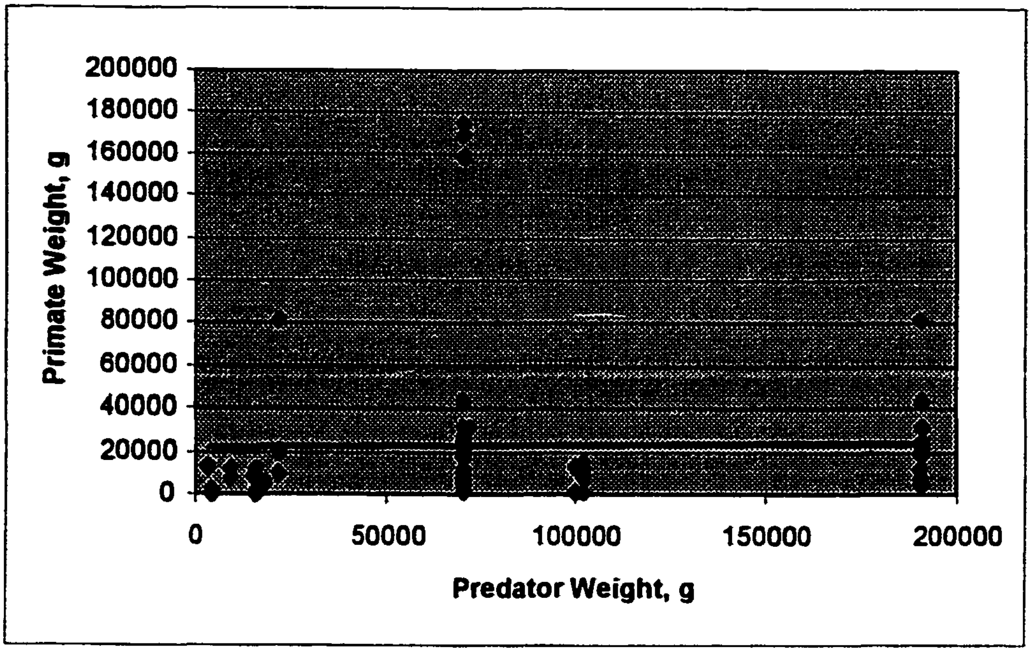


Fig.6.9. Regression line shows straight line fit between primate prey weights and felid weights for recorded predation events (n=737) (r^2=0.0008).

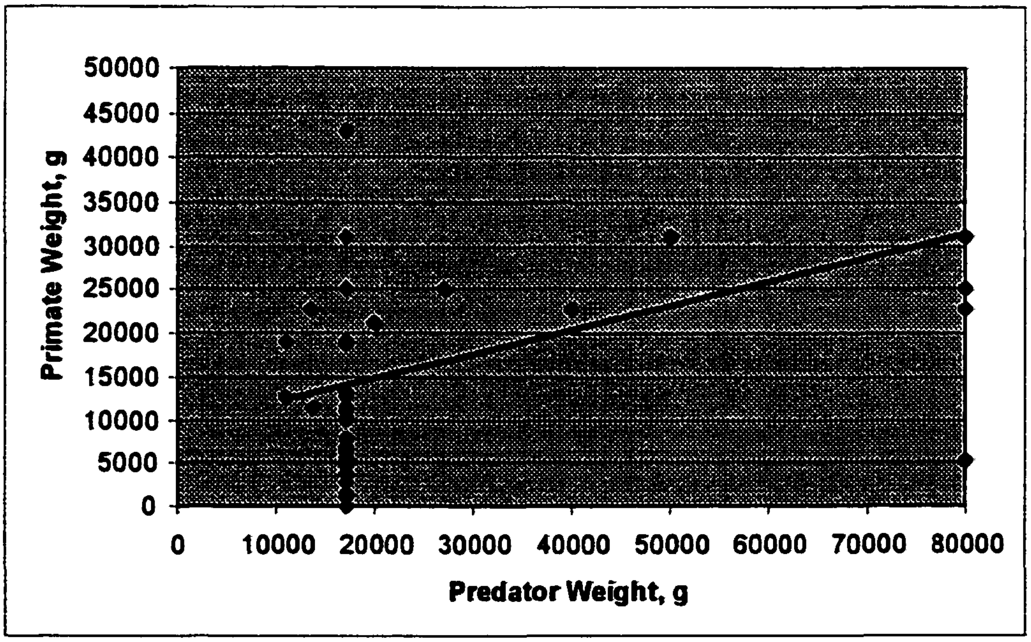


Fig.6.10. Regression line shows straight line fit between primate prey weights and canid/hyaenid weights for recorded predation events (n=126) (r^2=0.3546).

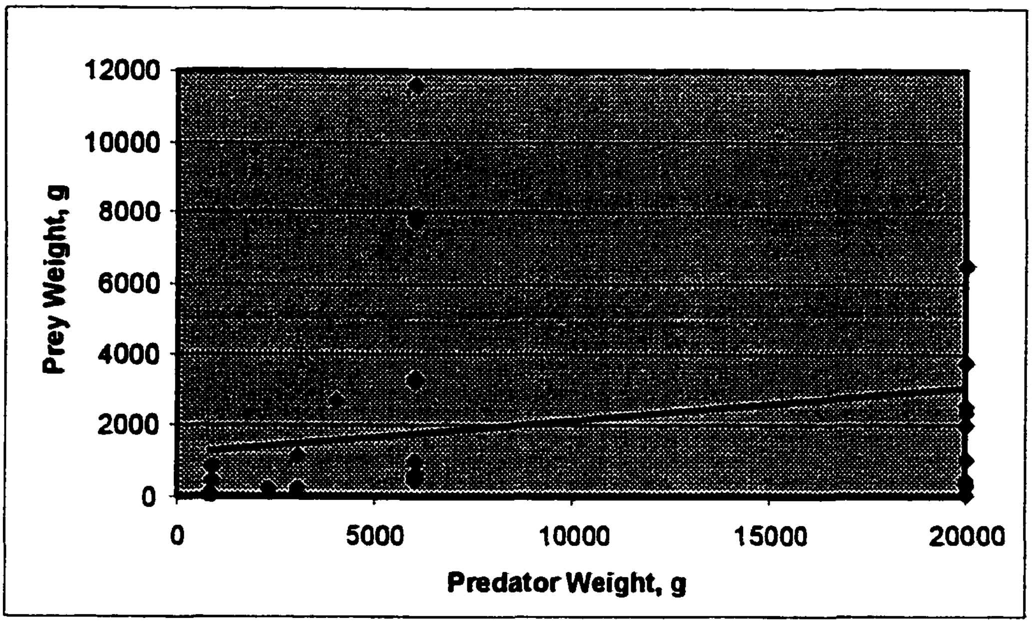


Fig.6.11. Regression line shows straight line fit between primate prey weights and small carnivore weights for recorded predation events (n=93) (r^2=0.0875).

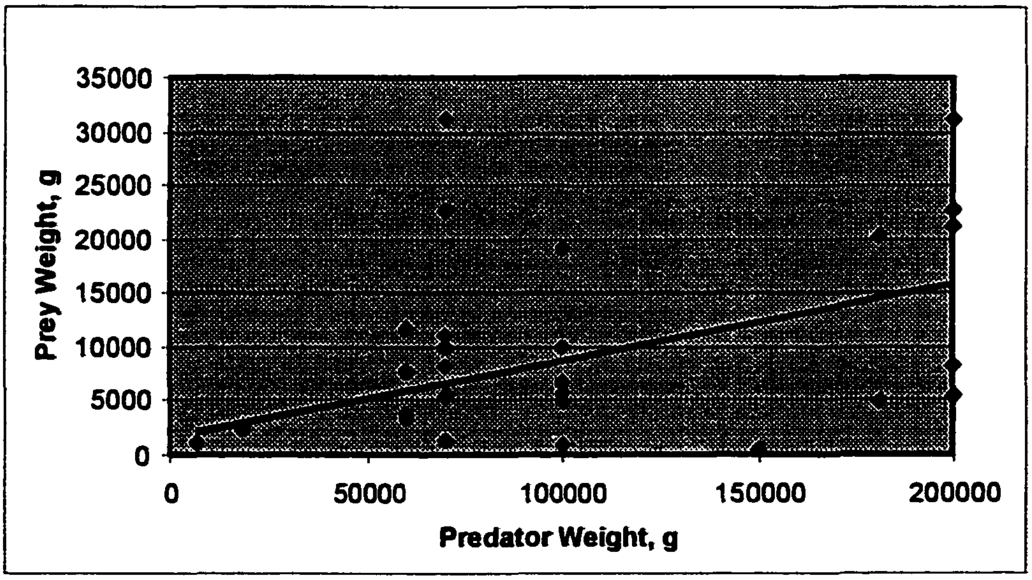


Fig.6.12. Regression line shows straight line fit between primate prey weights and reptile weights for recorded predation events (n=70) (r^2=0.2326).

due to greater densities of small predators in comparison to large predators which may underestimate the intensity of predation on arboreal primates (Isbell 1994a).

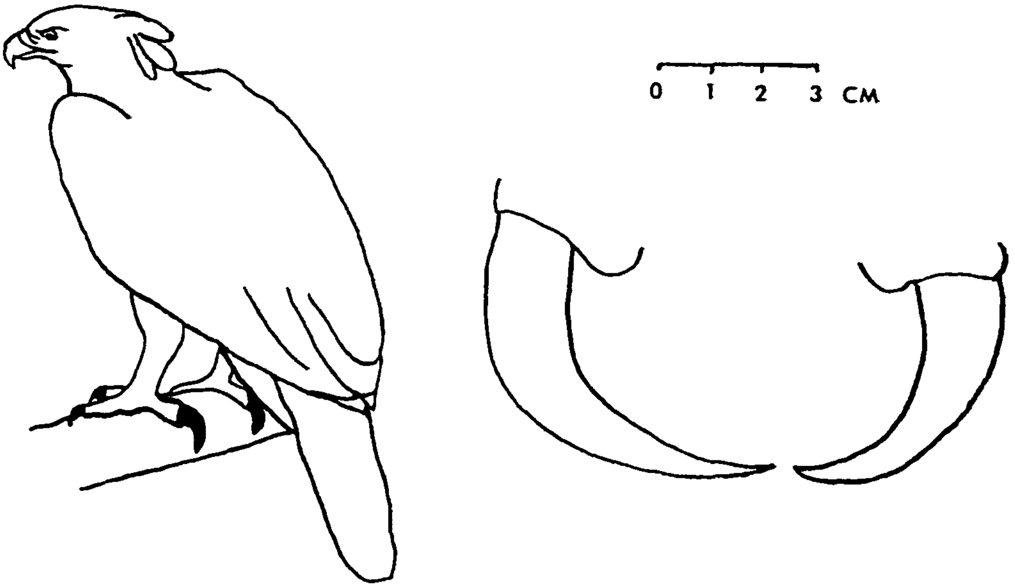
Nonetheless, arboreality has been hypothesized to confer some protection from predation because all primates (with the exception of gorillas, the largest species) sleep in trees, cliffs, or off the ground in some manner (Busse 1977, Isbell 1994a). Examining the size relationships of primates and predators ranked by arboreal competence suggests that primates can avoid many arboreal predators -- but few terrestrial predators -- by being larger than they are. This statement is underscored by the high maximum prey size of felids in Fig.6.5, which represents predation on two of the largest primate species, e.g., leopard predation on gorillas in the Central African Republic (Fay et al. 1995), leopard predation on chimpanzees in the Tai Forest (Boesch 1991), and lion predation on chimpanzees in the Mahale Mountains (Tsukahara 1993).

Eagles and hawks are the major -- and most competent -- predators on primates worldwide (Dittus 1975, Struhsaker 1975, Charles-Dominique 1977, Rettig 1978, Terborgh 1983, Wright 1985), and most primate species are larger than most raptor species. Many birds of prey are to a large degree "all feathers," efficient killing machines that weigh little and, with very few exceptions, take prey that is half or less the bird's own weight (Brown and Amadon 1989). The crowned eagle is an exception to this rule and kills extremely large prey for a raptor, e.g. adult male colobus monkeys, juvenile mandrills, and juvenile baboons. But, since adult primate weights were used throughout the data analysis, the maximum prey weight (*Papio ursinus*, 31200 g) for crowned eagles in Table 6.5 (and the raptor category in Table 6.4) is no doubt higher than the weight of the actual prey animal.

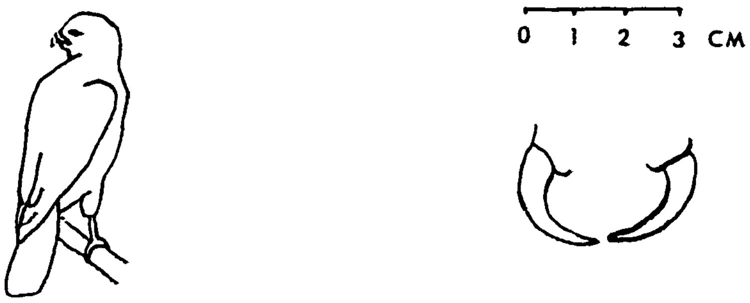
One analysis of raptor predation found that nine primate species weighing less than 2 kg were preyed upon by five confirmed and nine suspected avian predators, while eight primate species weighing over 5 kg had only one confirmed and two suspected raptor predators (Cheney and Wrangham 1987). An analysis of the data collected for this thesis produced compatible results: Twenty-four primate species weighing less than 2 kg were preyed upon by 32 confirmed avian predators, while twenty-four primate species weighing over 5 kg had 15 confirmed and two suspected raptor predators.

While large raptors can kill small prey, small birds of prey do not take large primates (Terborgh 1983). Fig.6.13 compares the relative body and talon sizes of the harpy (*Harpia harpyja*), the largest Neotropical eagle (7600 g), to one of the smaller birds of prey, the grey hawk (*Buteo nitidus*) (460 g). Both species are known predators of primates (Rettig 1978, Boinski 1987), but their "predation potential" (Voous 1969) -- a measure of strength which places raptors in an ecological hierarchy -- is indicated by body size plus talon length and dictates the size of their prey.

Intense predation has been speculated to be the cause of many behavior patterns observed in lion tamarins (*Leontopithecus rosalia*), a callitrichid weighing only 500 g (Coimbro-Filho 1978). Their constant state of alertness, readiness for swift flight, and descent to lower strata in the forest when sensing danger may be indicative of the large number of diurnal raptors that prey on the tamarins. Neotropical hawk species are twice as common as Old World species mainly because of the added small-sized forest falcons of the genus *Micrastur* (Thiollay 1985). Early retirement to night shelters and the small diameter of shelter openings suggest that nocturnal predators, such as the great horned owl (*Bubo virginianus*), also put lion tamarins at risk (Coimbro-Filho 1978).



Female harpy eagle (7600 g)



Female grey hawk (460 g)

Fig.6.13. Comparison of harpy eagle (*Harpia harpyja*) and grey hawk (*Buteo nitidus*) body sizes and talon lengths. (Redrawn after Voous 1969.)

The majority of small carnivores are outweighed by the majority of primate species. Many of the small carnivores, especially the genets, are nocturnal and highly arboreal which allows them access to small canopy-dwelling primates. Like raptors, though, small carnivores are eliminated as predators when primate species reach certain critical weights. The elongated bodies, speed, and maneuverability of many small carnivores make them rapacious predators, but they are constrained when trying to kill animals larger than themselves that are active and capable of defensive movements (Ben-David et al. 1991). For example, the tayra, a fairly large mustelid weighing 6000 g, has been recorded preying only on callitrichids and small cebids weighing between 500-3000 g (Moynihan 1970, Galef et al. 1976, Hernandez-Camacho and Cooper 1976, Izawa 1978, Defler 1980, Ramirez 1989, Stafford and Ferreira 1995).

All snakes are capable tree climbers. However, only the smaller snakes, those about 2 m or less in length, are arboreal predators (Grzimek 1975, Pfeffer 1989). Furthermore, snakes, like raptors, tend to hunt prey significantly smaller than themselves. Snakes are inhibited in their intake of large prey both because they must swallow their prey whole (Shine 1991) and because satiated immobilization may occur after ingestion of animals above a certain ratio to the snake's own weight (Mehrtens 1987). It appears that most primate species are too large to be attractive prey to snake species that hunt arboreally.

While the bulk of their hunting activities are terrestrial, most felids have some arboreal competence. Small openings to lion tamarin night shelters may reflect a risk of predation by scansorial or arboreal Neotropical felids, such as ocelots (*Felis pardalis*), margays (*F. wiedii*), jaguarundis (*F. yagouaroundi*), and oncillas (*F. tigrina*) (Coimbro-

Filho 1978). Size is a less important limiting factor with felids than with predators discussed above, since the maximum size prey many wild cats are able to kill is exponentially related to their own body size (Kruuk 1986, Kitchener 1991). For example, ocelots weigh an average of 15 kg and prey on animals weighing up to 12 kg (Kitchener1991). However, caracals (*F. caracal*) weighing approximately 18 kg, prey on animals twice their own mass (Kitchener 1991), and tigers (*Panthera tigris*) are able to kill animals four times their own weight (Hoogerwerf 1970). Lions (*P. leo*) have the added advantage of social grouping, and the size of prey increases with the number of lions present at the hunt (Kruuk and Turner 1967). Few primate species are larger than felid predators, and even the largest primates are within the size range of felid prey (see Fay et al. 1995).

Canids and hyaenids have terrestrial lifestyles. Most of these predators are larger than the majority of primates. In addition, most canids and hyaenids employ a cooperative hunting strategy, which reduces the protective role of large size in their prey. Even smaller canids, such as golden jackals (*Canis aureus*), use cooperative hunting methods to capture colobines weighing 6000-7000 g (Newton 1985, Stanford 1989, 1990, 1991). Very few primates are protected from canid and hyaenid predation by size alone.

Crocodilians are aquatic in lifestyle, and monitors may be terrestrial, aquatic, or arboreal (Hoogerwerf 1970). Crocodiles cannot pursue prey but must take advantage of prey species' dependence on water. False gharials (*Tomistoma schlegeli)* were observed preying upon crab-eating macaques (*Macaca fascicularis*) and proboscis monkeys (*Nasalis larvatus)* as the primates crossed rivers during foraging (Galdikas and Yeager 1984, Galdikas 1985, Yeager 1991). For crocodilians, there is a direct relationship between the size of the individual crocodile and the size of the prey taken. Over 60.0% of the diet of large crocodiles consists of mammals; mature individuals do not expend energy on very small prey even if it is available (Pooley 1989). Most primate species are within the size range of monitor prey and all are within the size range for crocodilians.

The limits of a predator's ability to kill and consume prey are based on size relationships (Vezina 1985). As a result, the number of predators on primate species should decrease as primate body weight increases. While the number of total predators will decrease, results of data analysis show that size increase may confer protection for primates only within some groups of predators. There is a clear tendency for primate species to be larger than most arboreal predator species, but smaller than most terrestrial predator species.

Eagles and hawks have relatively little variation in body size across the globe, and Old World monkeys may have employed increased body weight as an adaptation to avoid predation from raptors (Wright 1985). When the whole range of arboreal and terrestrial predators are considered, the smaller size of vervet monkeys (*Cercopithecus aethiops*) makes them vulnerable to four times as many predators as baboons (*Papio* spp.) and makes it necessary for vervets to remain close to the safety of trees (Struhsaker 1967b).

Terborgh (1983) discussed size and escape from predation for the Neotropical primates at Cocha Cashu, Peru. He identified three distinct strategies by Neotropical primates to thwart predation: Crypticity, group-living, and escape through an increase in size. The smallest primates under 1500 g spend many hours per day in safe hiding places. Slightly larger species, such as *Cebus* and *Saimiri* seek protection in groups. The latter strategy – size increase -- applies to adults of the largest species (i.e., *Ateles*, *Lagothrix*, and *Alouatta*). These primates are often found at rest in conspicuous exposed perches in the canopy (Terborgh 1983). From such vantage points, the larger primates scan for the largest eagles, harpy and Guiana crested (*Morphnus guianensis*), species in which a few birds are highly dispersed over huge territories. Increased size, combined with group-living and agility may render the larger Neotropical primates very difficult prey even for the harpy eagle (Sherman 1991). Howler monkeys were observed to evade and chase a harpy eagle that attacked one of their group (Eason 1989), but the successful capture of a fully-grown adult male howler by a harpy eagle was witnessed, even though smaller individuals were in the same group and available as prey (Peres 1990). However, it is more common for harpy eagles to prey on medium-sized capuchins (*Cebus apella* and *C. albifrons*), sakis (*Pithecia pithecia, P monachus, P. irrorata,* and *P albicans*), and bearded sakis (*Chiropotes satanas* and *C. albinasus*) (Peres 1990). Medium-sized monkeys in the range of 2000-4000 g constitute regular prey for harpy eagles (Voous 1969).

It is difficult to separate consequence from causation. There are 81 species of diurnal raptors, owls, and other predatory birds known or suspected to prey on primates (cf. Table 2.1). Many of the smaller birds (<1000 g), e.g., toucans (*Ramphastos sulfuratus, R. swainsonii, Andigena hypoglauca*), owls (*Tyto alba affinis, T. a. guatemalae, T. soumagnei, Asio madagascariensis, Athene cunicularia, Otus rutilus*), kites (*Milvus migrans, Haliastur indus, Leptodon cayanensis, Harpagus bidentatus*), cuckoos (*Piaya cayana*), vangas (*Vanga curvirostris*), crows (*Corvus albus, C. macrorhynchos*), small hawks and falcons (*Accipiter bicolor, A. francesii, Polyboroides typus, Leucopternis albicollis, Micrastur mirandollei, M. ruficollis, M. semitorquatus,* *Buteo nitidus, B. magnirostris, Falco newtoni, F. zoniventris, Aviceda madagascariensis, Herpetotheres cachinnans*), and caracaras (*Daptrius americanus, Polyborous plancus*) prey on only the smallest primates (Terborgh 1983, Boinski 1987, Mitchell et al. 1991, Goodman et al. 1993c, and additional sources listed in Appendix 1). A clear consequence of most primate species size is that they are too large to be attractive prey to many of the predators most active in their arboreal habitats.

It appears that the first primates were arboreal and small and that increased size was a later adaptation (Conroy 1990). "Large body size may be seen as an evolutionary response to greater predation risk that has resulted in lower predation rates" (Isbell 1994a, p. 68).

Observations presented here are consistent with the hypothesis that size increase was, at least in part, an evolutionary response to predation. However, it is unlikely that predation is the *sole* explanation for primate species' size increases. Examining Table 6.3 suggests that most of the "gain" (escape from predators through growth) is in the 25th-50th percentile weight range of primates. Below this range, there must be advantages to small size that outweigh greater vulnerability to predation. Above this range, there is little gain in terms of safety from predators, so it seems likely that size increase above this level was driven by different rewards.

SUMMARY

- Most primate species are larger than most of the arboreal predators (birds, small carnivores, and snakes approximately 2 m in length) that prey upon them.

- Most primate species are smaller than most of the terrrestrial predators (felids, canids and hyaenids, large snakes, monitors, and crocodiles) that prey upon them.
- Based on recorded predation events, felids had the highest mean primate prey body weights; raptors and small carnivores had the lowest means.
- Overall, predator weight is not a good predictor of primate prey weight.
- The first primates were arboreal and small. The emergence of larger arboreal primates may have been, in part, an evolutionary response to arboreal predation.
- Reduced predation is unlikely to have been the only reward for increased size; many larger primate species show size increases unlikely to confer increased protection from predation.

CHAPTER VII.

COUNTERING PREDATION: ASPECTS OF PRIMATE BEHAVIOR

"A pride of lions was taking its midday siesta close to a drinking-pool when a troop of baboons was heard approaching. At once the lions lay flat, except two lionesses, which getting up, strolled off into a neighbouring patch of bush, about a hundred yards away. The baboons came on unsuspectingly, and when they were well inside the trap the two lionesses suddenly rushed out, with the effect of sending the whole panic-stricken horde straight into the jaws of the rest of the pride. A complete massacre ensued. The baboons were apparently too terrified even to try to escape up any of the surrounding trees, and hid their faces in their hands while the lions simply struck them down right and left with blows of their paws." (Stevenson-Hamilton 1947, p. 262)

INTRODUCTION

There is basic asymmetry in the evolutionary rate of prey defenses and the predatory mechanisms challenging them. This imbalance is called the "life/dinner" principle: A missed predation attempt saves the life of the prey, but only loses a meal for the predator, so defense mechanisms are more strongly selected for than counter-defenses (Endler 1991).

Anti-predation behavior has been a frequent subject of primate studies, both in the field and in the laboratory. Anti-predation behavior exhibited by individual animals is employed along with adaptive strategies, such as group living, polyspecific associations, and nocturnality, to thwart predators. Morphological characteristics comprise yet another method of defense against predation. A combination of several anti-predator defenses may be necessary for primates undergoing severe predator pressure (Sussman 1999), e.g., the rain forest potto (*Perodicticus potto*) or the savannah patas monkey (*Erythrocebus patas*). The potto is a nocturnal prosimian with a wide array of defense mechanisms including: a scapular shield used in defensive postures, muscular and vascular enhancement of the limbs which allows a strong grip on branches while dealing with predators, a repertoire of behaviors to confuse predators (i.e., dropping to the ground, running a short distance and freezing), slow, cryptic locomotion, and a disagreeable odor (Charles-Dominique 1977). Patas monkeys are renowned for their speed during flight from predators. In addition, they scan for predators bipedally and live a silent, furtive life in small, highly-dispersed groups (Kummer 1971). A conspicuous male stays on the periphery to distract potential predator's attention away from his group of females and young (Hall 1965). Patas give birth diurnally to avoid olfactory cues to nocturnal mammalian predators, and females and infants have cryptic coloration (Chism and Rowell 1988).

A review of recent ethological literature reveals that all predation may be divided into six stages (Endler 1991): encounter, detection, identification, approach, subjugation, and consumption. For each of these stages, prey adapt by developing specific anti-predator defenses.

Primate behavior fits into many of these stages. To cite a small number of examples, alarm vocalizations are a common primate anti-predator strategy to offset the encounter stage of predation (Cheney and Wrangham 1987); crypsis is a typical anti-predator strategy observed in small primates to prevent detection by predators (Charles-Dominique 1974, 1977, Terborgh 1983, Caine 1987); male baboons (*Papio* spp.) employ threat behaviors to foil the approach/attack stage of predation (Altmann and Altmann

1970, Stoltz and Saayman 1970). Chemical defense mechanisms, such as toxins, have also evolved in primates (Alterman 1995). Increase in body size, another morphological adaptation to predation (Terborgh 1983), has been discussed previously in Chapter VI.

Predation is an important source of evolutionary change (Vermeij 1982). The total range of taxa that prey on primates (see Appendix I) cannot be viewed as a single entity or their evolutionary influences as a single phenomenon. Each taxon of predators may have promoted varying types of adaptations. The resulting primate anti-predator defenses are species-specific and geared to compensate for the morphology, behavior, or ecology of their predators.

In this chapter, I discuss the act of predation from the predator's viewpoint, showing correlation between primate anti-predation behaviors observed by field and laboratory researchers and the behavior of the predators that trigger defensive responses.

METHODS

Questionnaires One, Two, and Three, sent to primate researchers, predator researchers, and naturalists/park personnel, contained an inquiry about anti-predation behaviors exhibited by primates in study populations. I provided a nucleus of eight common defense behaviors and asked respondents to list any other behaviors they had observed. A total of 14 anti-predation behaviors emerged from the questionnaires and were entered as data (i.e., scanning, crypsis, mobbing, fleeing to trees or cliffs, alarm vocalization, running on the ground, fleeing through the canopy to the tree trunk, diving to the ground, charge/attack, breaking or dropping branches, chestbeat, defensive posture, strong body odor, and the disruption of ranging/sleeping behavior).

I assessed these behaviors in two ways: (a) the predator taxa which elicited the behavior, and (b) the primate family or subfamily exhibiting the behavior. For the latter, the behavior was divided into percentages directed at specific predator taxa. In addition, I searched the literature for further examples of primate defense strategies. I used Endler's (1991) outline of predation and corresponding anti-predator defenses as a template upon which to correlate primate defense behaviors as they related to predator actions. Anti-predation behaviors from both questionnaires and the literature were grouped by the predator action that had initiated a primate counteraction.

RESULTS

Respondents to questionnaires noted 1036 instances of anti-predation behavior. In Fig.7.1, I give the frequencies of the 14 categories of defense behaviors. Alarm vocalizations were the most frequently-observed defense strategy used by primates (30.7%). This was followed in frequency by scanning (15.7%), mobbing (13.5%), fleeing to trees or cliffs (12.9%), charge/attack against predator (8.3%), crypsis (5.3%), defensive posture (5.2%), running on the ground (5.0%), fleeing through the canopy to the tree trunk (1.4%), breaking or dropping branches (1.4%), diving to the ground from the trees (0.2%), chestbeat (0.1%), strong body odor (0.1%), disruption of ranging and sleeping behavior (0.1%).

In Table 7.1, I have calculated the predator taxa that elicited the 14 anti-predation behaviors. Alarm vocalizations, the most frequently observed behavior, were used as a defense strategy against all five categories of predator taxa -- felids, raptors, canids/hyaenids, small carnivores, and reptiles. This is also the case with scanning,

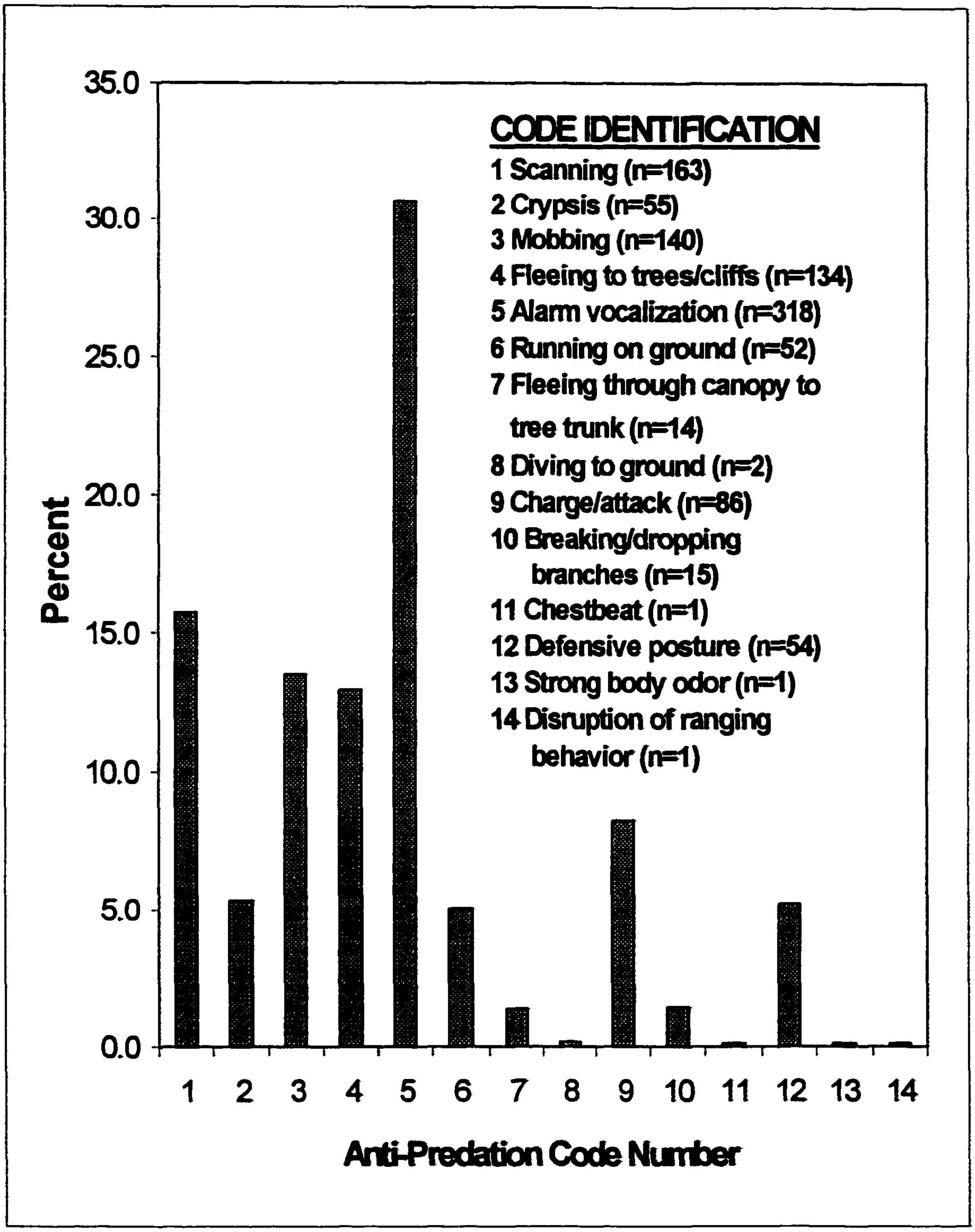


Fig.7.1. Frequencies of anti-predation behaviors.

TABLE 7.1. Primate anti-predator behaviors; percentage directed at predator taxa.

Anti-Predation Behavior	Felids (%)	Raptors (%)	Canids/ Hyaenids (%)	Small Carnivores (%)	Reptiles (%)
Scanning (n=163)	22.1	30.7	27.0	6.1	14.1
Crypsis (n=55)	12.7	45.4	16.4	16.4	9.1
Mobbing (n=140)	35.0	12.9	17.8	13.6	20.7
Fleeing to trees/cliffs (n=134)	28.6	11.6	41.3	8.3	10.5
Alarm vocalization (n=318)	23.9	34.6	20.4	6.9	14.2
Running on ground (n=52)	23.1	7.7	63.5	1.9	3.8
Fleeing through canopy to tree trunk (n=14)	7.1	78.6	--	14.3	--
Diving to ground (n=2)	--	100.0	--	--	--
Charge/attack (n=86)	26.8	26.8	30.2	8.1	8.1
Breaking/ Dropping branches (n=15)	33.4	--	13.3	13.3	40.0
Chestbeat (n=1)	--	--	100.0	--	--
Defensive posture (n=54)	22.2	25.9	29.6	9.3	13.0
Strong body odor (n=1)	100.0	--	--	--	--
Disruption of ranging behavior (n=1)	100.0	--	--	--	--

mobbing, crypsis, fleeing to trees/cliffs, running on the ground, charge/attack, and defensive posture. Other behaviors were directed exclusively at specific categories of predators. For example, diving to the ground from a tree was a reaction directed only at raptors; additionally, more than 78.0% of the time primates fled through the canopy to the tree trunk, it was because raptors were present. Breaking and dropping branches was a behavior directed at terrestrial predators only and was never used to defend against raptors. Three behaviors were specific to gorillas: chestbeat, which was elicited only by canids/hyaenids, and strong body odor and disruption of ranging/sleeping behavior evoked by felids.

Tables 7.2a and 7.2b classify anti-predation behavior observed by questionnaire respondents in two ways: a) the family or subfamily of primates that exhibited the behavior and (b) the predator groups to which the behavior was directed. More data were available for lemurs, callitrichids, cebids, cercopithecines, colobines and pongids than were available for cheirogaleids, indriids, and gibbons. No data on anti-predation behavior was provided by questionnaire respondents for lorisids or tarsiers.

- Cheirogaleidae: These exclusively nocturnal primates used only one of the anti-predation behaviors, alarm vocalization, as a defense against owls.
- Lemuridae: Scanning and alarm vocalizations were the most frequently noted behaviors; these were most often used as a defense against raptors. Raptors were also the most frequent elicitors of crypsis, mobbing, running on the ground, fleeing to trees, fleeing within the canopy, charge/attacks, and defensive postures.
- Indriidae: Raptors and small carnivores were the only predators that elicited defensive behavior. Scanning and charge/attacks were used exclusively against

TABLE 7.2a. Anti-predation behaviors exhibited by primate families, %. (F=felids; Ra=raptors; C/H=canids/hyaenids; Sm C=small carnivores; Re=reptiles.)

Family or Subfamily	Scanning	Crypsis	Mobbing	Fleeing to trees/cliffs	Alarm vocalization	Running on ground	Fleeing through canopy to tree trunk
Cheirogaleidae					(n=1) Ra=100.0		
Lemuridae	(n=15) F= 6.7 Ra= 53.3 C/H= 13.3 Sm C= 26.7	(n=7) Ra= 57.1 Sm C= 42.9	(n=8) F= 12.5 Ra= 25.0 C/H= 37.5 Sm C= 12.5 Re= 12.5	(n=12) F= 8.3 Ra= 50.0 C/H= 16.7 Sm C= 25.0	(n=23) F= 4.3 Ra= 73.9 C/H= 13.0 Sm C= 8.7	(n=1) Ra=100.0	(n=4) Ra=100.0
Indriidae	(n=7) Ra=100.0	(n=5) Ra= 60.0 Sm C= 40.0			(n=11) Ra= 72.7 Sm C= 27.3		(n=2) Ra= 50.0 Sm C= 50.0
Lorisidae							
Tarsiidae							
Callitrichidae	(n=4) Ra=100.0	(n=5) Ra= 80.0 Sm C= 20.0	(n=14) F= 28.6 C/H= 14.3 Sm C= 50.0 Re= 7.1	(n=7) Ra= 14.3 C/H= 28.6 Sm C= 28.6 Re= 28.6	(n=25) F= 4.0 Ra= 60.0 C/H= 12.0 Sm C= 16.0 Re= 8.0	(n=3) Ra= 25.0 C/H= 75.0	

CONTINUED … TABLE 7.2a. Anti-predation behaviors exhibited by primate families, %. (F=felids; Ra=raptors; C/H=canids/hyaenids; Sm C=small carnivores; Re=reptiles.)

Family or Subfamily	Scanning	Crypsis	Mobbing	Fleeing to trees/cliffs	Alarm vocalization	Running on ground	Fleeing through canopy to tree trunk
Cebidae	(n=44) F= 20,5 Ra= 31,8 Sm C= 13,6 Re= 25,0	(n=16) F= 37,5 Ra= 12,5 Sm C= 18,8 Re= 31,2	(n=41) F= 26,8 Ra= 12,2 C/H= 9,8 Sm C= 17,1 Re= 34,1	(n=30) F= 36,7 Ra= 6,7 C/H= 20,0 Sm C= 20,0 Re= 16,7	(n=76) F= 26,3 Ra= 23,7 C/H= 10,5 Sm C= 17,1 Re= 22,4	(n=2) C/H=100,0	(n=5) F= 20,0 Ra= 60,0 Sm C= 20,0
Cercopithecinae	(n=74) F= 31,1 Ra= 17,6 C/H= 39,2 Re= 12,2	(n=20) F= 5,0 Ra= 60,0 C/H= 35,0	(n=57) F= 40,4 Ra= 15,8 C/H= 22,8 Sm C= 5,3 Re= 15,8	(n=69) F= 30,4 Ra= 8,7 C/H= 55,1 Re= 5,8	(n=137) F= 30,7 Ra= 27,8 C/H= 29,2 Re= 12,4	(n=41) F= 29,3 Ra= 4,9 C/H= 61,0 Sm C= 2,4 Re= 2,4	(n=1) Ra=100,0
Colobinae	(n=11) F= 18,1 Ra= 9,1 C/H= 81,8 Re= 9,1	(n=1) C/H=100,0	(n=15) F= 60,0 Ra= 13,3 C/H= 13,3 Sm C= 6,7 Re= 6,7	(n=13) F= 23,1 Ra= 7,7 C/H= 53,8 Re= 15,4	(n=33) F= 27,3 Ra= 30,3 C/H= 30,3 Re= 12,1	(n=4) C/H=100,0	
Hylobatidae	(n=3) Ra= 66,7 Re= 33,3		(n=2) Re=100,0		(n=4) Ra= 50,00 Re= 50,00		(n=2) Ra=100,0

CONTINUED ... TABLE 7.2a. Anti-predation behaviors exhibited by primate families, %. (F=felids; Ra=raptors; C/H=canids/hyaenids; Sm C=small carnivores; Re=reptiles.)

Family or Subfamily	Scanning	Crypsis	Mobbing	Fleeing to trees/cliffs	Alarm vocalization	Running on ground	Fleeing through canopy to tree trunk
Pongidae	(n=3) F= 33.3 C/H= 33.3 Re= 33.3	(n=1) C/H=100.0	(n=2) F= 50.0 Re= 50.0	(n=3) F= 66.7 Re= 33.3	(n=7) F= 42.9 C/H= 14.3 Re= 42.9	(n=1) Re=100.0	

TABLE 7.2b. Anti-predation behaviors exhibited by primate families, %. (F=felids; Ra=raptors; C/H=canids/hyaenids; Sm C=small carnivores; Re=reptiles.)

Family or Subfamily	Diving to ground	Charge/ attack	Breaking/ Dropping branches	Chestbeat	Defensive Posture	Strong body odor	Disruption of ranging behavior
Cheirogaleidae							
Lemuridae		(n=4) Ra=100.0			(n=2) Ra=100.0		
Indriidae		(n=3) Ra=100.0					
Lorisidae							
Tarsiidae							
Callitrichidae		(n=4) Ra= 50.0 C/H= 50.0			(n=3) Ra= 25.0 C/H= 75.0		
Cebidae	(n=2) Ra=100.0	(n=20) F= 40.0 Ra= 5.0 C/H= 5.0 Sm C= 30.0 Re= 20.0	(n=15) F= 33.3 C/H= 13.3 Sm C= 13.3 Re= 40.0		(n=26) F= 26.9 Ra= 15.4 C/H= 15.4 Sm C= 19.2 Re= 23.1		
Cercopithecinae		(n=47) F= 27.7 Ra= 25.5 C/H= 42.6 Sm C= 2.1 Re= 2.1			(n=18) F= 27.8 Ra= 27.8 C/H= 38.9 Re= 5.6		

CONTINUED ... TABLE 7.2b. Anti-predation behaviors exhibited by primate families, %. (F=felids; Ra=raptors; C/H=canids/hyaenids; Sm C=small carnivores; Re=reptiles.)

Family or Subfamily	Diving to ground	Charge/ attack	Breaking/ Dropping branches	Chestbeat	Defensive Posture	Strong body odor	Disruption of ranging behavior
Colobinae		(n=4) Ra= 25.0 C/H= 75.0			(n=5) Ra= 40.0 C/H= 60.0		
Hylobatidae							
Pongidae		(n=3) F= 66.7 Re= 33.3		(n=1) C/H=100.0		(n=1) F=100.0	(n=1) F=100.00

raptors. Crypsis, alarm vocalizations, and fleeing through the canopy were used against both birds of prey and small carnivores.

- Callitrichidae: Tamarins and marmosets reacted to all predator groups, but raptors elicited the majority of scanning, crypsis, and alarm vocalizations. Reactions to domestic dogs included mobbing, fleeing to trees and running on the ground, alarm vocalization, charge/attack, and defensive posture. Encounters with reptiles evoked mobbing, fleeing to trees, and alarm vocalization. Mobbing was the major reaction against felids. Small carnivores -- the tayra (*Eira barbara*), coatis (*Nasua nasua*), raccoons (*Procyon cancrivorus*) – and the Neotropical opossums (*Didelphis marsupialis*) caused the most mobbing incidents, but crypsis, fleeing to trees, and alarm vocalizations were used also.
- Cebidae: Cebids employed a wide range of defensive strategies, but alarm vocalizations were used at least 1.7 times more often than any other anti-predation behavior. Cebids were the only primate family to dive to the ground from trees or break and drop branches as defenses against predators; raptors caused all instances of diving, and felids and reptiles were the animals that most often caused the branch breaking and dropping behavior. Cebids employed charge/attack as a strategy against all predator taxa.
- Cercopithecinae: Cercopithecines reacted to predators twice as often with alarm calls than with any other defensive behavior; alarm vocalizations were given to felids, raptors, and canid/hyaenids at nearly the same frequencies, but less often to reptiles. Small carnivores seldom elicited any anti-predation behaviors. Canid/hyaenids and felids evoked the most scanning, mobbing, runnning on the

ground, charge/attacks, defensive posture, and fleeing to trees or cliffs. Raptors were most often met with crypsis.

- Colobinae: Colobines used alarm vocalizations twice as often as any other form of defensive behavior. Canids and hyaenids were most often the cause of scanning, crypsis, fleeing to trees, running on the ground, charge/attack, and defensive posture. Felids were the predator group most often mobbed by colobines.
- Hylobatidae: Only four of the anti-predation behaviors were employed by gibbons – scanning, mobbing, alarm vocalization, and fleeing through the canopy. Reptiles or raptors elicited all of the observed defensive actions.
- Pongidae: The most frequently observed behavior was alarm calling. Felids evoked two of the three charge/attacks and escape to trees. Scanning was evenly directed toward felids, canid/hyaenids, and reptiles; mobbing was evenly divided between felids and reptiles. Gorillas used three unique behaviors – chestbeat, strong body odor and disruption of ranging behavior.

After analyzing the data from questionnaires, I turned to the literature for additional descriptions of primate defensive behaviors and strategies. In Table 7.3, I identify where, in relation to the predator's action, primate defensive behaviors and strategies are emphasized within the context of Endler's stages of predation and corresponding anti-predator defenses.

Primates interrupt the encounter stage of predatory action with apparent rarity and one-upmanship. The detection stage of predation is countered with crypsis, confusion, and limits to sensory perception. No primate defensive strategies have evolved to counter

TABLE 7.3. The six stages of predation and corresponding anti-predator defenses; primate defense strategies are shown in bold and underlined (after Endler 1991).

1 ENCOUNTER, or get within a distance from which predator can detect prey

- A *Rarity*: reduces the random encounter rate between predator and prey. Rarity makes predator specialization unlikely
- **B *Apparent rarity*: similar effects to rarity, but without the mate-finding and other costs**
  - **(i) Differences between predator and prey in activity times or seasons**
  - **(ii) Hiding or inconspicuous resting places**
  - (iii) Polymorphism
  - (iv) Seasonal changes in color patterns or other signals
- **C *One-upmanship*: greater detection distance of predators by prey than vice versa**

2 DETECTION of prey as objects which are distinct from the background

- **A *Immobility*: for any sensory mode which detects motion; may depend upon seasonal changes in color patterns**
- **B *Crypsis*: reduces signals of prey in predator's sensory field**
- **C *Confusion*: makes detection of a single individual more difficult, or makes it difficult to 'fix' on a single individual for long enough to identify it as edible**
  - **(i) Random or unpredictable movement; may also shift predator's attention to other objects or other prey species**
  - (ii) Movement between contrasting sensory backgrounds
  - (iii) Random or unpredictable sensory effects, especially when enhanced by, and genetically correlated with, color patterns
  - (iv) Extreme abundance: predator saturation; concerted behaviors
  - (v) Polymorphism
- **D *Sensory limits and perception***
  - **(i) Minimum distance for detection of any spot or pattern element**
  - **(ii) Minimum distance for detection of color**
  - (iii) Flicker fusion
  - (iv) 'Private wavelengths'
  - (v) Sealed shells to prevent leakage of chemical cues

3 IDENTIFICATION as profitable or edible prey and decision to attack

- A *Masquerade* (special resemblance to inedible objects)
- B *Confusion*
- C *Aposematism* (conspicuousness associated with distastefulness)

CONTINUED ... TABLE 7.3. The six stages of predation and corresponding anti-predator defenses; primate defense strategies shown in bold and underlined (after Endler 1991).

- D *Mullerian mimicry* (less distasteful species strongly resembling more distasteful species
- E *Batesian mimicry* (palatable species strongly resembling distasteful species
- F *Honest signaling of unprofitability*

4 APPROACH (attack)

- **A *Mode of fleeing***
  - **(i) Speed**
  - **(ii) Sprint to cover**
  - **(iii) Different style than predator (flying, running, swimming)**
- **B *Unpredictable behavior* (same as 2C and 2D above)**
- **C *Rush for cover* or other predator-inaccessible microhabitat**
- **D *Startle, bluffing and threat behavior***
- E *Redirection*
- F *Encouraging premature attack*
- **G *Aggregation and predator saturation***

5 SUBJUGATION (prevent escape)

- **A *Strength to escape***
- **B *Mechanical methods***
  - (i) Physical toughness to withstand handling
  - (ii) Mucus or slime
  - (iii) Autotomy of body parts (e.g. salamander and lizard tails)
  - **(iv) Spines or other structures**
- **C *Noxiousness***
  - (i) Spines and prickles
  - **(ii) Jaws and claws (bite and scratch at predator)**
  - **(iii) Bad tastes, toxins, stings**
- **D *Lethality***
- **E *Group defense, mobbing, etc.***
- F *Resistance to venom*

6 CONSUMPTION

- A *Safe passage through the gut* (e.g. snails & bivalves)
- B *Emetic*
- C *Poisonous*
- D *Lethal*

the identification stage of predation. The approach stage of predation is met with different modes of fleeing, unpredictable behavior, rushing for cover, startling, bluffing, threats, and predator saturation. The subjugation stage of predation is countered with strength, body structures that deter the predator, noxiousness, lethality, and mobbing. Primates have not evolved anti-predator defenses to counter the consumption stage of predation.

DISCUSSION

Predators of primates employ all of the six stages of predation – encounter, detection, identification, approach, subjugation, consumption. Prey have available numerous behaviors, strategies, and adaptations to avoid predation. These are specifically oriented to certain phases of predation; not all anti-predation defenses are appropriate for all of the phases (Vermeij 1982). Primates, as an order, respond by adopting a repertoire of anti-predator defense behaviors to interrupt the process at only four of these stages of predatory activity – encounter, detection, approach, and subjugation.

The encounter stage of predation

At this stage the predator is searching for prey, but no specific prey has been identified. For carnivores, this stage can be initiated by prey stimulus, hunt rhythm (the diurnal or nocturnal activity cycle of the predator), or hunger (Elliot et al. 1977). Many reptilian predators hunt by speculation, wandering around until they come within range of suitable prey (Cloudsley-Thompson 1994). Ocelots (*Felis pardalis*) may travel more than 12 hours without rest looking for prey (Emmons et al.1989). Knowledge of the geography and topography of the environment is crucial for the predator at this stage (Peters and Mech 1975), and an ongoing *strategy* of movement is more efficient for the predator than completely random movement patterns (Krebs 1975). The search stage has been defined as "the reduction of predator-prey distance for prey which has not been specifically located" (Elliot et al. 1977:1813). Success at this stage is dependent on the rate of movement of the predator in relation to the dispersion and rate of movement of the prey (Elliot et al. 1977).

Primate anti-predator defenses at the encounter stage include adaptive strategies such as nocturnality, found in many small prosimians (Charles-Dominique and Petter 1980) and the owl monkey (*Aotus trivirgatus*) (Wright 1982). The timing of births in primate species is also an encounter stage defense. Nocturnal primates tend to give birth during the day in the safety of their sleeping shelters, while diurnal monkeys give birth at night so females are not left behind by their troop and become vulnerable to predators (Jolly 1972). Patas monkeys, however, are an exception and give birth during the day to avoid predation because their group composition and open savannah habitat make them particularly vulnerable at night (Chism et al. 1983). Nine species of carnivores are potential nocturnal predators of patas: lions (*Panthera leo*), leopards (*P. pardus*), caracal (*Felis caracal*), serval (*F. serval*), golden jackal (*Canis aureus*), blackbacked jackal (*C. mesomelas*), side striped jackal (*C. adustus*), spotted hyena (*Crocuta crocuta*), and striped hyena (*Hyaena hyaena*). To counter this array of nocturnal predators, patas have adapted by emphasizing unpredictability, wide dispersal, and concealment in their sleeping patterns; nocturnal births would provide olfactory cues to their location and undermine the other defense strategies (Chism et al. 1983).

Callitrichids are among the primate species with the most adaptations to high levels of predation (Caine 1993, 1998). A complex of behaviors for safe retirement at night, including torpor, careful selection of sleeping sites, entry into nests before dusk, and prolonged vigilance, are adaptations observed by researchers (Moynihan 1970, Coimbra-Filho 1978, Caine 1987, 1993).

Inaccessible nocturnal shelters in the tallest trees, on cliffs, or on sheer rock walls are sought by all species of baboons (Hall 1960, Bert et al. 1967, Anderson 1981b, Byrne 1982). Proboscis monkeys (*Nasalis larvatus*) and crab-eating macaques (*Macaca fascicularis*) select trees growing along river banks for nighttime nests (Fittinghoff and Lindburg 1985, Bismark 1990), while black and white colobus (*Colobus guereza*) were observed to be more tightly clustered in their sleeping trees on nights when visibility was greater (von Hippel 1998). *Aotus*, being nocturnal, prefers sleeping sites in lodge trees with numerous lianas as a screen against diurnal predators (Garcia and Braza 1993). Milne-Edward's sifaka (*Propithecus diadema edwardsi*) day resting sites are positioned lower than feeding sites to avoid avian predation, and night sleeping sites are higher to avoid predation from fossa (*Cryptoprocta ferox*) (Wright 1998). The more vulnerable immatures in Hanuman langur (*Presbytis entellus*) bands avoid the periphery of sleeping trees and huddle close together (Sommer et al. 1998). However, in baboon troops, the young sleep closest to the top of the tree with the strongest adults close to the trunk to prevent leopards from climbing up (Verschuren 1958). This is also the positioning that white-handed gibbons (*Hylobates lar*) take in sleeping trees, with infants using thinner branches and higher sections of the tree (Uhde and Sommer 1998).

It is an advantage to prey to be aware of a predator before the predator is aware of the prey (Edmunds 1974) since early detection of the predator usually means escape of the prey (Bertram 1978). Alarm calls are typically given after a predator has been sighted (Harvey and Greenwood 1978). But, one-upmanship is a delicate balance for prey. While alarm calling enables prey to adjust to the presence of a predator, rather than being caught unaware and forced into panic flight, it also draws attention to the individual sounding the alarm (Edmunds 1974). As highly social species, it is not unexpected that primate alarm vocalizations – often individually disadvantageous, but socially advantageous (Maynard Smith 1965) -- exceed other forms of anti-predation behaviors.

Struhsaker (1967a) identified species-specific alarm calling in vervets that could be divided into distinct sounds associated with aerial and terrestrial predators. A long-term study of vervet monkey (*Cercopithecus aethiops*) vocalizations has been carried out in Amboseli Reserve, Kenya in which learned predator-specific alarm calls for leopards, small carnivores, eagles, snakes, baboons and unfamiliar humans have been identified (Seyfarth and Cheney 1980, 1986, Seyfarth et al. 1980a, Cheney and Seyfarth 1981). Captive Japanese macaques (*Macaca fuscata*) also exhibit specificity in alarm calling (Fedigan 1974). Free-ranging rhesus macaques (*M. mulatta*) on Cayo Santiago responded with alarm calls to the unusual appearance of a raptor, but never gave alarm calls to other large, non-predatory birds (Chapais and Schulman 1980). Neotropical callitrichids (Pola and Snowdon 1975, Moody and Menzel 1976, Vencl 1977, Neyman 1977) and cebids (Norris 1990, Fedigan et al. 1996) also exhibit predator-specific alarm calls. This sophisticated defense mechanism is not limited to anthropoids; Sussman (1977), Sauther (1989), Macedonia (1990a, 1990b), and Pereira and Macedonia (1991) recorded species-specific alarm calls in ringtailed lemurs (*Lemur catta*).

Alarm vocalizations may be given and interpreted interspecifically. Ringtailed lemurs respond to predator alarm calls given by Verreaux's sifakas (*Propithecus verreauxi*) (Oda and Masataka 1996). Vervets respond to the alarm signal of the superb starling (*Spreo superbus*) (Hauser 1988). Redtailed monkeys (*Cercopithecus ascanius*), blue monkeys (*C. mitis*), and red colobus (*Colobus badius*) can distinguish between the calls of potential predators, resource competitors, and non-competitors (Hauser and Wrangham 1990). Recognition of raptor versus other non-predatory bird calls occurs in captive Geoffroy's marmoset (*Callithrix geoffroyi*) (Searcy and Caine 1998).

In the ongoing adaptations between predator and prey, some predators have evolved the capacity to localize alarm calls given by prey species (Harvey and Greenwood 1978). The alarm vocalizations emitted by Kloss's gibbons (*Hylobates klossii*) are wide-frequency, extremely loud, and repetitious, giving rise to speculation that predators can localize the sounds (Tenaza and Tilson 1977).

Scanning, the second most frequent anti-predation behavior, is consistent with a taxon dependent more on visual cues than odors (Richard 1985). Scanning is one of the benefits from group living, since the more detectors, the higher the probability of detecting the predator before it detects its prey (Bertram 1978, Terborgh 1990a).

Vigilance against predators, defined by Treves (1999) as "scanning beyond arm's reach," has been the focus of many primate field studies, particularly centered on the concept of the role it plays in promoting benefits to members of large primate groups and polyspecific associations (Struhsaker 1969, Altmann 1974, Waser and Homewood 1979, van Schaik et al. 1983b, Addicott 1984, Pulliam and Caraco 1984, de Ruiter 1986, Stacey 1986, Gautier-Hion and Tutin 1988, Srikosamatara 1988, Terborgh 1990a, Fleagle 1994, Rose and Fedigan 1995, Gould et al. 1997, Hardie and Buchanan-Smith 1997).

Polyspecific associations are permanent or semi-permanent mixed species groupings of primates, such as red colobus and diana monkeys (*Cercopithecus diana*) (Bshary and Noë 1997b, Noë and Bshary 1997), tamarins (*Saguinus labiatus* and *S. fuscicollis*) (Buchanan-Smith 1990, Hardie and Buchanan-Smith 1997), squirrel monkeys (*Saimiri* spp.) and capuchins (*Cebus* spp.) (Terborgh 1983), African guenons (Gartlan and Struhsaker 1972, Gautier and Gautier-Hion 1983, Gautier-Hion 1988), and guenons, colobus, and mangabeys (Struhsaker 1981).

One of the most vulnerable periods in primate life is the time of dispersal or emigration from the natal group (Hall 1965, Dittus 1975, 1977a, Sugiyama 1976, Harcourt 1978, Cheney and Seyfarth 1983). Since philopatry enhances familiarity with a home range and, therefore, reduces the need to learn about predators in a new territory, it may be selected for as an anti-predation adaptation (Isbell et al. 1990a, 1993, Isbell 1994a).

Troop progressions, the order or form in which groups of baboons travel to maximize the safety of group members, was identified in pioneering field studies as a defensive strategy wherein dominant males protected adult females and infants in the center of the group while subordinate males and juveniles were a first line of defense in the front and back (DeVore and Washburn 1963). This "idealized" order was disputed by other researchers who hypothesized that baboons travel in random order (Altmann 1979).

Still others found systematic positioning of adult males toward the front and back, particularly in potentially dangerous situations, and identified it as an adaptation for terrestrial coexistence with predators (Rhine and Westlund 1981). Although no particular placement of age or gender was noted, chimpanzees (*Pan troglodytes*) formed large parties containing adult males as a defense strategy when traveling through open, non-forested habitat in Senegal (Tutin et al. 1983).

Total avoidance of predators is the ultimate goal in one-upmanship, since it completely interrupts the encounter stage. Rhesus macaques rapidly shifted a distance of 12 km after hearing the roar of a tiger (*Panthera tigris*) (Lindburg 1977). In 33 of 34 observed dangerous situations, hamadryas baboons (*Papio hamadryas*) silently moved away from the danger zone (Sigg 1980). Captive tamarins (*Saguinus labiatus* and *S. oedipus)*) exhibited an innate recognition of fecal scents, showing more avoidance and anxiety toward Neotropical predator scents than control scents (Caine and Weldon 1989, Buchanan-Smith et al. 1993).

Snakes, in particular, have success catching their prey by inconspicuously lying in wait for it to approach (Cloudsley-Thompson 1994). Avoidance of snakes is a well-documented behavior in primates (cf. van Schaik and Mitrasetia 1990, Vitale et al. 1991, Nunes et al. 1998) although primates sometimes approach them out of curiosity (Dittus 1977b). There is support both for theories that this is innate behavior – see, for example, studies on chacma baboons (*Papio ursinus*) (Bolwig 1959), squirrel monkeys (*Saimiri sciureus*) (Masataka 1993), and different species of callitrichids (Ziegler and Heymann 1996) – and the theory that it is learned behavior, e.g., studies on squirrel monkeys

(Osada 1991), macaques (Joslin et al. 1964, Bertrand 1969, Mineka et al. 1980, Cook and Mineka 1990), and lemurs (Bayart and Anhouard 1992).

The detection stage of predation

The detection, or orientation, stage of predation involves a reduction in the distance between the predator and prey, which has been located but which is unaware or minimally alarmed by the predator (Elliot et al. 1977, Caro 1980). For felids, this is the critical stage in predation. Once the prey has been located, if there is any reciprocal detection of the felid predator, the cat will abandon the hunt (Schaller 1972, Bertram 1978). Visual stimuli are the major inputs of sensory information to prey during the process of stalking (Elliot et al. 1977). Mechanisms used by prey at this stage are in the category of *primary* defenses because they go into force before a potential predator launches pursuit or attack (Whitfield 1978). This is a key stage for prey since primary defenses reduce the possibility that prey will need to actively fight off the onslaught of the predator (Kruuk 1986). Predatory mammals usually have post-detection predation success of less than 50% (Vermeij 1982), but snakes have no chance of a successful kill if the prey discovers them at this stage (Owen 1980).

Crypsis, combined with camouflage color patterns, is a common anti-predator strategy that makes detection difficult for predators (Alcock 1993). Crypsis, as a defense mechanism for primates, may be particularly advantageous in dense rain forest environments where detection by predators can be minimized (Wright 1998). Another theory poses that small callitrichids, such as pygmy marmosets (*Cebuella pygmaea*) and cottontop tamarins (*Saguinus geoffroyi*) who are exudate feeders, exhibit the most cryptic pelage coloration because they feed on exposed tree trunks (Ramirez 1989). The coloration of the pygmy marmoset is highly cryptic, as is their propensity for frozen immobility (Moynihan 1976a). These two defense strategies are used by most species of tamarins and marmosets (Sussman and Kinzey 1984) but are also found in Old World monkeys. De Brazza's monkey (*Cercopithecus neglectus*) curls itself into a ball to cover facial and rump markings when perceiving danger and will remain immobile for several hours (Gautier-Hion and Gautier 1978, Wahome et al. 1993).

Confusion of the predator is employed to thwart the detection stage of predation. For example, marmosets huddle together in a large ball at night which may be perceived as one large animal by a predator (Ferrari and Lopes-Ferrari 1990). When tamarins group tightly together, they have been observed to mimic a termite nest (Dawson 1979).

Disruption of ranging and sleeping behavior by western lowland gorillas (*Gorilla g. gorilla*) (C. Olejniczak, pers.comm.) when predators are in the vicinity is an example of unpredictable or random movement to shift the predator's attention away from the primate prey. Slow and silent locomotion, interspersed with immobility, manifests the same strategy in the lorisines (Charles Dominique 1974, 1977).

Protective coloration and pelage patterns that confound the sensory perception of predators are found in the bright golden shade of lion tamarins (*Leontopithecus rosalia*) (Coimbra-Filho and Mittermeier1973), the dull green-gray of the olive colobus (*Colobus verus*) (Noë 1996), and the brown-gray agouti fur of some cercopithecines (Kingdon 1988).

The approach stage of predation

The approach or attack stage of predation actively maximizes the probability of predator-prey contact (Elliot et al. 1977). The predator ignores discovery by the prey at this stage; stealth is used, but there may be follow through even if the prey becomes aware of the predator (Elliot et al. 1977). The exact point of awareness by prey will influence whether the predator takes up a chase, continues it, or gives up (Curio 1976). Carnivores exhibit the most diversification of hunting methods in the approach stage of predation (Kruuk 1986). Felids, canids, hyaenids, and mustelids use a slow and partly concealed approach to their intended prey, their bodies held lower than the normal position (Kruuk 1972b, Lloyd 1980, Pounds 1981, Welch and Bekoff 1982). Felids stalk their prey in elaborate fashion before rushing; crouching over periods of several minutes up to an hour, making considerable use of cover, the stalk is facilitated by feline morphology and camouflaged coloration (Kruuk 1986). For felids, the minimum distance covered in the final charge is strongly correlated with a successful kill (Sunquist and Sunquist 1989). Nile crocodiles (*Crocodylus niloticus*) also exhibit a burst of speed as they attack prey and are capable of chasing prey on land at the speed of 10 km/h (Cloudsley-Thompson 1994).

Patas monkeys employ vigilance and speed as defenses against this stage of predation (Hall 1965). Male patas have an effective defense in their speed, since the predator may give up pursuit when the prey has outdistanced it or does not fall back soon enough (Curio 1976). Rapid escape from predators is also used by bushbabies (*Galago* spp.) (Charles-Dominique 1977) and squirrel monkeys (Terborgh 1983).

Talapoins (*Miopithecus talapoin*) react to the approach of a predator by changing the medium in which pursuit must take place. Talapoin sleeping trees overhang water, and when nocturnal predators enter their trees, individuals closest to the ground drop into the water and swim away (Gautier-Hion and Gautier 1971, Gautier-Hion 1973). Pottos, particularly in encounters with arboreal snakes, will suddenly drop to the ground, run quickly for a short distance and then freeze in order to confuse the predator (Charles-Dominique 1977).

Arboreal agility is the major defense against diurnal predators for cercopithecines (Struhsaker 1967b), lemurs (Albignac 1973), and colobines (Gebo et al. 1994). Fleeing to trees or cliffs, fleeing through the canopy to the tree trunk, and diving to the ground comprised a total of 14.5% of all observed defense behaviors reported by questionnaire respondents. The chief mechanism of defense in langurs is fleeing to trees, causing them to stay close to trees when they are on the ground (Beck and Tuttle 1972, Vogel 1976). Woolly monkeys (*Lagothrix lagotricha*) flee through the canopy to the tree trunk when attacked by Isidor's eagles (*Spizaetus isidori*) (Lehmann 1959). Blue monkeys (*Cercopithecus mitis*) flee to understory trees when crowned eagles (*Stephanoaetus coronatus*) are in the vicinity (Cordeiro 1992). Goeldi's monkeys (*Callimico goeldii*) rush downward and into denser vegetation when they become alarmed (Pook and Pook 1981), as do buffy-headed marmosets (*Callithrix flaviceps*) (Ferrari and Lopes Ferrari 1990) and crowned lemurs (*Lemur coronatus*) (Wilson et al. 1989). Tamarins (*Saguinus mystax* and *S. fuscicollis*) dive downward in trees in reaction to alarming stimuli (Heymann 1990). Pursuit by predators triggered running on the ground in only 5.0% of the anti-predation behaviors observed by questionnaire respondents. Explosive startle reactions followed by flight were evidenced by captive *Cercopithecus ascanius*, *C. diana*, and *C. l'hoesti* when exposed to a fear-inducing event (Macdonald and Pinel 1991).

Assuming a defensive posture comprised 5.2% of all observations of anti-predator behavior by questionnaire respondents. Pottos and angwantibos (*Arctocebus calabarensis*) tuck their heads between their forelimbs in a defensive posture; the potto makes violent thrusts at the predator with its scapular shield and the angwantibo will lift its leg and bite its attacker while in a defensive posture (Charles-Dominique 1977).

Chestbeating, accompanied by screams, are used as warning threats by gorillas (Zahl 1960, Schaller 1963). Calls that mimic sounds of other predators can also be used as a threat against an approaching predator (Klump and Shalter 1984). Many bird species use this tactic when approached at the nest, but other than *Aotus* hooting like an owl (Moynihan 1976b), primates do not seem to employ this defensive strategy.

Aggregation and predator saturation are used to foil the attack stage of predation. Synchronous births in squirrel monkeys (*Saimiri oerstedi*) and guenons may reduce the risk of predation to mothers and their infants by producing a predator-swamping effect (Butynski 1988, Boinski 1989). A saturation effect can also occur during the confusion of flight from a predator. A "flurry of animals" running in every direction makes it difficult for a leopard to catch another baboon if it misses its first intended victim (Altmann and Altmann 1970). An "explosion of prey" as the result of an attack has also been observed in vervets (Struhsaker 1967a).

The subjugation stage of predation

At this stage of predation, contact is made between predator and prey with the intent of immobilizing the prey (Kruuk 1986). *Secondary* defenses, either passive or active, are now employed by prey to increase chances of surviving the assault (Whitfield 1978). Passive secondary defenses in primates can be morphological or chemical. The scapular shield, which is formed from vertebral protuberances, is a morphological defense mechanism that is used by pottos for protection and thrusting attacks when a predator cannot be evaded by other means (Charles-Dominique 1977). Additionally, pottos have unique vascular bundles in their limbs that allow them to maintain a strong grip on branches for long periods during encounters with predators without experiencing muscle fatigue (Suckling et al. 1969). Pottos also exhibit great strength to escape from predators. When attacked in a tree by a carnivore, the potto can topple a predator three times its weight to the ground (Charles-Dominique 1977).

Chemical secondary defenses include the noxious taste and unpleasant odor of tarsiers (*Tarsius* spp.) that serve to inhibit predators (MacKinnon and MacKinnon 1980). Initial research has indicated that chemical signals of toxicity given off by slow loris (*Nycticebus coucang*) may be recognizable to mammalian predators (Alterman 1995). Both pottos and slender loris (*Loris tardigradus*) have a disagreeable odor which may serve as a warning or distraction to predators (Petter and Hladik 1970, Charles-Dominique 1977).

In contrast to secondary defenses of a passive nature, active secondary defenses aim to inflict serious injury on the predator (Whitfield 1978). This last line of defense, termed "protective aggression" is intended to drive the predator completely away or sufficiently interrupt the predation so prey can escape (Archer 1988). Active defenses by primates may be in the general mammalian category, employing teeth or nails and claws – e.g., the angwantibo biting a predator on the nose (Charles-Dominique 1974, 1977) -- or they may be uniquely primate, such as using sticks or branches as weapons.

Approximately 8.0% of the observed anti-predator behaviors from questionnaire respondents were classified as charge/attacks. Male sexual dimorphism, e.g., characteristics such as larger size and canine length, are associated with group defense from predators as well as intrasexual and intertroop competition (Washburn and Hamburg 1968, Crook 1972, Leutenegger and Kelley 1977, Harvey et al. 1978). Adult males will charge and attack raptors (Gonzales 1968, Boggess 1976, Eason 1989, Gautier-Hion and Tutin 1988, Struhsaker and Leakey 1990), felid predators (DeVore and Washburn 1963, Hamburg 1971, Baenninger et al. 1977), canid predators (DeVore and Washburn 1963), and mustelids (Klein 1974). Adult females also act aggressively toward predators, particularly in defense of an infant. For example, most threat and attack behaviors by female baboons involve an infant (Hamburg 1971), and a female indri (*Indri indri*) successfully stopped an attack on her infant by a Madagascar harrier hawk (*Polyboroides radiatus*) (J. Powzyk, pers. comm.). A captive ruffed lemur (*Varecia variegata*) matriarch regularly attacked carnivores that came into the lemur compound (Macedonia 1993). A female chimpanzee being rehabilitated into the wild in Mt. Assirik, Senegal took the lead in charging a leopard that was flushed from cover (Gandini and Baldwin 1978).

Mobbing has been defined as several or all individuals of a group gathering around giving alarm cries, approaching, and even attacking a predator (Bartecki and

Heymann 1987). Snake mobbing has been reported in groups of tamarins (Bartecki and Heymann 1987), langurs (Srivastava 1991), and lemurs (Colquhoun 1993). Mobbing of a leopard by langurs was witnessed (Ross 1993), as well as a tiger being mobbed by gibbons (Uhde and Sommer 1998). Marmosets have mobbed margays (*Felis wiedii*) (Passamani 1995) and capuchins have mobbed tayras (Phillips 1995). Captive marmosets were observed mobbing a dead predator (Chamove 1996).

In a field experiment, wild chimpanzees were presented with a stuffed leopard which they attacked with sticks and small trees (Kortlandt 1967). Chacma baboons threw stones at human observers in conjunction with typical fear and escape behaviors (Hamilton et al. 1975). Breaking off or dropping branches was only observed in members of the family Cebidae by questionnaire respondents, and all aggressive retaliation of this kind was directed at felids and reptiles. Captive capuchins (*Cebus apella*) were found to be capable of aimed throwing of stones (Westergaard and Suomi 1994), and a wild white-faced capuchin (*C. capucinus*) clubbed a venomous snake (*Bothrops asper*) to death (Boinski 1988).

Killing the predator is the ultimate act of defense. Out of eleven aggressive retaliations against leopards by baboons, the leopard was killed in four instances (Turnbull-Kemp 1963, Altmann and Altmann 1970, Saayman 1971, Goodall 1986). Chimpanzees in Mahale attacked a female leopard and killed her cub (Hiraiwa-Hasegawa et al. 1986, Byrne and Byrne 1988), while a single dominant male chacma baboon maimed or killed three or four large dogs when they attacked his troop (Stoltz and Saayman 1970).

SUMMARY

- According to data gathered from questionnaires, alarm vocalizations were used more frequently by primates than other defensive strategies. Alarm calls were used by all primate families and subfamilies for which data were available and were used against all predator taxa.
- Scanning was the second most frequently used defense strategy by primates. The need for vigilance against predators promotes larger group size and polyspecific associations that provide "more eyes" for scanning.
- Basic ethological principles can be used to classify primate anti-predation behavior. Primates incorporate many of the same anti-predator defenses as other vertebrate taxa.
- Using Endler's stages of predation as a template for predator-prey interactions, primates are able to interrupt predation during the encounter, detection, approach, and subjugation stages with evolved anti-predator adaptations.

CHAPTER VIII.

COMPARISON OF PRIMATES TO OTHER PREY SPECIES

> *"It is a well known fact that monkeys in forests live generally in company with deer such as chital, and on the slightest suspicion of danger, specially at the approach of their deadly foe, the leopard, the chital give the warning cry and the monkeys in their turn take up the alarm and jump away from tree to tree to safer quarters."* (Alikhan 1938, pp. 556-557)

INTRODUCTION

An emphasis on research into the social responses used by primates in the face of predation has tended to obscure other avenues of study, such as the similarities between primates and other mammals in their ecological responses to predation (Isbell 1990a). Ungulates (hoofed animals) often serve as models of "typical" prey animals. A removal rate of approximately 9.0-10.0% of the total ungulate population per year is the level of mortality due to predation estimated for African ungulates that have co-evolved with large carnivores (Schaller 1972). Many primate populations also sustain 10.0% or higher predation rates (see Table 4.2).

There may be similarities in the pressure exerted on ungulates and primates by large carnivores. Wildebeest (*Connochaetes taurinus*) and patas monkeys (*Erythrocebus patas*), both terrestrial species that inhabit African savannahs and are prey for large carnivores, have converged in one anti-predation strategy by selectively giving birth diurnally when the likelihood of encountering their nocturnal predators is less (Chism et al. 1983).

Raptors, a major category of primate predators, are limited in their prey choice by size; only the largest eagles can prey on the smaller species of ungulates (Brown 1971a, 1977). Large reptiles, such as pythons and anacondas, frequently capture antelope, forest deer, and wild pigs (Hoogerwerf 1970, Pope 1980, Branch 1991, Nettlebeck 1995, Shine et al. 1998). The only category of primate predator that does not also kill ungulates is the small carnivore.

The overall population numbers of ungulates (particularly gazelles, wildebeest, and zebra of East African savannahs) are much higher than primate species. However, prey species susceptibility to predation cannot be gauged by the total number of animals. A better indicator is the estimated predation rate (the percentage of the prey population killed by predators annually) compared to the recruitment rate (new individuals added by birth to the population).

METHODS

Based on the estimated predation rates (EPR) that I gathered from questionnaires and the scientific literature (see Chapter IV), I calculated the mean EPR for each family or subfamily of primates for which I have data. For the cercopithecines and colobines, I also calculated EPR's by region to compare them to Asian and African ungulates.

I conducted a literature search to find estimated predation rates for ungulate species. The EPR's for primates were based on predation offtake as a percentage of population numbers, but some ungulate estimated predation rates are based on biomass of prey (Tamang 1982, Emmons 1987). Numbers of prey animals are estimated and multiplied by average weights to give the biomass; if the weight of prey eaten by a predator (the offtake) is estimated, calculations can be made concerning the proportion of available prey eaten each year by one or a set of predators (Emmons 1991). If a single average weight of the prey species is used in the calculations, biomass EPR equals population count EPR, making it feasible to compare data from the two methods.

I compared EPR's for individual species or sympatric groups of ungulates with species of primates that inhabit the same biome by calculating the mean EPR for each primate species that inhabited the three biomes for which ungulate data were available.

RESULTS

Estimated predation rates for ungulates were limited and referred only to predation by large carnivores, such as felids, canids, and hyaenids. A tendency in the literature to combine many species of ungulates (as well as other related prey species) together made it impossible to compare individual primate species and individual ungulate species in all cases.

In Table 8.1, the mean estimated predation rates by primate family and subfamily are given, based on the individual EPR's found in Table 4.2. Since estimated predation rates of ungulates often combine many species together as "large prey" of carnivores, I calculated the mean estimated predation rates of whole groups of primates to compare primates and ungulates. Thus, based on the available data, Neotropical primates have a mean estimated predation rate that ranges between 5.8-15.0%; African monkeys range from 4.6-5.6%, and Asian monkeys range from 3.1-3.5%.

TABLE 8.1. Estimated predation rates of primates by family, subfamily, and region.

PRIMATE FAMILIES, SUBFAMILIES, AND GEOGRAPHIC REGIONS	MEAN ESTIMATED PREDATION RATE (%)
Cheirogaleidae	25.0
Indriidae	7.1
Lorisidae	11.8
Callitrichidae	15.0
Cebidae	5.8
Cercopithecinae (African species)	5.6
Cercopithecinae (Asian species)	3.1
Colobinae (African species)	4.6
Colobinae (Asian species)	3.5
Hylobatidae	5.0
Pongidae	5.9

In Table 8.2, I compare the estimated predation rates of ungulates in three biomes – African savannah, Asian moist deciduous forest, and Neotropical rain forest -- to primate species that also inhabit those biomes. Three large herbivorous rodents, the agouti (*Dasyprocta variegata*), paca (*Agouti paca*), and capybara (*Hydrochaeris hydrochaeris*), are included with Neotropical ungulates since they fill the same niche and are preyed upon at the same rates by jaguar (*Panthera onca*) and puma (*Felis concolor*) (Emmons 1987).

Large Serengeti predators combined are estimated to kill 9.0-10.0% of all ungulate prey (Schaller 1972). The mean estimated predation rate is 6.2% for all primate species that live in the same savannah habitat as East African ungulates and for which I have data, viz., vervets (*Cercopithecus aethiops*), patas monkeys (*Erythrocebus patas*),

TABLE 8.2. Comparison of estimated predation rates between ungulates and primates in selected biomes.

BIOME	UNGULATE PREY	PREDATOR	ESTIMATED PREDATION RATE, %	SOURCE	PRIMATE PREY	MEAN ESTIMATED PREDATION RATE, %
African savannah	Wildebeest (*Connochaetes taurinus*)	Lion	2.2-3.3	Schaller 1972	Vervet (*Cercopithecus aethiops*)	9.8
	Wildebeest (*C. taurinus*)	Spotted hyena	1.6-2.6	Kruuk 1972	Patas monkey (*Erythrocebus patas*)	7.5
	Wildebeest (*C. taurinus*)	Spotted hyena	11.1	Kruuk 1972	Chacma baboon (*Papio ursinus*)	7.7
	Zebra (*Equus burchelli*)	Lion	5.9-7.2	Schaller 1972	Olive baboon (*P. anubis*)	1.7
	Zebra (*E. burchelli*)	Spotted hyena	9.4	Kruuk 1972	Yellow baboon (*P. cynocephalus*)	6.4
	Zebra (*E. burchelli*)	Spotted hyena	1.7-2.3	Kruuk 1972		
	Zebra (*E. zebra hartmannae*)	Spotted hyena	2.2	Henschel and Tilson 1988		
	Gazelles (*Gazella grantii, G. thomsonii*)	Spotted hyena	3.4	Kruuk 1972		
	Gazelles (*G. grantii, G. thomsonii*)	Spotted Hyena	2.2-6.5	Kruuk 1972		
	Gemsbok (*Oryx gazella*)	Spotted hyena	14.3	Henschel and Tilson 1988		

CONTINUED ... TABLE 8.2. Comparison of estimated predation rates between ungulates and primates in selected biomes.

BIOME	UNGULATE PREY	PREDATOR	ESTIMATED PREDATION RATE, %	SOURCE	PRIMATE PREY	MEAN ESTIMATED PREDATION RATE, %
Asian moist deciduous forest	Chital (*Axis axis*), hog deer, (*A. porcinus*), sambar (*Cervus unicolor*), barking deer (*Muntiacus muntjak*), wild boar (*Sus scrofa*)	Tiger	8.0-10.0	Sunquist 1981	Hanuman langur (*Presbytis entellus*)	4.0
	Chital (*A. axis*), hog deer (*A. porcinus*), sambar (*C. unicolor*), barking deer (*M. muntjak*), wild boar (*S. scrofa*)	Tiger	7.0	Tamang 1982	Nilgiri langur (*P. johnii*)	3.5
					Crab-eating macaque (*Macaca fascicularis*)	6.5

CONTINUED … TABLE 8.2. Comparison of estimated predation rates between ungulates and primates in selected biomes.

BIOME	UNGULATE PREY	PREDATOR	ESTIMATED PREDATION RATE, %	SOURCE	PRIMATE PREY	MEAN ESTIMATED PREDATION RATE, %
					Rhesus macaque (*M. mulatta*)	2.1
					Bonnet macaque (*M. radiata*)	3.0
					Thibetan macaque (*M. thibetana*)	3.3
Neotropical rain forest (prey includes large rodents)	Peccary (*Tayassu tajacu*), brocket deer (*Mazama americana*), agouti (*Dasyprocta variegata*), paca (*Agouti paca*), capybara (*Hydrochaeris hydrochaeris*)	Jaguar, puma	8.0	Emmons 1987	Saddle-back Tamarin (*Saguinus fuscicollis*)	15.0

CONTINUED … TABLE 8.2. Comparison of estimated predation rates between ungulates and primates in selected biomes.

BIOME	UNGULATE PREY	PREDATOR	ESTIMATED PREDATION RATE, %	SOURCE	PRIMATE PREY	MEAN ESTIMATED PREDATION RATE, %
					Emperor tamarin (*S. imperator*)	15.0
					Squirrel monkey (*Saimiri boliviensis*)	1.0
					Squirrel monkey (*S. oerstedii*)	5.7
					Squirrel monkey (*S. sciureus*)	2.5
					Red howler (*Alouatta seniculus*)	0.5
					Tufted capuchin (*Cebus Apella*)	14.0
					White-throated capuchin (*C. Capucinus*)	10.0
					Wedge-capped capuchin (*C. Nigrivittatus*)	3.0

CONTINUED … TABLE 8.2. Comparison of estimated predation rates between ungulates and primates in selected biomes.

BIOME	UNGULATE PREY	PREDATOR	ESTIMATED PREDATION RATE, %	SOURCE	PRIMATE PREY	MEAN ESTIMATED PREDATION RATE, %
					Woolly monkey (*Lagothrix lagotricha*)	3.0

and baboons (*Papio* spp.). Primates have an EPR that is 2.8-3.8% less than the ungulate population; however, when individual species in a specific location are compared, the difference between ungulate and primate predation rates is minimal. For example, lions (*Panthera leo*) in the Serengeti take approximately 5.9-7.2% of the zebra (*Equus burchelli*) population per year (Schaller 1972) and spotted hyenas (*Crocuta crocuta*) take 1.7-2.3% (Kruuk 1972a), for a total EPR of 7.6-9.5%. Vervets, patas monkeys, and yellow baboons (all indigenous to the same area of East Africa) have mean EPR's of 9.8%, 7.5%, and 6.4% respectively.

EPR's for ungulates vary by geographic location. Spotted hyenas in Ngorongoro Crater kill 11.1% of the wildebeest population, 9.4% of the zebra population, and 3.4% of the estimated population of all species of gazelle (Kruuk 1972a). In the Serengeti, spotted hyenas ate lower proportions of their main prey species – 1.6-2.6% of the adult wildebeest, 1.7-2.3% of zebra, and 2.2-6.5% of all gazelle species combined (Kruuk 1972a).

Tigers (*Panthera tigris*) kill 7.0-10.0% of the standing crop of prey per year (Sunquist 1981, Tamang 1982). The Asian primates that coexist with tigers -- Hanuman langurs (*Presbytis entellus*), Nilgiri langurs (*P. johnii*), crab-eating macaques (*Macaca fascicularis*), rhesus macaques (*M. mulatta*), bonnet macaques (*M. radiata*), and thibetan macaques (*M. thibetana*) -- have an overall mean estimated predation rate of 3.9%. EPR's for individual species in this group of primates range between 2.1-6.5%.

Pumas and jaguars at Cocha Cashu, Peru remove an estimated 8% of large terrestrial mammalian prey each year (Emmons 1987). Primates living in ecosystems containing pumas and jaguars have an overall mean estimated predation rate of 7.2%.

EPR's for individual genera or species in this group are: tamarins (*Saguinus* spp.), mean EPR=15.0%; titi monkeys (*Callicebus moloch*), mean EPR=4.5%; squirrel monkeys (*Saimiri* spp.), mean EPR=3.7%; howler monkeys (*Alouatta seniculus*), mean EPR=0.5%; capuchins (*Cebus* spp.), mean EPR=10.3%; woolly monkeys (*Lagothrix lagotricha*), mean EPR=3.0%.

DISCUSSION

For ungulates, the general pattern of predation is similar over many species (Hirst 1969). Juveniles and subadults bear the brunt of predation, animals in their prime, i.e., early adulthood, have the highest resistance, and remaining classes have a uniform degree of susceptibility (Hirst 1969). The similarity of the predation rates by large carnivores (between 7.0-10.0%) across species and geographic areas may reflect a limiting equilibrium state for large predators and their large prey (Emmons 1987).

Precise comparison is not possible between estimated predation rates of ungulates and primates because the variables in the predator base (number of predator species that were integrated into calculation of the EPR) are not consistent. In Table 8.2, the predation rate of 8.0% on Neotropical deer, peccaries, and large rodents is due to jaguars and pumas (Emmons 1987). Jaguars and puma prey on Neotropical cebids (Schaller 1983, Emmons 1987, Peetz et al. 1992, Olmos 1994, Jorgenson and Redford 1995) and ocelots (*Felis pardalis*) prey on callitrichids (Emmons 1987, Goldizen 1987). The EPR's for the primate species in Table 8.2 in that biome, however, represent predation by raptors or an unidentified predator base. Some primate species used in the comparison in Table 8.2, such as vervets, are preyed upon by large carnivores, raptors and reptiles. One vervet EPR represented predation sustained from four predator species, while another EPR represented predation from only two predator species (Cheney and Wrangham 1987). Any comparisons between primate and ungulate estimated predation rates can only be viewed in the most general terms; nevertheless, Neotropical primates and East African terrestrial primates have similar predation rates to ungulates in the same biomes.

The hyrax (*Procavia capensis*) is an African prey species that is more equivalent in size to many primates than are ungulates. Hyrax weigh approximately 4 kg and are heavily preyed upon by some of the same predators as primates, e.g., crowned eagles (*Stephanoaetus coronatus*), Verreaux's eagles (*Aquila verreauxii*), and leopards (*Panthera pardus*) (Brown 1955, 1966, Gargett 1971, 1990, Brain 1981). A study in Zimbabwe calculated that Verreaux's eagles would take 3.0-6.0% of the hyrax population annually in the Matopo Hills, and with mortality from leopards and other predators factored in, the overall predation rate on hyrax would be under 10.0% (Gargett 1990). This is a comparable figure to the vervet, patas monkeys, and baboon EPR's that range from 6.4-9.8%.

An alternative way of comparing primates to other prey species is to identify in what circumstances predators feed primarily on primates. Such a study was undertaken to identify the environmental correlates where primates comprise a major portion of large felid diets in South Asian habitats (Seidensticker 1983, 1985, 1991) with the following results: If there were abundant ungulate species in the <50 kg range, leopards ate fewer primates. If ungulates in this size class were present but at low density, leopards had intermediate numbers of primates 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: a) tigers and leopards switched to primate prey in the absence of ungulates at Meru-Betiri Park, Indonesia (Seidensticker and Suyono 1980); b) in the Periyar Tiger Reserve, India where the Nilgiri langur comprises 81.4% of the leopard diet, a small ungulate, the Nilgiri tahr (*Hemitragus hylocrius*), occurs only in isolated pockets (Srivastava et al. 1996); c) at another site in India, Eravikulam National Park, tahr, sambar (*Cervus unicolor*), and barking deer (*Muntiacus muntjak*) were common and formed 77.0% of the leopard diet while primates, porcupines, rodents, reptiles, and insects constituted the remainder (Rice 1986); d) unlike East Africa, Niokolo-Koba National Park in Senegal does not have dense concentrations of ungulates, and Guinea baboons (*Papio papio*) are the commonest large mammal (Byrne 1982). A high risk of predation from relatively dense concentrations of both diurnal (African hunting dog *Lycaon pictus*) and nocturnal predators (leopard, lion, and spotted hyena) was inferred from alarm vocalizations, unusually large groups, extreme wariness of open spaces, and a paucity of secure sleeping sites (Byrne 1982).

SUMMARY

- As wholly terrestrial species, ungulates are preyed upon most commonly by large carnivores. Although raptors and reptiles also prey on ungulates (especially their young), ungulates do not have as wide a range of predators as primates.
- There may be a limiting equilibrium for large predators and their large ungulate prey. Seven to ten percent removal rate per year by predators has been estimated for East African grasslands, South Asian deciduous forests, and Neotropical rain forests.

- A comparison of ungulates and primates sharing three biomes found some primate EPR's were comparable to some groups of ungulates, but several variables in data collection and computation make comparisons imprecise.
- Leopards switch to primates as major prey if ungulates <50 kg are missing from the ecosystem.
- It is probable that primates have similar levels of predation-induced mortality as other prey animals, although sparse data currently make it impossible to confirm this.

CHAPTER IX.

CONCLUSIONS

"In 1909 I met a farmer at Harrismith in the Transvaal who had a pair of Verreaux's [eagles] *resident on his estate. He told me they lived almost entirely on hyrax, an occasional young rhebok and many young baboons; they never raided his poultry or lambs, and in return for keeping the baboon in check he never molested the eagles."* (Meinertzhagen 1959, p. 117)

In this thesis, I have collected and analyzed the data currently available on predation of primates. To summarize:

- 81 species of diurnal raptors, owls, and other birds, 35 large carnivores, 22 species in five families of small carnivores, 36 species of reptiles, and two species of sharks are known or suspected to prey on primates. Primates sustain levels of predation that designate them as a resource base for certain species of predators.
- Eyewitness accounts of predation were documented throughout the range of extant primate species -- Africa, Madagascar, Asia and the Neotropics. Observed predation events are published for ten non-human primate families; the subfamily Cercopithecinae accounts for the highest percentage of observed predations.
- No region, weight, activity cycle, or stratum could be identified in which primates were free of predation.
- Estimated typical predation rates on primates varied from 0-25.0%. Limited evidence points to small, nocturnal, arboreal primates having higher predation

rates than larger, diurnal, or terrestrial species. The frequency of occurrence of primates in the diets of predators ranges from 0.03-87.9%; raptors and felids have the highest percentages of primates in their diets.

- Eleven primate specialists could be determined based on the level of recorded predations as a function of the median percentage of primates in the predator's diet. I tentatively identified leopards (*Panthera pardus*), harpy eagles (*Harpia harpyja*), crowned eagles (*Stephanoaetus coronatus*), and fossa (*Cryptoprocta ferox*) as "dedicated" predators on primates based on evidence of significant predation by both quantitative and qualitative measurements.
- Overall, predator weight was not a good predictor of primate prey weight.
- The first primates were arboreal and small, and the emergence of larger arboreal primates may have been an evolutionary response to arboreal predation.
- Primates are able to interrupt predation with anti-predator adaptations during four stages of predatory action -- the encounter, detection, approach, and subjugation stages. Coevolution between primates and predators is inferred based on predator strategies and anti-predator defenses.
- It is probable that primates have similar levels of predation-induced mortality as other prey animals, although sparse data currently make this difficult to confirm.

In addition to the above summary, four cardinal insights, which I discuss below, are suggested by the data:

1) Primates are "generalist" prey

Despite the evidence found to identify certain predators as primate specialists (see Chapter V), I take the position that primates are "generalist" prey in the sense that, as a taxon, they range in size from 60 g to 169 kg, they inhabit geographic ranges throughout the tropics, subtropics, and a few temperate forests, they range from totally arboreal to totally terrestrial, and they include both nocturnal and diurnal species. Their successful radiation into many niches carried with it the potential to interact with many predators. The list of known and potential predators I have identified (see Appendix 1) contains mostly generalist and opportunist feeders. While there are dedicated primate specialists among these species -- viz., crowned eagles, harpy eagles, leopards, and fossa -- there are no examples of predators with a rigidly narrow food base. There are no mammalian predators, for example, comparable in their food selectivity to aardwolves (*Proteles cristatus*) that eat only termites or baleen whales that must strain tiny crustaceans known as krill from sea water (Nowak 1991). There are no birds of prey employing hunting strategies that limit their prey, such as bat falcons (*Falco rufigularis*) and bat hawks (*Machaerhamphus alcinus*) both of which take only flying animals (e.g., bats, swallows, swifts, hummingbirds, insects) on the wing at great speed (Brown and Amadon 1989). There are no reptiles with morphological adaptations that exclude normal-sized prey, such as the African slender-snouted crocodile (*Crocodylus cataphractus*) which is similar to no other member of its genus with its radically modified snout limiting it to a diet of crabs, frogs, and snakes (Ross and Magnusson 1989).

The closest examples of non-generalist feeders that are also primate predators are two genera of eagles, the snake eagles of Africa and Asia, and the African and Malagasy fish eagles. There are three species of snake eagles (*Circaetus cinereus*, *C. gallicus*, and *C. pectoralis*); 70.0-95.0% of their diet is reptiles, although they will hunt and eat mammalian prey (Brown and Amadon 1989). Members of this genus possess long legs covered with rough hexagonal scales believed to be an adaptation to deflect snake bites (Brown 1971a). Toes are short and similarly scaled; talons are also short (Brown and Amadon 1989). African fish eagles (*Haliaeetus vocifer*) and Madagascar fish eagles (*H. vociferoides*) rarely catch or eat mammals (Steyn 1982). Fish, both dead and alive, constitute approximately 90.0% of their diets (Brown and Amadon 1989). The two fish eagle species have long claws with spicules on the pads of their feet for grasping slippery fish (Steyn 1982).

One felid species, the cheetah (*Acinonyx jubatus*), might be considered a non-generalist in comparison to other wild cats that prey on primates. Cheetah differ radically from other cats in both generalized morphology and hunting techniques (Sunquist and Sunquist 1989). Unlike the other members of the family Felidae, their bodies are geared for high-speed pursuit of prey, not stealthy ambush (Eaton 1974, Hamilton 1981). Cheetah prey are smaller in size than prey of felids of comparable weight, and their non-retractile claws make them completely terrestrial (Sunquist and Sunquist 1989). Compared to the other large cats, few records exist of cheetah predation on primates. Two unsuccessful attacks on baboons were reported (Stevenson-Hamilton 1947, DeVore and Washburn 1963), and one successful kill of a chacma baboon (*Papio ursinus*) was recorded in Kruger National Park (Pienaar 1969).

2) Current predation on primates reflects predation on early hominids

Predation on living primates may reflect predation on early hominids (Brain 1981). The first primates were arboreal and small (Conroy 1990); the emergence of larger arboreal primates may have been partly an evolutionary response to arboreal predation by raptors and small carnivores. After the australopithecine transfer to a terrestrial bipedal existence, raptors were virtually eliminated as predators due to size constraints. The large terrestrial carnivores, however, were powerful predators of these hominids. The Sterkfontein, Swartkrans, and Kromdraai caves in South African contain australopithecine and baboon fossils. These fossils are thought to be discarded food remains, and the potential predators that either brought the primates into the caves or preyed on primates sleeping there include leopards, false saber-tooth cats (*Dinofelis* spp.), saber-tooth cats (*Megantereon* spp.), along with hyenas (*Crocuta* and *Hyaena*) and cursorial hunting hyenas (*Euryboas* spp.) (Brain 1981).

When Brain formulated his hypotheses about predators of australopithecines and baboons at Swartkrans, he found it "a remarkable state of affairs" that over 50.0% of all the animals in the Member 1 macrovertebrate assemblages were hominids or cercopithecoids. He questioned why fossil leopards had concentrated so intensively on this kind of prey when studies of contemporary leopards suggested that primates formed only a small part of leopard diets. Other assemblages, where baboons constituted only 3.0% of the remains, conformed more closely to the assumption of low leopard predation on baboons.

Recent data on primate predators have implications on the interpretation of fossil hominid and baboon remains. Three of the four large Old World felids of the genus

Panthera are now known to prey on apes: lions on chimpanzees (Tsukahara 1993), leopards on chimpanzees and gorillas (Boesch 1991, Tutin and Benirschke 1991, Fay et al. 1995), and tigers on orangutans (Rijksen 1978). The frequency of occurrence of primates in leopard diets ranges as high as 81.4% (Srivastava et al. 1996).

Brain (1981) constructed two hypotheses to explain the high percentages of hominid and baboon remains: a) there was an unknown predator that specialized in primates, or b) leopards took advantage of primates that were using the cave as a sleeping refuge. Both of these hypotheses may be correct. However, a third possibility exists that -- particularly if <50 kg ungulates were less available -- leopards were acting as primate specialists in the Pleistocene.

3) Predation rate versus predation risk

Predation rate involves the annual mortality of a certain percentage of a primate population due to predators. Predation risk involves the entire spectrum of compensations primates must make to offset predation. Direct observation by researchers substantiates that predation risk is constant in the daily lives of primates (Terborgh 1983, Dunbar 1988). Predation rates are variable, but, " ... events have a powerful selective effect if the event completely eliminates an individual's genetic contribution to the next generation ... for a dead individual, any [predation] rate above zero is highly significant..." (Anderson 1986a:24).

Terborgh (1983) postulated that predation was, of necessity, a rare event at the level of a whole primate group. He speculated, for example, that a *Cebus apella* troop could not sustain more than one loss to predation per year since the replacement level (i.e., birth rate) is only 1-2 infants per year. Estimated typical predation rates in the database I collected varied from 0% to 25.0%. Limited evidence pointed to small, nocturnal, arboreal primates having higher predation rates than larger, diurnal, or terrestrial species.

A predation rate of 25.0% annually for mouse lemurs (*Microcebus murinus*) (Goodman et al. 1993c), seems to belie Terborgh's cautionary comments. Higher predation rates are acceptable only if the species' potential reproductive rate is high enough to compensate for losses to predation (Hill and Dunbar 1998). The mouse lemur is able to sustain a predation rate of 25.0% because the species, for a primate, has a high reproductive capacity (Martin 1972, Goodman et al. 1993c). *Microcebus* has two litters per rainy season to offset predation; an average annual production of four offspring per breeding female with a 50.0% infant survival rate provides the mouse lemur with the ability to rapidly replace its population (Martin 1972). This description of reproductive capability in *Microcebus* calls into question the accuracy of considering the very high rates (16.8-32.9%) of chimpanzee predation on red colobus at Gombe National Park (Stanford et al. 1994a) as anything other than an aberrant situation.

Predation risk not predation rate, nevertheless, is what drives the animal's anti-predation behavior (Hill and Dunbar 1998). Unsuccessful predation attempts, i.e., the failure of predators to catch prey, underlie selection for defense behaviors (Vermeij 1982). Cowlishaw (1997a) constructed a field experiment to measure perceived versus actual risk in chacma baboons (*Papio cynocephalus*). He found that females in small groups are expected to be at the greatest risk from predators and that they perceived the greatest risk, but males had equal or higher mortality rates. These results suggest that females invest highly in anti-predator behavior which compensates for their susceptibility to predators.

Animals strive to reduce their predation risk because it represents the sum total of all past unsuccessful encounters with predators plus their perception of the likelihood of future attack (Young 1994, Hill and Dunbar 1998). Behavior is predicated on predation risk not predation rate because animals react to unsuccessful attacks, but die from successful ones.

4) Primates have selected strategies to offset predation at its earliest stages

Primates, as intelligent mammals, focus on the prevention of predation at the earliest stage of predatory action. Prey are able to interrupt predation during any of six stages: the encounter stage, the detection stage, the identification stage, the approach stage, the subjugation stage, and the consumption stage (Endler 1991). The advantage lies with prey that interrupt the predation sequence at the earliest stage because: a) the risk of a successful predation is reduced, causing b) less current energy to be expended in defensive behavior, allowing c) future fitness to be enhanced through the channeling of saved energy into growth and reproduction, given the fact that d) the relative frequency of the early stages of predation will be higher than later stages (Endler 1991).

Prey animals face the dilemma of being preyed on by more than one species or group of predators. Their difficulty lies in evolving defense strategies that are effective in all circumstances (Bertram 1979). The early predation stages are more general (Endler 1991); therefore, more different types of predators can be countered with a similar defensive strategy if prey respond in the earliest stages.

Primate anti-predator adaptations are centered on the first stage of predator activity – the encounter stage. Alarm vocalizations, scanning, social grouping, and polyspecific associations to enhance vigilance are all methods to achieve what Endler has termed "one-upmanship," or detection of the predator before the predator has detected the prey. Alarm vocalizations were used more frequently than other defensive strategies by primates according to the data I collected from questionnaires. Alarm calls were used by all primate families and subfamilies for which there were data and were used against all predator groups. Scanning was the second most frequently used defense strategy and was also used against all categories of predators.

The choice of defenses used by prey depends on the relative cost and benefits and the evolutionary history of the taxon (Endler 1986). Most diurnal primates live in a social group which results in more effective vigilance to locate predators than is possible for a solitary individual (Bertram 1978). Nocturnal primates do not use group size as an anti-predator defense (Hill and Dunbar 1998), but nocturnality is, itself, a defense strategy countering the first stage of predation.

Primates have evolved a variety of strategies to keep the predation sequence from passing into later stages. Evidence exists that the need for vigilance promotes mixed species associations that provide "more eyes" for a primate group (Gautier and Gautier-Hion 1983, Gautier-Hion 1988, Buchanan-Smith 1990). Further, predator specific alarm vocalizations that identify raptors, snakes, or terrestrial carnivores are found in Old World and Neotropical monkeys and lemurs (Struhsaker 1967a, Sussman 1977, Cheney and Seyfarth 1981, Sauther 1989, Macedonia 1990a, 1990b, Norris 1990, Fedigan et al. 1996). Additionally, tamarin sleep behavior is a suite of adaptations including retirement before dusk with up to an hour of monitoring before entering sleeping holes (Caine 1984, 1987, Peres 1993, Boinski and Chapman 1995).

* * * * * *

Predation as a demographic parameter in primate populations has been one of the least studied areas because little empirical information on predation has been available. Predation is undoubtedly significant and may be the leading source of mortality in populations of primates (Terborgh 1983). It is the main conclusion of my study that species of primates are influenced to varying degrees by predation and that major morphological, ecological and behavioral adaptations have evolved in response to predators.

Primates are at risk from predation; at question is only the *degree* to which it influences the life history of the individual or shapes the phylogeny of a species. Insights into the individual and phylogenetic impacts on primates from predation will come only from increasingly sophisticated field studies that emphasize the inter-relationship between primate prey and their predators.

BIBLIOGRAPHY

Addicott, J. 1984. Mutualistic interactions in population and community processes. In: A New Ecology: Novel Approaches to Interactive Systems, P. Price, C. Slobodchikoff, and W. Gaud (eds.). John Wiley & Sons Publications, New York. pp. 437-455.

Agoramoorthy, G. 1992. Reproductive biology of the Hanuman langur, *Presbytis entellus*, in Jodhpur, western India. *Journal of Bombay Natural History Society* 89(1):84-93.

Albignac, R. 1970. Notes ethologiques sur quelque carnivores Malgaches: Le *Cryptoprocta ferox* (Bennet). *Terre Vie* 24:395-402.

_____. 1973. Mammiferes Carnivores, Faune de Madagascar, Vol. 36. ORSTOM/CNRS, Paris. pp. 180-189.

_____. 1984. The carnivores. In: Madagascar, A. Jolly, P. Oberle, and R. Albignac (eds.). Pergamon Press, Oxford. pp. 167-177.

Alcock, J. 1993. Animal Behavior: An Evolutionary Approach, 5th edition. Sinauer Associates, Inc., Sunderland. pp. 353-393.

Alderton, D. 1991. Crocodiles and Alligators of the World. Facts on File, New York.

Aldrich-Blake, F. 1970a. Problems of social structure in forest monkeys. In: Social Behaviour in Birds and Mammals: Essays on the Social Ethology of Animals and Man, J. Crook (ed.). Academic Press, London. pp. 79-101.

_____. 1970b. The ecology and behaviour of the blue monkey, *Cercopithecus mitis stuhlmanni*. Ph.D. dissertation, University of Bristol, Bristol, United Kingdom.

Alexander, J. 1992. Alas, poor *Notharctus*. *Natural History* 9:54-59.

Alexander, R. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics* 5:1-35.

Alikhan, I. 1938. Method adopted by leopards in hunting monkeys. *Journal of the Bombay Natural History Society* 40:555-557.

Allen, G., and A. Loveridge. 1933. Reports on the scientific results of an expedition to the southwestern highlands of Tanganyika Territory. II. Mammals. *Bulletin of the Musueum of Comparative Zoology, Harvard.* 75:45-140.

Alonzo, C. and A. Langguth. 1989. Ecologia e comportamento de *Callithrix jacchus* numa ilha de Floresta Atlântica. *Rev. Nordestina Biol.* 6:105-137.

Alp, R. 1993. Meat eating and ant dipping by wild chimpanzees in Sierra Leone. *Primates* 34(4):463-468.

Alp, R. and A. Kitchener. 1993. Carnivory in wild chimpanzees, *Pan trogloytes verus*, in Sierra Leone. *Mammalia* 57(2):273-274.

Alterman, L. 1995. Toxins and toothcombs: Potential allospecific chemical defenses in *Nycticebus* and *Perodicticus*. In: Creatures of the Dark: The Nocturnal Prosimians, L. Alterman, G. Doyle and M. Kay Izard (eds.). Plenum Press, New York. pp. 413-424.

Altmann, S. 1974. Baboons, space, time, and energy. *American Zoology* 14:221-248.

_____. 1979. Baboon progressions: Order or chaos? A study of one-dimensional group geometry. *Animal Behaviour* 27:46-80.

Altmann, S. and J. Altmann. 1970. Baboon Ecology. University of Chicago Press, Chicago.

Alvard, M. 1994. The sustainability of primate hunting in the Neotropics: Data from native communities. *American Journal of Physical Anthropology* 49 (Supplement 18).

Alvard, M. and H. Kaplan. 1991. Procurement technology and prey mortality among indigenous neotropical hunters. In: Human Predators and Prey Mortality, M. Steiner (ed.). Westview Press, Boulder. pp. 79-104.

Alvarez, J., Jr. 1970. A report on the 1969 status of the monkey-eating eagle of the Philippines. IUCN (International Union for the Conservation of Nature and Natural Resources) Publication N. S. 18:68-73.

Anderson, C. 1980. Chacma baboon (*Papio ursinus*) social groups and their interrelationships in the Suikerbosrand Reserve, South Africa. Ph.D. dissertation, University of California, Riverside, California.

_____. 1981a. Subtrooping in a chacma baboon (*Papio ursinus*) population. *Primates* 22:445-458.

_____. 1981b. Intertroop relations of chacma baboons (*Papio ursinus*). *International Journal of Primatology* 2:285-310.

_____. 1986a. Predation and primate evolution. *Primates* 27(1):15-39.

Anderson, J. 1986b. Encounters between domestic dogs and free-ranging non-human primates. *Applied Animal Behaviour Science* 15(1):71-86.

Andrews, P. 1990. Owls, Caves and Fossils: Predation, Preservation, and Accumulation of Small Mammal Bones in Caves, with an Analysis of the Pleistoncene Cave Faunas from Westbury-Sub-Mendip, Somerset, United Kindom. The University of Chicago Press, Chicago.

Aranda, M. 1993. Habitas alimentarios del jaguar (*Panthera onca*) en la Reserva de la Biosfera de Calakmul, Campeche. In: Avances en el Studio de los Mamiferos de Mexico, Publcaciones Especiales, Vol. I., R. Medellin y G. Ceballos (eds.). Asociacion Mexicana de Mastozoologi, A.C., Mexico.

Archer, J. 1988. The Behavioural Biology of Aggression. Cambridge University Press, Cambridge.

Ayres, J. 1986. Uakaris and the Amazonian flooded forests. Museu Goeldi, Belém, Pará, Brazil. Unpublished manuscript.

Badrian, N. and R. Malenky. 1984. Feeding ecology of *Pan paniscus* in the Lomako forest, Zaire. In: The Pygmy Chimpanzee: Evolutionary Biology and Behavior, R. Susman (ed.). Plenum Press, New York. pp. 275-99.

Baenninger, R., R. Estes, and S. Baldwin. 1977. Anti-predator behavior of baboons and impalas toward a cheetah. *East African Wildlife Journal* 15(4):327-330.

Bakker, R. 1983. The deer flees, the wolf pursues: Incongruencies in predator-prey coevolution. In: Coevolution, D. Futuyma and M. Slatkin (eds.). Sinauer Associates, Inc., Sunderland. pp. 350-382.

Bakuneeta, C. (in prep). The ecology and behaviour of chimpanzees in Budongo Forest Reserve, Uganda: Responses to timber-harvesting operations. Ph.D. dissertation, Makerere University, Kampala, Uganda.

Bakuneeta, C., H. Inagaki, and V. Reynolds. 1993. Identification of wild chimpanzee hair samples from feces by electron microscopy. *Primates* 34(2):233-235.

Baldellou, M. and S. Henzi. 1992. Vigilance, predator detection, and the presence of supernumerary males in vervet monkey troops. *Animal Behavior* 43(3):451-461.

Barnett, R. and R. Rudd. 1983. Feral dogs of the Galapagos Islands: Impact and control. *International Journal for the Study of Animals Problems* 4:44-58.

Bartecki, U. and E. Heymann. 1987. Field observation of snake-mobbing in a group of saddle-back tamarins (*Saguinus fuscicollis nigrifrons*). *Folia Primatologica* 48:199-202.

Bartlett, T., R. Sussman, and J. Cheverud. 1993. Infant killing in primates: a review of observed cases with specific references to the sexual selection hypothesis. *American Anthropologist* 95:958-990.

Barton, R. 1989. Foraging strategies, diet and competition in olive baboons. Ph.D. dissertation, University of St. Andrews, United Kingdom.

Bates, R. 1956. Monkeys and panther. *Journal of the Bombay Natural History Society* 53:254-255.

Baumgartel, W. 1976. Up Among the Mountain Gorillas. Hawthorn Books, Inc., New York.

Bayart, F. and M. Anthousard. 1992. Responses to a live snake by *Lemur macaco macaco* and *Lemur fulvus mayottensis* in captivity. *Folia Primatologica* 58(1):41-46.

Bearder, S. 1977. Feeding habits of spotted hyena in a woodland habitat. *East African Wildlife Journal* 15:263-280.

Beck, B. and R. Tuttle. 1972. The behavior of gray langurs at a Ceylonese water hole. In: The Functional and Evolutionary Biology of Primates, R. Tuttle (ed.). Aldine, Chicago. pp. 351-377.

Ben-David, M., S. Pellis, and V. Pellis. 1991. Feeding habits and predatory behaviour in the marbled polecat (*Vormela peregus nasyriaca*): I. Killing methods in relation to prey size and prey behaviour. *Behaviour* 118(1-2):127-143.

Bennett, E. 1983. The banded langur: Ecology of a colobine in west Malaysian rain-forest. Ph.D. dissertation, University of Cambridge, Cambridge, United Kingdom.

Bennett, E. and A. G. Davies. 1994. The ecology of Asian colobines. In: Colobine Monkeys: Their Ecology, Behaviour and Evolution, A. G. Davies and J. Oates (eds.). Cambridge University Press, Cambridge. pp. 129-171.

Berkelman, J. 1993. Ecology of the Madagascar buzzard, *Buteo brachypterus*, in the rain forest of the Masoala Peninsula. Master's thesis, Boise State University, Idaho.

Bernstein, I. 1967. A field study of the pigtail monkey. *Primates* 8:217-228.

Bert, J., H. Ayats, A. Martino, and H. Colomb. 1967. Le sommeil nocturne chez le babouin *Papio papio* – observations en milieu naturel et données éléctrophysiologiques. *Folia Primatologica* 6:28-43.

Bertram, B. 1978. Living in groups: Predators and prey. In: Behavioural Ecology: An Evolutionary Approach, 1st edition, J. Krebs and N. Davies (eds.). Blackwell Scientific Publications, Oxford, London. pp. 64-96.

_____. 1979. Serengeti predators and their social systems. In: Serengeti: Dynamics of an Ecosystem, A. Sinclair and M. Norton-Griffiths (eds.). University of Chicago Press, Chicago. pp. 221-248.

_____. 1982. Leopard ecology as studied by radio-tracking. *The Symposium of the Zoological Society of London* 49:341-352.

Bertrand, M. 1969. The Behavioral Repertoire of the Stumptail Macaque. S. Karger, Basel. 273 pp.

Bhatnagar, P. and R. Mathur. 1994. Association of rhesus males with a langur group. Paper presented at: Symposium on Behavioral Processes.

_____. (In prep.). Response to alarm situations in langur mother-infant dyads.

Biquand, S., V. Biquand-Guyot, A. Boug, and J. Gautier. 1994. The distribution of *Papio hamadryas* in Saudi Arabia: Ecological correlates and human influence. *International Journal of Primatology* 13(3):223-243.

Biquand, S., V. Urios, A. Boug, C. Vila, J. Castroviejo, and I. Nader. 1994. Fishes as diet of a wolf (*Canis lupus arabs*) in Saudi Arabia. *Mammalia* 58(3):492-494.

Bisbal, F. 1986. Food habits of some neotropical carnivores in Venezuela (Mammalia, Carnivora). *Mammalia* 50:329-339.

Bishop, N. 1975. Social behavior of langur monkeys (*Presbytis entellus*) in a high altitude environment. Ph.D. dissertation, University of California, Berkeley, California.

Bismark, M. 1990. [Night nesting habits of the proboscis monkey in the mangrove forest of the Kutai National Park.] *Buletin Penelitian Hutan* 527:33-40.

Blakey, M. 1994. Two together: Fossas look a lot more social. *BBC Wildlife* 12(5):11.

Boesch, C. 1991. The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour* 117(3-4):220-242.

_____. 1992. Predation by leopards on chimpanzees and its impact on social grouping. *Bulletin of the Chicago Academy of Science* 15(1):5 (Abstract).

_____. 1994a. Chimpanzees-red colobus monkeys: A predator-prey system. Animal Behaviour 47(5):1135-1148.

_____. 1994b. Cooperative hunting in wild chimpanzees. *Animal Behaviour* 48(3):653-667.

_____. 1994c. Hunting strategies of Gombe and Tai chimpanzees. In: Chimpanzee Cultures, R. Wrangham, W. McGrew, F. de Waal, et al. (eds.). Harvard University Press, Cambridge. pp. 77-92.

Boesch, C. and H. Boesch. 1989. Hunting behavior of wild chimpanzees in the Tai National Park, Ivory Coast. *American Journal of Physical Anthropology* 78(4):547-574.

Boggess, J. 1976. The social behavior of the Himalayan langur (*Presbytis entellus*) in eastern Nepal. Ph.D. dissertation, University of California, Berkeley, California.

Boinski, S. 1987. Birth synchrony in squirrel monkeys: A strategy to reduce neonatal predation. *Behavioural Ecology and Sociobiology* 21(6):393-400.

_____. 1988. Use of club by a wild white-faced capuchin to attack a venomous snake. *American Journal of Primatology* 14(2):177-179.

_____. 1992. Monkeys with inflated sex appeal. *Natural History* 7:42-48.

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

Bolwig, N. 1959. A study of the behaviour of the chacma baboon, *Papio ursinus*. *Behaviour* 14:136-163.

Boonratana, R. 1994. The ecology and behaviour of the proboscis monkey (*Nasalis larvatus*) in the Lower Kinabatangan, Saba. Ph.D. dissertation, Mahidol University, Thailand.

Boshoff, A. and N. Palmer. 1980. Macro-analysis of prey remains from Martial Eagle nests in the Cape Province. *Ostrich* 51:7-13.

Boshoff, A., N. Palmer, and G. Avery. 1990. Regional variation in the composition, diversity and species richness of martial eagle prey in the Cape Province. *South African Journal of Wildlife Research* 20:57-68.

Boshoff, A., N. Palmer, G. Avery, R. Davies and M. Jarvis. 1991. Biogeographical and topographical variation in the prey of the black eagle in the Cape Province, South Africa. *Ostrich* 62:59- 72.

Boshoff, A., N. Palmer, C. Vernon, and G. Avery. 1994. Comparison of the diet of crowned eagles in the savanna and forest biomes of southeastern South Africa. *South African Journal of Wildlife Research* 24:26-31.

Bothma, J. du. 1966. Notes on the stomach contents of certain Carnivora (Mammalia) from the Kalahari Gemsbok Park. *Koedoe* 9:37-39.

Bothma, J. du and E. Le Riche. 1984. Aspects of the ecology and behaviour of the leopard in the Kalahari Desert. *Koedoe* (supplement) 1984:259-279.

_____. 1986. Prey preference and hunting efficiency of the Kalahari Desert leopard. In: In: Cats of the World: Biology, Conservation and Management, S. Miller and D. Everett (eds.). National Wildlife Federation, Washington, D.C. pp. 389-414.

Bourliere, F. 1963. Specific feeding habits of African carnivores. *African Wild Life* 17:21-27.

_____. 1979. Significant parameters of environmental quality for nonhuman primates. In: Primate Ecology and Human Origins, I. Bernstein and E. Smith (eds.). Garland, New York. pp. 23-46.

Bourliere, F., C. Hunkeler, and M. Bertrand. 1970. Ecology and behaviour of Lowe's guenon (*Cercopithecus campbelli lowei*) in the Ivory Coast. In: Old World Monkeys, J. Napier and P. Napier (eds.). Academic Press, New York. pp. 297-350.

Brain, C. 1970. New finds at the Swartkrans Australopithecine site. *Nature* (London) 225:1112-1119.

_____. 1978. Interpreting the bone accumulation from the Sterkfontein Valley caves. *Ann. Natal Mus.* 23:465-468.

_____. 1981. The Hunters or the Hunted? University of Chicago Press, Chicago.

Branch, R. 1991. Unusual herpetological observations in the Kruger National Park. *African Herp News* 16:39-40.

Brander, A. 1939. Behaviour of monkeys when attacked. *Journal of Bombay Natural History Society* 41:165.

Brooks, D. (In press.) Notes from the Paraguayan Chaco on the night monkey (*Aotus azarae*). *Neotropical Primates.*

Brown, L. 1952. On the biology of the large birds of prey of the Embu District, Kenya Colony. *Ibis* 94:577-620.

_____. 1953. On the biology of the large birds of prey of Embu District, Kenya Colony. *Ibis* 95:74-114.

_____. 1955. Supplementary notes on the biology of the large birds of prey of Embu District, Kenya Colony. *Ibis* 97:38-64;183-221.

_____. 1965. Observations on Verreaux's eagle owl. *Journal of East African Natural History Society* 25:101-107.

_____. 1966. Observations on some Kenya eagles. *Ibis* 108:531-572.

_____. 1971a. African Birds of Prey. Houghton Mifflin Company, Boston.

_____. 1971b. The relations of the crowned eagle, *Stephanoaetus coronatus*, and some of its prey animals. *Ibis* 113:240-243.

_____. 1977. Eagles of the World. Universe Books, New York.

_____. 1982. The prey of the crowned eagle, *Stephanoaetus coronatus*, in central Kenya. *Scopus* 6:91-94.

Brown, L. and D. Amadon. 1989. Eagles, Hawks and Falcons of the World, Wellfleet, Secaucus, NJ.

Brown, L., E. Urban, and K. Newman. (eds.) 1982. Birds of Africa Vol. I: Ostriches to Birds of Prey. Academic Press, New York.

Bryden, B. 1976. The biology of the African lion (*Panthera leo*, Linn 1758) in the Kruger National Park. Master's thesis, University of Pretoria, South Africa.

Brynard, A. and U. de V. Pienaar. 1960. Annual report of the biologist, 1958-1959. Kruger National Park. *Koedoe* 3:1-205.

Bshary, R. and R. Noë. 1997a. Anti-predation behaviour of red colobus monkeys in the presence of chimpanzees. *Behavioural Ecology and Sociobiology* 41:321-333.

_____. 1997b. Red colobus and Diana monkeys provide mutual protection against predators. *Animal Behaviour* 54:1461-1474.

Buchanan-Smith, H. 1990. Polyspecfic association of two tamarin species, *Saguinus labiatus* and *Saguinus fuscicollis*, in Boliva. *American Journal of Primatology* 22:205-214.

Buchanan-Smith, H., D. Anderson, and C. Ryan. 1993. Responses of cotton-top tamarins (*Saguinus oedipus*) to faecal scents of predators and non-predators. *Animal Welfare* 2:17-32.

Bueler, L. 1973. Wild Dogs of the World. Stein and Day, New York.

Bulger, J. and W. Hamilton III. 1987. Rank and density correlates of inclusive fitness measures in natural chacma baboon (*Papio ursinus*) troop. *International Journal of Primatology* 8:635-650.

Burbridge, B. 1928. Gorilla: Tracking and Capturing the Ape Man of Africa. The Century, Co., New York.

Busse, C. 1977. Chimpanzee predation as a possible factor in the evolution of red colobus monkey social organization. *Evolution* 31:907-911.

_____. 1978. Do chimpanzees hunt co-operatively? *American Naturalist* 112:767-770.

_____. 1980. Leopard and lion predation upon chacma baboons living in the Moremi Wildlife Reserve. *Botswana Notes Records* 26:132-160.

Butynski, T. 1982a. Blue monkey predation on galagos. *Primates* 23(4):563-566.

_____. 1982b. Vertebrate predation by primates. A review of hunting patterns and prey. *Journal of Human Evolution* 11:421-430.

_____. 1988. Guenons' birth seasons. In: A Primate Radiation: Evolutionary Biology of the African Guenons, A. Gautier-Hion, F. Bourliere, J. Gautier, and J. Kingdon (eds.). Cambridge University Press, Cambridge. pp. 316-322.

_____. 1990. Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high and low density subpopulations. *Ecological Monographs* 60:1-26.

Byrne, R. 1982. Distance vocalisations of Guinea baboons (*Papio papio*) in Senegal: An analysis of function. *Behaviour* 78:283-312.

Byrne, R. and J. Byrne. 1988. Leopard killers of Mahale. *Natural History* 97(3):22-26.

Byrne, R. and A. Whiten. 1990. Tactical deception in primates: The 1990 database. *Primate Report* (27):1-101.

Caine, N. 1987. Vigilance, vocalization, and cryptic behaviour at retirement in captive groups of red-bellied tamarins (*Saguinus labiatus*). *American Journal of Primatology* 12:241-250.

_____. 1990. Unrecognized anti-predator behavior can bias observational data. *Animal Behaviour* 39(1):195-197.

_____. 1993. Flexibility and co-operation as unifying themes in *Saguinus* social organization and behaviour: The role of predation pressures. In: Marmosets and Tamarins: Systematics, Behaviour, and, Ecology, A. Rylands (ed.) Oxford University Press, Oxford. pp. 200-219.

_____. 1998. Cutting costs in response to predatory threat by Geoffroy's marmosets (*Callithrix geoffroyi*). *American Journal of Primatology* 46(3):187-196.

Caine, N. and P. Weldon. 1989. Responses by red-bellied tamarins (*Saguinus labiatus*) to fecal scents of predatory neotropical mammals. *Biotropica* 21(2):186-189.

Caro, T. 1980. The effects of experience on the predatory patterns of cats. *Behavioral and Neural Biology* 29:1-28.

Caro, T. and C. Fitzgibbon. 1992. Large carnivores and their prey: The quick and the dead. In: Natural Enemies: The Population Biology of Predators, Parasites and Diseases, M. Crawley (ed.). Blackwell Scientific Publications, London. pp. 117-142.

Carpenter, C. 1934. A field study of the behavior and social relations of howling monkeys. *Comp. Psychol. Monogr.* 10:1-168.

Cavallo, J. 1991. Leopards and human evolution. In: Great Cats: Majestic Creatures of the Wild, J. Seidensticker and S. Lumpkin (eds.). Rodale Press, Emmaus, Pennsylvania. pp. 208.

Chamove, A. 1996. Predator (*Mustela nivalis*) responses in captive-bred *Callithrix jacchus*. *Neotropical Primates* 4(2):56-57.

Channer, O. 1895. The food of the python. *Journal of Bombay Natural History Society* 9:491.

Chapais, B. and S. Schulman. 1980. Alarm responses to raptors by rhesus monkeys at Cayo Santiago. *Journal of Mammalogy* 61(4):739-741.

Chapin, J. 1925. The crowned eagle, ogre of Africa's monkeys. *Natural History* 25:459-469.

_____. 1932. The birds of the Belgian Congo. (I.) *Bulletin of the American Museum of Natural History* 65(1):534-655.

Chapman, C. 1986. Boa constrictor predation and group response in white-faced cebus monkeys. *Biotropica* 18(2):171-172.

Charles-Dominique, P. 1974. Ecology and feeding behavior of five sympatric lorisids in Gabon. In: Prosimian Biology, R. Martin, G. Doyle, and A. Walker (eds.). Gerald Duckworth & Co., Ltd., London. pp. 135-150.

_____. 1977. Ecology and Behaviour of Nocturnal Primates: Prosimians of Equatorial West Africa. Duckworth, London.

Charles-Dominique, P, and J. Petter. 1980. Ecology and social life of *Phaner furcifer*. In: Nocturnal Malagasy Primates: Ecology, Physiology, and Behavior, P. Charles-Dominque, H. M. Cooper, A. Hladik, C. Hladik, E. Pages, G. Pariente, A. Petter-Rousseaux, J. Petter, and A. Schilling (eds.). Academic Press, New York. pp. 75-95.

Cheney, D., P. Lee, and R. Seyfarth. 1981. Behavioral correlates of non-random mortality among free-ranging adult female vervet monkeys. *Behavioural Ecology and Sociobiology* 9:153-161.

Cheney, D. and R. Seyfarth. 1981. Selective forces affecting the predator alarm calls of vervet monkeys. *Behaviour* 76:25-61.

_____. 1983. Non-random dispersal in free-ranging vervet monkeys: Social and genetic consequences. *American Naturalist* 122:392-412.

Cheney, D., R. Seyfarth, S. Andelman, and P. Lee. 1988. Reproductive success in vervet monkeys. In: Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems, T. Clutton-Brock (ed.). University of Chicago Press, Chicago. pp. 384-402.

Cheney, D. and R. Wrangham. 1987. Predation. In: Primate Societies, B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker (eds.). The University of Chicago Press, Chicago. pp. 227-239.

Chiarello, A. and M. Passamani. 1993. A reintroduction program for Geoffroy's marmoset, Callithrix geoffroyi. *Neotropical Primates* 1(3):6-7.

Chism, J., D. Olson, and T. Rowell. 1983. Diurnal births and perinatal behavior among wild patas monkeys. *International Journal of Primatology* 4:167-184.

Chism, J. and W. Rogers. (submitted). Male competition, mating success and female choice in patas monkeys in Kenya. *Behavioral Ecology and Sociobiology.*

Chism, J. and T. Rowell. 1988. The natural history of patas monkeys. In: A Primate Radiation: Evolutionary Biology of the African Guenons, A. Gautier-Hion, F. Bourliere, J. Gautier, and J. Kingdon (eds.). Cambridge University Press, Cambridge. pp. 412-437.

Cilliers, W. 1963. Lions apparently do eat baboons. *African Wild Life* 17:17-18.

Clark, J. 1970. Observations on the crowned eagle, *Polemaetus coronatus. The Lammergeyer* 12:74-77.

Clifton, M. 1977. Attack on a colobus monkey. *East Africa Natural History Society* Vol. 5.

Cloudsley-Thompson, J. 1994. Predation and Defence Amongst Reptiles. R & A Publishing Ltd, England.

Coimbra-Filho, A. 1978. Natural shelters of *Leontopithecus rosalia* and some ecological implications (Callitrichidae: Primates). In: The Biology and Conservation of the Callitrichidae, D. Kleiman (ed.). Smithsonian Institution Press, Washington. pp. 79-89.

Coimbra-Filho, A. and R. Mittermeier. 1973. Distribution and ecology of the genus *Leontopithecus* (Lesson, 1840) in Brazil. *Primates* 14(1):47-66.

Colquhoun, I. 1993. The socioecology of *Eulemur macaco*: A preliminary report. In: Lemur Social Systems and Their Ecological Basis, P. Kappeler and J. Ganzhorn (eds.). Plenum Press, New York. pp. 11-23.

Collar, J. 1989. Harpy eagle. *World Birdwatch* 11(3):5.

Collins, D. 1984. Spatial patterns in a troop of yellow baboons (*Papio cynocephalus*) in Tanzania. *Animal Behaviour* 32:536- 553.

Condit, V. and E. Smith. 1994. Predation on a yellow baboon (*Papio cynocephalus cynocephalus*) by a lioness in the Tana River National Primate Reserve, Kenya. *American Journal of Primatology* 33:57-64.

Conroy, G. 1990. Primate Evolution. W. W. Norton, New York.

Cook, M. and S. Mineka. 1990. Selective associations in the observational conditioning of fear in rhesus monkeys. Journal of Experimental Psychology: *Animal Behavior Processes* 16(4):372- 389.

Cooper, S. 1990. The hunting behaviour of spotted hyenas (*Crocuta crocuta*) in a region containing both sedentary and migratory populatons of herbivores. *African Journal of Ecology* 28:131-141.

Corbet, G. and J. Hill. 1991. A World List of Mammalian Species, Third Edition. Oxford University Press, Oxford.

Cordeiro, N. 1992. Behaviour of blue monkeys (*Cercopithecus mitis*) in the presence of crowned eagles (*Stephanoaetus coronatus*). *Folia Primatologica* 59(4):203-207.

Correa, H. and P. Coutinho. 1997. Fatal attack of a pit viper, *Bothrops jararaca*, on an infant buffy-tufted ear marmoset (*Callithrix aurita*). *Primates* 38(2)215-217.

Coryndon, S. 1964. Bone remains in the caves. *Studies in Speleology* 1(1):60-63.

Cott, H. 1961. Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. *Trans. Zool. Soc. London* 29:211-356.

Cowlishaw, G. 1994. Vulnerability to predation in baboon populations. *Behaviour* 131(3-4):293-304.

_____. 1997a. Alarm calling and implications for risk perception in a desert baboon population. *Ethology* 103(5):384-394.

_____. 1997b. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour* 53(4):667-686.

Crook, J. 1970. The socioecology of primates. In: Social Behaviour in Birds and Mammals, J. Crook (ed.). Academic Press, London. pp. 103-159.

_____. 1972. Sexual selection, dimorphism, and social organization in the primates. In: Sexual Selection and the Descent of Man, B. Campbell (ed.). Aldine, Chicago. pp. 231-281.

Crook, J. and J. Gartlan. 1966. Evolution of primate societies. *Nature* 210:1200-1203.

Curio, E. 1976. The Ethology of Predation. Springer-Verlag, Berlin.

Curtin, R. 1975. The socioecology of the common langur, *Presbytis entellus*, in the Nepal Himalaya. Ph.D. dissertation, University of California, Berkeley, California.

Daly, M. and M. Wilson. 1988. Evolutionary social psychology and family homicide. *Science* 242:519-524.

Daneel, A. 1979. Prey size and hunting methods of the crowned eagle. *Ostrich* 50:120-121.

Davies, A. G. 1994. Colobine populations. In: Colobine Monkeys: Their Ecology, Behaviour and Evolution, A. G. Davies and J. Oates (eds.). Cambridge University Press, Cambridge. pp. 285-310.

Davies, R. 1990. Sighting of a clouded leopard (*Neofelis nebulosa*) in a troop of pigtail macaques (*Macaca nemestrina*) in Khao Yai National Park, Thailand. *National History Bulletin of the Siam Society* 38(1):95-96.

_____. 1994. Black eagle, *Aquila verreauxii*, rock hyrax, *Procavia capensis*, and other prey in the Karoo. Ph.D. dissertation, University of Pretoria, Pretoria, South Africa.

Davis, D. 1962. Mammals of the lowland rainforests of North Borneo. *Bulletin of the National Museum of Singapore* 31:1-129.

Dawson, G. 1976. Behavioral ecology of the Panamanian tamarin, *Saguinus oedipus* (Callitrichidae: Primates). Ph.D. dissertation, Michigan State University, Ann Arbor, Michigan.

_____. 1979. The use of time and space by the Panamanian tarmarin, *Saguinus oedipus*. *Folia Primatologica* 31:253-284.

Dawson, G., and W. Dukelow. 1976. Reproductive characteristics of free-ranging Panamanian tamarins (*Saguinus oedipus geoffroyi*). *Journal of Medical Primatology* 5:266-275.

Decker, B. 1994. Effects of habitat disturbance on the behavioral ecology and demographics of Tana River red colobus. *International Journal of Primatology* 15(5):703-738.

Decker, B., and M. Kinnaird. 1992. Tana River red colobus and crested mangabeys: Results of recent censuses. *American Journal of Primatology* 26(1):47-52.

Defler, T. 1980. Notes on interactions between the tayra (*Eira barbara*) and the white-fronted capuchin (*Cebus albifrons*). *Journal of Mammalogy* 61:156.

de Ruiter, J. 1986. The influence of group size on predator scanning and foraging behaviour of wedgecapped capuchin monkeys (*Cebus olivaceus*). *Behaviour* 98:240-258.

DeVore, I. and K. Hall. 1965. Baboon ecology. In: Primate Behavior: Field Studies of Monkeys and Apes, I. DeVore (ed.). Holt, Rinehart, and Winston, New York. pp. 20-52.

DeVore, I. and S. Washburn. 1963. Baboon ecology and human evolution. In: African Ecology and Human Evolution, C. Howell and F. Bouliere (eds.). Aldine, New York. pp. 335-367.

deVries, A. 1991. Translocation of mantled howling monkeys (*Alouatta palliata*) in Guanacaste, Costa Rica. Master's thesis, University of Calgary, Alberta, Canada.

Dittus, W. 1975. Population dynamics of the toque monkey, *Macaca sinica*. In: Socioecology and Psychology of Primates, R. Tuttle (ed.). Mouton, The Hague. pp. 125-152.

_____. 1977a. The social regulation of population density and age-size distribution in the toque monkey, *Macaca sinica*. *Behaviour* 63:281-322.

_____. 1977b. The socioecological basis for the conservation of the toque monkey (*Macaca sinica*) of Sri Lanka (Ceylon). In: Primate Conservation, HRH Rainier III and G. Bourne (eds.). Academic Press, New York. pp. 237-265.

_____. 1979. The evolution of behaviors regulating density and age-specific sex ratios in a primate population. *Behaviour* 69:265-302.

_____. 1980. The social regulation of primate populations. In: The Macaques, D. Lindburg (ed.). Van Nostrand Reinhold. pp. 263-284.

Dixon, J. 1968. Prey of large raptors. *The Ostrich* 39(3):203-204.

Dunbar, R. 1988. Primate Social Systems. Comstock Publications, Ithaca.

Dunning, J. (ed.) 1993. CRC Handbook of Avian Body Masses. CRC Press, Boca Raton.

Eason, P. 1989. Harpy eagle attempts predation on adult howler monkey. *Condor* 91(2):469-470.

Eaton, R. 1974. The Cheetah: The Biology, Ecology, and Behavior of an Endangered Species. Van Nostrand Reinhold, New York. pp. 41-87.

Edmunds, M. 1974. Defence in Animals: A Survey of Anti-Predator Defences. Longman, London.

Eisenberg, J. 1981. The Mammalian Radiations: An Analysis of Trends in Evolution, Adaptation, and Behavior. University of Chicago Press, Chicago.

_____. 1989. Mammals of the Neotropics: The Northern Neotropics, Vol. I. University of Chicago Press, Chicago.

Eisenberg, J. and P. Leyhausen. 1972. The phylogenesis of predatory behavior in mammals. *Zeitschrift fuer Tierpsychologie* 30(1):59-93.

Eisenberg, J. and M. Lockhart. 1972. An ecological reconnaissance of Wilpattu National Park, Ceylon. *Smithsonian Contributions to Zoology* (101):1-118.

Eisenberg, J., N. Muckenhirn and R. Rudran. 1972. The relation between ecology and social structure in primates. *Science* 176:863-874.

Elliott, J., I. Cowan, and C. Holling. 1977. Prey capture in the African lion. *Canadian Journal of Zoology* 55:1811-1828.

Ellis, R. 1996. The Book of Sharks. Alfred A. Knopf, New York.

Eloff, F. 1973. Lion predation in the Kalahari Gemsbok National Park. *Journal of the South African Wildlife Management Association* 3:59-63.

Emmons, L. 1987. Comparative feeding ecology of felids in a neotropical rainforest. *Behavioural Ecology and Sociobiology* 20:271-283.

_____. 1988. A field study of ocelots (*Felis pardalis*) in Peru. *Revue d'Ecologie la Terre et la Vie* 43:133-157.

_____. 1989. Ocelot behavior in moonlight. In: Advances in Neotropical Mammalogy, K. Redford and J. Eisenberg (eds.). Sandhill Crane Press, Gainesville. pp. 233-242.

_____. 1991. Body size and feeding tactics. In: Great Cats: Majestic Creatures of the Wild, J. Seidensticker and S. Lumpkin (eds.). Rodale Press, Emmaus, Pennsyl vania. pp. 62.

Endler, J. 1986. Natural Selection in the Wild. Princeton University Press, Princeton, New Jersey.

_____. 1991. Interactions between predators and prey. In: Behavioural Ecology: An Evolutionary Approach, Third Edition, J. Krebs and N. Davies (ed.). Blackwell Scientific Publications, New York. pp. 169-196.

Estes, R. 1967. Predators and scavengers. *Natural History*, New York 76:21-29.

Estes, R. and J. Goddard. 1967. Prey selection and hunting behavior of the African wild dog. *Journal of Wildlife Management* 31:52-70.

Everett, M. 1977. A Natural History of Owls. The Hamlyn Publishing Group, Ltd., London.

Ewer, R. 1973. The Carnivores. Cornell University Press, New York.

Fairgrieve, C. 1996. The comparative ecology of blue monkeys (*Cercopithecus mitis*) in logged and unlogged forest in the Budongo Forest, Uganda. Ph.D. dissertation, University of Edinburgh, Edinburgh, United Kingdom.

Fannin, A. and D. Webb 1975. Notes on the breeding of the crowned eagle. *Honeyguide* 82:36.

Fay, J., R. Carroll, J. Kerbis Peterhans, and D. Harris. 1995. Leopard attack on and consumption of gorillas in the Central African Republic. *Journal of Human Evolution* 29(1):93-99.

Fedigan, L. 1974. The classification of predators by Japanese macaques (*Macaca fuscata*) in the mesquite chaparral habitat of south Texas. *American Journal of Physical Anthropology* 40(1):135.

_____. 1991. History of the Arashiyama west Japanese macaques in Texas. In: The Monkeys of Arashiyama, L. Fedigan and P. Asquith (eds.). SUNY Press, Albany. pp. 54-73.

Fedigan, L., A. Rosenberger, S. Boinski, M. Norconk, and P. Garber. 1996. Critical issues in cebine evolution and behavior. In: Adaptive Radiation of Neotropical Primates, M. Norconk, A. Rosenberger, and P. Garber (eds.). Plenum Press, New York. pp. 219-228.

Fellowes, J. 1992. Hong Kong macaques: Final report to the World Wildlife Fund Hong Kong Projects Committee. Unpublished manuscript.

Ferrari, S. 1988. The behaviour and ecology of the buffy-headed marmoset, *Callithrix flaviceps*. Ph.D. dissertation, University College, London, United Kingdom.

Ferrari, S. and M. Lopes Ferrari. 1990. Predator avoidance behaviour in the buffy-headed marmoset (*Callithrix flaviceps*). *Primates* 31(2):323-338.

Fischer, W. 1984. Zum nahrungserwerb, zur beuteauswahl und zur okologischen einordnung der harpyie, *Harpia harpyia* L. *Der Zoologische Garten, Jena* 54(6):412-426.

Fittinghoff, N. and D. Lindburg. 1985. Riverine refuging in East Bornean *M. fascicularis*. In: The Macaques: Studies in Ecology, Behavior and Evolution, D. Lindburg (ed.). Van Nostrand Reinhold, New York. pp. 182-214.

Fleagle, J. 1988. Primate Adaptation and Evolution. Academic Press, San Diego.

_____. 1994. Polyspecific associations: An anti-predator tactic? *Evolutionary Anthropology* 3(2):68.

Floyd, T., L. Mech, and P. Jordan. 1978. Relating wolf scat content to prey consumed. *Journal of Wildlife Management* 42:528-532.

Fogden, M. 1974. A preliminary field study of the western tarsier (*Tarsius bancanus*, Horsfield). In: Prosimian Biology, R. Martin, G. Doyle, and A. Walker (eds.). Duckworth, London. pp. 151-167.

Foster, J. and D. Kearney. 1967. Nairobi National Park game census, 1966. *East African Wildlife Journal* 5:112-120.

Fowler, J. and J. Cope. 1964. Notes on harpy eagle in British Guiana. *Auk* 81:257-273.

Frank, N. and E. Ramus. 1995. A Complete Guide to Scientific and Common Names of Reptiles and Amphibians of the World. NG Publishing, Pottsville, PA.

Freeland, W. 1977. Blood sucking flies and primate polyspecific associations. *Nature* 269:801-802.

Freese, C. and J. Oppenheimer. 1981. The capuchin monkeys, genus *Cebus*. In: Ecology and Behavior of Neotropical Primates, A. Coimbra-Filho and R. Mittermeier (eds.). Acacemia Braziliera de Ciencias, Rio de Janeiro. pp 331-390.

Fuller, T. and P. Kat. 1990. Movements, activity, and prey relationships of African wild dogs (*Lyaon pictus*) near Aitong, southwestern Kenya. *African Journal of Ecology* 28:330-350.

Galdikas, B. 1985. Crocodile predation on a proboscis monkey in Borneo. *Primates* 26(4):495-496

Galdikas, B. and C. Yeager. 1984. Crocodile predation on a crab-eating macaque in Borneo. *American Journal of Primatology* 6(1):49-51.

Galef, B., Jr., R. Mittermeier, and R. Bailey. 1976. Predation by the tayra (*Eira barbara*). *Journal of Mammalogy* 57:760-761.

Galetti, M. 1990. Antipredatory behavior in four species of neotropical primates. In: Joint Meeting of the Argentine Mammal Society (SAREM) and the American Society of Mammalogists (ASM): Buenos Aires, Argentina, 17-20 June 1990. Unpublished manuscript. 22 pp.

Gandini, G. and P. Baldwin. 1978. An encounter between chimpanzees (*Pan troglodytes*) and a leopard (*Panthera pardus*) in Senegal. *Carnivore* 1(1):107-121.

Ganzhorn, J., and P. Kappeler. 1996. Lemurs of the Kirindy Forest. *Primate Report* 46-1:257-274.

Garcia, J. and F. Braza. 1993. Sleeping sites and lodge trees of the night monkey (*Aotus azarae*) in Bolivia. *International Journal of Primatology* 14(3):467-477.

Gardner, P. 1972. The Paliyans. In: Hunters and Gatherers Today, M. Bicchieri (ed.). Holt, Rinehart and Winston, New York. pp. 404-447.

Gargett, V. 1971. Some observations on black eagles in the Matopos, Rhodesia. *Ostrich (Supplement)* 9:91-124.

_____. 1990. The Black Eagle. A Study of Verreaux's Eagle in Southern Africa. Academic Press, London.

Gartlan, J. and C. Brain. 1968. Ecology and social variability in *Cercopithecus aethiops* and *Cercopithecus mitis*. In: Primates: Studies in Adaptation and Variability, P. Jay (ed.). Holt, Rinehart, & Winston, New York. pp. 253-292.

Gartlan, J. and T. Struhsaker. 1972. Polyspecific associations and niche separation of rainforest anthropoids in Cameroon, West Africa. *Journal of Zoology, London*. 168:221-266.

Gautier, J. and A. Gautier-Hion. 1983. Comportement vocal des males adultes et organisation dans les troupes polyspecifiques de cercopitheques. *Folia Primatologica* 40:161-174.

Gautier-Hion, A. 1973. Social and ecological features of talapoin monkey. In: Comparative Ecology and Behaviour of Primates, R. Michael and J. Crook (eds.). Academic Press, London. pp. 147-170.

_____. 1988. Polyspecific associations among forest guenons. In: A Primate Radiation: Evolutionary Biology of the African Guenons, A. Gautier-Hion, F. Bourliere, J. Gautier, and J. Kingdon (eds.). Cambridge University Press, Cambridge. pp. 454-473.

Gautier-Hion, A. and J. Gautier. 1971. La nage chez les cercopitheques arboricoles du Gabon. *La Terre et la Vie* 25(118):67-75.

_____. 1978. Le singe De Brazza: Une strategie originale. *Zeitschrift fuer Tierpsychologie* 46:84-104.

Gautier-Hion, A., R. Quris, and J. Gautier. 1983. Monospecific vs. polyspecific life: A comparative study of foraging and anti-predatory tactics in a community of *Cercopithecus* monkeys. *Behavioural Ecology and Sociobiology* 12(4):325-335.

Gautier-Hion, A. and C. Tutin. 1988. Mutual attack by a polyspecific association of monkeys against a crowned hawk eagle. *Folia Primatologica* 51:149-151.

Gebo, D., C. Chapman, L. Chapman, and J. Lambert. 1994. Locomotor response to predator threat in red colobus monkeys. *Primates* 35(2):219-223.

Gebo, D. and E. Simons. 1984. Puncture marks on early African anthropoids. *American Journal of Physical Anthropology* 65(1):31-36.

Ghiglieri, M. 1984. The Chimpanzees of Kibale Forest. Columbia University Press, New York.

Gillard, L. 1979. Giant eagle owl. *Witwatersrand Bird Club News* 104:5-6.

Glanz, W. 1991. Neotropical mammal densities: How unusual is the community on Barro Colorado Island, Panama? In: Four Neotropical Rainforests, A. Gentry (ed.). Yale University Press, New Haven. pp. 287-313.

Goldizen, A. 1987. Tamarins and marmosets: Communal care of offspring. In: Primate Societies, B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham and T. Struhsaker (eds.). University of Chicago Press, Chicago. pp. 34-43.

Gonzales, R. 1968. A study of the breeding biology and ecology of the monkey-eating eagle. *Silliman Journal* 15:461-491.

Goodall, J. 1965. Chimpanzees of the Gombe Stream Reserve. In: Primate Behavior: Field Studies of Monkeys and Apes, I. De Vore (ed.). Holt, Rinehart, and Winston, New York. pp. 425-473.

_____. 1977. Infant killing and cannibalism in free-living chimpanzees. *Folia Primatologica* 28:259-282.

_____. 1986. The Chimpanzees of Gombe: Patterns of Behavior. Harvard University Press, Cambridge.

Goodman, S. 1994a. Description of a new species of subfossil eagle from Madagascar: *Stephanoaetus* from the deposits of Ampasamba Zimba. Unpublished manuscript.

_____. 1994b. The enigma of antipredator behavior in lemurs: Evidence of a large extinct eagle on Madagascar. *International Journal of Primatology* 15(1):129-135.

Goodman, S., G. Creighton, and C. Raxworthy. 1991. The food habits of the Madagascar long-eared owl, *Asio madagascariensis*, in southeastern Madagascar. *Bonn. zool. Beitr.* 42(1):21-26.

Goodman, S. and O. Langrand. 1993. Food habits of the barn owl, *Tyto alba*, and the Madagascar long-eared owl, *Asio madagascariensis*, on Madagascar: Adaptation to a changing environment. The Proceedings of the 8th Pan-African Ornithological Congress: Birds and the Environment, R. Trevor Wilson (ed.). pp. 118-120.

_____. 1996. Food remains found in a nest of the Madagascar buzzard (*Buteo brachypterus*) in the Vohibasia Forest. *Newsletter of the Working Group on Birds of the Madagascar Region* 6:13-14.

Goodman, S., O. Langrand, and B. Rasolonandrasana. 1997. The food habits of *Cryptoprocta ferox* in the high mountain zone of the Andringitra Massif, Madagascar. *Mammalia* 61(2):185-192.

Goodman, S., O. Langrand, and C. Raxworthy. 1993a. Food habits of the Madagascar long-eared owl, *Asio madagascariensis*, in two habitats in southern Madagascar. *Ostrich* 64:79-85.

_____. 1993b. The food habits of the barn owl (*Tyto alba*) at three sites on Madagascar. *Ostrich* 64:160-171.

Goodman, S., S. O'Connor, and L. Langrand. 1993c. A review of predation on lemurs: Implications for the evolution of social behavior in small, nocturnal primates. In: Lemur Social Systems and Their Ecological Basis, P. Kappeler and J. Ganzhorn (eds.). Plenum Press, New York. pp. 51-66.

Goodman, S., L. de Roland, and R. Thorstrom. 1998. Predation on the eastern woolly lemurs (*Avahi laniger*) and other vertebrates by Henst's goshawk (*Accipiter henstii*). *Lemur News* (3):14-15.

Goodman, S. and R. Thorstrom. 1998. The diet of the Madagascar red owl (*Tyto soumagnei*) on the Masoala peninsula, Madagascar. *Wilson Bulletin* 110(3):417-421.

Gould, L., L. Fedigan, and L. Rose. 1997. Why be vigilant? The case of the alpha anaimal. *International Journal of Primatology* 18(3):401-414.

Gouzoules, H., L. M. Fedigan, and L. Fedigan. 1975. Responses of a transplanted troop of Japanese macaques (*Macaca fuscata*) to bobcat (*Lynx rufus*) predation. *Primates* 16(3):335-349.

Green, R. 1991. Wild Cat Species of the World. Basset Publications, Plymouth.

Greene, H. 1997. Snakes: The Evolution of Mystery in Nature. University of California Press, Berkeley. pp. 59-73.

Greene, H. and M. Santana. 1983. Field studies of hunting behavior by bushmasters. *American Zoologist* 23:879.

Grobler, J. and V. Wilson. 1972. Food of the leopard, *Panthera pardus* (Linn.), in the Rhodes Matopos National Park, Rhodesia, as determined by fecal analysis. *Arnoldia* (Rhodesia) 5(34):1- 10.

Grzimek, B. 1975. Grzimek's Animal Life Encyclopedia. Vol. 6: Reptiles. Van Nostrand Reinhold Company, New York.

Gunderson, V. 1977. Some observations on the ecology of *Colobus badius temmincki*, Abuko Nature Reserve, The Gambia, West Africa. *Primates* 18:305-314.

Guggisberg, C. 1963. Simba: The Life of the Lion. Chilton Books, Philadelphia.

_____. 1975. Wild Cats of the World. Taplinger Publishing Company, New York.

Haddow, A. 1952. Field and laboratory studies on an African monkey, *Cercopithecus ascanius schmidtii* Matschie. *Proceedings, Zoological Society of London* 122:297-398.

Hall, K. 1960. Social vigilance behaviour of the chacma baboon, *Papio ursinus*. *Behaviour* 16:261-294.

_____. 1963. Variations in the ecology of the chacma baboon, *Papio ursinus*. *Symposia, Zoological Society of London* 10:1- 28.

_____. 1965. Ecology and behavior of baboons, patas and vervet monkeys in Uganda. In: The Baboon in Medical Research, H. Vagtborg (ed.). University of Texas, San Antonio. pp. 43-61.

_____. 1966. Distribution and adaptation of baboons. *Symposium of the Zoological Society of London* 17:49.73.

Hamai, M., T. Nishida, H. Takasaki, L. Turner. 1992. New records of within-group infanticide and cannibalism in wild chimpanzees. *Primates* 33:151-162.

Hamburg, D. 1971. Aggressive behavior of chimpanzees and baboons in natural habitats. *Journal of Psychiatric Research* 8:385-398.

Hamilton, P. 1981. The leopard *Panthera pardus* and the cheetah *Acinonyx jubatus* in Kenya. Unpublished report for the U.S. Fish and Wildlife Service, the African Wildlife Leadership Foundation and the Government of Kenya.

_____. 1986. Status of the leopard in Kenya, with reference to sub-saharan Africa. In: Cats of the World: Biology, Conservation, and Management, S. Miller and D. Everett (eds.). National Wildlife Federation, Washington, D.C. pp. 447-457.

Hamilton, W., R. Buskirk, and W. Buskirk. 1975. Defensive stoning by baboons. *Nature* 256:488-489.

Hanif, M. 1970. The harpy eagle (*Harpia harpyja*) at Georgetown Zoo. In: International Zoo Yearbook, Vol. 10, J. Lucas (ed.). Zoological Society of London. pp. 24-25.

Harcourt, A. 1978. Strategies of emigration and transfer by primates. *Zeitschrift fuer Tierpsychologie* 48:401-420.

Hardie, S., and H. Buchanan-Smith. 1997. Vigilance in single- and mixed-species groups of tamarins (*Saguinus labiatus* and *Saguinus fuscicollis*). *International Journal of Primatology* 18(2):217-234.

Hart, J. 1978. From subsistence to market: A case study of the Mbuti net hunters. Human Ecology 6(3):325-353.

Hart, J., M. Katembo and K. Punga. 1996. Diet, prey selection and ecological relations of leopard and golden cat in the Ituri Forest, Zaire. *African Journal of Ecology* 34:364-379.

Harvey, P. and P. Greenwood. 1978. Anti-predator defense strategies: Some evolutionary problems. In: Behavioural Ecology: An Evolutionary Approach, First Edition, J. Krebs and N. Davies (eds.). Blackwell Scientific Publications, Oxford, London. pp. 129-151.

Harvey, P., M. Kavanagh, and T. Clutton-Brock. 1978. Sexual dimorphism in primate teeth. *Journal of Zoology, London* 186:475-485.

Hauser, M. 1988. How infant vervet monkeys learn to recognize starling alarm calls: The role of experience. *Behaviour* 105(3- 4):187-201.

Hauser, M. and R. Wrangham. 1990. Recognition of predator and competitor calls in nonhuman primates and birds: A preliminary report. *Ethology* 86(2):116-130.

Hausfater, G. 1976. Predatory behavior of yellow baboons. *Behaviour* 56:44-68.

Hausfater, G. and S. Hrdy (eds.). 1984. Infanticide: Comparative and Evolutionary Perspectives. Aldine Publishing, New York.

Henschel, J. and R. Tilson. 1988. How much does a spotted hyaena eat? Perspective from the Namib Desert. *Afr. Journal of Ecology* 26:247-255.

Hernandez-Camacho, J. and R. Cooper. 1976. The nonhuman primates of Colombia. In: Neotropical Primates: Field Studies and Conservation, R. Thorington, Jr. and P. Heltne (eds.). National Academy of Sciences, Washington, D.C. pp. 35-69.

Hershkovitz, P. 1969. The evolution of mammals on southern continents, VI. The recent mammals of the neotropical region: A zoogeographic and ecological review. *Quarterly Review of Biology* 44:1-70.

Heymann, E. 1987. A field observation of predation on a moustached tamarin (*Saguinas mystax*) by an anaconda. *International Journal of Primatology* 8(2):193-195.

_____. 1990. Reactions of wild tamarins, *Saguinus mystax* and *Saguinus fuscicollis* to avian predators. *International Journal of Primatology* 11(4):327-337.

Hill, R. and P. Lee. 1998. Predation risk as an influence on group size in cercopithecoid primates: Implications for social structure. *Journal of Zoology* 245(Pt. 4):447-456.

Hill, R. and R. Dunbar. 1998. An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping behaviour. *Behaviour* 135(4):411-430.

Hiraiwa-Hasegawa, M., R. Byrne, H. Takakaki, and J. Byrne. 1986. Aggression toward large carnivores by wild chimpanzees of Mahale Mountains National Park, Tanzania. *Folia Primatologica* 47(1):8- 13.

Hirst, S. 1969. Predation as a regulating factor of wild ungulate populations in a Transvaal lowveld nature reserve. *Zoologica Africana* 4:199-230.

Hladik, A. 1980. The dry forest of the west coast of Madagascar: Climate, phenology, and food available for prosimians. In: Nocturnal Malagasy Primates: Ecology, Physiology, and Behavior, P. Charles-Dominique, H. Cooper, A. Hladik, C. Hladik, E. Pages, G. Pariente, A. Petter-Rousseaux, and A. Schilling (eds.). Academic Press, New York. pp. 3-40.

Hladik, C. 1979. Ecology, diet, and social patterning in Old and New World primates. In: Primate Ecology, R. Sussman (ed.). Wiley, New York. pp. 513-542.

Hladik, C., P. Charles-Dominque, and J. Petter. 1980. Feeding strategies of five nocturnal prosimians in the dry forest of the West Coat of Madagascar. In: Nocturnal Malagasy Primates: Ecology, Physiology and Behaviour, P. Charles-Dominque, H. Cooper, A. Hladik, C. Hladik, E. Pages, G. Pariente, A. Petter-Rousseaux, A. Schilling, and J. Petter (eds.). Academic Press, New York. pp. 41-74.

Holcroft, R. 1951. The crowned hawk-eagle: A diary of observations. *African Wildlife* 5:107-110.

Hoogerwerf, A. 1970. Udjung Kulon, The Land of the Last Javan Rhinoceros. E. J. Brill, Leiden.

Hoppe-Dominik, B. 1984. Prey frequency of the leopard (*Panthera pardus*) in the Tai National Park of the Ivory Coast. *Mammalia* 48(4):477-488.

Hosaka, K. 1995. Chimpanzee predation on red colobus in Mahale Mountains National Park, Tanzania. *Anthropological Science* 103(2):160 (Abstract).

Howard, R. and A. Moore. 1991. A Complete Checklist of the Birds of the World, Second Edition. Academic Press, London.

Howell, S. and S. Webb. 1995. A Guide to the Birds of Mexico and Northern Central America. Oxford University Press, Oxford.

Hrdy, S. 1974. Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatologica* 22:19-58.

_____. 1977a. Infanticide as a primate reproductive strategy. *American Scientist* 65:40-49.

_____. 1977b. The Langurs of Abu. Harvard University Press, Cambridge.

_____. 1979. Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology* 1:13-40.

Hrdy, S., C. Janson, and C. van Schaik. 1995. Infantcide: Let's not throw out the baby with the bath water. *Evolutionary Anthropology* 3(5):151-154.

Ihobe, H. 1997. Anti-predator strategy of red colobus monkeys: Changes of activity and height. *Anthropological Science* 105(1):49 (Abstract).

Inagaki, H. and T. Tsukahara. 1991. [Some features of hairs detected in feces of feral lion.] *Reichorui Kenkyu Nempo* 7(2):159.

_____. 1993. A method of identifying chimpanzee hairs in lion feces. *Primates* 34(1):109-112.

Isbell, L. 1990a. Influences of predation and resource competition on the social system of vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya. Ph.D. dissertation, University of California, Davis, California.

_____. 1990b. Sudden short-term increase in mortality of vervet monkeys (*Cercopithecus aethiops*) due to leopard predation in Amboseli National Park, Kenya. *American Journal of Primatology* 21(1):41-52.

_____. 1994a. Predation on primates: Ecological patterns and evolutionary consequences. *Evolutionary Anthropology* 3(2):61-71.

_____. 1994b. The vervet's year of doom. *Natural History* 103(8):48-55.

Isbell, L., D. Cheney, and R. Seyfarth. 1990. Costs and benefits of home range shifts among vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya. *Behavioral Ecology and Sociobiology* 27:351-358.

_____. 1993. Are immigrant vervet monekys, *Cercopithecus aethiops*, at greater risk of mortality than residents? *Animal Behaviour* 45:729-734.

Isbell, L. and T. Young. 1993. Human presence reduces predation in a free-ranging vervet monkey population in Kenya. *Animal Behaviour* 45:1233-1235.

Isemonger, R. 1962. Snakes of Africa: Southern, Central and East. Thomas Nelson and Sons, Johannesburg.

Islam, M. and K. Husain. 1982. A preliminary study on the ecology of the capped langur. *Folia Primatologica* 39:145-159.

Iwamoto, T., A. Mori, and M. Kawai. 1995. [Antipredatory behaviour of gelada baboon.] *Reichorui Kenkyu/Primate Research* 11(3):286.

Iwamoto, T., A. Mori, M. Kawai, and A. Bekele. 1996. Antipredator behaviors of gelada baboons. *Primates* 37(4):389-397.

Izawa, K. 1978. A field study of the ecology and behavior of the black-mantled tamarin (*Saguinus nigricollis*). *Primates* 19:241-274.

Izawa, K. and J. Itani. 1966. Chimpanzees in Kasakati Basin, Tanganyika: I. Ecological study in the rainy season 1963-1964. *Kyoto University African Studies* 1:73-156.

Izawa, K., and T. Nishida. 1963. Monkeys living in the northern limits of their distribution. *Primates* (4):67-88.

Izor, R. 1985. Sloths and other mammalian prey of the harpy eagle. In: The Evolution and Ecology of Armadillos, Sloths, and Vermilinguas, G. Montgomery (ed.). Smithsonian Institution Press, Washington, D.C. pp. 343-346.

Janson, C. 1984. Female choice and mating system of the brown capuchin monkey, *Cebus apella* (Primates: Cebidae). *Zeitschrift fuer Tierpsychologie* 65:177-200.

Janson, C. and C. van Schaik. 1993. Ecological risk aversion in juvenile primates: Slow and steady wins the race. In: Juvenile Primates: Life History, Development, and Behavior, M. Pereira and L. Fairbanks (eds.). Oxford University Press, New York. pp. 57-74.

Janzen, D. 1980. When is it coevolution? *Evolution* 34:611- 612.

Jarvis, M., M. Currie, and N. Palmer. 1980. Food of the crowned hawk eagle in the Cape Province, South Africa. *Ostrich* 51:215- 218.

Johnsingh, A. 1980. Ecology and behavior of the dhole or Indian wild dog, *Cuon alpinus* Pallas 1811, with special reference to predator-prey relations at Bandipur. Ph.D. dissertation, Madurai University, Tamil Nadu, India.

_____. 1983. Large mammalian prey-predators in Bandipur. *Journal of the Bombay Natural History Society* 80(1):1-57.

Johnson, M. 1931. Congorilla. Harcourt and Brace, New York.

Jolly, A. 1972. Hour of birth in primates and man. *Folia Primatologica* 18:108-121.

Jones, C. 1969. Notes on ecological relationship of four lorisids in Rio Muni, West Africa. *Folia Primatologica* 11:255-267.

Jorgenson, J. and K. Redford. 1993. Humans and big cats as predators in the Neotropics. In: Mammals as Predators, N. Dunstone and M. Gorman (eds.). Clarendon Press, Oxford. pp. 367-390.

Joslin, J., H. Fletcher, and J. Emlen. 1964. A comparison of the responses to snakes of lab and wild reared rhesus monkeys. *Animal Behaviour* 22:348-352.

Jouventin, P. 1975. Observations sur le socio-ecologie du mandrill. *Terre Vie* 29:493-532.

Julliot, C. 1994. Predation of a young spider monkey (*Ateles paniscus*) by a crested eagle (*Morphnus guianensis*). *Folia Primatologica* 63(2):75-77.

Kalin, N. 1991. Rhesus monkey defensive behavior: Environmental cues and neurochemical regulation. *Aggressive Behavior* 17(2):77-78.

Kano, T. 1972. Distribution and adaptation of chimpanzees on the eastern shore of Lake Tanganyika. *Kyoto University African Studies* 7:37-129.

Kawabe, M. 1966. One observed case of hunting behavior among wild chimpanzees living in the savanna woodland of western Tanzania. *Primates* 7:393-396.

Kemp, A. 1990. What is a raptor? In: Birds of Prey, I. Newton (ed.). Facts on File, New York. pp. 14-31.

Kennedy, R. 1977. Notes on the biology and population status of the monkey-eating eagle of the Philippines. *Wilson Bulletin* 89(1):1-20.

_____. 1981. The air's noblest flier. *The Filipinas Journal of Science and Culture* 2:33-48.

_____. 1985. Conservation research of the Phillipine eagle. *National Geographic Society Research Reports* 18:401-414.

Kerbis Peterhans, J. 1990. The roles of porcupines, leopards, and kyenas in ungulate carcass dispersal: Implications for paleoanthropology. Ph.D. dissertation, University of Chicago, Chicago, Illinois.

Kern, J. 1964. Observations on the habits of the proboscis monkey made in the Brunei Bay Area, Borneo. *Zoologica* 149:183-191.

Kingdon, J. 1974. East African Mammals, Vol. I. University of Chicago Press, Chicago.

_____. 1977. East African Mammals: An Atlas of Evolution in Africa, Vol. 3(A). Carnivores. Academic Press, New York.

_____. 1988. The role of face patterns in guenons. In: A Primate Radiation: Evolutionary Biology of the African Guenons, A. Gautier-Hion, F. Bourliere, J. Gautier, and J. Kingdon (eds.). Cambridge University Press, Cambridge. pp. 228-243.

Kinzey, W., A. Rosenberger, P. Heisler, D. Prowse, and J. Trilling. 1977. A preliminary field investigation of the yellow handed titi monkey, *Callicebus torquatus torquatus*, in northern Peru. *Primates* 18:159-181.

Kitchener, A. 1991. The Natural History of the Wild Cats. Comstock Publishing Associates, Ithaca.

Klein, L. 1974. Agonistic behavior in neotropical primates. In: Primate Aggression, Territoriality, and Xenophobia, R. Holloway (ed.). Academic Press, New York. pp. 77-122.

Klump, G. and M. Shalter. 1984. Acoustic behaviour of birds and mammals in the predator context. I: Factors affecting the structure of alarm signals. II: The functional significance and evolution of alarm signals. *Zeitschrift fuer Tierpsychologie* 66:189-226.

Kortlandt, A. 1967. Experimentation with chimpanzees in the wild. In: Neue Ergenbnisse der Primatologie Progress in Primatology, First Congress of the International Primatological Society, Frankfurt (May 26-July 30, 1966), D. Starck, R. Schneider, and H. Kuhn (eds.). Gustav Fischer Verlag, Stuttgart. pp. 208-224.

Krebs, J. 1975. Behavioral aspects of predation. In: Perspectives in Ethology, Vol. I, P. Bateson and P. Klopfer (eds.). Plenum Press, New York. pp. 73-111.

Krishnan, M. 1972. An ecological survey of the larger mammals of peninsular India. Part I. *Journal of Bombay Natural History Society* 68:503-555.

Kruuk, H. 1970. Interactions between populations of spotted hyaenas (*Crocuta crocuta*, Erxleben) and their prey species. In: Animal Populations in Relation to Their Food Resources, A. Watson (ed.). Blackwell Scientific, Oxford. pp. 359-374.

_____. 1972a. The Spotted Hyena: A Study of Predation and Social Behavior. University of Chicago Press, Chicago.

_____. 1972b. Surplus killing by carnivores. *Journal of Zoology, London* 166:233-244.

_____. 1975. Functional aspects of social hunting by carnivores. In: Function and Evolution in Behaviour, G. Baerends, C. Beer, and A. Manning (eds.). Clarendon Press, Oxford. pp. 119-141.

_____. 1986. Interactions between Felidae and their prey species: A review. In: Cats of the World: Biology, Conservation and Management, S. Miller and D. Everett (eds.). National Wildlife Federation, Washington, D.C. pp. 353-374.

Kruuk, H. and M. Turner. 1967. Comparative notes on predation by lion, leopard, cheetah, and wild dog in the Serengeti area, East Africa. *Mammalia* 31(1):1-27.

Kummer, H. 1968. Social Organization of Hamadryas Baboons: A Field Study. University of Chicago Press, Chicago.

_____. 1971. Primate Societies. Aldine-Atherton, Chicago.

_____. 1995. In Quest of the Sacred Baboon: A Scientist's Journey. Princeton University Press, Princeton.

Kuroda, S., S. Suzuki, and T. Nishihara. 1996. Preliminary report on predatory behavior and meat sharing in tschego chimpanzees (*Pan troglodytes troglodytes*) in the Nkoki Forest, northern Congo. *Primates* 37(3):253-259.

Lamprecht, J. 1978. The relationship between food competition and foraging group size in some large carnivores: A hypothesis. *Zeitschrift fuer Tierpsychologie* 46:337-343.

Langrand, O. 1990. Guide to the Birds of Madagascar. Yale University Press, New Haven.

Lehmann, F. 1959. Contribuciones al estudio de la faune de Colombia. XIV. Neuvas observaciones sobre *Oroaetus isidori* (Des Murs). *Novedades Colombianas: Contribuciones Cientificas del Museo der Historia Natural der la Universidad del Cauca, Popayan-Colombia* 1(4):169-195.

Leland, L. and T. Struhsaker. 1993. Teamwork tactics: Kibale forest's monkeys and eagles each depend on strategic cooperation for survival. *Natural History* 102(4):42-48.

le Roux, P. and J. Skinner. 1989. A note on the ecology of the leopard (*Panthera pardus*, Linnaeus) in the Londolozi Game Reserve, South Africa. *African Journal of Ecology* 27:167-171.

Leutenegger, W. and J. Kelley. 1977. Relationship of sexual dimorphism in canine size and body size to social, behavioral, and ecological correlates in anthropoid primates. *Primates* 18:117-136.

Lindburg, D. 1971. The rhesus monkey in North India. In: Primate Behavior, Vol. 2, L. Rosenblum (ed.). Academic Press, New York. pp. 1-106.

_____. 1977. Feeding behaviour and diet of rhesus (*Macaca mulatta*) in a Siwalik Forest in North India. In: Primate Ecology, T. Clutton-Brock (ed.). Academic Press, London. pp. 223-249.

Lindsay, N. 1979. A report on the field study of Geoffroy's tamarin, *Saguinus oedipus geoffroyi. Dodo, Journal of the Jersey Wildlife Preservation Trust* 16:27-51.

Lineaweaver, T. and R. Backus. 1970. The Natural History of Sharks. Lyons & Burford Publishers, New York.

Lloyd, H. 1980. The Red Fox. Batsford, London.

Lockie, J. 1959. The estimation of the food of foxes. *Journal of Wildlife Management* 23:224-227.

Lumpkin, S. 1993. Great Creatures of the World: Big Cats. Facts on File, New York.

Macdonald, D. (ed.). 1984a. All the World's Animals: Primates. Torstar Books, New York.

_____. 1984b. The Encyclopedia of Mammals, Facts on File, New York.

_____. 1992. The Velvet Claw: A Natural History of the Carnivores. BBC Books, London.

MacDonald, S. and J. Pinel. 1991. Information gathering: A component of the defensive behavior of rats and Old-World monkeys. *Psychological Record* 41(2):207-215.

Macedonia, J. 1990a. Vocal communication and anti-predator behavior in the ringtailed lemur *(Lemur catta)*. Ph.D. dissertation, Duke University, Durham, North Carolina.

_____. 1990b. What is communicated in the anti-predator calls of lemurs: Evidence from playback experiments with ringtailed and ruffed lemurs. *Ethology* 86(3):177-190.

_____. 1993. Adaptation and phylogenetic constraints in the antipredator behavior of ringtailed and ruffed lemurs. In: Lemur Social Systems and Their Ecological Basis, P. Kappeler and J. Ganzhorn (eds.). Plenum Press, New York. pp. 67-84.

MacKinnon, J. 1974. The behavior and ecology of wild orang-utans (*Pongo pygmaeus*). *Animal Behaviour* 22:3-74.

MacKinnon, J. and K. MacKinnon. 1980. The behavior of wild spectral tarsiers. *International Journal of Primatology* 1:361- 379.

Maclatchey, A. 1937. Etude des oiseau de Gabon. *Oiseau* 7:71- 76.

Maclean, G. 1985. Roberts' Birds of Southern Africa. New Holland, Amsterdam.

Maisels, F., J. Gautier, A. Cruickshank, and J. Bosefe. 1993. Attacks by crowned hawk eagles (*Stephanoaetus coronatus*) on monkeys in Zaire. *Folia Primatologica* 61(3):157-159.

Makacha, S. and G. Schaller. 1969. Observations on lions in the Lake Manyara National Park, Tanzania. *East African Wildlife Journal* 7:99-103.

Manley, G. 1985. Primates and predators: The example of *Presbytis senex*. *Dyn* 8:1-17.

Mansfield, E. 1986. Basic Statistics with Application. W.W. Norton, New York.

Marais, E. 1939. My Friends the Baboons. Human and Rousseau, Capetown.

Martin, R. 1972. A preliminary field study of the lesser mouse lemur (*Microcebus murinus* J. Miller 1777). *Zeitschrift fur Tierpsychologie* 9:43-89.

Martin, R. and S. Bearder. 1979. Radio bush baby. *Natural History* 88(8):76-81.

Masataka, N. 1993. Categorical responses to natural and synthesized alarm calls in Goeldi's monkeys (*Callimico goeldii*). *Primates* 24:40-51.

Mattison, C. 1988. Keeping and Breeding Snakes. Blandford Press, London.

_____. 1995. The Encyclopedia of Snakes. Facts on File, New York.

Maynard Smith, J. 1965. The evolution of alarm calls. *American Naturalist* 100:637-650.

McConnell, E., P. Basson, V. DeVos, B. Myers, and R. Kuntz. 1974. A survey of diseases among 100 free-ranging baboons (*Papio ursinus*) from the Kruger National Park. *Onderstepoort Journal of Veterinary Research* 41:97-168.

McDougal, C. 1977. The Face of the Tiger. Rivington Books, London.

McFarland, K. 1994. Update on gorillas in Cross River State, Nigeria. *Gorilla Conservation News* 8:13-14.

McGrew, W. 1976. An encounter between a leopard and a group of chimpanzees at Gombe National Park. Report. 11 pp.

_____. 1979. Evolutionary implications of sex differences in chimpanzee predation and tool use. In: The Great Apes, D. Hamburg and E. McCown (eds.). Cummings, Menlo Park. pp. 441-463.

McGrew, W., C. Tutin, and P. Baldwin. 1978. Primates preying upon vertebrates: New records from west Africa. *Carnivore* 1:41-45.

_____. 1979. New data on meat-eating by wild chimpanzees. *Current Anthropology* 20:238-239.

McKenzie, A. 1991. Co-operative hunting in the black-backed jackal *Canis mesomelas*. *Dissertation Abstracts International Science and English* B52(4):1902.

Mehrtens, J. 1987. Living Snakes of the World. Sterling Publications, New York.

Meinertzhagen, R. 1959. Pirates and Predators. Oliver and Boyd, Edinburgh.

Mills, M. 1978. Foraging behaviour of the brown hyena (*Hyaena brunnea* Thunberg, 1820) in the southern Kalahari. *Z. Tierpshychol.* 48:113-141.

_____. 1989. The comparative behavioral ecology of hyenas: The importance of diet and food dispertion. In: Carnivore Behavior, Ecology and Evolution, J. Gittleman (ed.). Cornell University Press, Ithaca. pp. 125-142.

Mills, M. and H. Biggs. 1993. Prey apportionment and related ecological relationships between large carnivores in Kruger National Park. In: Mammals as Predators, N. Dunstone and M. Gorman (eds.) Clarendon Press, Oxford. pp. 253-268.

Mineka, S., R. Keir, and V. Price. 1980. Fear of snakes in wild- and laboratory-reared rhesus monkeys (*Macaca mulata*). *Animal Learning Behavior* 8:653-663.

Mitchell, B., J. Shenton, and J. Uys. 1965. Predation on large mammals in the Kafue National Park, Zambia. *Zoologica Africana* 1(2):297-318.

Mitchell, C., S. Boinski, and C. van Schaik. 1991. Competitive regimes and female bonding in two species of squirrel monkeys (*Saimiri oerstedi* and *S. sciureus*). *Behavioral Ecology and Sociobiology* 28:55-60.

Mittermeier, R. 1987. Effects of hunting on rain forest primates. In: Primate Conservation in the Tropical Rain Forest, C. Marsh and R. Mittermeier (eds.). Alan R. Liss, New York. pp. 109-146.

Mittermeier, R. and D. Cheney. 1987. Conservation of primates and their habitats. In: Primate Societies, B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker (eds.). University of Chicago Press, Chicago. pp. 477-496.

Mittermeier, R. and A. Coimbra-Filho. 1977. Primate conservation in Brazilian Amazonia. In: Primate Conservation, HRH Rainier and G. Bourne (eds.) Academic Press, New York. pp. 117- 166.

Mondolfi, E. 1986. Notes on the biology and status of the small wild cats in Venezuela. In: Cats of the World: Biology, Conservation, and Management, S. Miller and D. Everett (eds.). National Wildlife Federation. pp. 125-146.

Montgomery, G. and A. Rand. 1978. Movements, body temperature and hunting strategy of a boa constrictor. *Copeia* 1978:532-533.

Moody, M. and E. Menzel. 1976. Vocalizations and their behavioral contexts in the tamarin, *Saguinus fuscicollis*. *Folia Primatologica* 25:73-94.

Moore, J. 1984. Female transfer in primates. *International Journal of Primatology* 5:537-589.

Montgomery, G. and A. Rand. 1978. Movements, body temperature and hunting strategy of a boa constrictor. *Copeia* 1978:532-533.

Moynihan, M. 1970. Some behavior patterns of platyrrhine monkeys, II: *Saguinus geoffroyi* and some other tamarins. *Smithsonian Contributions to Zoology* 28:1-77.

_____. 1976a. Notes on the ecology and behavior of the pygmy marmoset (*Cebuella pygmaea*) in Amazonian Colombia. In: Neotropical Primates: Field Studies and Conservation, R. Thorington, Jr. and P. Heltne (eds.). National Academy of Science, Washington, D.C.

_____. 1976b. The New World Primates: Adaptive Radiation and the Evolution of Social Behavior, Languages, and Intelligence. Princeton University Press, Princeton.

Msuya, C. 1993. Feeding habits of crowned eagles, *Stephanoaetus coronatus*, in Kiwengoma Forest Reserve, Matumbi Hills, Tanzania. In: Proceedings of the 8th Pan-African Ornithological Congress: Birds and the Environment, R. Trevor Wilson (ed.). pp. 118-120.

Muckenhirn, N. 1972. Leaf-eaters and their predators in Ceylon: Ecological roles of gray langurs, *Presbytis entellus*, and leopards. Ph.D. dissertation, University of Maryland, College Park, Maryland.

Muckenhirn, N. and J. Eisenberg. 1973. Home ranges and predation of the Ceylon leopard. In: The World's Cats: Ecology and Conservation, Vol. 1, R. Eaton (ed.) The Proceedings of an International Symposium held at Lion Country Safari, Laguna Hills, California, on March 15-17, 1971. World Wildlife Safari, Winston. pp. 142-175.

Mukherjee, A. and S. Gupta. 1965. Habits of the rhesus macaque *Macaca mulatta* (Zimmermann) in the Sunderbans, 24-Parganas, West Bengal. *Journal of the Bombay Natural History Society* 62:145-146.

Mukherjee, R. 1982. Phayre's leaf monkey (*Presbytis phayrei*, Blyth, 1847) of Tripura. *Journal of the Bombay Natural History Society* 79(1):47-56.

Müller, K. (undated). Ecology of the masked titi monkey (*Callicebus personatus melanochir*). Deutsches Primatenzentrum, Göttingen, Germany. Unpublished manuscript.

Murphy, J. and R. Henderson. 1997. Tales of Giant Snakes: A Historical Natural History of Anacondas and Pythons. Krieger Publishing Company, Malabar, Florida.

Nagel, C. 1973. A comparison of anubis baboons, hamadryas baboons, and their hybrids at a species border in Ethiopia. *Folia Primatologica* 19:104-165.

Nakamura, M. 1997. First observed case of chimpanzee predation on yellow baboons (*Papio cynocephalus*) at the Mahale Mountains National Park. *Pan Africa News* 4(2):9-11.

Nekaris, K. 2000. The socioecology of the Mysore slender loris (*Loris tardigradus lydekkerianus*) in Dindigul, Tamil Nadu, South India. Ph.D. dissertation, Washington University, St. Louis, Missouri.

Nettlebeck, A. 1995. Predation on barking deer by reticulated python and dholes in Kao Yai National Park. *Natural History Bulletin of the Siam Society* 43(2):369-373.

Newman, K. 1970. Giant eagle owl. *Witwatersrand Bird Club News Sheet* 71:16.

Newton, P. 1985. A note on golden jackals (*Canis aureus*) and their relationship with langurs (*Presbytis entellus*) in Kanha Tiger Reserve. *Journal of the Bombay Natural History Society* 82:633-636.

Neyman, P. 1977. Aspects of the ecology and social organization of free-ranging cotton-top tamarins (*Saguinus oedipus*) and the conservation status of the species. In: The Biology and Conservation of the Callitrichidae, D. Kleiman (ed.). Smithsonian Institution Press, Washington. pp. 39-72.

Niemitz, C. 1972. Puzzle about *Tarsius*. *Sarawak Mus. J.* 20:329-337.

Nishida, F. 1968. The social groups of wild chimpanzees in the Mahale mountains. *Primates* 9:167-224.

_____. 1972. A note on the ecology of the red colobus monkeys living in the Mahale mountains. *Primates* 13:57-64.

Nishida, T. and K. Kawanaka. 1985. Within-group cannibalism by adult male chimpanzees. *Primates* 26(3):274-284.

Nishida, T., H. Takasaki, and Y. Takahata. 1990. Demography and reproductive profiles. In: The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies, T. Nishida (ed.). University of Tokyo, Tokyo. pp. 63-97.

Nishida, T., S. Uehara, and R. Nyundo. 1979. Predatory behavior among wild chimpanzees of the Mahale mountains. *Primates* 20(1):1-20.

Noë, R. 1996. Anti-predation strategies of colobus monkeys in the Tai Park, Ivory Coast. *ISP/ASP Congress Abstracts* #019 (Abstract).

Noë, R., and R. Bshary. 1997. The formation of red colobus-diana monkey associations under predation pressure from chimpanzees. *Proceedings of the Royal Society of London* B264(1379):253-259.

Norikoshi, K. 1983. Prevalent phenomenon of predation observed among wild chimpanzees of the Mahale Mountains, Tanzania. *Journal of the Anthropological Society of Nippon* 91(4):475-480.

Norris, C. 1961. Relationship between predator and herbivore. *Loris; A Journal of Ceylon Wildlife* 9:83-89.

Norris, J. 1990. The semantics of *Cebus olivaceus* alarm calls: Object designation and attribution. *Dissertation Abstracts International* B52(3):1160

Norton, P., G. Avery, S. Henley, and, A. Lawson. 1986. Prey of leopards in four mountain areas of the southwestern Cape Province, South Africa. *South African Journal of Wildlife Research* 16(2):47-52.

Nowak, R. 1991. Walker's Mammals of the World, Vols. I and II. The Johns Hopkins University Press, Baltimore.

_____. 1999. Walker's Mammals of the World, Vol. I. The Johns Hopkins University Press, Baltimore.

Nowell, K. and P. Jackson. 1996. Wild Cats: Status Survey and Conservation Action Plan. IUCN/SSC Cat Specialist Group, Gland, Switzerland.

Nunes, C., J. Bicca-Marques, K. Schacht, and A. de Alencar Araripe. 1998. Reaction of wild emperor tamarins to the presence of snakes. *Neotropical Primates* 6(1):20.

Oates, J. 1977. The guereza and its food. In: Primate Ecology, T. Clutton-Brock (ed.). Academic Press, London. pp. 276-323.

Oda, R. and N. Masataka. 1996. Interspecific responses of ringtailed lemurs to playbacks of antipredator alarm calls given by sifakas. *International Primatological Society/American Society of Primatologists Congressional Abstracts* #501.

Olmos, F. 1994. Jaguar predation on muriqui, *Brachyteles arachnoides*. *Neotropical Primates* 2(2).

Oppenheimer, J. 1977. *Presbytis entellus*, the Hanuman langur. In: Primate Conservation, HRH Rainier III and G. Bourne (eds.). Academic Press, New York. pp. 469-512.

Osada, Y. 1991. [A comparision of fear responses to snakes of wild- and lab-reared squirrel monkeys.] *Reichorui Kenkyu Nempo* 7(2):131 (Abstract).

Overdorff, D. and S. Strait. 1995. Life history and predation in *Eulemur rubriventer* in Madagascar. *American Journal of Physical Anthropology* Suppl. 19:164-165.

Owen, D. 1980. Survival in the Wild: Camouflage and Mimicry. The University of Chicago Press, Chicago.

Owens, M. and D. Owens. 1978. Feeding ecology and its influence on social organization in brown hyenas (*Hyaena brunnea*) of the central Kalahari Desert. *East African Wildlife Journal* 16(2):113-136.

Packer, C., D. Scheel, and A. Pusey. 1990. Why lions form groups: Food is not enough. *American Naturalist* 136(1):1-19.

Paine, R. 1976. Size-limited predation. *Ecology* 57:858-873.

Passamani, M. 1995. Field observation of a group of Geoffroy's marmosets mobbing a margay cat. *Folia Primatologica* 64:163-166.

Passamani, M. and J. Passamani. 1995. Losses of reintroduced Geoffroy's marmoset (*Callithrix geoffroyii*). Manuscript. 3 pp.

Paulraj, S. 1995. Prey-predator relationships with special reference to the tiger, panther and dhole competitions in Kalakad-Mundanthurai Tiger Reserve (Tirunelveli District - Tamil Nadu). *Indian Forester* (October):922-30.

Payne, J. and A. Downey. 1949. Resented the spectators. *African Wild Life* 3:211.

Payne, R. 1971. Acoustic location of prey in barn owls (*Tyto alba*). *Journal of Experimental Biology* 54:535.

Peetz, A., M. Norconk, and W. Kinzey. 1992. Predation by jaguar on howler monkeys (*Alouatta seniculus*) in Venezuela. *American Journal of Primatology* 28:223-228.

Pereira, M. and J. Macedonia. 1991. Ringtailed lemur anti-predator calls denote predator class not response urgency. *Animal Behaviour* 41(3):543-544.

Peres, C. 1990. A harpy eagle successfully captures an adult male red howler monkey. *Wilson Bulletin* 102(3):560-561.

_____. 1991. Ecology of mixed-species groups of tamarins in Amazonian terra firme forests. Ph.D. dissertation, University of Cambridge, Cambridge, United Kingdom.

_____. 1993. Anti-predation benefits in a mixed-species group of Amazonian tamarins. *Folia Primatologica* 61:61-76.

Peters, R. and L. Mech. 1975. Behavioral and intellectual adaptations of selected mammalian predators to the problem of hunting large animals. In: Socioecology and Psychology of Primates, R. Tuttle (ed.). Mouton Publishers, The Hague. pp. 279-300.

Petter, J., R. Albignac, and Y. Rumpler. 1977. Faune de Madagascar 44: Mammiferes, Lemuriens (Primates Prosimiens). ORSTOM/CNRS, Paris.

Petter, J. and C. Hladik. 1970. Observations sur le domaine vital et la densité de population de *Loris tardigradus* dans les forêts de Ceylan. *Mammalia* 3:394-409.

Pfeffer, P. 1989. Predators and Predation: The Struggle for Life in the Animal World, P. Pfeffer (ed.). Facts on File, Inc., New York.

Phillips, K. 1995. Differing responses to a predator (*Eira barbara*) by *Alouatta* and *Cebus*. *Neotropical Primates* 3(2):45-46.

Phythian-Adams, E. 1939. Behaviour of monkeys when attacked. *Journal of Bombay Natural History Society* 41:653.

Pienaar, U. 1969. Predator-prey relationships among the larger mammals of the Kruger National Park. *Koedoe* (12):108-176.

Pitman, C. and J. Adamson. 1978. Notes on the ecology and ethology of the giant eagle owl, *Bubo lacteus*. *Honeyguide* 96:26-43.

Pitts, A. 1996. Predation by *Eulemur fulvus rufus* on an infant *Lemur catta* at Berenty Reserve, Madagascar. *Folia Primatologica* 66:169-171.

Pocock, T. 1939. Fauna of British India. Mammalia I. Primates and Carnivora. Taylor & Francis, London.

Poirier, F. 1970. The Nilgiri langur (*Presbytis johnii*) of South India. In: Primate Behaviour: Developments in Field and Laboratory Research, Vol. I, L. Rosenblum (ed.). Academic Press, New York. pp. 251-283.

Pola, Y. and C. Snowdon. 1975. The vocalizations of pygmy marmosets (*Cebuella pygmaea*). *Animal Behaviour* 23:826-842.

Pook, A. and G. Pook. 1981. A field study of the socio-ecology of the Goeldi's monkey in northern Bolivia. *Folia Primatologica* 35:288-312.

Pooley, A. 1989. Food and feeding habits. In: Crocodiles and Alligators, C. Ross (ed.). Facts on File, New York. pp. 76-91.

Pooley, A. and C. Gans. 1976. The Nile crocodile. *Scientific American* 234:114-124.

Pope, C. 1980. The Giant Snakes: The Natural History of the Boa Constrictor, the Anaconda, and the Largest Pythons. Alfred A. Knopf, New York.

Popp, J. 1978. Male baboons and evolutionary principles. Ph.D. dissertation, Harvard University, Cambridge, Massachusetts.

Pounds, C. 1981. Niche overlap in sympatric populations of stoats (*Mustela erminea*) and weasels (*M. nivalis*) in northeast Scotland. Ph.D. dissertation, University of Aberdeen, Scotland.

Powell, R. 1978. A comparison of fisher and weasel hunting behavior. *Carnivore* 1:28-34.

Powzyk, J. 1997. The socioecology of two sympatric indrids, *Propithecus diadema diadema* and *Indri indri*: A comparision of feeding strategies and their possible repercussions on species-specific behaviors. Ph.D. dissertation, Duke University, Durham, North Carolina.

Prater, S. 1971. The Book of Indian Animals, Third Edition. Bombay Natural History Society, Bombay.

Price, C. 1985. Swayambu rhesus monkeys: A behavioral study, Kathmandu, Nepal. Senior thesis, University of Wisconsin, Madison.

Printes, R., C. Costa, and K. Strier. 1996. Possible predation on two infant muriquis, *Brachyteles arachnoides*, at the Estacao Biologica de Caratinga, Minas Gerais, Brazil. *Neotropical Primates* 4(3):85-86.

Pulliam, H. and T. Caraco. 1984. Living in groups: Is there an optimal group size? In: Behavioural Ecology: An Evolutionary Approach, 2nd edition, J. Krebs and N. Davies (eds.). Blackwell Scientific Publications, New York. pp. 122-147.

Queiroz, H. 1994. Uso dos recursos, do tempo e do es paco pelos mammiferos folivoros arboricolas dos matas do médio solimoes. Master's thesis, Federal University of Pará, Brasil.

Rabinowitz, A. 1988. The clouded leopard in Taiwan. *Oryx* 22:46-47.

_____. 1991. Chasing the Dragon's Tail: The Struggle to Save Thailand's Wild Cats. Doubleday, New York.

Rabinowitz, A. and B. Nottingham. 1986. Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. *Journal of Zoology, London* A210:145-159.

Raemaekers, J. and D. Chivers. 1980. Socioecology of Malayan forest primates. In: Malayan Forest Primates: Ten Years' Study in Tropical Rain Forest, D. Chivers (ed.). Plenum Press, New York. 279-331.

Rahaman, H. 1973. The langurs of the Gir Sanctuary (Gujarat): A preliminary survey. *Journal of the Bombay Natural History Society* 70:295-314.

Rahm, U. 1967. Observations during chimpanzee capture in the Congo. In: Neue Ergenbnisse der Primatologie Progress in Primatology, First Congress of the International Primatological Society, Frankfurt (May 26-July 30, 1966), D. Starck, R. Schneider, and H. Kuhn (eds.). Gustav Fischer Verlag, Stuttgart. pp. 197-207.

Rajaram, A. and R. Menon. 1986. A scanning electron microscope study of the hair keratins of some animals of the Indian subcontinent: A preliminary report. *Journal of the Bombay Natural History Society* 83(2):427-429.

Rajpurohit, L. S. and V. Sommer. 1991. Sex differences in mortality among langurs (*Presbytis entellus*) of Jodhpur, Rajasthan. *Folia Primatologica* 56:17-27.

Rakotondravony, D., S. Goodman, and V. Soarimalala. 1998. Predation on *Hapalemur griseus griseus* by *Boa manditra* (Boidae) in the littoral forest of eastern Madagascar. *Folia Primatologica* 69(6):405-408.

Ramakrishnan, U., R. Coss, and N. Pelkey. (In press.). Tiger decline caused by the reduction of large ungulate prey: Evidence from a study of leopard diet in southern India. *Biological Conservation.*

Ramirez, M. 1989. Feeding ecology and demography of the moustached tamarin (*Saguinus mystax*) in northeastern Peru. Ph.D. dissertation, The City University of New York, New York.

Ransom, T. 1981. Beach Troop of the Gombe. Associated University Press, East Brunswick, New Jersey.

Rasmussen, D. 1983. Correlates of patterns of range use of a troop of yellow baboons (*Papio cynocephalus*). II. Spatial structure, cover density, food gathering and individual behaviour patterns. *Animal Behaviour* 31:834-56.

Rasmussen, K. 1980. Consort behaviour and mate selection in yellow baboons (*Papio cynocepalus*). Ph.D. dissertation, University of Cambridge, Cambridge, United Kingdom.

Rasoloarison, M. 1994. Contribution a l'etude de l'alimentation de deux rapaces nocturnes: *Tyto alba* Scopoli 1769 et *Asio madagascariensis* Smith 1834 par analyse des pelotes de rejection aboutissant a l'inventaire faunistique des forets de la region de Morondava. Ph.D. dissertation, Universite d'Antananarivo, Antananarivo, Madagascar.

Rasoloarison, R., B. Rasolonandrasana, J. Ganzhorn, and S. Goodman. 1995. Predation on vertebrates in the Kirindy Forest, Western Madagascar. *Ecotropica* 1:59-65.

Rasolonandrasana, B. 1994. Contribution a l'etude de l'alimentation de *Cryptoprocta ferox* Bennet (1833) dans son milieu naturel. Ph.D. dissertation, Universite d'Antananarivo, Antananarivo, Madagascar.

Ratsirarson, J. 1985. Contribution a l'etude comparative de l'ecoethologie de *Lemur catta* dans deux habitats diferents de la reserve speciale de Beza-Mahafaly. Memoire de fin d'etudes, Universite de Madagascar, Antananarivo, Madagascar.

Rautenbach, I. and J. Nel. 1978. Coexistence in Transvaal carnivora. *Bulletin of the Carnegie Museum of Natural History* 6:138-145.

Redmond, I. 1998. The African Bushmeat Trade – A Recipe for Extinction. Ape Alliance, UK. 4 pp.

Rettig, N. 1977. In quest of the snatcher. *Audubon Magazine* 79:26-49.

_____. 1978. Breeding behavior of the harpy eagle (*Harpia harpyja*). *Auk* 95:629-643.

_____. 1995. Remote world of the harpy eagle. *National Geographic Magazine* 187(2):40-49.

Rhine, R. 1975. The order of movement of yellow baboons (*Papio cynocephalus*). *Folia Primatologica* 23:72-104.

Rhine, R. and B. Westlund. 1981. Adult male positioning in baboon progressions: Order and chaos revisited. *Folia Primatologica* 35:77-116.

Rice, C. 1986. Observations on predators and prey at Eravikulam National Park, Kerala, India. *Journal of the Bombay Natural History Society* 83(2):283-305.

Richard, A. 1978. Behavioral Variation: Case Study of a Malagasy Lemur. Bucknell University Press, Lewisburg, Pennsylvania.

_____. 1985. Primates in Nature. W. H. Freeman and Company, New York.

Richard, A., P. Rakotomanga, and M. Schwartz. 1991. Demography of *Propithecus verreauxi* at Beza Mahafaly, Madagascar: Sex ratio, survival, and fertility 1984-1988. *American Journal of Physical Anthropology* 84:307-322.

Rijksen, H. 1978. A Field Study on Sumatran Orangutans, (*Pongo pygmaeus abelii*): Ecology, Behaviour and Conservation. Veenman and Zonen, Wageningen.

Rijksen, H. and A. Rijksen-Graatsma. 1975. Orang-utan rescue work in north Sumatra. *Oryx* 13(1):63-73.

Ripley, S. 1965. The ecology and social behavior of the Ceylon gray langur (*Presbytis entellus thersites*). Ph.D. dissertation, University of California, Berkeley, California.

_____. 1970. Leaves and leaf monkeys: The social organization of foraging in gray langurs (*Presbytis entellus thersites*). In: Old World Monkeys, J. Napier and P. Napier (eds.). Academic Press, New York. pp. 481-509.

Rodman, P. 1988. Resources and group sizes of forest primates. In: The Ecology of Social Behaviour, C. Slobodchikoff (ed.). Academic Press, New York. pp. 83-108.

Ron, T. 1993. The dynamics of social relationships among female chacma baboons (*Papio cynocephalus ursinus*) in Julułand. Ph.D. dissertation. University of Natal, South Africa.

Roonwal, M., and S. Mohnot. 1977. Primates of South Asia. Harvard University Press, Cambridge.

Rose, L. and L. Fedigan. 1995. Vigilance in white-faced capuchins, *Cebus capucinus*, in Costa Rica. *Animal Behavior* 49:63-70.

Rosenzweig, M. 1966. Community structure in sympatric Carnivora. *Journal of Mammalogy* 47:602-612.

Rosevear, D. 1974. The Carnivores of West Africa. British Museum of Natural History, London.

Ross, C. 1993. Predator mobbing by an all-male band of Hanuman langurs (*Presbytis entellus*). *Primates* 34(1):105-107.

Ross, C. A. (ed.) 1989. Crocodiles and Alligators. Facts on File, New York.

Ross, C. A. and W. Magnusson. 1989. Living Crocodilians. In: Crocodiles and Alligators, C. Ross (ed.). Facts on File, New York. pp. 58-73.

Roughgarden, J. 1983. The theory of coevolution. In: Coevolution, D. Futuyma and M. Slatkin (eds.). Sinauer Associates, Sunderland. pp. 33-64.

Rowe-Rowe, D. 1978. Comparative prey capture and food studies of South African mustelids. *Mammalia* 42:175-196.

Rowell, T. 1969. Long-term changes in a population of Ugandan baboons. *Folia Primatologica* 11:241-254.

Rudran, R. 1978. Socioecology of the blue monkeys (*Cercopithicus mitis stuhlmanni*) of the Kibale Forest, Uganda. *Smithsonian Contributions to Zoology* (249):1-88.

Russell, R. 1977. The behavior, ecology, and physiology of a nocturnal primate, *Lepilemur mustelinus*. Ph.D. dissertation, Duke University, Durham, North Carolina.

Rylands, A. 1981. Preliminary field observations on the marmoset, *Callithrix humeralifer intermedius* (Hershkovitz, 1977) at Dardanelos, Rio Aripuana, Mato Grosso. *Primates* 22(1):46-59

Saayman, G. 1971. Baboons responses to predators. *African Wild Life* 25(2):46-49.

Sauther, M. 1989. Anti-predation behavior in troops of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *International Journal of Primatology* 10(6):595-606.

Schaller, G. 1963. The Mountain Gorilla. University of Chicago Press, Chicago.

_____. 1967. The Deer and the Tiger. University of Chicago Press, Chicago.

_____. 1972. The Serengeti Lion. A Study of Predator-Prey Relations. University of Chicago Press, Chicago.

_____. 1983. Mammals and their biomass on a Brazilian ranch. *Arquivos de Zoologia,* Vol. 31, Fasciculo I. Museu de Zoologia da Universidade de São Paulo, Brasil.

Schaller, G. and P. Crawshaw. 1980. Movement patterns of jaguar. *Biotropica* 12(3):161-168.

Schaller, G., H. Jinchu, P. Wenshi, and Z. Jing. 1985. The Giant Pandas of Wolong. University of Chicago Press, Chicago.

Schaller, G., H. Li, J. Ren, M. Qiu, and H. Wang. 1987. Status of large mammals in the Taxkorgan Reserve, Xinjiang, China. *Biological Conservation* 42:53-71.

Schaller, G. and J. Vasconcelos. 1978. Jaguar predation on capybara. *Zeitschrift fuer Saugetierkunde* 43:296-301.

Searcy, Y. and N. Caine. 1998. Reactions of captive Geoffroy's marmosets to experimentally presented calls of a raptorial and non-raptorial bird. *American Journal of Primatology* 45(2):206 (Abstract).

Seidensticker, J. 1976. On the ecological separation between tigers and leopards. *Biotropica* 8:225-234.

_____. 1983. Predation by *Panthera* cats and measures of human influence in habitats of South Asian monkeys. *International Journal of Primatology* 4(3):323-327.

_____. 1985. Primates as prey of *Panthera* cats in South Asian habitats. Paper given at the seventh annual meeting of the American Society of Primatologists, University of Buffalo State University of New York, Niagra Falls, New York, June 1-4, 1985.

_____. 1991. Leopards. In: Great Cats: Majestic Creatures of the Wild, J. Seidensticker and S. Lumpkin (eds.). Rodale Press, Emmaus, Pennsylvania. pp. 106-115.

Seidensticker, J. and C. McDougal. 1993. Tiger predatory behaviour, ecology and conservation. In: Mammals as Predators, N. Dunstone and M. Gorman (eds.). Clarendon Press, Oxford. pp. 105-125.

Seidensticker, J. and I. Suyono. 1980. The Javan Tiger and the Meru-Betiri Reserve, a Plan for Management. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.

Selous, E. and E. Banks. 1935. The clouded leopard of Sarawak. *Sarawak Musuem Journal* 4(3):263-266.

Sessions, P. 1966. Notes on the birds of Lengetia farm Mau Narok. *Journal of East African Natural History Society* 26(1):18-48.

Seth-Smith, D. 1910. On the monkey-eating eagle of the Philippines (*Pithecophaga jefferyi*). *Ibis* 4 (9th Series):285-290.

Seyfarth, R. and D. Cheney. 1980. The ontogeny of vervet monkey (*Cercopithecus aethiops*) alarm calling behavior: A preliminary report. *Zeitschrift fuer Tierpsychologie* 54(1):37-56.

_____. 1986. Vocal development in vervet monkeys. *Animal Behaviour* 34:1640-1658.

Seyfarth, R., D. Cheney, and P. Marler. 1980a. Monkey responses to three different alarm calls: Evidence for predator classification and semantic communication. *Science* 210:801-803.

_____. 1980b. Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behaviour* 28:1070-1094.

Sharma, B. 1994. High Altitude Wildlife of India. Oxford & IBH Publishing Company, New Dehli.

Sherman, P. 1991. Harpy eagle predation on a red howler. *Folia Primatologica* 56(1):53-56.

Shine, R. 1991. Why do larger snakes eat larger prey items? *Functional Ecology* 5(4):493-502.

Shine, R., P. Harlow, J. Keogh, and Boeadi. 1998. The influence of sex and body size on food habits of a giant tropical snake, *Python reticulatus*. *Functional Ecology* 12(2):248-258.

Sigg, H. 1980. Differentiation of female positions in hamadryas one-male units. *Zeitschrift fuer Tierpsychologie* 53:265-302.

Silva-López, G., F. Garcia-Orduña, and E. Rodríguez-Luna. 1988. The status of *Ateles geoffroyi* and *Alouatta palliata* in disturbed forest areas of Sierra de Santa Martha, Mexico. *Primate Conservation* 9:53-61.

Silva-López, G., J. Jiménez-Huerta, and J. Benítez-Rodríguez. 1993. Availability of resources to primates and humans in a forest fragment of Sierra de Santa Martha, Mexico. *Neotropical Primates* 1(4):3-6.

Simonds, P. 1965. The bonnet macaque in South India. In: Primate Behavior: Field Studies of Monkeys and Apes, I. DeVore (ed.). Holt, Rinehart, and Winston, New York. pp. 175-196.

Simons, J. 1966. The presence of leopard and a study of food debris in the leopard lairs of the Mount Suswa Caves, Kenya. *Bulletin of Cave Exploration Group East Africa* 1:51-69.

Sinha, D. 1972. The Birhors. In: Hunters and Gatherers Today, M. Bicchieri (ed.). Holt, Rinehart, and Winston, New York. pp. 371-403.

Skinner, J. 1976. Ecology of the brown hyaena, *Hyaena brunnea*, in the Transvaal with a distribution map for Southern Africa. *South African Journal of Science* 72:262-269.

Skinner, J. and R. Smithers. 1990. The Mammals of the Southern African Sub-Region. University of Pretoria Press, Pretoria.

Skorupa, J. 1989. Crowned eagles, *Stephanoaetus coronatus*, in rainforest: Observations on breeding chronology and diet at a nest in Uganda. *Ibis* 131:294-298.

Skorupa, J., J. Kalina, T. Butynski, G. Tabor, and E. Kellog. 1985. Notes on the breeding biology of Cassin's hawk eagle *Hieraaetus africanus*. *Ibis* 127:120-122.

Smeenk, C. 1974. Comparative ecological studies of some East African birds of prey. *Ardea* 62:1-97.

Smith, R. 1978. Movement patterns and feeding behavior of the leopard in the Rhodes Matopos National Park, Rhodesia. *Carnivore* 1:58-69.

Smithers, R. 1968. A Check List and Atlas of the Mammals of Botswana. Trustees of the National Museum of Rhodesia. 169 pp.

_____. 1971. The mammals of Botswana. *Mem. Natn. Mus. Rhodesia* 4.

Smuts, B. 1985. Sex and Friendship in Baboons. Aldine de Gruyter Press, New York.

Sokal, R. and J. Rohlf. 1981. Biometry: The Principles and Practice of Statistics in Biological Research, Second Edition. W.H. Freeman, New York.

Sommer, V., D. Mendoza-Grandados, and U. Reichard. 1998. Predation risk causes grouping pattern in Hanuman langurs (*Presbytis entellus*). *Folia Primatologica* 69(4):223-224 (Abstract).

Srikosamatara, S. 1988. Group size in wedge-capped capuchin monkeys (*Cebus olivaceus*): Vulnerability to predators, intragroup and intergroup feeding competition. *Dissertation Abstracts International* B48(8):2235.

Srivastava, A. 1991. Cultural transmission of snake-mobbing in free-ranging hanuman langurs. *Folia Primatologica* 56(2):117- 120.

Srivastava, K., A. Bhardwaj, C. Abraham, and V. Zacharias. 1996. Food habits of mammalian predators in Periyar Tiger Reserve, South India. *Indian Forester* 122(10:877-883.

Stacey, P. 1986. Group size and foraging efficiency in yellow baboons. *Behavioural Ecology and Sociobiology* 18:175-187.

Stafford, B., and F. Ferreira. 1995. Predation attempts on Callitrichids in the Altantic coastal rain forest of Brazil. *Folia Primatologica* 65(4):229-233.

Stafford-Deitsch, J. 1987. Sharks: A Photographer's Story. Sierra Club Books, San Francisco.

Stander, P. 1992. Foraging dynamics of lions in a semi-arid environment. *Canadian Journal of Zoology* 70(1):8-21.

Stanford, C. 1989. Predation on capped langurs (*Presbytis pileata*) by cooperatively hunting jackals (*Canis aureus*). *American Journal of Primatology* 19:53-56.

_____. 1990. The capped langur (*Presbytis pileata*) in Bangladesh: Ecology and social behavior of a primate living in one-male groups. Ph.D. dissertation, University of California, Berkeley, California.

_____. 1991. The capped langur in Bangladesh: Behavioral ecology and reproductive tactics. *Contributions to Primatology* 26:1-198.

_____. 1995a. Chimpanzee hunting behavior and human evolution. *American Scientist* 83(3):255-261.

_____. 1995b. The influence of chimpanzee predation on group size and anti-predator behaviour in red colobus monkeys. *Animal Behaviour* 49(3):577-587.

_____. 1996. The hunting ecology of wild chimpanzees: Implications for the evolutionary ecology of Pliocene hominids. *American Anthropologist* 98(1):96-113.

_____. 1998. Predation and male bonds in primate societies. *Behaviour* 135(4):513-533.

Stanford, C., J. Wallis, H. Matama, and J. Goodall. 1994a. Patterns of predation by chimpanzee on red colobus monkeys in Gombe National Park, 1982-1991. *American Journal of Physical Anthropology* 94(2):213-228.

Stanford, C., J. Wallis, E. Mpongo, and J. Goodall. 1994b. Hunting decisions in wild chimpanzees. *Behaviour* 131(1-2):1-18.

Stanford, C. and R. Wrangham. 1998. Chimpanzee and Red Colobus: The Ecology of Predator and Prey. Harvard University Press, Cambridge.

Starin, E. 1978. A preliminary investigation of home range use in the Gir Forest langur. *Primates* 19(3):551-568.

_____. 1991. Socioecology of the red colobus monkey in The Gambia with particular reference to female-male differences and transfer patterns. Ph.D. dissertation, The City University of New York, New York.

Starin, E. and G. Burghardt. 1992. African rock pythons in the Gambia: Observations on natural history and interactions with primates. *Snake* 24(1):50-62.

Stelzner, J. and K. Strier. 1981. Hyena predation on an adult male baboon. *Mammalia* 45:259-260.

Sterck, E. (In press.). The langurs of the Gunung Leuser National Park. In: The Gunung Leuser National Park: Home of the Orangutan, C. van Schaik and J. Supriatna (eds.).

Stevenson, P. and M. Quinoñes. 1993. Vertical stratification of four New World primates at Tinigua National Park, Colombia. *Field Studies of New World Monkey, La Macarena, Colombia* 8:11-18.

Stevenson-Hamilton, J. 1947. Wildlife in South Africa. Cassell and Co., London.

Steyn, P. 1973. Observations on the tawny eagle. *The Ostrich* 44:1-22.

_____. 1980. Bateleur: Breeding and food. *The Ostrich* 51(3):168-178.

_____. 1982. Birds of Prey of Southern Africa. David Philip, Capetown.

Stoltz, L. 1977. The population dynamics of baboons (*Papio* ursinus) Kerr 1792, in the Transvaal. Ph.D. dissertation, University of Pretoria, Pretoria, South Africa.

Stoltz, L. and G. Saayman. 1970. Ecology and behaviour of baboons in the Northern Transvaal. *Ann. Transvaal Mus.* 26:99-143.

Struhsaker, T. 1967a. Auditory communication among vervet monkeys (*Cercopithecus aethiops*). In: Social Communication Among Primates, S. Altmann (ed.). University of Chicago Press, Chicago. pp. 281-324.

_____. 1967b. Ecology of vervet monkeys (*Cercopithecus aethiops*) in the Masai-Amboseli Game Reserve, Kenya. *Ecology* 48:891-904.

_____. 1969. Correlates of ecology and social organization among African cercopithecines. *Folia Primatologica* 11:80-118.

_____. 1970. Notes on *Galagoides demidovii* in Cameroon. *Mammalia* 34:207-211

_____. 1975. The Red Colobus Monkey. University of Chicago Press, Chicago.

_____. 1981. Polyspecific association among tropical rainforest primates. *Zeitschrift fuer Tierpsychologie* 57:268-304.

Struhsaker, T. and J. Gartlan. 1970. Observations on the behaviour and ecology of the patas monkey (*Erythrocebus patas*) in the Waza Reserve, Cameroon. *Journal of the Zoological Society, London* 161:49-63.

Struhsaker, T. and M. Leakey. 1990. Prey selectivity by crowned hawk-eagles on monkeys in the Kibale Forest, Uganda. *Behavioural Ecology and Sociobiology* 26(6):435-443.

Suckling, J., E. Suckling, and A. Walker. 1969. Suggested function of the vascular bundles in the limbs of *Perodictus potto*. *Nature* 221:379-380.

Sugardjito, J., Nurhuda. 1981. Meat-eating behavior in wild orangutan *Pongo pymaeus*. *Primates* 22:414-416.

Sugiyama, Y. 1976. Life history of male Japanese monkeys. *Advances in the Study of Behavior* 7:255-284.

Sunquist, M. 1981. The social organization of tigers (*Panthera tigris*) in Royal Chitwan National Park, Nepal. *Smithsonian Contributions to Zoology* 336:1-98.

Sunquist, F. and M. Sunquist. 1988. Tiger Moon. University of Chicago Press, Chicago.

Sunquist, M. and F. Sunquist. 1989. Ecological constraints on predation by large felids. In: Carnivore Behavior, Ecology, and Evolution, J. Gittleman (ed.). Cornell University Press, Ithaca. pp. 283-301.

Sunquist, M., F. Sunquist, and D. Daneke. 1989. Ecological separation in Venezuelan llanos carnivore community. In: Advances in Neotropical Mammalogy, K. Redford and J. Eisenberg (eds.). The Sandhill Crane Press, Gainesville. pp. 197-232.

Sussman, R. 1974. Ecological distinctions in sympatric species of *Lemur*. In: Prosimian Biology, R. Martin, G. Doyle and A. Walker (eds.). Duckworth, London. pp. 75-108.

_____. 1977. Feeding behaviour of *Lemur catta* and *Lemur fulvus*. In: Primate Ecology, T. Clutton-Brock (ed.). Academic Press, London. pp. 1-37.

_____. 1999. Primate Ecology and Social Structure, Volume I. Lorises, Lemurs and Tarsiers. Pearson Costum Publishing, Needham, Massachusetts.

Sussman, R., J. Cheverud, and T. Bartlett. 1995. Infant killing as an evolutionary strategy: Reality or myth? *Evolutionary Anthropology* 3(5):149-151.

Sussman, R. and W. Kinzey. 1984. The ecological role of the Callitrichidae: A review. *American Journal of Physical Anthropology* 64:419-449.

Suzuki, A. 1971. Carnivory and cannibalism observed among forest-living chimpanzees. *Journal of the Anthropological Society of Nippon* 79:30-48.

Takahata, Y. 1985. Adult male chimpanzees kill and eat a male newborn infant: Newly observed intragroup infanticide and cannibalism in Mahale National Park, Tanzania. *Folia Primatologica* 44:121-128.

Takahata, Y., T. Hasegawa, and T. Nishida. 1984. Chimpanzee predation in the Mahale mountains from August 1979 to May 1982. *International Journal of Primatology* 5:213-233.

Takahata, Y., S. Suzuki, N. Okayasu, and D. Hill. 1994. Troop extinction and fusion in wild Japanese macaques of Yakushima Island, Japan. *American Journal of Primatology* 33:317-322.

Tamang, K. 1982. The status of the tiger, *Panthera tigris tigris* and its impact on principal prey populations in the Royal Chitawan National Park, Nepal. Ph.D. dissertation, Michigan State University, Ann Arbor, Michigan.

Tarboton, W. 1989. African Birds of Prey. Cornell University Press, Ithaca.

Tarboton, W. and D. Allan. 1984. The Status and Conservation of Birds of Prey in the Transvaal. Transvaal Museum, Pretoria.

Taylor Halvorsen, K. 1986. Combining results from independent investigations: Meta-analysis in medical research. In: Medical Uses of Statistics, J. Bailar and F. Mosteller (eds.). New England Journal of Medicine Books, Waltham, Massachusetts. pp. 392-416.

Teleki, G. 1973a. The omnivorous chimpanzee. *Scientific American* 228:32-42.

_____. 1973b. The Predatory Behavior of Wild Chimpanzees. Bucknell University Press, Lewisburg, Pennsylvania.

_____. 1975. Primate subsistence patterns, collector predators, and gatherer hunters. *Journal of Human Evolution* 4(2):125-184.

Teleki, G., E. Hunt Jr., and J. Pfifferling. 1976. Demographic observations (1963-1973) on the chimpanzees of Gombe National Park, Tanzania. *Journal of Human Evolution* 5:559-598.

Tenaza, R. and R. Tilson. 1977. Evolution of long-distance alarm calls in Kloss's gibbon. *Nature* 268:233-235.

Terborgh, J. 1983. Five New World Primates: A Study in Comparative Ecology. Princeton University Press, Princeton.

_____. 1986. The social systems of New World primates: An adaptionist view. In: Primate Ecology and Conservation, J. Else and P. Lee (eds.). Cambridge University Press, Cambridge. pp. 199-211.

_____. 1990a. Mixed flocks and polyspecific associations: Cost and benefits of mixed groups to birds and monkeys. *American Journal of Primatology* 21(2):87-100.

_____. 1990b. The role of felid predators in Neotropical forests. *Vida Silvestre Neotropica* 2:3-5.

Terborgh, J. and C. Janson. 1986. The socioecology of primate groups. *Annual Review of Ecology and Systematics* 17:111-135.

Thapar, V. 1986. Tiger: Portrait of a Predator. Facts on File Publications, New York.

Thiollay, J. 1985. Species diversity and comparative ecology of rainforest falconiforms on three continents. In: Conservation Studies on Raptors, I. Newton and R. Chancellor (eds.). ICBP Technical Publication No. 5, Cambridge. pp. 155-166.

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

Treves, A. 1997. Self-protection in primates. Ph.D. dissertation, Harvard University, Cambridge, Massachusetts.

_____. 1999. Has predation shaped the social systems of arboreal primates? *International Journal of Primatology* 20(1):35-67.

Tsukahara, T. 1993. Lions eat chimpanzees: The first evidence of predation by lions on wild chimpanzees. *American Journal of Primatology* 29(1):1-11.

Turnbull-Kemp, P. 1967. The Leopard. Howard Timmins, Capetown.

Tutin, C. and K. Benirschke. 1991. Possible osteomyelitis of skull causes death of a wild lowland gorilla in the Lopé Reserve, Gabon. *Journal of Medical Primatology* 20:357-360.

Tutin, C. and M. Fernandez. 1993. Predation by chimpanzees. *American Journal of Primatology* 30:195-211.

Tutin, C., W. McGrew, and P. Baldwin. 1981. Responses of wild chimpanzees to potential predators. In: Primate Behavior and Sociobiology, B. Chiarelli and R. Corruccini (eds.). Springer-Verlag, Berlin. pp. 136-141.

_____. 1983. Social organization of savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Senegal. *Primates* 24:154-173.

Uehara, S., T. Nishida, M. Hamai, T. Hasegawa, H. Hayaki, M. Huffman, K. Kawanaka, S. Kobayashi, J. Mitani, U. Takahata, H. Takasaki, and T. Tsukahara. 1992. Characteristics of predation by the chimpanzees in the Mahale Mountains National Park, Tanzania. In: Topics in Primatology, Human Origins, Volume 1, T. Nishida, W. McGrew, P. Marler, M. Pickford, and F. de Wall (eds.). University of Tokyo Press, Tokyo. pp. 143-158.

Uhde, N. and V. Sommer. 1998. The importance of predation risk for gibbon behavior and evolution. *Folia Primatologica* 69(4):224 (Abstract).

Utami, S. and J. van Hooff. 1997. Meat-eating by adult female Sumatran orangutans (*Pongo pygmaeus abelii*). *American Journal of Primatology* 43:159-165.

van Eyssen, J. 1949. Rogue elephant's dramatic charge into van. *African Wild Life* 3(1):7-16.

van Lawick-Goodall, J. 1968a. A preliminary report on expressive movements and communication in the Gombe Stream chimpanzees. In: Primates: Studies in Adaptation and Variability, P. Jay (ed.). Holt, Rinehart, and Winston, New York. pp. 313-350.

_____. 1968b. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs* 1:165-311.

van Orsdol, K. 1984. Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. *African Journal of Ecology* 22(2):79-99.

van Schaik, C. 1983. Why are diurnal primates living in groups? *Behaviour* 87(1-2):120-143.

van Schaik, C. and M. Horstermann. 1994. Predation risk and the number of adult males in a primate group: A comparative test. *Behavioural Ecology and Sociobiology* 35:261-272.

van Schaik, C. and T. Mitrasetia. 1990. Changes in the behaviour of wild long-tailed macaques (*Macaca fascicularis*) after encounters with a model python. *Folia Primatologica* 55(2):104-108.

van Schaik, C. and J. van Hooff. 1983. On the ultimate causes of primate social systems. *Behaviour* 85:91-117.

van Schaik, C. and M. van Noordwijk. 1985. Evolutionary effect of absence of felids on the social organization of the macaques on the island of Simeulue (*Macaca fascicularis fusca*, Miller 1903). *Folia Primatologica* 44:138-147.

_____. 1989. The special role of male *Cebus* monkeys in predation avoidance and its effects on group composition. *Behavioural Ecology and Sociobiology* 24:265-276.

van Schaik, M. van Noordwijk, R. de Boer, and I. den Tonkelaar. 1983a. The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). *Behavioural Ecology and Sociobiology* 13:173-181.

van Schaik, C., M. van Noordwijk, B. Warsono, and E. Sutriono. 1983b. Party size and early detection of predators in Sumatran forest primates. *Primates* 24(2):211-221.

Vencl, F. 1977. A case of convergence in vocal signals between marmosets and birds. *American Naturalist* 111:777-782.

Vermeij, G. 1982. Unsuccessful predation and evolution. *American Naturalist* 120:701-720.

Vernon, C. 1965. The black eagle survey in the Matopos, Rhodesia. *Arnoldia (Rhodesia)* 2(6):1-9.

_____. 1972. An analysis of owl pellets collected in southern Africa. *Ostrich* 43(2):109-113.

_____. 1980. Prey remains from nests of Bateleur Eagles. *Honeyguide* 103/4:22-25.

Verschuren, J. 1958. Ecologie et biologie des grandes mammiferes. Exploration du Parc National de Garamba (Inst. Parcs Nat. Congo Belge: Brussels) 9.

Vezina, A. 1985. Empirical relationships between predator and prey size among terrestrial vertebrate predators. *Oecologia* 67:555-565.

Vitale, A., E. Visalberghi, and C. de Lillo. 1991. Responses to a snake model in captive crab-eating macaques (*Macaca fascicularis*) and captive tufted capuchins (*Cebus apella*). *International Journal of Primatology* 12(3):277-286.

Vogel, C. 1976. Oekologie, lebensweise und socialverhalten der grauen languren (*Presbytis entellus*, Dufresne 1797) in un terschiedlichen biotopen indiens. *Fortschritte der Verhaltens borschung* 17:1-160.

von Hippel, F. 1998. Use of sleeping trees by black and white colobus monkeys (*Colobus guereza*) in the Kakamega Forest, Kenya. *American Journal of Primatology* 45(3):281-290.

Voous, K. 1969. Predation potential in birds of prey from Surinam. *Ardea* 57:117-148.

_____. 1988. Owls of the Northern Hemisphere. MIT Press, Cambridge.

Wahome, J., T. Rowell, and H. Tsingalia. 1993. The natural history of de Brazza's monkey in Kenya. *International Journal of Primatology* 14(3):445-466.

Wahungu, G. 1993. Niche overlap and competition between the Tana crested mangabey and yellow baboon. Master's thesis, Moi University, Kenya.

Wall, F. 1921. *Ophidia taprobanica* or the Snakes of Ceylon. H.R. Cottle, Colombo. pp. 56-63.

Waser, P. 1980a. Polyspecific associations of *Cercocebus albigena*: Geographic variation and ecological correlates. *Folia Primatologica* 33:57-76.

_____. 1980b. Small nocturnal carnivores: Ecological studies in the Serengeti. *African Journal of Ecology* 18:167-185.

_____. 1984. "Chance" and mixed-species associations. *Behavioural Ecology and Sociobiology* 15:197-202.

Waser, P. and K. Homewood. 1979. Cost-benefit approaches to territoriality. *Behavioural Ecology and Sociobiology* 6:115-119.

Washburn, S. and D. Hamburg. 1968. Aggressive behavior in Old World monkeys and apes. In: Primates: Studies in Adaptation and Variability, P. Jay (ed.). Holt, Rinehart, and Winston, New York. pp. 458-478.

Watson, R. 1986. Ecology, biology and population dynamics of the bateleur eagle *Terathopius ecaudatus*. Ph.D. dissertation, University of Witwatersrand, South Africa.

Webb, D. and A. Fannin. 1975. Notes on the breeding of the crowned eagle. *Honeyguide* 82:36-37.

Welch, M. and M. Bekoff. 1982. Predation by wild coyotes: Behavioral and ecological analyses. *Journal of Mammalogy* 63:118-127.

Westergaard, G. and S. Suomi. 1994. Aimed throwing of stones by tufted capuchin monkeys (*Cebus apella*). *Human Evolution* 9(4):323-329.

Whitacre, D., R. Thorstrom, N. Rettig, J. Madrid, H. Madrid, M. Córdova, J. Lopez, and J. Sutter. 1994. Nest observations and new distributional records for the crested eagle (*Morphnus guianensis*). The Peregrine Fund, Boise, ID. Unpublished manuscript.

Whiten, A. and R. Byrne. 1988. Tactical deception in primates. *Behavioral and Brain Sciences* 11:233-244.

Whitfield, P. 1978. The Hunters. Simon and Schuster, New York.

Whitten, A. 1980. The Kloss gibbon in the Siberut rain forest. Ph.D. dissertation, University of Cambridge, Cambridge, United Kingdom.

Wiens, F., and A. Zitzmann. 1999. Predation on a wild slow loris, *Nycticebus coucang* by a reticulated python, *Python reticulatus*. *Folia Primatologica* 70:362-364.

Willis, M. 1995. Dental variation in Asian colobines. Ph.D. dissertation, Washington University, St. Louis, Missouri.

Wilson, J., P. Stewart, G. Ramangason, A. Denning, and M. Hutchings. 1989. Ecology and conservation of the crowned lemur, *Lemur coronatus*, at Ankarana, N. Madagascar. *Folia Primatologica* 52(1-2):1-26.

Wilson, V. 1976. The leopard in eastern Zambia. In: The World's Cats: Contributions to Biology, Ecology, Behavior and Evolution, Volume 3, No. 2, R. Eaton (ed.). Carnivore Research Institute c/o Burke Museum, University of Washington, Seattle. pp. 29-38.

Wolfheim, J. 1983. Primates of the World: Distribution, Abundance, and Conservation. University of Washington Press, Seattle.

Wrangham, R. 1974. Predation by chimpanzees in the Gombe National Park, Tanzania. *Primate Eye* 2:6.

_____. 1979. On the evolution of ape social systems. *Social Science Inf.* 18:335-368.

_____. 1980. An ecological model of female-bonded primate groups. *Behaviour* 75:262-300.

Wrangham, R. and E. Bergmann Riss. 1990. Rates of predation on mammals by Gombe chimpanzees. *Primates* 31:157-170.

Wright, B. 1960. Predation on big game in East Africa. *Journal of Wildlife Management* 24:1-15.

Wright, P. 1982. Adaptive advantages of nocturnality in *Aotus*. *American Journal of Physical Anthropology* 57(2):242.

_____. 1984. Biparental care in *Aotus trivirgatus* and *Callicebus moloch*. In: Female Primates: Studies by Women Primatologists, M. Small (ed.). Alan R. Liss, New York. pp. 59-75.

_____. 1985. The costs and benfits of nocturnality of *Aotus trivirgatus* (the night monkey). Ph.D. dissertation, The City University of New York, New York.

_____. 1989. The nocturnal primate niche in the New World. *Journal of Human Evolution* 18:635-658.

_____. 1994. The behavior and ecology of the owl monkey. In: Aotus: The Owl Monkey, J. Baer, R. Weller, and I. Kakoma (eds.). Academic Press, San Diego. pp. 97-112.

_____. 1995. Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *International Journal of Primatology* 16(5):835-854.

_____. 1998. Impact of predation risk on the behaviour of *Propithecus diadema edwardsi* in the rain forest of Madagascar. *Behaviour* 135(4):483-512.

Wright, P., S. Heckscher and A. Dunham. 1997. Predation on Milne-Edward's sifaka (*Propithecus diadema edwardsi*) by the fossa (*Cryptoprocta ferox*) in the rain forest of southeastern Madagascar. *Folia Primatologica* 68(1):34-43.

_____. 1998. Predation of rain forest prosimians in Ranomafana National Park, Madagascar. *Folia Primatologica* 69(Suppl. 1):401 (Abstract).

Wright, P. and L. Martin. 1995. Predation, pollination and torpor in two nocturnal prosimians: *Cheirogaleus major* and *Microcebus rufus* in the rainforest of Madagascar. In: Creatures of the Dark: The Nocturnal Prosimians, L. Alterman, G. Doyle, and M. Izard, (eds.). Plenum Press, New York. pp. 45-60.

Yeager, C. 1991. Possible anti-predator behavior associated with river crossings by proboscis monkeys (*Nasalis larvatus*). *American Journal of Primatology* 24(1):61-66.

Yost, J. and P. Kelley. 1983. Shotguns, blowguns, and spears: The analysis of technological efficiency. In: Adaptive Responses of Native Amazonians, R. Hames and W. Vickers (eds.). Academic Press, New York. pp. 189-224.

Young, T. 1994. Predation risk, predation rate, and the effectiveness of anti-predator traits. *Evolutionary Anthropology* 3(2):67.

Zahl, P. 1960. Face to face with gorillas in Central Africa. *National Geographic Magazine* 117:114-137.

Zapfe, H. 1981. Ein schadel von *Mesopithecus* mit biss-spuren. [A skull of *Mesopithecus* with bite marks.] *Folia Primatologica* 35:248-258.

Ziegler, T., and E. Heymann. 1996. Response to snake models in different species of Callitrichidae. *Primate Report* 44:58-59.

Zueberbuehler, K., R. Noë, and R. Seyfarth. 1997. Diana monkey long-distance calls: Messages for conspecifics and predators. *Animal Behaviour* 53(3):589-604.

APPENDIX 1.

Table A1.1 provides the published source or personal communication by questionnaire used to designate 176 species as observed or suspected primate predators.

TABLE A1.1. Sources for known or suspected primate predators.

DIURNAL RAPTORS, OWLS, AND OTHER PREDATORY BIRDS		SOURCE
Madagascar cuckoo hawk	*Aviceda madagascariensis*	Charles-Dominique & Petter (1980)
Grey-headed kite	*Leptodon cayanensis*	Printes et al. (1996)
Double-toothed kite	*Harpagus bidentatus*	E. Heymann (pers. comm.)
Black kite	*Milvus migrans*	Sauther (1989)
Brahminy kite	*Haliastur indus*	Dittus (1975)
White-bellied sea eagle	*Haliaeetus leucogaster*	Dittus (1975)
African fish eagle	*H. vocifer*	Steyn (1982)
Madagascar fish eagle	*H. vociferoides*	Wilson et al. (1989)
Tank eagle	*Ichthyophaga ichthyaetus*	Dittus (1975)
Short-toed eagle	*Circaetus gallicus*	Brown (1971a)
Black-chested snake eagle	*C. pectoralis*	Seyfarth et al. (1980b)
Brown snake eagle	*C. cinereus*	Brown (1971a)
Bateleur	*Terathopius ecaudatus*	Steyn (1982)
Crested serpent eagle	*Spilornis cheela*	Boonratana (1994)
Madagascar serpent eagle	*Eutriorchis astur*	R. Thorstrom (pers. comm.)
African harrier hawk	*Polyboroides typus*	Richard (1978)
Madagascar harrier hawk	*P. radiatus*	Langrand (1990)
Madagascar goshawk	*Accipiter francesii*	Wilson et al. (1989)
Madagascar sparrow hawk	*A. madagascariensis*	Langrand (1990)
Bi-colored hawk	*A. bicolor*	Terborgh (1983)
Henst's goshawk	*A. henstii*	Goodman et al. (1998)
Slate-colored hawk	*Leucopternis schistacea*	Glanz (1991)
White hawk	*L. albicollis*	Boinski (1987)
Common black hawk	*Buteogallus anthracinus*	Lindsay (1979)
Great black hawk	*B. urubitinga*	Lindsay (1979)
Crowned solitary eagle	*Harpyhaliaetus coronatus*	Garcia & Braza (1993)
Black-collared hawk	*Busarellus nigricollis*	Heymann (1990)
Grey hawk	*Buteo nitidus*	Boinski (1987)
Roadside hawk	*B. magnirostris*	Boinski (1987)

Madagascar buzzard	*B. brachypterus*	Sauther (1989)
Guiana crested eagle	*Morphnus guianensis*	Mitchell et al. (1991)
Harpy eagle	*Harpia harpyja*	Voous (1969)
Philippine eagle	*Pithecophaga jefferyi*	Kennedy (1977)
Asian black eagle	*Ictinaetus malayensis*	Stanford (1989)
Lesser spotted eagle	*Aquila pomarina*	Treves (1997)
Tawny eagle	*A. rapax*	Brown (1971a)
Imperial eagle	*A. heliaca*	Brown (1971a)
Golden eagle	*A. chrysaetos*	Izawa & Nishida (1963)
Verreaux's eagle	*A. verreauxii*	Gargett (1971)
Wahlberg's eagle	*Hieraaetus wahlbergi*	Steyn (1982)
Bonelli's eagle	*H. fasciatus*	Brown (1971)
African hawk eagle	*H. spilogaster*	Steyn (1982)
Chestnut-bellied hawk eagle	*H. kienerii*	Manley (1985)
Black and white hawk eagle	*Spizastur melanoleucus*	Mitchell et al. (1991)
Martial eagle	*Polomaetus bellicosus*	Brown & Amadon (1989)
Cassin's hawk eagle	*Spizaetus africanus*	Skorupa et al. (1985)
Crested hawk eagle	*S. cirrhatus*	Manley (1985)
Hodgson's hawk eagle	*S. nipalensis*	Manley (1985)
Black hawk eagle	*S. tyrannus*	Fischer (1984)
Ornate hawk eagle	*S. ornatus*	Boinski (1987)
Isidor's eagle	*S. isidori*	Fischer (1984)
Crowned eagle	*Stephanoaetus coronatus*	Brown (1971b)
Red-throated caracara	*Daptrius americanus*	Boinski (1987)
Common caracara	*Polyborus plancus*	L. Rose (pers. comm.)
Laughing falcon	*Herpetotheres cachinnans*	L. Rose (pers. comm.)
Barred forest falcon	*Micrastur ruficollis*	Izawa (1978)
Slaty-backed forest falcon	*M. mirandollei*	Rylands (1981)
Collared forest falcon	*M. semitorquatus*	Boinski (1987)
Madagascar kestrel	*Falco newtoni*	Wilson et al. (1989)
Madagascar banded kestrel	*F. zoniventris*	Wilson et al. (1989)
Madagascar red owl	*Tyto soumagnei*	Goodman & Thorstrom (1998)
Barn owl (Madagascar)	*T. alba affinis*	Langrand (1990)
Barn owl (Neotropics)	*T. a. guatemalae*	A. Baker (pers. comm.)
Madagascar scops owl	*Otus rutilus*	Wilson et al. (1989)
Great horned owl	*Bubo virginianus*	Wright (1994)
Northern eagle owl	*B. bubo*	J. Moore (pers. comm.)
Desert eagle owl	*B. ascalaphus*	Brown (1971a)
Spotted eagle owl	*B. africanus*	Steyn (1982)
Fraser's eagle owl	*B. poensis*	Kingdon (1974)
Forest eagle owl	*B. nipalensis*	Dittus (1975)
Shelley's eagle owl	*B. shelleyi*	Kingdon (1974)

Verreaux's eagle owl	*B. lacteus*	Brown (1971a)
Brown fish owl	*B. zeylonensis*	Dittus (1975)
Burrowing owl	*Athene cunicularia*	Stafford & Ferreira (1995)
Madagascar long-eared owl	*Asio madagascariensis*	Goodman et al. (1991)
Squirrel cuckoo	*Piaya cayana*	H. Queiroz (pers. comm.)
Grey-breasted mountain toucan	*Andigena hypoglauca*	M. Norconk (pers. comm.)
Keel-billed toucan	*Ramphastos sulfuratus*	Dawson (1976)
Chestnut-mandibled toucan	*R. swainsonii*	Boinski (1987)
Hook-billed vanga	*Vanga curvirostris*	Goodman et al. (1993c)
Jungle crow	*Corvus macrorhynchos*	Manley (1985)
Pied crow	*C. albus*	Wilson et al. (1989
FELIDS		**SOURCE**
Lion	*Panthera leo*	Kingdon (1974)
Jaguar	*P. onca*	Schaller & Vasconcelos (1978)
Leopard	*P. pardus*	Smithers (1971)
Tiger	*P. tigris*	Sunquist & Sunquist (1989)
Cheetah	*Acinonyx jubatus*	Kingdon (1974)
Clouded leopard	*Neofelis nebulosa*	Nowell & Jackson (1996)
African golden cat	*Felis aurata*	Nowell & Jackson (1996)
Leopard cat	*F. bengalensis*	Bishop (1975)
Caracal	*F. caracal*	Kingdon (1974)
Feral cat	*F. catus*	MacKinnon & MacKinnon (1980)
Jungle cat	*F. chaus*	Bishop (1975)
Puma	*F. concolor*	Jorgenson & Redford (1993)
Ocelot	*F. pardalis*	Hershkovitz (1969)
Rusty-spotted cat	*F. rubignosa*	Manley (1985)
Serval	*F. serval*	Kingdon (1974)
African wildcat	*F. silvestris lybica*	Struhsaker (1967b)
Asiatic golden cat	*F. temmincki*	MacKinnon (1974)
Oncilla	*F. tigrina*	Nowell & Jackson (1996)
Fishing cat	*F. viverrina*	Manley (1985)
Margay	*F. wiedii*	Hershkovitz (1969)
Jaguarundi	*F. yagouroundi*	Dawson (1976)
CANIDS		**SOURCE**
Side-striped jackal	*Canis adustus*	Chism et al. (1983)
Golden jackal	*C. aureus*	Stanford (1989)

Blackbacked jackal	*C. mesomelas*	Chism et al. (1983)
Domestic dog	*C. familiaris*	Kingdon (1974)
Coyote	*C. latrans*	Wright (1985)
Wolf	*C. lupus*	Biquand et al. (1994)
African hunting dog	*Lycaon pictus*	Kingdon (1974)
Dhole	*Cuon alpinus*	Johnsingh (1983)
Raccoon dog	*Nyctereutes procyonoides*	N. Itoigawa (pers. comm.)
Red fox	*Vulpes vulpes*	N. Itoigawa (pers. comm.)
HYAENIDS		**SOURCE**
Spotted hyena	*Crocuta crocuta*	Kingdon (1974)
Brown hyena	*Hyaena brunnea*	Kingdon (1974)
Striped hyena	*H. hyaena*	Kingdon (1974)
URSIDS		**SOURCE**
Asian black bear	*Selenarctos thibetanus*	Bishop (1975)
VIVERRIDS		**SOURCE**
African linsang	*Poiana richardsoni*	Charles Dominique (1977)
Small spotted genet	*Genetta genetta*	Kingdon (1977)
Servaline genet	*G. servalina*	Charles-Dominique (1977)
Large spotted genet	*G. tigrina*	Kingdon (1974)
Giant genet	*G. victoriae*	Kingdon (1977)
Indian civet	*Viverricula indica*	Colquhoun (1993)
African civet cat	*Civettictis civetta*	Charles-Dominique (1977)
African palm civet	*Nandinia binotata*	Charles-Dominique (1977)
Sulawesi civet	*Macrogalidia musschenbroekii*	MacKinnon & MacKinnon (1980)
Malagasy civet	*Fossa fossana*	Colquhoun (1993)
Fossa*	*Cryptoprocta ferox*	Sauther (1989)
HERPESTIDS		**SOURCE**
Ring-tailed mongoose	*Galidia elegans*	Colquhoun (1993)
Broad-striped mongoose	*Galidictis* (spp.)	Petter et al. 1977
Narrow-striped mongoose	*Mungotictis decemlineata*	Macdonald (1992)
Malagasy brown-tailed mongoose	*Salanoia concolor*	Albignac (1973)
Striped-necked mongoose	*Herpestes vitticollis*	Manley (1985)
Marsh mongoose	*Atilax paludinosus*	Charles-Dominique (1977)
Black-legged mongoose	*Bdeogale nigripes*	Charles-Dominique (1977)

PROCYONIDS		**SOURCE**
Coati	*Nasua nasua*	Boinski (1992)
Crab-eating raccoon	*Procyon cancrivorus*	Ferrari (1988)
MUSTELIDS		**SOURCE**
Tayra	*Eira barbara*	Ramirez (1989)
DIDELPHIDS		**SOURCE**
Neotropical opossum	*Didelphis marsupialis*	Boinski (1992)
REPTILES		**SOURCE**
Common caiman	*Caiman crocodilus*	Klein (1974)
Indopacific crocodile	*Crocodylus porosus*	Boonratana (1994)
Mugger crocodile	*C. palustris*	Roonwal & Mohnot (1977)
Nile crocodile	*C. niloticus*	Goodman et al. (1993c)
False gharial	*Tomistoma schlegeli*	Galdikas (1985)
Tegu	*Tupinambis* (spp.)	M. Monteiro da Cruz (pers. comm.)
African monitor	*Varanus niloticus*	Starin & Burghardt (1992)
Asian water monitor	*V. salvator*	Yeager (1991)
Komodo dragon	*V. komodoensis*	Pfeffer (1989)
Reticulated python	*Python reticulatus*	Boonratana (1994)
Indian python	*P. molurus*	Wall (1921)
African python	*P. sebae*	Kingdon (1974)
Malagasy boa constrictor	*Acrantophis madagascariensis*	Colquhoun (1993)
Malagasy tree boa	*Sanzinia madagascariensis*	Goodman et al. (1993c)
Rainbow boa	*Epicrates cenchria*	Wright (1985)
Emerald tree boa	*Corallus canima*	Bartecki & Heymann (1987)
Amazon tree boa	*C. enydris*	Bartecki & Heymann (1987)
Boa constrictor	*Boa constrictor*	Chapman (1986)
Anaconda	*Eunectes murinus*	Heymann (1987)
Madagascar forest night snake	*Ithycyphys miniatus*	Richard (1978)
Yellow rat snake	*Elaphe quadrivittata*	R. Fontaine (pers. comm.)
Malagasy giant hognose snake	*Leioheterodon madagascariensis*	Sauther (1989)

Mussurana	*Clelia clelia*	Bartecki & Heymann (1987)
Boomslang	*Dispholidus typus*	Izawa & Itani (1966)
Egyptian cobra	*Naja haje*	Bourlière et al. (1970)
Black cobra	*N. nigricollis*	Izawa & Itani (1966)
Black mamba	*Dendroaspis polylepsis*	Seyfarth et al. (1980b)
Green mamba	*D. viridis*	Starin & Burghardt (1992)
Common mamba	*D. angusticeps*	Seyfarth et al. (1980b)
Jameson's mamba	*D. jamesonii*	Struhsaker (1970)
Puff adder	*Bitis arietans*	Kingdon (1974)
Gaboon viper	*B. gabonicus*	Jones (1969)
Neotropical rattlesnake	*Crotalus durissus*	S. Perry (pers. comm.)
Fer-de-lance	*Bothrops asper*	Boinski (1988)
Jararaca pit viper	*B. jararaca*	Correa & Coutinho (1997)
Bushmaster	*Lachesis muta*	Bartecki & Heymann (1987)
SHARKS		**SOURCE**
Wolf shark	*Alopias vulpinus*	Mukhergee & Gupta (1965)
Requiem shark	*Carcharhinus gangeticus*	Mukhergee & Gupta (1965)

APPENDIX 2.

Table A2.1 synthesizes the current literature regarding primate predators and their primate prey. Further information on this topic is available from references included in the bibliography.

TABLE A2.1. Primates preying on other primates.

PRIMATE PREDATOR	**PRIMATE PREY**	**SOURCES**
Cheirogaleidae		
Mirza coquereli	*Microcebus murinus*	Hladik 1980
Lemuridae		
Eulemur fulvus rufus	*Lemur catta*	Pitts 1996
Cebidae		
Cebus apella	*Callicebus moloch* *Aotus trivirgatus*	Freese and Oppenheimer 1981, Wright 1984
C. albifrons	*C. moloch* *A. trivirgatus*	Wright 1984
Cercopithecidae		
Cercopithecus mitis	*Galago* spp.	Butynski 1982a, 1982b
Papio cynocephalus	*G. senegalensis* *Cercopithecus aethiops*	Kingdon 1974, Teleki 1975, Hausfater 1976, Cheney et al. 1988
Pongidae		
Pongo pygmaeus	*Nycticebus coucang* *Hylobates* spp.	Sugardjito and Nurhuda 1981, Utami and van Hooff 1997

CONTINUED ...TABLE A2.1. Primates preying on other primates.

PRIMATE PREDATOR	PRIMATE PREY	SOURCES
Pongidae (con't.)		
Pan troglodytes	*Perodicticus potto* *Galago* spp. *G. crassicaudatus* *G. alleni* *G. senegalensis* *Cercopithecus ascanius* *C. pogonias* *C. cephus* *C. mitis* *C. aethiops* *C. campbelli* *C. diana* *Cercocebus atys* *Colobus badius* *C. polykomos* *C. verus* *C. guereza* *Papio anubis* *P. cynocephalus* *Pan troglodytes*	Goodall 1965, 1977, 1986, Kawabe 1966, van Lawick-Goodall 1968a, 1968b, Suzuki 1971, Nishida 1972, Teleki 1973a, 1973b, 1975, Kingdon 1974, Wrangham 1974, Busse 1977, 1978, McGrew et al. 1978, 1979, McGrew 1979, Nishida et al. 1979, 1990, Ransom 1981, Norikoshi 1983, Ghiglieri 1984, Takahata et al. 1984, Nishida & Kawanaka 1985, Takahata 1985, Cheney & Wrangham 1987, Boesch & Boesch 1989, Wrangham & Bergmann Riss 1990, Hamai et al. 1992, Uehara et al. 1992, Alp 1993, Alp & Kitchener 1993, Bakuneeta et al. 1993, Tutin & Fernandez 1993, Boesch 1994a, 1994b, 1994c, Stanford et al. 1994a, 1994b, Hosaka 1995, Stanford 1995a, 1995b, 1996, 1998, Kuroda et al. 1996, Bshary & Noë 1997a, Ihobe 1997, Nakamura 1997, Noë & Bshary 1997, Stanford & Wrangham 1998

APPENDIX 3.

The data on observed predation events presented in Chapter III were drawn from the following published sources:

Agoramoorthy, G. 1992. Reproductive biology of the Hanuman langur, *Presbytis entellus*, in Jodhpur, western India. *Journal of Bombay Natural History Society* 89(1):84-93.

Alikhan, I. 1938. Method adopted by leopards in hunting monkeys. *Journal of the Bombay Natural History Society* 40:555-557.

Alonzo, C. and A. Langguth. 1989. Ecologia e comportamento de *Callithrix jacchus* numa ilha de Floresta Atlântica. *Rev. Nordestina Biol.* 6:105-137.

Altmann, S. and J. Altmann. 1970. Baboon Ecology. University of Chicago Press, Chicago.

Anderson, J. 1986. Encounters between domestic dogs and free-ranging non-human primates. *Applied Animal Behaviour Science* 15(1):71-86.

Badrian, N. and R. Malenky. 1984. Feeding ecology of *Pan paniscus* in the Lomako forest, Zaire. In: The Pygmy Chimpanzee: Evolutionary Biology and Behavior, R. Susman (ed.). Plenum Press, New York. pp. 275-99.

Baldellou, M. and S. Henzi. 1992. Vigilance, predator detection, and the presence of supernumerary males in vervet monkey troops. *Animal Behavior* 43(3):451-461.

Bartecki, U. and E. Heymann. 1987. Field observation of snake-mobbing in a group of saddle-back tamarins (*Saguinus fuscicollis nigrifrons*). *Folia Primatologica* 48:199-202.

Baumgartel, W. 1976. Up Among the Mountain Gorillas. Hawthorn Books, Inc., New York.

Bernstein, I. 1967. A field study of the pigtail monkey. *Primates* 8:217-228.

Boinski, S. 1987. Birth synchrony in squirrel monkeys: A strategy to reduce neonatal predation. *Behavioural Ecology and Sociobiology* 21(6):393-400.

Boonratana, R. 1994. The ecology and behaviour of the proboscis monkey (*Nasalis larvatus*) in the Lower Kinabatangan, Saba. Ph.D. dissertation, Mahidol University, Thailand.

Brain, C. 1981. The Hunters or the Hunted? University of Chicago Press, Chicago.

Brander, A. 1939. Behaviour of monkeys when attacked. *Journal of Bombay Natural History Society* 41:165.

Brown, L. 1955. Supplementary notes on the biology of the large birds of prey of Embu District, Kenya Colony. *Ibis* 97:38-64;183-221.

_____. 1966. Observations on some Kenya eagles. *Ibis* 108:531-572.

_____. 1971. The relations of the crowned eagle, *Stephanoaetus coronatus*, and some of its prey animals. *Ibis* 113:240-243.

Brown, L. and D. Amadon. 1989. Eagles, Hawks and Falcons of the World, Wellfleet, Secaucus, NJ.

Brynard, A. and U. de V. Pienaar. 1960. Annual report of the biologist, 1958-1959. Kruger National Park. *Koedoe* 3:1-205.

Bulger, J. and W. Hamilton III. 1987. Rank and density correlates of inclusive fitness measures in natural chacma baboon (*Papio ursinus*) troop. *International Journal of Primatology* 8:635-650.

Burbridge, B. 1928. Gorilla: Tracking and Capturing the Ape Man of Africa. The Century, Co., New York.

Busse, C. 1980. Leopard and lion predation upon chacma baboons living in the Moremi Wildlife Reserve. *Botswana Notes Records* 26:132-160.

Butynski, T. 1990. Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high and low density subpopulations. *Ecological Monographs* 60:1-26.

Carpenter, C. 1934. A field study of the behavior and social relations of howling monkeys. *Comp. Psychol. Monogr.* 10:1-168.

Channer, O. 1895. The food of the python. *Journal of Bombay Natural History Society* 9:491.

Chapin, J. 1925. The crowned eagle, ogre of Africa's monkeys. *Natural History*, New York 25:459-469.

_____. 1932. The birds of the Belgian Congo. (I.) *Bulletin of the American Museum of Natural History* 65(1):534-655.

Chapman, C. 1986. Boa constrictor predation and group response in white-faced cebus monkeys. *Biotropica* 18(2):171-172.

Charles-Dominique, P. 1977. Ecology and Behaviour of Nocturnal Primates: Prosimians of Equatorial West Africa. Duckworth, London.

Charles-Dominique, P, and J. Petter. 1980. Ecology and social life of *Phaner furcifer*. In: Nocturnal Malagasy Primates: Ecology, Physiology, and Behavior, P. Charles-Dominque, H. M. Cooper, A. Hladik, C. Hladik, E. Pages, G. Pariente, A. Petter-Rousseaux, J. Petter, and A. Schilling (eds.). Academic Press, New York. pp. 75-95.

Cheney, D., R. Seyfarth, S. Andelman, and P. Lee. 1988. Reproductive success in vervet monkeys. In: Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems, T. Clutton-Brock (ed.). University of Chicago Press, Chicago. pp. 384-402.

Cheney, D. and R. Wrangham. 1987. Predation. In: Primate Societies, B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker (eds.). The University of Chicago Press, Chicago. pp. 227-239.

Chism, J., D. Olson, and T. Rowell. 1983. Diurnal births and perinatal behavior among wild patas monkeys. *International Journal of Primatology* 4:167-184.

Chism, J. and T. Rowell. 1988. The natural history of patas monkeys. In: A Primate Radiation: Evolutionary Biology of the African Guenons, A. Gautier-Hion, F. Bourliere, J. Gautier, and J. Kingdon (eds.). Cambridge University Press, Cambridge. pp. 412-429; 432-437.

Cilliers, W. 1963. Lions apparently do eat baboons. *African Wild Life* 17:17-18.

Clark, J. 1970. Observations on the crowned eagle, *Polemaetus coronatus*. *The Lammergeyer* 12:74-77.

Clifton, M. 1977. Attack on a colobus monkey. *East Africa Natural History Society* Vol. 5.

Collins, D. 1984. Spatial patterns in a troop of yellow baboons (*Papio cynocephalus*) in Tanzania. *Animal Behaviour* 32:536- 553.

Colquhoun, I. 1993. The socioecology of *Eulemur macaco*: A preliminary report. In: Lemur Social Systems and Their Ecological Basis, P. Kappeler and J. Ganzhorn (eds.). Plenum Press, New York. pp. 11-23.

Condit, V. and E. Smith. 1994. Predation on a yellow baboon (*Papio cynocephalus cynocephalus*) by a lioness in the Tana River National Primate Reserve, Kenya. *American Journal of Primatology* 33:57-64.

Correa, H. and P. Coutinho. 1997. Fatal attack of a pit viper, *Bothrops jararaca*, on an infant buffy-tufted ear marmoset (*Callithrix aurita*). *Primates* 38(2)215-217.

Cowlishaw, G. 1994. Vulnerability to predation in baboon populations. *Behaviour* 131(3-4):293-304.

Daneel, A. 1979. Prey size and hunting methods of the crowned eagle. *Ostrich* 50:120-121.

Davies, A. G. 1994. Colobine populations. In: Colobine Monkeys: Their Ecology, Behaviour and Evolution, A. G. Davies and J. Oates (eds.). Cambridge University Press, Cambridge. pp. 285-310.

Davis, D. 1962. Mammals of the lowland rainforests of North Borneo. *Bulletin of the National Museum of Singapore* 31:1-129.

Dawson, G. 1976. Behavioral ecology of the Panamanian tamarin, *Saguinus oedipus* (Callitrichidae: Primates). Unpublished Ph.D. dissertation, Michigan State University, Ann Arbor, Michigan.

Defler, T. 1980. Notes on interactions between the tayra (*Eira barbara*) and the white-fronted capuchin (*Cebus albifrons*). *Journal of Mammalogy* 61:156.

DeVore, I. and S. Washburn. 1963. Baboon ecology and human evolution. In: African Ecology and Human Evolution, C. Howell and F. Bouliere (eds.). Aldine, New York. pp. 335-367.

Dittus, W. 1975. Population dynamics of the toque monkey, *Macaca sinica*. In: Socioecology and Psychology of Primates, R. Tuttle (ed.). Mouton, The Hague. pp. 125-152.

Eason, P. 1989. Harpy eagle attempts predation on adult howler monkey. *Condor* 91(2):469-470.

Emmons, L. 1988. A field study of ocelots (*Felis pardalis*) in Peru. *Revue d'Ecologie la Terra et la Vie* 43:133-157.

Ewer, R. 1973. The Carnivores. Cornell University Press, New York.

Fairgrieve, C. 1996. The comparative ecology of blue monkeys (*Cercopithecus mitis*) in logged and unlogged forest in the Budongo Forest, Uganda. Ph.D. dissertation, University of Edinburgh, United Kingdom.

Fowler, J. and J. Cope. 1964. Notes on harpy eagle in British Guiana. *Auk* 81:257-273.

Freeland, W. 1977. Blood sucking flies and primate polyspecific associations. *Nature* 269:801-802.

Galdikas, B. 1985. Crocodile predation on a proboscis monkey in Borneo. *Primates* 26(4):495-496

Galdikas, B. and C. Yeager. 1984. Crocodile predation on a crab-eating macaque in Borneo. *American Journal of Primatology* 6(1):49-51.

Galef, B., Jr., R. Mittermeier, and R. Bailey. 1976. Predation by the tayra (*Eira barbara*). *Journal of Mammalogy* 57:760-761.

Gargett, V. 1971. Some observations on black eagles in the Matopos, Rhodesia. *Ostrich Supplement* 9:91-124.

Gartlan, J. and T. Struhsaker. 1972. Polyspecific associations and niche separation of rainforest anthropoids in Cameroon, West Africa. *Journal of Zoology, London.* 168:221-266.

Gautier-Hion, A., R. Quris, and J. Gautier. 1983. Monospecific vs. polyspecific life: A comparative study of foraging and anti-predatory tactics in a community of *Cercopithecus* monkeys. *Behavioural Ecology and Sociobiology* 12(4):325-335.

Gautier-Hion, A. and C. Tutin. 1988. Mutual attack by a polyspecific association of monkeys against a crowned hawk eagle. *Folia Primatologica* 51:149-151.

Goldizen, A. 1987. Tamarins and marmosets: Communal care of offspring. In: Primate Societies, B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham and T. Struhsaker (eds.). University of Chicago Press, Chicago. pp. 34-43.

Gonzales, R. 1968. A study of the breeding biology and ecology of the monkey-eating eagle. *Silliman Journal* 15:461-491.

Goodman, S., L. de Roland, and R. Thorstrom. 1998. Predation on the eastern woolly lemurs (*Avahi laniger*) and other vertebrates by Henst's goshawk (*Accipiter henstii*). *Lemur News* (3):14-15.

Goodman, S., O. Langrand, and C. Raxworthy. 1993. Food habits of the Madagascar long-eared owl, *Asio madagascariensis*, in two habitats in southern Madagascar. *Ostrich* 64:79-85.

Goodman, S., S. O'Connor, and L. Langrand. 1993. A review of predation on lemurs: Implications for the evolution of social behavior in small, nocturnal primates. In: Lemur Social Systems and Their Ecological Basis, P. Kappeler and J. Ganzhorn (eds.). Plenum Press, New York. pp. 51-66.

Gouzoules, H., L. M. Fedigan, and L. Fedigan. 1975. Responses of a transplanted troop of Japanese macaques (*Macaca fuscata*) to bobcat (*Lynx rufus*) predation. *Primates* 16(3):335-349.

Guggisberg, C. 1963. Simba: The Life of the Lion. Chilton Books, Philadelphia.

Haddow, A. 1952. Field and laboratory studies on an African monkey, *Cercopithecus ascanius schmidtii* Matschie. *Proceedings, Zoological Society of London* 122:297-398.

Hall, K. 1963. Variations in the ecology of the chacma baboon, *Papio ursinus*. *Symposia, Zoological Society of London* 10:1-28.

Hernandez-Camacho, J. and R. Cooper. 1976. The nonhuman primates of Colombia. In: Neotropical Primates: Field Studies and Conservation, R. Thorington, Jr. and P. Heltne (eds.). National Academy of Sciences, Washington, D.C. pp. 35-69.

Heymann, E. 1987. A field observation of predation on a moustached tamarin (*Saguinas mystax*) by an anaconda. *International Journal of Primatology* 8(2):193-195.

Hladik, A. 1980. The dry forest of the west coast of Madagascar: Climate, phenology, and food available for prosimians. In: Nocturnal Malagasy Primates: Ecology, Physiology, and Behavior, P. Charles-Dominique, H. Cooper, A. Hladik, C. Hladik, E. Pages, G. Pariente, A. Petter-Rousseaux, and A. Schilling (eds.). Academic Press, New York. pp. 3-40.

Hoogerwerf, A. 1970. Udjung Kulon, The Land of the Last Javan Rhinoceros. E. J. Brill, Leiden.

Hrdy, S. 1977. The Langurs of Abu. Harvard University Press, Cambridge.

Isemonger, R. 1962. Snakes of Africa: Southern, Central and East. Thomas Nelson and Sons, Johannesburg.

Islam, M. and K. Husain. 1982. A preliminary study on the ecology of the capped langur. *Folia Primatologica* 39:145-159.

Iwamoto, T., A. Mori, and M. Kawai. 1995. [Antipredatory behaviour of gelada baboon.] *Reichorui Kenkyu/Primate Research* 11(3):286.

Izawa, K. 1978. A field study of the ecology and behavior of the black-mantled tamarin (*Saguinus nigricollis*). *Primates* 19:241-274.

Janson, C. 1984. Female choice and mating system of the brown capuchin monkey, *Cebus apella* (Primates: Cebidae). *Zeitschrift fuer Tierpsychologie* 65:177-200.

Jarvis, M., M. Currie, and N. Palmer. 1980. Food of the crowned hawk eagle in the Cape Province, South Africa. *Ostrich* 51:215-218.

Jones, C. 1969. Notes on ecological relationship of four lorisids in Rio Muni, West Africa. *Folia Primatologica* 11:255-267.

Jouventin, P. 1975. Observations sur le socio-ecologie du mandrill. *Terre Vie* 29:493-532.

Julliot, C. 1994. Predation of a young spider monkey (*Ateles paniscus*) by a crested eagle (*Morphnus guianensis*). *Folia Primatologica* 63(2):75-77.

Kano, T. 1972. Distribution and adaptation of chimpanzees on the eastern shore of Lake Tanganyika. *Kyoto University African Studies* 7:37-129.

Kennedy, R. 1977. Notes on the biology and population status of the monkey-eating eagle of the Philippines. *Wilson Bulletin* 89(1):1-20.

Kern, J. 1964. Observations on the habits of the proboscis monkey made in the Brunei Bay Area, Borneo. *Zoologica* 149:183-191.

Kingdon, J. 1974. East African Mammals, Vol. 1. University of Chicago Press, Chicago.

Kinzey, W., A. Rosenberger, P. Heisler, D. Prowse, and J. Trilling. 1977. A preliminary field investigation of the yellow handed titi monkey, *Callicebus torquatus torquatus*, in northern Peru. *Primates* 18:159-181.

Kruuk, H. and M. Turner. 1967. Comparative notes on predation by lion, leopard, cheetah, and wild dog in the Serengeti area, East Africa. *Mammalia* 31(1):1-27.

Kummer, H. 1971. Primate Societies. Aldine-Atherton, Chicago.

_____. 1995. In Quest of the Sacred Baboon: A Scientist's Journey. Princeton University Press, Princeton.

Leland, L. and T. Struhsaker. 1993. Teamwork tactics: Kibale forest's monkeys and eagles each depend on strategic cooperation for survival. *Natural History* 102(4):42-48.

le Roux, P. and J. Skinner. 1989. A note on the ecology of the leopard (*Panthera pardus*, Linnaeus) in the Londolozi Game Reserve, South Africa. *African Journal of Ecology* 27:167-171.

Lindburg, D. 1977. Feeding behaviour and diet of rhesus (*Macaca mulatta*) in a Siwalik Forest in North India. In: Primate Ecology, T. Clutton-Brock (ed.). Academic Press, London. pp. 223-249.

MacKinnon, J. and K. MacKinnon. 1980. The behavior of wild spectral tarsiers. *International Journal of Primatology* 1:361-379.

Maisels, F., J. Gautier, A. Cruickshank, and J. Bosefe. 1993. Attacks by crowned hawk eagles (*Stephanoaetus coronatus*) on monkeys in Zaire. *Folia Primatologica* 61(3):157-159.

Manley, G. 1985. Primates and predators: The example of *Presbytis senex*. *Dyn* 8:1-17.

Masataka, N. 1983. Categorical responses to natural and synthesized alarm calls in Goeldi's monkeys (*Callimico goeldii*). *Primates* 24:40-51.

McConnell, E., P. Basson, V. DeVos, B. Myers, and R. Kuntz. 1974. A survey of diseases among 100 free-ranging baboons (*Papio ursinus*) from the Kruger National Park. *Onderstepoort Journal of Veterinary Research* 41:97-168.

McGrew, W. 1976. An encounter between a leopard and a group of chimpanzees at Gombe National Park. Report. 11 pp.

Meinertzhagen, R. 1959. Pirates and Predators. Oliver and Boyd, Edinburgh.

Mills, M. and H. Biggs. 1993. Prey apportionment and related ecological relationships between large carnivores in Kruger National Park. In: Mammals as Predators, N. Dunstone and M. Gorman (eds.). Clarendon Press, Oxford. pp. 253-268.

Moynihan, M. 1970. Some behavior patterns of platyrrhine monkeys, II: *Saguinus geoffroyi* and some other tamarins. *Smithsonian Contributions to Zoology* 28:1-77.

______. 1976. The New World Primates: Adaptive Radiation and the Evolution of Social Behavior, Languages, and Intelligence. Princeton University Press, Princeton.

Muckenhirn, N. 1972. Leaf-eaters and their predators in Ceylon: Ecological roles of gray langurs, *Presbytis entellus*, and leopards. Ph.D. dissertation, University of Maryland, College Park, Maryland.

Muckenhirn, N. and J. Eisenberg. 1973. Home ranges and predation of the Ceylon leopard. In: The World's Cats: Ecology and Conservation, Vol. 1, R. Eaton (ed.) The Proceedings of an International Symposium held at Lion Country Safari, Laguna Hills, California, on March 15-17, 1971. World Wildlife Safari, Winston. pp. 142-175.

Mukherjee, R. 1982. Phayre's leaf monkey (*Presbytis phayrei*, Blyth, 1847) of Tripura. *Journal of the Bombay Natural History Society* 79(1):47-56.

Nagel, C. 1973. A comparison of anubis baboons, hamadryas baboons, and their hybrids at a species border in Ethiopia. *Folia Primatologica* 19:104-165.

Newton, P. 1985. A note on golden jackals (*Canis aureus*) and their relationship with langurs (*Presbytis entellus*) in Kanha Tiger Reserve. *Journal of the Bombay Natural History Society* 82:633-636.

Neyman, P. 1977. Aspects of the ecology and social organization of free-ranging cotton-top tamarins (*Saguinus oedipus*) and the conservation status of the species. In: The Biology and Conservation of the Callitrichidae, D. Kleiman (ed.). Smithsonian Institution Press, Washington. pp. 39-72.

Nowell, K. and P. Jackson. 1996. Wild Cats: Status Survey and Conservation Action Plan. IUCN/SSC Cat Specialist Group, Gland, Switzerland.

Payne, J. and A. Downey. 1949. Resented the spectators. *African Wild Life* 3:211.

Peres, C. 1990. A harpy eagle successfully captures an adult male red howler monkey. *Wilson Bulletin* 102(3):560-561.

Petter, J., R. Albignac, and Y. Rumpler. 1977. Faune de Madagascar 44: Mammiferes, Lemuriens (Primates Prosimiens). ORSTOM/CNRS, Paris.

Pocock, T. 1939. Fauna of British India. Mammalia I. Primates and Carnivora. Taylor & Francis, London.

Poirier, F. 1970. The Nilgiri langur (*Presbytis johnii*) of South India. In: Primate Behaviour: Developments in Field and Laboratory Research, Vol. I, L. Rosenblum (ed.). Academic Press, New York. pp. 251-283.

Popp, J. 1978. Male baboons and evolutionary principles. Ph.D. dissertation, Harvard University, Cambridge, Massachusetts.

Powzyk, J. 1997. The socioecology of two sympatric indrids, *Propithecus diadema diadema* and *Indri indri*: A comparision of feeding strategies and their possible repercussions on species-specific behaviors. Ph.D. dissertation, Duke University, Durham, North Carolina.

Rahaman, H. 1973. The langurs of the Gir Sanctuary (Gujarat): A preliminary survey. *Journal of the Bombay Natural History Society* 70:295-314.

Rahm, U. 1967. Observations during chimpanzee capture in the Congo. In: Neue Ergenbnisse der Primatologie Progress in Primatology, First Congress of the International Primatological Society, Frankfurt (May 26-July 30, 1966), D. Starck, R. Schneider, and H. Kuhn (eds.). Gustav Fischer Verlag, Stuttgart. pp. 197-207.

Rajpurohit, L. S. and V. Sommer. 1991. Sex differences in morality among langurs (*Presbytis entellus*) of Jodhpur, Rajasthan. *Folia Primatologica* 56:17-27.

Rakotondravony, D., S. Goodman, and V. Soarimalala. 1998. Predation on *Hapalemur griseus griseus* by *Boa manditra* (Boidae) in the littoral forest of eastern Madagascar. *Folia Primatologica* 69(6):405-408.

Ramirez, M. 1989. Feeding ecology and demography of the moustached tamarin (*Saguinus mystax*) in northeastern Peru. Ph.D. dissertation, The City University of New York, New York.

Rasmussen, D. 1983. Correlates of patterns of range use of a troop of yellow baboons (*Papio cynocephalus*). II. Spatial structure, cover density, food gathering and individual behaviour patterns. *Animal Behaviour* 31:834-56.

Rasmussen, K. 1980. Consort behaviour and mate selection in yellow baboons (*Papio cynocepalus*). Ph.D. dissertation, University of Cambridge, United Kingdom.

Ratsirarson, J. 1985. Contribution a l'etude comparative de l'ecoethologie de *Lemur catta* dans deux habitats diferents de la reserve speciale de Beza-Mahafaly. Memoire de fin d'etudes, Universite de Madagascar, Antananarivo.

Rettig, N. 1995. Remote world of the harpy eagle. *National Geographic Magazine* 187(2):40-49.

Richard, A. 1978. Behavioral Variation: Case Study of a Malagasy Lemur. Bucknell University Press, Lewisburg, Pennsylvania.

Rijksen, H. 1978. A Field Study on Sumatran Orangutans, *(Pongo pygmaeus abelii)*: Ecology, Behaviour and Conservation. Veenman and Zonen, Wageningen.

Ripley, S. 1965. The ecology and social behavior of the Ceylon gray langur (*Presbytis entellus thersites*). Ph.D. dissertation, University of California, Berkeley, California.

_____. 1970. Leaves and leaf monkeys: The social organization of foraging in gray langurs (*Presbytis entellus thersites*). In: Old World Monkeys, J. Napier and P. Napier (eds.). Academic Press, New York. 481-509.

Rodman, P. 1988. Resources and group sizes of forest primates. In: The Ecology of Social Behaviour, C. Slobodchikoff (ed.). Academic Press, New York. pp. 83-108.

Rudran, R. 1978. Socioecology of the blue monkeys (*Cercopithicus mitis stuhlmanni*) of the Kibale Forest, Uganda. *Smithsonian Contributions to Zoology* (249):1-88.

Russell, R. 1977. The behavior, ecology, and physiology of a nocturnal primate, *Lepilemur mustelinus*. Ph.D. dissertation, Duke University, Durham, North Carolina.

Rylands, A. 1981. Preliminary field observations on the marmoset, *Callithrix humeralifer intermedius* (Hershkovitz, 1977) at Dardanelos, Rio Aripuana, Mato Grosso. *Primates* 22(1):46-59

Schaller, G. 1963. The Mountain Gorilla. University of Chicago Press, Chicago.

_____. 1967. The Deer and the Tiger. University of Chicago Press, Chicago.

_____. 1972. The Serengeti Lion. A Study of Predator-Prey Relations. University of Chicago Press, Chicago.

_____. 1983. Mammals and their biomass on a Brazilian ranch. *Arquivos de Zoologia*, Vol. 31, Fasciculo I. Museu de Zoologia da Universidade de São Paulo, Brasil.

Seidensticker, J. and I. Suyono. 1980. The Javan Tiger and the Meru-Betiri Reserve, a Plan for Management. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.

Selous, E. and E. Banks. 1935. The clouded leopard of Sarawak. *Sarawak Musuem Journal* 4(3):263-266.

Sessions, P. 1966. Notes on the birds of Lengetia farm Mau Narok. *Journal of East African Natural History Society* 26(1):18-48.

Seyfarth, R., D. Cheney, and P. Marler. 1980. Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behaviour* 28:1070-1094.

Sherman, P. 1991. Harpy eagle predation on a red howler. *Folia Primatologica* 56(1):53-56.

Simonds, P. 1965. The bonnet macaque in South India. In: Primate Behavior: Field Studies of Monkeys and Apes, I. DeVore (ed.). Holt, Rinehart, and Winston, New York. pp. 175- 196.

Skinner, J. and R. Smithers. 1990. The Mammals of the Southern African Sub-Region. University of Pretoria Press, Pretoria.

Smuts, B. 1985. Sex and Friendship in Baboons. Aldine de Gruyter Press, New York.

Stafford, B., and F. Ferreira. 1995. Predation attempts on Callitrichids in the Altantic coastal rain forest of Brazil. *Folia Primatologica* 65(4):229-233.

Stanford, C. 1991. The capped langur in Bangladesh: Behavioral ecology and reproductive tactics. *Contributions to Primatology* 26:1-198.

Starin, E. 1978. A preliminary investigation of home range use in the Gir Forest langur. *Primates* 19(3):551-568.

_____. 1991. Socioecology of the red colobus monkey in the Gambia with particular reference to female-male differences and transfer patterns. Ph.D. dissertation, The City University of New York, New York.

Stelzner, J. and K. Strier. 1981. Hyena predation on an adult male baboon. *Mammalia* 45:259-260.

Sterck, E. (In press.). The langurs of the Gunung Leuser National Park. In: The Gunung Leuser National Park: Home of the Orangutan, C. van Schaik and J. Supriatna (eds.).

Stevenson, P. and M. Quinoñes. 1993. Vertical stratification of four New World primates at Tinigua National Park, Colombia. *Field Studies of New World Monkey, La Macarena, Colombia* 8:11-18.

Stevenson-Hamilton, J. 1947. Wildlife in South Africa. Cassell and Co., London.

Steyn, P. 1982. Birds of Prey of Southern Africa. David Philip, Capetown.

Stoltz, L. and G. Saayman. 1970. Ecology and behaviour of baboons in the northern Transvaal. *Ann. Transvaal Mus.* 26:99- 143.

Struhsaker, T. 1967. Ecology of vervet monkeys (*Cercopithecus aethiops*) in the Masai-Amboseli Game Reserve, Kenya. *Ecology* 48:891-904.

_____. 1969. Correlates of ecology and social organization among African cercopithecines. *Folia Primatologica* 11:80-118.

_____. 1970. Notes on *Galagoides demidovii* in Cameroon. *Mammalia* 34:207-211

_____. 1975. The Red Colobus Monkey. University of Chicago Press, Chicago.

_____. 1981. Polyspecific association among tropical rainforest primates. *Zeitschrift fuer Tierpsychologie* 57:268-304.

Struhsaker, T. and J. Gartlan. 1970. Observations on the behaviour and ecology of the patas monkey (*Erythrocebus patas*) in the Waza Reserve, Cameroon. *Journal of the Zoological Society, London* 161:49-63.

Struhsaker, T. and M. Leakey. 1990. Prey selectivity by crowned hawk-eagles on monkeys in the Kibale Forest, Uganda. *Behavioural Ecology and Sociobiology* 26(6):435-443.

Terborgh, J. 1983. Five New World Primates: A Study in Comparative Ecology. Princeton University Press, Princeton.

Thapar, V. 1986. Tiger: Portrait of a Predator. Facts on File Publications, New York.

Turnbull-Kemp, P. 1967. The Leopard. Howard Timmins, Capetown.

van Eyssen, J. 1949. Rogue elephant's dramatic charge into van. *African Wild Life* 3(1):7-16.

van Schaik, C. and M. Horstermann. 1994. Predation risk and the number of adult males in a primate group: A comparative test. *Behavioural Ecology and Sociobiology* 35:261-272.

van Schaik, C. and M. van Noordwijk. 1989. The special role of male *Cebus* monkeys in predation avoidance and its effects on group composition. *Behavioural Ecology and Sociobiology* 24:265-276.

van Schaik, M. van Noordwijk, R. de Boer, and I. den Tonkelaar. 1983. The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). *Behavioural Ecology and Sociobiology* 13:173-181.

Wahome, J., T. Rowell, and H. Tsingalia. 1993. The natural history of de Brazza's monkey in Kenya. *International Journal of Primatology* 14(3):445-466.

Wall, F. 1921. *Ophidia taprobanica* or the Snakes of Ceylon. H.R. Cottle, Colombo. pp. 56-63.

Waser, P. 1980. Polyspecific association of *Cercocebus albigena*: Geographic variation and ecological correlates. *Folia Primatologica* 33:57-76.

Wilson, V. 1976. The leopard in eastern Zambia. In: The World's Cats: Contributions to Biology, Ecology, Behavior and Evolution, Volume 3, No. 2, R. Eaton (ed.). Carnivore Research Institute c/o Burke Museum, University of Washington, Seattle. pp. 29-38.

Wright, B. 1960. Predation on big game in East Africa. *Journal of Wildlife Management* 24:1-15.

Wright, P. 1985. The costs and benfits of nocturnality of *Aotus trivirgatus* (the night monkey). Ph.D. dissertation, The City University of New York, New York.

_____. 1994. The behavior and ecology of the owl monkey. In: Aotus: The Owl Monkey, J. Baer, R. Weller, and I. Kakoma (eds.). Academic Press, San Diego. pp. 97-112.

Wright, P., S. Heckscher and A. Dunham. 1998. Predation of rain forest prosimians in Ranomafana National Park, Madagascar. *Folia Primatologica* 69(Suppl. 1):401 (Abstract).

Wright, P. and L. Martin. 1995. Predation, pollination and torpor in two nocturnal prosimians: *Cheirogaleus major* and *Microcebus rufus* in the rainforest of Madagascar. In: Creatures of the Dark: The Nocturnal Prosimians, L. Alterman, G. Doyle, and M. Izard, (eds.). Plenum Press, New York. pp. 45-60.

Yeager, C. 1991. Possible anti-predator behavior associated with river crossings by proboscis monkeys (*Nasalis larvatus*). *American Journal of Primatology* 24(1):61-66.

APPENDIX 4.

SAMPLE QUESTIONNAIRES

Three questionnaires dealing with predation on primates were sent to field researchers and naturalists. Questionnaire One was distributed to 1928 primate researchers. Questionnaire Two was disseminated to 236 researchers who study predators. Questionnaire Three was sent to 62 government wildlife departments, national parks, and naturalists in Africa, Madagascar, Asia, and the Neotropics.

I wish to acknowledge the kind assistance of Dr. Richard Wrangham who supplied a sample questionnaire which had been used to gather information later published in Cheney and Wrangham (1987). This prototype was very helpful in constructing the three questionnaires I used for gathering data.

Questionnaires One, Two, and Three are reproduced on subsequent pages.

[QUESTIONNAIRE ONE]

PRIMATE PREDATION QUESTIONNAIRE

This questionnaire is designed to gather information on one species at one site; however, data collected over many years of research may be combined on a single questionnaire. If you have studied more than one primate species at one site or many primate species at many sites, please photocopy or request more questionnaires so that each primate species at each site is dealt with on a separate questionnaire. Thanks for assisting this research.

1. Primate species:____

2. Study site:____

3. Were other researchers concurrently studying the same population of primates? Yes ____ No ____
   Name(s) of other researcher(s): ________________________
   ____

4. Habitat description (check one):
   Tropical rain forest ____ Monsoon forest ____
   Tropical montane forest ____ Temperate rain forest ___
   Temperate deciduous/evergreen forest _____
   Shrubland ____ Savanna ____ Other __________________

5. Total research time at site: _______ months
   Currently ongoing? Yes ____ No ____ If not currently ongoing, during which year(s) did research occur:_____________

6. Number of observation hours: Diurnal ____ Nocturnal ____

7. Number of animals in your study group (give average figure over research period):________________________
   Number of animals in population containing your study group (give average figure over research period): ___________

8. Has there been an attempt/intent to document or estimate predation? Yes ____ No ____

9. Predator species actually observed (by you or other researchers) preying upon or known to have killed individuals in your study population. Please give specific and common names. Include dogs, people and any other "unnatural" predators:
   (1) *Most important*____________________________________
   (2)____
   (3)____
   (4)____
   (5)____

10. Predator species, other than those above, suspected to have killed individuals in your study population:

(1) *Most important*____________________
(2)____________________
(3)____________________
(4)____________________
(5)____________________

11. Predator species that are present but appear not to be important predators. Include only species that might reasonably be expected to kill primates:

(1) *Most important*____________________
(2)____________________
(3)____________________
(4)____________________
(5)____________________

12. Predator species that elicit behavioral reactions from primates. Please match anti-predator behaviors below to the predator responsible for them:

(1)____________________
(2)____________________
(3)____________________
(4)____________________
(5)____________________

Scanning = *SC*
Crypsis = *CR*
Mobbing = *M*
Fleeing to trees = *FL*
Charge/attack = *C/A*
Alarm vocalization = *AV*
Defensive posture = *DP*
Running on ground = *RU*
Other ____________________ = *O*

13. Total number of predations actually observed during your study: _____

14. Total number of predations suspected to have occurred during your study: _____

15. Were there unexplained night-time disappearances in study population? Yes ____ No ____
If so, which age/sex classes were involved? Adult Male ____
Adult Female ____ Subadult Male ____ Subadult Female ____
Infant ____
Do you suspect predation? All ____ Some ____ % ____
Why? ____________________

16. Based on observations throughout the study, is it possible to give an *estimated predation rate* (percent of population taken by predators per year) for the primates you studied?
Yes ____ No ____
If yes, what is your estimate? ______%
(Error estimate for above, e.g., maximum and minimum): _____
If possible, briefly describe how this estimated predation rate was determined: ____________________
____
____

17. Based on observations throughout the study, is it possible to give the proportion of all predation deaths occurring in each age/sex class? Yes ____ No ____

If yes, see below. If numerical data are not available, feel free to comment where possible (e.g., "none"):

Infants (<1 year old)____________________
Juvenile/subadult males____________________
Juvenile/subadult females__________________
Adult males______________________________
Adult females_____________________________

Total number of predations on which above data are based: ______

18. Anecdotal observations and/or comments from indigenes regarding predation on primates:

19. How should your data be cited?

20. Are there researchers working at or near your site studying predatory species that prey on primates? If so, please provide their names and mailing addresses below:

Name and address of individual completing questionnaire:

[QUESTIONNAIRE TWO]

PRIMATE PREDATION QUESTIONNAIRE

1. Predator species (indicate family and order): ____________
____
Diurnal ____ Nocturnal ____
Terrestrial ____ Arboreal ____ Aquatic _____
Approximate adult weight ________________
If sexually dimorphic: Male wt. _____ Female wt. ______

2. Study site: ______________________________
Country: ______________________________

3. Habitat description (check one):
Tropical rain forest ____ Monsoon forest ____
Tropical montane forest ____ Temperate rain forest ___
Temperate deciduous/evergreen forest _____
Shrubland ____ Savanna ____ Other ______________

4. Study duration: Years ____ Months ____
Currently ongoing? Yes ____ No ____ If not currently ongoing, during which year(s) did research occur? ________

5. Number of observation hours: Diurnal ____ Nocturnal ______

6. Primate species found in study area: ________________
____
____
____
____
____
____
____
____

7. Did you ever observe predation on primates? Yes ___ No ___
If so, which species? ______________________________
____
____
____

8. Estimated number of primates killed by predators during study: ___________

9. What age/sex classes of primates were killed? Give percentages if available, or comment where possible (e.g., "none"):
   Infants (<1 year old)___________________________
   Juvenile/subadult males_________________________
   Juvenile/subadult females_______________________
   Adult males_____________________________________
   Adult females___________________________________

   Total number of predations on which above data are based:
   ____

10. Methodology used to analyze predator's diet:
   Fecal sampling ____ Direct observation of kills _____
   Analysis of prey carcass ____ Raptor nest remains ____
   Stomach contents ____ Other __________________________

11. Frequency of occurrence of primates in predator's diet (i.e., primates as a *percentage* of all food consumed): _____

12. Estimated predation rate on primates (i.e., percentage of primate population removed annually by study population of predators): __________
   Error estimate (e.g., maximum and minimum), if available:
   ____

13. Primates as a percentage of biomass consumed by predator species being studied: ________
   If available, estimated total prey biomass of ecosystem:
   ____

14. If direct observation of primate-predator interactions was recorded, what anti-predator defenses did primates employ? If more than one behavior, number in sequence:
   Scanning ____ Crypsis ____ Charge/attack _____
   Alarm vocalizations ____ Defensive posture ____
   Mobbing ____ Fleeing to trees ____
   Running on ground ____ Other __________________

15. What is the estimated percentage of instances in which these defenses were successful? _____

16. Anecdotal observations and/or comments of indigenes regarding predation on primates:

17. How should your data be cited?

18. For the species or genera you have studied, please list any published sources containing information about predation on primates:

19. **Can you recommend other researchers to whom this questionnaire may be sent? Please list names and mailing addresses:**

Name and address of individual completing questionnaire:

[QUESTIONNAIRE THREE]

PRIMATE PREDATION QUESTIONNAIRE

1. Name of reserve or national park: ____________________
____

2. Location: ____________________________________

3. Habitat description (check one):
    Tropical rain forest ____ Monsoon forest ____
    Tropical montane forest ____ Temperate rain forest ___
    Temperate deciduous/evergreen forest ____
    Shrubland ____ Savanna ____ Other ______________

4. What species of predators are present that might reasonably be expected to kill primates? (Please indicate both common and specific names):

Raptors: ____________________________________
____
____
____
____

Large carnivores: ______________________________
____
____
____
____

Small carnivores: ______________________________
____
____
____
____

Snakes: ____________________________________
____
____
____
____

Crocodiles and other reptiles: ____________________
____
____
____
____

1

5. What species of primates are present? (Please give estimated population size of each species if known):

6. Are records kept of observed predation? Yes ____ No ____
Who is in charge of keeping records? Park rangers ____
Naturalists ____ Guides ____ Visitors ____

7. How many primates were killed by predators in each of the years in which records are available?

Primate Species	No. Killed	Year	Predator

8. Is there an estimated predation rate on primates (i.e., percentage of primate population removed annually by predators)? Yes ____ No ____
If yes, please estimate each species of primate separately:

9. Is the frequency of occurrence of primates in predator diets known for any predatory species (i.e., primates as a percentage of all food consumed)? Yes ____ No ____
If yes, please give frequency of occurrence percentage for each species of predator separately:

10. Direct observations of behavioral reactions by primates to predators. If more than one behavior, number in sequence:
Scanning ____ Crypsis ____ Charge/attack ____
Alarm vocalizations ____ Defensive posture ____
Mobbing ____ Fleeing to trees ____
Running on ground ____ Other ____________

11. Are there any unusual observations concerning primates and their predators?

12. Name and address of individual filling out questionnaire:

13. Names and mailing addresses of individuals who may have information concerning predation on primates to whom this questionnaire may be sent: (Continue on back if necessary.)

APPENDIX 5.

ACKNOWLEDGMENTS TO RESPONDENTS

The time and attention to detail involved in completing a questionnaire makes it a task not easily undertaken. I want to acknowledge and thank the researchers listed below for the effort they expended to insure the accuracy of this thesis and increase the understanding of predation on primate species.

RESPONSES TO QUESTIONNAIRE ONE:

Amran Achmad
Dept. of Forestry
Hassanuddin University
Ujung Pandang, South Sulawesi
Indonesia

G. Agoramoorthy
Department of Biology
National Sun-yat Sen University
Kaohsiung, 80424
Taiwan
Republic of China

Ms. Rosalind Alp
c/o Tradelinks
10 Rawdon Street
PMB 833
Freetown
Sierra Leone
West Africa

Jeanne Altmann
Dept. of Ecology and Evolution
University of Chicago
Chicago, IL 60637

James R. Anderson
Centre de Primatologie
Université Louis Pasteur Strasbourg
Fort Foch
F 67207 Niederhausbergen
France

Anonymous
Department of Anthropology
University of Durham
43 Old Elvet
Durham DH1 3HN
England
United Kingdom

Anonymous
Kirkcaldy
United Kingdom

Ryosuke Asaba
Imajayama Monkey Park
Genrokuyamacho 8
Arashiyama, Saikyoku
Kyoto
Japan

Jose M. Ayres
Museu Goeldi
C.P. 399
Belem, Para
Brazil

Shigeru Azuma
Primate Research Institute
Kyoto University
Inuyama City, Aichi 484
Japan

Anne Baker
Burnet Park Zoo
1 Conservation Place
Syracuse, NY 13204

Mary Baker
Dept. of Anthropology
University of California
Riverside, CA 92521

Christopher Bakuneeta,
Budongo Forest Project
P.O. Box 362
Masindi
Uganda

Robert A. Barton
Dept. of Anthropology
Univ. of Durham
43 Old Elvet
Durham, DH1 3H
United Kingdom

Mark Beeson
Easdon Farmhouse
Manaton, Devon TQ13 9XB
United Kingdom

Jorge Benitez-Rodriquez
Facultad de Biologia
Universidad Veracruzana
A.P.. 270
91000 Xalapa, Ver.
Mexico

Elizabeth Bennett
7 Jalan Ridgeway
93200 Kuching
Sarawak
Malaysia

David Bergeson
Department of Anthropology
Washington University
Campus Box 1114
St. Louis, MO 63130

Hari Bhat
107 Awanti Apartments
OPP: Kamala Nehru Park
Erandawana
Pune-411004
India

P. S. Bhatnagar
Dept. of Zoology
University of Rajasthan
Jaipur 302.004, Rajasthan
India

Amanda Biggs
10 Pulford Avenue
Prenton
Birkenhead
Merseyside, L43 0TB
United Kindom

C.R. Birkinshaw
The Orchard
Stanedge Road
Bakewell Derbyshire DE45 1DG
United Kingdom

Naomi Bishop
Department of Anthropology
California State University, Northridge
18111 Nordhoff Street
Northridge, CA 91330-8244

William Bleisch
Wildlife Conservation Society
Bronx, NY 10564

Christopher Boehm
Director Jane Goodall Research Center
University of Southern California
Anthropology Department
Social Science 154
Los Angeles, CA 90089-0032

Christophe Boesch
Institute of Zoology
University of Basel
Rheinsprung 9
CH-4051
Basel
Switzerland

Sue Boinski
Dept. of Anthropology
1350 Turlington Hall
University of Florida
Gainesville, FL 32611

Ramesh Boonratana
Center for Conservation Biology
Dept. of Biology, Faculty of Science
Mahidol University
Rama VI Road
Bangkok 10400
Thailand

Warren Brockelman
Center for Conservation Biology
Department of Biology
Faculty of Science
Mahidol University
Rama 6 Rd., Bangkok 10400
Thailand

Daniel Brooks
Department of Biology
University of Houston-Downtown
Houston, TX 77030

Hannah Buchanan-Smith
Dept. of Psychol.
Univ. of St. Andrews
St. Andrews, Fife KY16 9JU
Scotland
United Kingdom

Tom Butynski
Zoo Atlanta
P.O. Box 24434
Nairobi
Kenya

Eva and David Bynum
1126 John Jones Road
Bahama, NC 27503

Rogerio Castro
Dept. of Biology
Washington University
St. Louis, MO 63130

Colin Chapman
University of Florida
Department of Zoology
Gainesville, FL 32611

Adriano G. Chiarello
Wildlife Research Group – Department of Anatomy
University of Cambridge
Downing Street
Cambridge CB2 3DY
England
United Kingdom

Janice Chism
Dept. of Biology
Winthrop University
Rock Hill, SC 29733

Margaret R. Clarke
Tulane Regional Primate Center
18703 Three Rivers Road
Covington, LA 70433

Ian C. Colquhoun
Dept. of Anthropol.
Univ. of Western Ontario
London, Ontario N6A 5C2
Canada

Vicki Condit
Department of Anthropology
Emory University
Atlanta, GA 30322

Marina Cords
Anthropology Department
Columbia University
452 Schermerhorn
New York, NY 10027

Carolyn Crockett
Washington Primate Center
SJ-50
University of Washington
Seattle, WA 98195

Ian Martin Coulson
Sengwa Wildlife Research Institute
Private Bag 6002
Gokwe
Zimbabwe

Marian Dagosto
Department of Cell, Molecular, and Structural Biology
Northwestern University Medical School
303 E. Chicago Avenue
Chicago, IL 60611-3008

Andrew De Vries
Axys Environmental Consulting, Ltd.
Suite 2630
1075 W. Georgia
Vancouver, BC v6E 3C9
Canada

Barbara Decker
236 Big Canoe
Big Canoe, GA 30143

Mario Di Bitteti
Department of Ecology and Evolution
State University of New York at Stony Brook
Stony Brook, NY 11794-5245

Lee Drucraner
Department of Zoology
Southern Illinois University – Carbondale
Carbondale, IL 62901

Robin Dunbar
Department of Psychology
Liverpool University
P.O. Box 147
Liverpool L69 3BX
United Kingdom

Joe Erwin
Diagnon Corporation
Division of Neurobiology and Behavior
9600 Medical Center Drive
Rockville, MD 20850-3336

Chris Fairgrieve
ICA PB
University of Edinburgh
Kings Buildings
West Mairs Road
Edinburgh EH9 3JT
Scotland
United Kingdom

Linda M. Fedigan
Department of Anthropology
University of Alberta
Edmonton, Alberta T6G 2H4
Canada

John Fellowes
Department of Zoology
Univerity of Hong Kong
Pokfulam Road
Hong Kong

Alison Fletcher
Department of Zoology, School of
Biological Sciences
University of Bristol
Woodland Road
Bristol BS8 1UG
United Kingdom

Roy Fontaine
Pennsylvania College of Technology
1 College Avenue
Williamsport, PA 17701

Debra Forthman
Conservation Arc.
Zoo Atlanta
800 Cherokee Avenue, SE
Atlanta, GA 30325-1440

Barbara Fruth
Forschungsstelle für Humanethologie
In der Max-Planck-Gesell Schaft
Von-Der-Tann-Strasse 3-5
D-82346 Andechs
Germany

Agustin Fuentes
Dept. of Anthropology
University of California at Berkeley
Berkeley, CA 94720

Paul Garber
Dept. of Anthropology
109 Davenport Hall
University of Illinois
Urbana, IL 61801

Kellen Gilbert
Department of Sociology, Social Work
and Criminal Justice
Southeastern Louisiana University
Hammond, LA 70902

Kenneth Glander
Duke University
Biological Anthropology
3705-B Erwin Road
Durham, NC 27705

Mary E. Glenn
204 Leeds Drive
Valparaiso, IN 46383

A.H. Harcourt
Dept. of Anthropology
University of California
Davis, CA 95616

Michele Goldsmith
Bai Hokou Gorilla Research Center
Dzanga-Ndoki National Park
Central African Republic

Yasumi Ishii
Copo Miyazima 205,
1-4-3 Maebara-higashi,
Funabashii City
Chiba, 274
Japan

Prof. N. Itoigawa
Dept. of Psychology
Faculty of Human Sciences
Osaka University
Suita, Osaka
Japan

Kosei Izawa
Miyagi University of Education
Aoba, Aramaki,
Sendai 980
Japan

Li Jin-hua
Department of Biology
Anhui University
Hefei, Anhui 230039
Republic of China

Alison Jolly
Dept. of Ecology and Evolutionary Biology
Princeton University
Princeton, NJ 08544

Catherine Julliot
Lab. d'Ecologie Generale
Museum National d'Histoire Naturelle
4 Av. du Petit Chateau
91800 Brunoy
France

Gladys Kalema
33 Albemarle Avenue
Potters Bar
Herts EN6 4NN
England
United Kingdom

Beth Kaplin
Department of Zoology
University of Wisconsin
430 Lincoln Drive
Madison, WI 53706

Ellen Kapsalis
P.O. Box 420375
Summerland Key, FL 33042

Margaret Kinnaird
Jl. Babe Palar 68
Manado 95117
Sulawesi Utara
Indonesia

Barbara Kirkevold
Dept. of Psychol.
NI-25
Univ. of Washington
Seattle, WA 98195

Karen Kool
School of Biological Sciences
University of New South Wales
Sydney, NSW 2052
Australia

Adriaan Kortlandt
8 Woodstock Road
Oxford OX2 7ND
United Kingdom

Naoki Koyama
405 Rumon Arashiyama
Nakaoshimocho 20-30
Nishikyoku, Kyoto 616
Japan

R. Krishnamani
Project "Singaalika"
Sithanadi BPO
Hebri 576 112
Karnataka
India

Hiroko Kudo-Hirotani
Prefectural Museum Construction
c/o Kanagawa Prefectural Education
Agency
33, Nihon-Odori, Naka-ku
Yokohama 231
Japan

Ajith Kumar
Salim Ali Centre for Ornithology and
Natural History
Coimbatore 641 010
India

Suehisa Kuroda
The University of Shiga Prefecture
2500 Hassaka-cho, Hikone
Shiga 522-8533
Japan

Jutta Küster
Ruhr-Universitat Bochum
Abteilung
Funktionelle Morphologie
Geb. MA 0/44
D-44780 Bochum
Germany

Mukesh Kumar Chalise
Department of Biology
Kathmandu University
Lazimpat cha-2-808
G.P.O. Box 2799
Kathmandu
Nepal

Isabelle Lardeux Gilloux
50 rue Edouard
Delanglado
13006 Marseille
France

M. J. Lawes
Department of Zoology &
Entomology
University of Natal
P.O. Box 375
3200 Pietermaritzburg
South Africa

Phyllis C. Lee
Department of Biol. Anthropology
University of Cambridge
Downing Street
Cambridge CB2 3DZ
United Kingdom

Suzi Leonard
Apto. 668
Iquitos
Peru

Donald Lindburg
Zoological Society of San Diego
Post Office Box 551
San Diego, CA 92112-0551

Iqbal Malik
540 Asian Games Village
New Delhi 110069
India

Nobuo Masataka
Kyoto Primate Research Institute
Inuyama City
Aichi, 484
Japan

Reena Mathur
Dept. of Zoology
University of Rajasthan
Jaipur 302.004, Rajasthan
India

Shuichi Matsumura
Primate Research Institute
Kyoto University
Inuyama, Aichi 484
Japan

Kelley McFarland
Department of Anthropology
CUNY-Graduate School
33 West 42nd Street
New York, NY 10036

Carol McMillan
Wenatchee Valley College
Omak Campus
P.O. Box 2058
Omak, WA 98841

Francisco Dyonisio Cardoio Mendes
Rua Maranhas 1019 5° and
Sao Paulo, SP 0124-001
Brazil

Shaily Menon
384 King Avenue
Columbus, OH 43201

Russell Mittermeier
Conservation International
1015 18th Street, N.W.
Suite 1000
Washington, D.C. 20036

Jim Moore
Dept. of Anthropology
9500 Gilman Road - Dept. 0101
University of California-San Diego
La Jolla, CA 92093

Klaus Muller
Deutches Primatenzentrum
Kellnerweg 4,
37077 Gottingen
Germany

Mr. Philip Muruthi
Mpala Research Centre
P.O. Box 555
Nanyuki
Kenya

Joel Mwangi Gathua
Nat. Museums of Kenya
Mammalogy Dept.
P.O. Box 40658
Nairobi
Kenya

Tilo Nadler
Cuc Phuong National Park
Nho Quan District
Ninh Binh Province
Vietnam

Marilyn A. Norconk
Kent State University
123 Lowry Hall
Dept. of Anthropology
Kent, OH 44242

Pia Nystrom
Dept. of Anthropology
Washington University
Campus Box 1114
St. Louis, MO 63130

Timothy O'Brien
Jl. Babe Palar 68
Manado 95117
Sulawesi Utara
Indonesia

Toru Oi
Forestry and Forest Products Res. Inst.
Tohoku Research Center
Shimokuriyagawa, Morioka 02001
Japan

Ms. Claudia Olejniczak
Department of Anthropology
Washington University
Campus Box 1114
St. Louis, MO 63130

Maria Adelia Oliveira-Monteiro
da Cruz
Rua General Abreu e Lima, 186
Rosarinho Recife-PE
CEP 52041-040
Brazil

William Olupot
MUIENR
P.O. Box 10066
Kampala
Uganda

Deborah Overdorff
Duke University
Biological Anthropology and Anatomy
3705-B Erwin Road-Wheeler
Durham, NC 27705

Amy Parish
Department of Anthropology
University of California, Davis
Davis, CA 95616

Marcelo Passamani
Depto. de Zoologia/Instituto de Ciencias
Biologicas
Universidade Federal de Minas Gerais
Av. Antonio Carlos
6627 Belo Horizonte - MG
31270.901
Brazil

Claudio Pereira-Nogueira
Estacao Biologica de Caratinga
Caixa Postal 82
Ipanema-MG 36950-000
Brazil

Susan Perry
Dept. of Anthropology
1054 LSA Building
University of Michigan
Ann Arbor, MI 48109-1382

Andrew Petto
Center for Biology Education
660 WARF
University of Wisconsin
610 N. Walnut Street
Madison, WI 53705-2397

Kim Phillips
Dept. of Psychology
University of Georgia
Athens, GA 30602-3013

Sharon T. Pochron
Department of Anthropology
University of New Mexico
Albuquerque, NM 87131

Doris Podzuweit
Institute of Anthropology
Buergerstrasse 50
D-37073 Goettingen
Germany

Joyce Powzyk
346 D Street
Springfield, OR 97477

Cristofer S. Price
Building 112, Room 205
NIH Animal Center
Elmer School Road
Poolesville, MD 20837

Sydney Purloe
Department of Psychology
Haverford College
370 Lancaster Avenue
Haverford, PA 19041-1392

Wenyuan Qu
Biology Dept.
Henaa Normal University
Zinxiang 453002
People's Republic of China

Helder L. Queiroz
Projeto Mamirsus
Caixa Postal 38
Tefé – Amazonas
Brazil

Ulrich Reichard
Institut für Anthropolgie
Burgerstrasse 50
37073 Göttingen
Germany

Rosalind Ribnick
1505 P Street
Eureka, CA 95501-2545

Martha Robbins
Department of Zoology
Birge Hall
430 Lincoln Drive
University of Wisconsin
Madison, WI 53706

Tamar Ron
Israel Nature Reserves Authority
78 Yirmeyahu Street
Jerusalem 94467
Israel

Ms. Lisa Rose
Department of Anthropology
Washington University
Campus Box 1114
St. Louis, MO 63130-4899

Thelma Rowell
Department of Integrative Biology
University of California - Berkeley
Berkeley, CA 94720

Anthony Rylands
Dept. Zoologia
Universidade Federal de Minas Gerais
31270-901 Belo Horizonte
Minas Gerais
Brazil

J. Sabater-Pi
Department de Psiquiatria i
Psicobiologia
Facultat de Psicolgia
Universitat de Barcelona
08028 Barcelona
Spain

Tom Sambrook
Psychology Department
University of St. Andrews
St. Andrews, Fife KY16 9JU
Scotland
United Kingdom

Robert Sapolsky
Dept. of Biol. Sci. & Neurosci.
Stanford University
Stanford, CA 94305

Michelle Sauther
Dept. of Anthropology
Washington University
Campus Box 1114
St. Louis, MO 63130

Anne Savage
Roger Williams Park Zoo
1000 Elmwood Avenue
Providence, RI 02907

Juan Carlos Serio-Silva
Calle 14-A #1532
Col. Federal CP 94570
Cordoba, Veracruz
Mexico

Lori Sheeran
Dept. of Anthropology
P.O. Box 34080
California State University-Fullerton
Fullerton, CA 92634-9480

Gilberto Silva-Lopez
Programa Bioconservacion
Instituto de Investigaciones Biologicas
Universidad Veracruzana
Aptd. Post. 294
Xalapa, Veracruz 91000
Mexico

Paul E. Simonds
Department of Antrhopology
University of Oregon
Eugene, OR 97403-1218

Hilary Simons-Morland
Wildlife Conservation Society
International Programs
Bronx, NY 10460

Barbara Smuts
Department of Psychology
University of Michigan
Ann Arbor, MI 48109

Volker Sommer
Department of Anthropology
University of California
Davis, CA 95616

C. H. Southwick
Dept. of Environmental, Population and
Organismic Biology
University of Colorado, Boulder
Boulder, CO 80309

Craig B. Stanford
Dept. of Anthropology
University of Southern California
Los Angeles, CA 90089-0032

Erica D. Starin
32B Warwick Avenue
London W9 2PT
United Kingdom

Romy Steenbeek
Ketambe Research Center
P.O. Box 4
Kutacane 24601
Aceh Tenggara
Sumatra
Indonesia

E.H.M. Sterck
University of Utrecht
Ethology & Socioecology
P.O. Box 60086
3508 TB Utrecht
The Netherlands

Eleanor Sterling
SPEF
BP 416
Toamasina 501
Madagascar

Pablo R. Stevenson
A.A. 18226
Santa Fe de Bogota
Colombia

Karen B. Strier
Dept. of Anthropology
University of Wisconsin-Madison
1180 Observatory Drive
Madison, WI 53706

Thomas Struhsaker
Duke University
Box 90383
Biological Anthropology and Anatomy
Durham, NC 27708-0383

Shirley C. Strum
Dept. of Anthropology
University of California - San Diego
La Jolla, CA 92093

Robert Sussman
Department of Anthropology
Washington University
Campus Box 1114
St. Louis, MO 63130

Yukio Takahata
Naruto University of Education
Takashima, Naruto-cho
Naruto 772
Japan

Patricia Teixidor
School of Psychology
University of St. Andrews
St. Andrews
Fife KY16 9JU
Scotland
United Kingdom

Kanaizuka Tsutomu
908-206 Ohonocho Saikigun
Hiroshima-Ken
Japan

Caroline E. G. Tutin
S.E.G.C.
B.P. 7847
Libreville
Gabon

Shigeo Uehara
Sapporo University
3-7-3-1 Nishioka, Toyohira-ku
Sapporo 062
Japan

C. P. van Schaik
Department of Biological Anthropology
and Anatomy
Duke University
Durham, NC 27705

Natalia Vasey
Department of Anthropology
Washington University
Campus Box 1114
St. Louis, MO 63130

Francois Vincent
Universite of Paris
10 rue de la Tuilerie
78650 Saulx-Marchais
France

Joseph M. Wahome
Department of Integrative Biology
University of California at Berkeley
Berkeley, CA 94720

Mwangi-Wahungu
Dept. of Wildlife Management
Moi University
P.O. Box 1125
Eldoret
Kenya

R.D. Warren
Dept. of Human Anatomy & Cell
Biology
University of Liverpool
P.O. Box 147
Liverpool L69 3BX
United Kingdom

Peter Waser
Department of Biological Sciences
Lilly Hall of Life Sciences
Purdue University
West Lafayette, IN 47907

Frances White
Duke University
Biological Anthropology and Anatomy
Wheeler Bldg.,
Box 90383
Durham, NC 27708

Frank Wiens
Abt. Funktionelle Morphologie
Geb. MA 0/44
Ruhr-Universitaet Bochum
D-44780 Bochum
Germany

R. W. Wrangham
Department of Anthropology
Peabody Museum
Harvard University
Cambridge, MA 02138

Juichi Yamagiwa
Primate Research Inst.
Kyoto University
Inuyama 484
Aichi
Japan

Tomoo Yoshimura
Japan Monkey Centre
Kanrin 26, Inuyama
Aichi 484
Japan

Anne Zeller
Dept. of Anthropology
University of Waterloo
Waterloo, Ontario
Canada N2L 3G1

Klaus Zuberbuhler
Ethologie und Wildforschung
Universität Zürick-Irchel
Winterthurerstrasse 190
CH-8057 Zürich
Switzerland

Gabriel Zunio
Museo Argentino de Ciencias Naturales
Av. Angel Gallardo 470
1405 Buenos Aires
Argentina

RESPONSES TO QUESTIONNAIRE TWO:

Senor Marcelo Aranda
Instituto de Ecologia
Apdo. Postal 63
Xalapa 91000, Veracruz
Mexico

James Berkelman
Department of Fisheries and Wildlife Sciences
Virginia Polytechnic Institute and State University
Blacksburg, VA 24061

Brian Bertram
Fieldhead
Amberley
Stroud, Glouchestershire GL5 5AG
United Kingdom

Christophe Boesch
Institute of Zoology
University of Basel
Rheinsprung 9
CH-4051
Basel
Switzerland

Prof. J. du P. Bothma
Centre for Wildlife Management
University of Pretoria
0002 Pretoria
South Africa

David Bygott
Box 161
Karatu
Tanzania

Tim Caro
Wildlife and Fisheries Biology
University of California
Davis, CA 95616

Scott Creel
Rockefeller University
Field Rsearch Center
Box 38B, RR. 2, Tyrrel Road
Millbrook, NY 12545

Rob Davies
P.O. Box 1390
Halfway House 1685
Midrand
South Africa

Mr. Divyabhanusinh
Vice-President, Northern Region
Taj Group of Hotels
Mandlik House
Mandlik Road
Bombay 400 001
India

Sarah Durant
Institute of Zoology
Zoological Society of London
London NW1 4RY
United Kingdom

Vincent Egan
Terrestrial Ecology Research Unit
Department of Zoology
University of Port Elizabeth
P.O. Box 1600
Port Elizabeth 6001
South Africa

John F. Eisenberg
Florida Museum of Natural History
Dept. of Natural Sciences
University of Florida
Gainesville, FL 32611-2035

Louise Emmons
Smithsonian Institution
Museum of Natural History
Division of Mammals
10th & Constitution, NW
Washington, DC 20560

Field Director
Similipal Tiger Reserve
Bhanjpur, Baripada
Orissa 757 002
India

George Frame
P.O. Box 822
Cape May Court House, NJ 08210-0822

Laurence Frank
Field Station for Behavioral Research
3210 Tolman Hall #1650
Berkeley, CA 94720-1650

Steven M. Goodman
Field Museum of Natural History
Roosevelt Road
Lake Shore Drive
Chicago, IL 60605

Ron Hartley
Zimbabwe Falconers Club
Falcon College
Esigodini
Zimbabwe

Jeannette Hanby
Box 161
Karatu
Tanzania

Rafael Hoogesteijn
P.O. Box 492
Melrose, FL 32666

David Jenny
Rechengasse 2
Bremgarten 5620
Switzerland

Karen Laurenson
Upland Research Group
The Game Conservancy
Crubenmore Lodge
Newtonmore PH20 1BE
Invernesshire
Scotland PH20 1BE
United Kingdom

Paul Leyhausen
Auf'm Driesch 22
D-51570 Windeck
Germany

Hector C. Miranda, Jr.
Philippine Eagle Foundation
Garnet cor. Diamond Sts. Marfori
Heights
Davao City 8000
Philippines

Fumi Mizutani
Lolldaiga Hills Ltd.
P.O. Box 26
Nanyuki
Kenya

Mr. Dieter Morsbach
Ministry of Environment and Tourism
Private Bag 13306
Windhoek 9000
Namibia

Paul Newton
Wolfson College
Oxford OX2 6UD
United Kingdom

Peter M. Norton
Eastern Cape Province
Cape Nature Conservation
Private Bag X1126
Port Elizabeth 6000
South Africa

Craig Packer
Department of Ecology, Evolution and
Behavior
University of Minnesota
100 Ecology Building
1987 Upper Buford Circle
St. Paul, MN 55108-6097

Bernardino Ragni
Istituto de Zoologia
Universita Degli Studi di Perugia
Via Elce di Sotto
Perugia 06100
Italy

Uma Ramakrishran
University of California – Davis
Department of Psychology
One Shields Avenue
Davis, CA 95616-8686

M. A. Rashid
Ketan Apartments
Flat 103
Fatehganj Camp
Baroda 390 002
India

Neil Rettig
Rural Route #1, Box 454
Prairie du Chien, WI 53821

George Schaller
NYZS/Wildlife Conservation Society
Southern Blvd.
Bronx, NY 10460

John Seidensticker
Curator of Mammals
National Zoological Park
Smithsonian Institution
Washington, D.C. 20008

P. E. Stander
Box 17
Grootfontein
Namibia

Simon Thomsett
P.O. Box 42818
Nairobi
Kenya

Russell Thorstrom
The Peregrine Fund
5666 W. Flying Hawk Lane
Boise, ID 83709

Carl Vernon
East London Museum
Box 11021
Southernwood 5213
South Africa

Richard Watson
The Peregrine Fund
5666 W. Flying Hawk Lane
Boise, ID 83709

David Whitacre
The Peregrine Fund
5666 W. Flying Hawk Lane
Boise, ID 83709

Shigeki Yasuma
23-11, Miyakubo 1-chome,
Ichikawa, Chiba 272
Japan

RESPONSES TO QUESTIONNAIRE THREE:

Ferdinand L. J. Baal
Nat. Conserv. Div.
Surinam Forest Svc.
Lands Bosbeheer
Cornelis Jongbawstraat 10
Paramaribo
Suriname

Matsunaga Katsutoshi
Kasungu National Park
P.O. Box 43
Kasungu
Malawi

K. Mohadin
Nature Conservation Division
Surinam Forest Service
P.O. Box 436
Paramaribo
Suriname

Nancy N. Moindi
Mpala Research Centre
P.O. Box 555
Nanyuki
Kenya

Basil Moss
Ruchomechi Camp
Chilindu
Zimbabwe

Bourama Niagate
Ingenieur des Eaux et Forets
Aménagiste de la Faune
Direction Nationale des Eaux et Forets
BP 275
Bamako
Mali

Troy Williamson
Ruckomechi Camp
Chilindu
Zimbabwe

APPENDIX 6.

The calculations below are an example of the methodology used to arrive at estimated predation rates, i.e. the percentage of a primate population that is removed yearly by predators.

Sample methodology for calculating estimated predation rate (EPR):

Wright, P., S. Heckscher and A. Dunham. 1997. Predation on Milne-Edward's sifaka (*Propithecus diadema edwardsi*) by the fossa (*Cryptoprocta ferox*) in the rain forest of southeastern Madagascar. *Folia Primatologica* 68(1):34-43.

- Milne-Edward's sifakas live in groups of 3-9 individuals. There were three groups under study – a maximum of 27 individuals.
- Fossas killed 7 individuals between 1990-1994 (4 years) from the 3 groups.
- Maximum 3-group size = 27 individuals. Deaths (n=7) divided by 27 = 0.2592 divided by 4 years = 0.065 (6.5%), estimated predation rate.

APPENDIX 7.

A qualitative comparison between data gathered from questionnaires and data found in published sources is presented in this appendix. This comparison was undertaken to ascertain the similarity between the two data sources. The questionnaire and literature data were compared by region and by predator taxa, using the number of predations as the evaluation criterion. Data gathered from the questionnaires and data found in published sources exhibited the same characteristics and followed the same trends, thus the two data sources were combined into one data set.

Sources of Data

Predation data collected in this study were gathered through two methods: (a) questionnaires sent to 2226 researchers, and (b) an exhaustive literature search. Two hundred seventy-seven responses were received from questionnaires and 253 applicable articles were found in the published literature; a total of 3592 primate predation events were reported from the combined questionnaires and literature. As shown in Fig.A7.1, questionnaires accounted for 37.0% of predations, while the literature accounted for 63.0%.

Data Set Comparison by Region

In Fig.A7.2, I compare the percentage of primate predations gathered from the questionnaires and published sources for each region. The questionnaire data and the literature data exhibited the same characteristics and trends. In both data sets the

APPENDIX 7.

A qualitative comparison between data gathered from questionnaires and data found in published sources is presented in this appendix. This comparison was undertaken to ascertain the similarity between the two data sources. The questionnaire and literature data were compared by region and by predator taxa, using the number of predations as the evaluation criterion. Data gathered from the questionnaires and data found in published sources exhibited the same characteristics and followed the same trends, thus the two data sources were combined into one data set.

Sources of Data

Predation data collected in this study were gathered through two methods: (a) questionnaires sent to 2226 researchers, and (b) an exhaustive literature search. Two hundred seventy-seven responses were received from questionnaires and 253 applicable articles were found in the published literature; a total of 3592 primate predation events were reported from the combined questionnaires and literature. As shown in Fig.A7.1, questionnaires accounted for 37.0% of predations, while the literature accounted for 63.0%.

Data Set Comparison by Region

In Fig.A7.2, I compare the percentage of primate predations gathered from the questionnaires and published sources for each region. The questionnaire data and the literature data exhibited the same characteristics and trends. In both data sets the

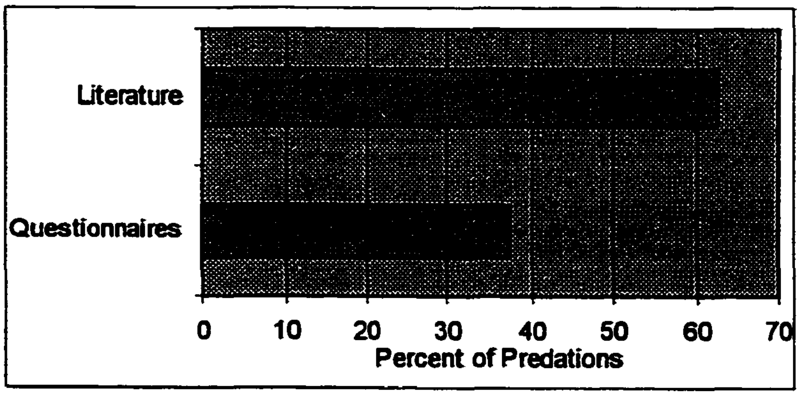


Fig.A7.1 Sources of primate predation data. Literature = 253 publications and 2262 primate mortalities. Questionnaires = 277 responses and 1330 primate mortalities.

majority of predation data was reported from Africa (50.0%, n=667, from the questionnaires compared to 61.0%, n=1378, from the literature). Both data sets recorded 7.0-8.0% (questionnaires, n=114, literature, n=172) of predations from Madagascar. Predations from Asia totaled 22.0% (n=303) from questionnaires compared to 15.0% (n=355) from the literature. Eighteen percent (n=248) of all predations were from the Neotropics in the questionnaire data set compared to 15.0% (n=355) from the literature.

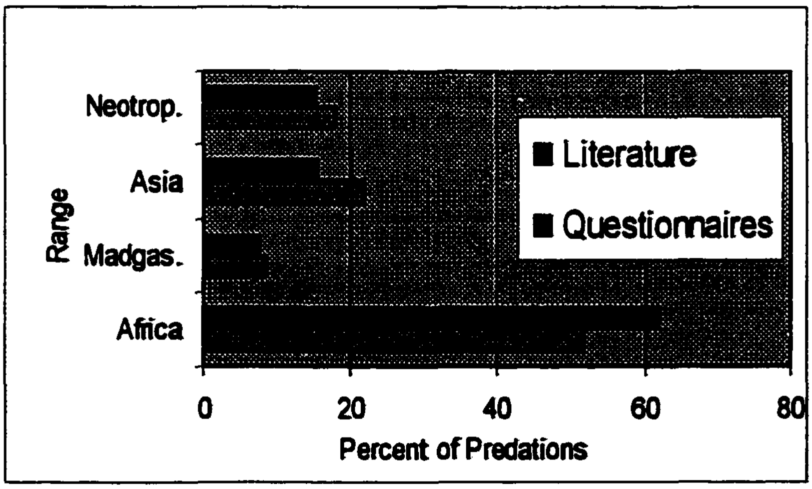


Fig.A7.2. Comparison of questionnaire data to literature data by region.

Data Set Comparison by Predator

The percentages of predations on primates gathered from questionnaires and data from published sources are compared for each predator group in Fig.A7.3. Data shown in this figure are for all four regions combined. As seen in the figure, questionnaire data and literature data again exhibited the same characteristics and trends. In both data sets, the majority of predations were reported for felids and raptors. Although there were more raptor predations found in the literature than from questionnaires and more felid predations found in questionnaire responses than in the literature, these reversals are not important because the most visible characteristic of the comparison is the domination of the data by these two taxa. The percentages of predations reported for canids/hyaenids, small carnivores, reptiles, and unknown predators were approximately 10.0% or less for each predator group.

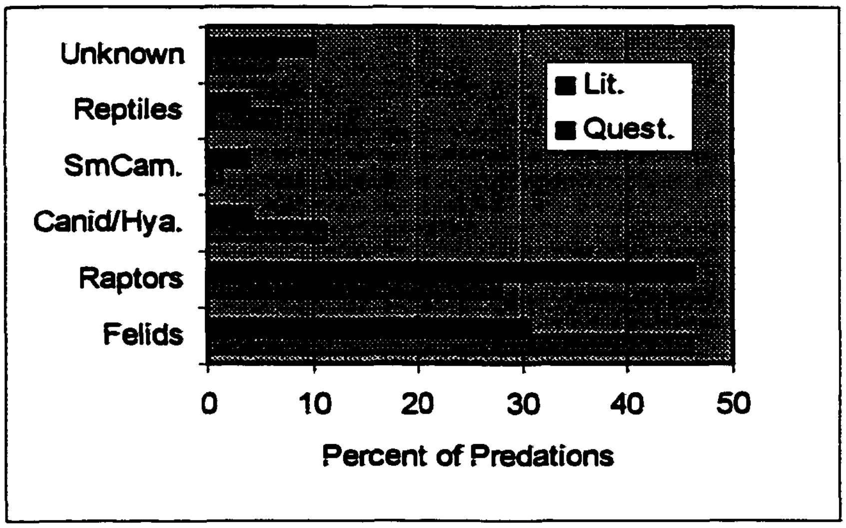


Fig.A7.3. Comparison of questionnaire data to literature data by predator group.

I took the data presented in Fig.A7.3 (all four regions combined) and then compared percentages of predator groups within each region: Fig.A7.4 -- Africa, Fig.A7.5 -- Madagascar, Fig.A7.6 -- Asia, and Fig.A7.7 -- Neotropics. For each region, the two sets of data, in general, had similar trends with the same predator categories dominating the data.

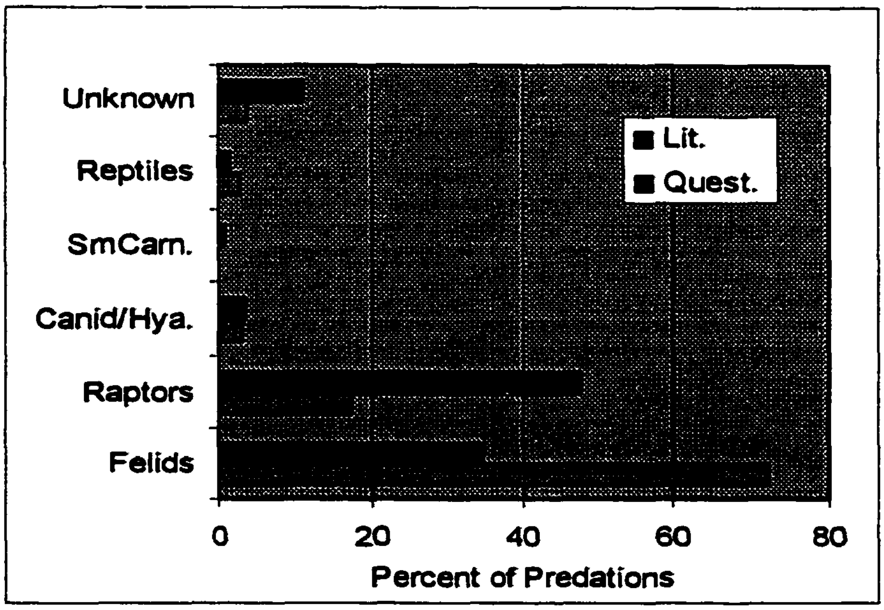


Fig.A7.4. Comparison of questionnaire data to literature data by predator group – Africa.

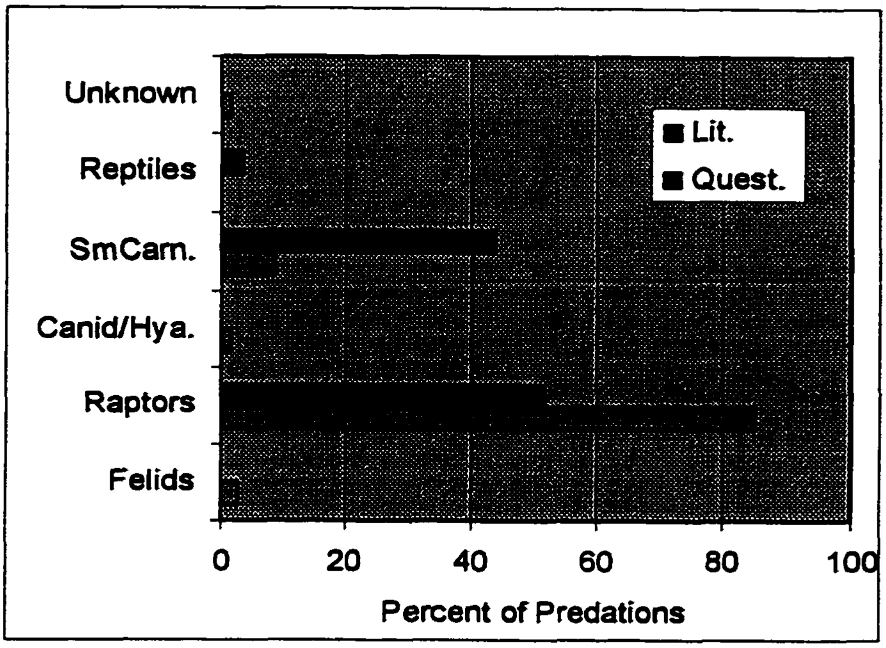


Fig.A7.5. Comparison of questionnaire data to literature data by predator group – Madgascar.

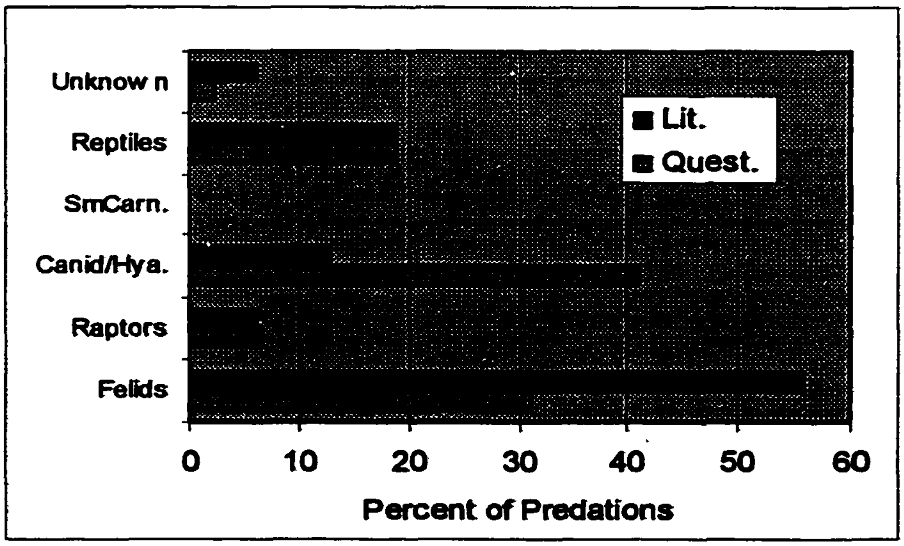


Fig.A7.6. Comparison of questionnaire data to literature data by predator group -- Asia.

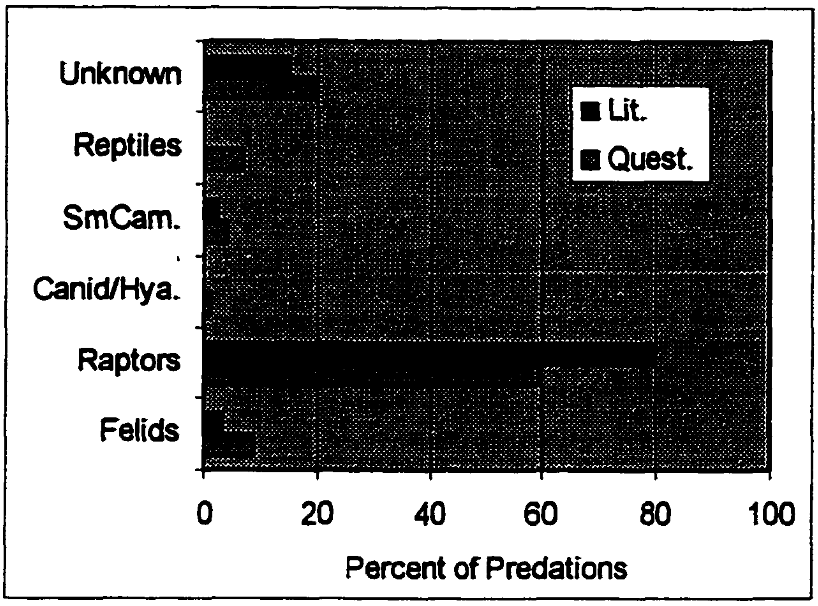


Fig.A7.7. Comparison of questionnaire data to literature data by predator group -- Neotropics.

APPENDIX 8.

An analysis of the relationship between recorded predation events and the number of sources (questionnaires and literature) from which they were drawn is summarized below:

- Total number of predation events = 3592
- Number of sources = 613
- Mean predation events per source = 5.9

The total number of predation events can be divided into suspected predations (n=684, mean predation events per source = 5.5), unsuccessful attacks (n=679, mean predation events per source = 4.5), and known predations (n=2229, mean predation events per source = 6.8). (See Figs.A8.1 and A8.2.)

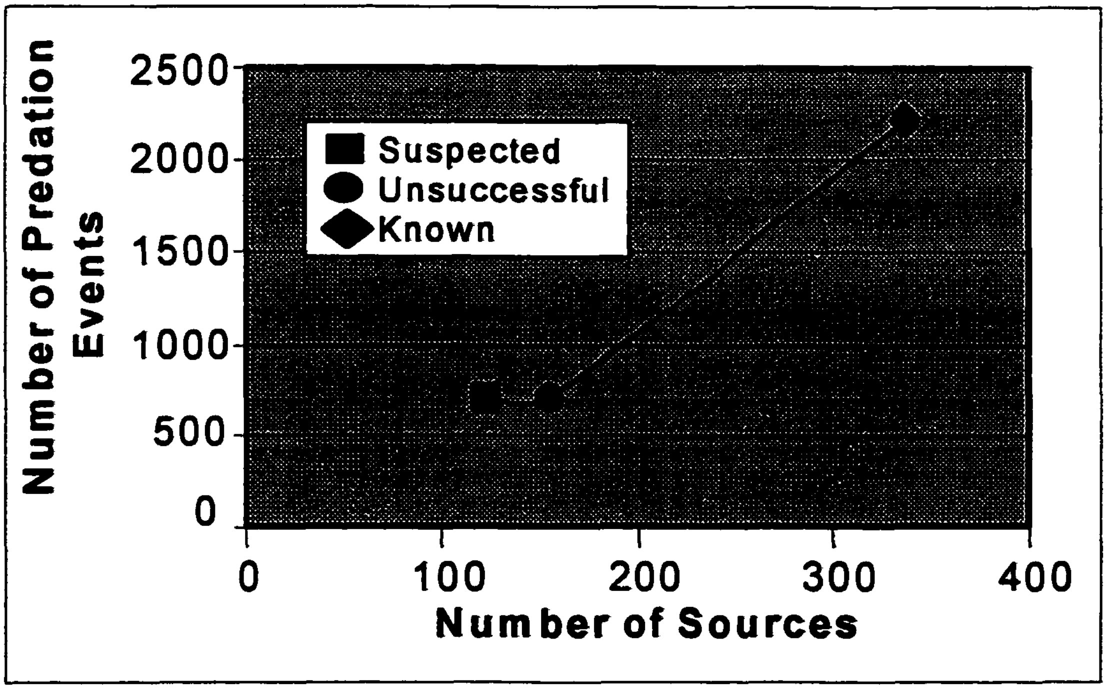


Fig.A8.1. Number of predation events as a function of number of sources.

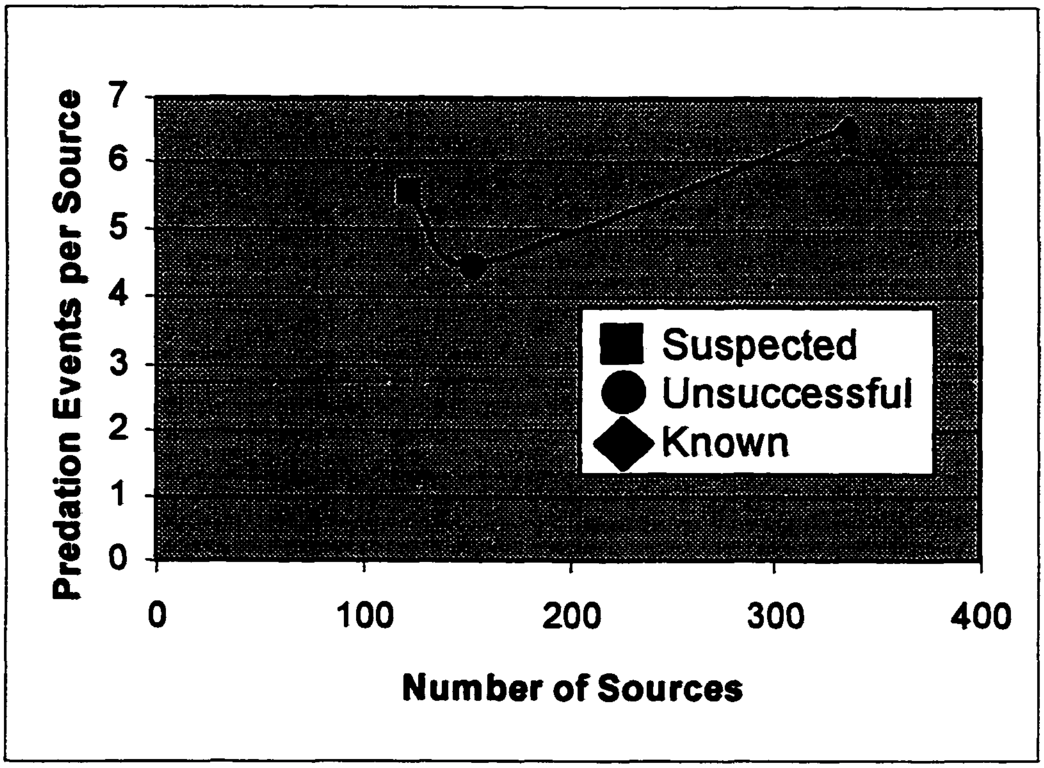


Fig.A8.2. Number of predation events per source as a function of number of sources.