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Predatory behavior of crowned hawk-eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda

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Abstract Evaluating the nature and significance of predation on populations of wild primates has been difficult given a paucity of data regarding the phenomenon. Here we addressed this problem in a 37-month study of the predatory behavior of crowned hawk-eagles living at the Ngogo study site in Kibale National Park, Uganda. We collected prey remains underneath the nests of two pairs of eagles and census data on potential prey species to investigate prey selection and the ecological impact of predation on the Ngogo primate population. Results indicate that primates form the vast majority of all prey items. Eagles prey selectively on monkeys according to sex and species. Male primates were taken more often than females, while two species, redtail monkeys and mangabeys, were captured significantly more and less, respectively, than chance expectation. In addition, there was no bias in the age of prey: adult and non-adults were killed in numbers roughly equal to their proportional representations in the forest. Further analyses indicate that a non-trivial fraction of the entire primate population at Ngogo succumbs to crowned hawk-eagle predation each year. These results reveal both parallels and contrasts with those reported previously. Some of the parallels are due to similarities in prey availability, while contrasts are likely related to methodological differences between studies, inter-individual variations in predator hunting styles, and differences in prey abundance, demography, and behavior.

Keywords Crowned hawk-eagle · Predation · Primates

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Introduction

Few topics have generated more debate in the study of primate behavioral ecology than the role played by predation in affecting anatomy, behavior, and social systems (Alexander 1974; Altmann 1974; Wrangham 1980; van Schaik 1983; Cheney and Wrangham 1987; Isbell 1994; Bshary and Noe 1997; Cowlishaw 1997; Hill and Lee 1998; Janson 1998). In a major review of the subject, Cheney and Wrangham (1987) concluded that predation does not exert a strong influence on the evolution of primate morphology and social structure. In contrast, others have argued that predation represents a principal selective force in the life of primates (van Schaik 1983; Terborgh and Janson 1986; Janson 1992).

These disparate views are maintained, in part, due to persistent gaps in observations. In fact, very few data exist on predation in the wild. Primate predation is inherently difficult to document since it is rare, occurs quickly, and is performed by animals who hunt at night and largely by stealth (review in Isbell 1994). While it has long been recognized that predation is best studied through investigation of predators directly and not their primate prey (Washburn et al. 1965; Cheney and Wrangham 1987; Isbell 1994; Boinski and Chapman 1995), such studies have been undertaken only rarely. In this context, it is no surprise that some of the best information regarding predation on primates from field work conducted on primates who themselves are predators (e.g., Strum 1981; Stanford 1998).

Raptors are an important class of predator known to prey on primates throughout their geographic range. There have been numerous reports of neotropical Harpy eagles and Asian monkey-eating eagles preying on primates (e.g., Kennedy 1977; Rettig 1978; Izor 1985; Peres 1990; Sherman 1991; Robinson 1994). In Africa, monkeys are a regular part of the diet of crowned hawk-eagles (*Stephanoaetus coronatus*) (Gautier-Hion and Tutin 1988; Skorupa 1989; Struhsaker and Leakey 1990; Cordeiro 1992; Maisels et al. 1993). Prior studies indicate that substantial information regarding the hunting behavior of crowned hawk-eagles can be gleaned by monitoring activities around their nests (Skorupa 1989; Struhsaker and Leakey 1990). We adopted this technique and present new observations on the predatory behavior of crowned hawk-eagles during a 37-month study in Kibale National Park, Uganda. By focusing on the behavior of predators rather than their prey, we circumvent some of the empirical problems associated with predation studies in the wild. Our results provide one of the largest databases for predation on wild primates and allow us to address several aspects of eagle predatory behavior, including prey selection and its ecological impact.

Methods

Study site

We conducted observations of crowned hawk-eagles and their primate prey over 37 months from July 1996 to August 1999 at the Ngogo study site in Kibale National Park, Uganda. Ngogo lies at an interface between lowland and montane rainforest and is covered primarily with moist, evergreen forest interspersed between large blocks of *Pennisetum purpureum* grassland (Struhsaker 1997). The 12-km^2 Ngogo study area has been the site of behavioral research on primates since 1974 (Struhsaker 1997). Ghiglieri (1984), Butynski (1990), and Struhsaker (1997) provide detailed descriptions of the study area.

Subjects

Primate prey

Eight diurnal anthropoid primates are commonly encountered at Ngogo: two colobines – black-and-white colobus (*Colobus guereza*) and red colobus (*Piliocolobus badius*); five cercopithecines – baboons (*Papio anubis*), blue monkeys (*Cercopithecus mitis*), l'Hoest's monkey (*Cercopithecus lhoesti*), mangabeys (*Lophocebus albigena*), and redtail monkeys (*Cercopithecus ascanius*); and a single ape, the chimpanzee (*Pan troglodytes*). Given their large body size (29–50 kg; Uehara and Nishida 1987), chimpanzees do not appear to be vulnerable to predation by the much smaller crowned hawk-eagles (3–4 kg; Brown et al. 1982). We have not witnessed any attacks by eagles on chimpanzees during concurrent field research focused on the latter species over 5 years (Watts 1998; Mitani and Watts 1999; Mitani et al. 1999, 2000a; Pepper et al. 1999; Watts 2000a, 2000b), nor do eagles prey on chimpanzees at other field sites (e.g., Goodall 1986; Nishida 1990). For these reasons, we excluded chimpanzees from consideration as potential prey for eagle predators.

Eagle predators

We monitored the predatory behavior of two mated pairs of crowned hawk-eagles during the 37-month study period. One pair was first observed at the start of the study in July 1996 and subsequently followed during the ensuing 3 years, while the other pair was observed over 3 months at the end of this study between June and August 1999. At the time of initial observation, the first pair of eagles maintained an active nest that contained a nestling which was approximately 1 month old. This nestling fledged in October 1996 and subsequently disappeared from the study area shortly after August 1997. The pair started to rebuild their nest and resumed breeding activities in September 1997. A breeding attempt failed in December 1997, apparently due to abnormally high levels of rainfall. Another successful breeding effort followed in the ensuing months, however, with the appearance of a nestling in May 1998. This nestling fledged toward the end of July 1998 and remained in its natal area until the end of this study, August 1999, at which time it was making journeys up to 2 km away from the nest. The mated pair continued to feed both offspring at the nest site during the extended 1-year, post-fledgling period that preceded juvenile dispersal. The pair itself fed sporadically near the nest at other times. A second mated pair of eagles was discovered toward the end of this study in June 1999. They maintained an active nest, with a recently fledged juvenile who remained nearby. We observed activities around this nest during the last 3 months of the study.

Primate prey censuses

We estimated the availability of potential primate prey through 64 censuses conducted over 32 months between January 1997 and August 1999. All censuses were performed by a single observer (J.S.L), who completed one census during each half of every month. We censused the seven cercopithecoids that occupied the study site, all of which are known to be preyed upon by crowned hawk-eagles (Brown et al. 1982; Skorupa 1989; Struhsaker and Leakey 1990).

We employed line transect methods to obtain census data (National Research Council 1981; Whitesides et al. 1988; Mitani et al. 2000b). All censuses were completed over the same, 4.4-km rectangular route, running about 1 km on each side and covering the middle of the Ngogo study area. All primates observed during censuses fell within the hunting range of crowned hawk-eagles monitored during this study. The first pair of eagles occupied a nest within 150 m of the southeast corner of the census route; the nest of the second pair was further away, approximately 2 km southeast of the census route. J.S.L varied the direction of travel along the census route to equalize the number started and stopped in either direction. All censuses were conducted between 0730 and 1330 hours. During each census, the observer walked slowly, traveling at approximately 1 km per hour, and pausing at regular intervals to scan the forest. Upon sighting primates, he stopped for no more than 10 min and recorded the species, time, location, number of individuals, and distance between himself and the first animal observed.

Eagle predation

We monitored the predatory behavior of the two crowned hawk-eagle pairs by picking up prey remains under their nests. Searches at the first nest were conducted about once a week during the nestling phase and period of eaglet dependence. At other times, searches were conducted sporadically, but typically never more than 2 weeks apart. The second nest discovered in 1999 was monitored for a short 3-month period on a biweekly basis. We additionally used observations of three predatory episodes and two carcasses recovered in the forest to assay predation by eagles. After a kill, crowned hawk-eagles typically process their prey on the ground by plucking them clean of their hair, leaving a dense mat of hair in a small area as an unambiguous signature of eagle hunting behavior.

We classified each specimen taxonomically as precisely as possible using reference collections from the American Museum of Natural History and The Field Museum. We used size and morphological criteria to make taxonomic assessments. We assigned specimens to two age classes, adults and non-adults. Postcrania were assumed to be from adult animals if the epiphyses were fused to the diaphyses and sutures were closed. If bones were adult or nearly adult sized, but epiphyses were not fully fused or were missing, the specimens were assigned to the non-adult category. Where possible, we relied on tooth emergence criteria to ascertain the age of specimens. Skulls were considered adult if they had all adult teeth in occlusion and a significant degree of fusion between cranial bones. We considered individuals non-adults if

M3/m3 were not fully erupted. We assigned the sex of specimens on the basis of robustness and size. In adult skulls, tooth size, particularly of canines, was taken to be a good indicator of sex. For all species considered, we noted substantial evidence of sexual dimorphism in long-bone length and scapular dimensions that facilitated our sex determinations.

We determined the number of individual organisms per taxon using a minimum number of individuals (MNI) method (Badgley 1986). This procedure is based upon counts of the most abundant element present from one side of the body, and was augmented by other considerations of the skeletal parts represented, including size, age, and species affiliation. An attempt was made to sort the material into species-specific or age-grade lots, and then to perform MNI estimates for each separately. This method is conservative and probably underestimates the overall number of individuals (Badgley 1986). It is appropriate, however, when the assumption can be made that association is high for the whole assemblage, as is the case for carcass accumulation in one area by predators or scavengers, even if the actual associations are not immediately evident (Badgley 1986).

Analyses

Prey availability

Primates are typically social and, as a result, encounters usually take place between eagle predators and groups of monkeys. We therefore used the densities of each primate species, measured in groups per km^2, to estimate their abundance and availability as prey. To derive these density estimates, we began by plotting a frequency distribution of sighting distances of primates made during censuses. From this frequency distribution, we estimated the "fall-off" distance, the first 10-m interval at which the number of detections of groups dropped to half or less that of the immediately previous interval (cf. Whitesides et al. 1988). The distributions of sighting distances did not differ between the three species, mangabeys, red colobus, and redtails, for which we had a sufficient number of observations for statistical comparison (Kolmogorov-Smirnov $P>0.20$ for all three comparisons), and for this reason, we lumped observations from all species to compute a single fall-off distance. Using this distance to estimate the effective width of the census route, we computed the total census area (A) as:

$$A=2wl$$

where w=effective width of the census route and l=census route length=4.4 km.

We estimated group densities (D) of each primate species according to the following formula:

$$D_i=G_i/2wl$$

where G_i=the number of groups of species i observed within the effective strip width w during each census and w and l are defined as above.

Eagle predation

We evaluated prey selectivity by comparing the minimum number of individuals recovered underneath the nests of the two mated pairs against those predicted to be caught by chance. We performed two analyses dividing primate prey according to subfamily and species. Calculations were conducted for each of the seven monkey species known to be preyed upon by crowned hawk-eagles. Chance expectations were generated based on each subfamily and species proportional representations in the forest as estimated by their group densities. We employed a χ^2-test to determine whether the observed number of colobines and cercopithecines in our sample of kills differed significantly from those expected by chance. Given a small expected number of kills for baboons, l'Hoest's monkeys, blue monkeys, and black-and-white colobus, χ^2-tests were inappropriate to test for differences between observed and expected numbers of kills for each prey species. To circumvent this problem, we employed a resampling technique to investigate whether the observed numbers of kills departed significantly from chance expectations (Good 1999). Here we compared the observed number of kills for each species against theoretical distributions of kills generated on the assumption that eagles hunt randomly and prey on monkeys in direct proportion to their representations in the forest. To generate these expected distributions, we used a random number generator to select numbers between 0 and 1. If the random number generator assigned a value equal to or less than the proportional representation of the species in question, we scored a hit or kill for that assignment. We iterated this assignment procedure 53 times, a number equal to the total observed kills in our sample. At the end of these 53 iterations, we tallied the number of times the random number generator assigned a successful kill. We used these summations as single data points to create the expected distribution of kills. Expected distributions were produced after iterating the assignment procedure 10,000 times. Comparing our observed number of kills to the 2.5% tails of the expected distributions provided a two-tailed statistical test of the null hypothesis that observed and expected number of kills for each species do not differ.

We used data compiled by Struhsaker and Leakey (1990) to estimate the number of adult and non-adult primates at Ngogo. These data were derived from observations of five of the seven potential primate species at the study site, namely black-and-white colobus, blue monkeys, mangabeys, red colobus, and redtail monkeys. Similar observations provided a means to estimate the number of potential male and female prey at Ngogo (Struhsaker and Leakey 1990). We compared the observed number of prey taken from the two age classes with those expected on the basis of chance using a χ^2-test. Chance expectations were generated on the assumption that if eagles hunt randomly, they would kill individuals in direct proportion to their numbers in the forest. Similar calculations were performed to investigate whether eagle offtake was random with respect to the sex of adult primate prey**.** We limited this analysis to adults, since it is difficult to sex immature animals and because the sex ratios of adult and non-adult primates typically differ.

Prey offtake

We employed the minimum number of individuals represented in the prey collection, the approximate hunting range of eagle pairs, and the population density of primate prey to assess prey offtake. We estimated the size of an eagle pair's hunting range by first measuring the distance between the nests of the two pairs using a Magellan GPS 315. We made the simplifying assumption that eagle pairs occupy circular, non-overlapping territories and took one-half the distance between nest sites as the radius of a hunting range. We employed this figure to estimate the hunting area, again assuming a circular range. We calculated the population density of each prey species at Ngogo by multiplying mean group size and group density. Information on group size was provided from the literature and our own field observations (Butynski 1990; Oates 1994; Struhsaker 1997; T.L. Windfelder and J.S. Lwanga, unpublished data), while current group densities were estimated using census data. We divided the observed number of kills made per year by the product of the hunting range of eagles and population density of primate prey to derive an estimate of eagle predation rates.

Results

Prey availability

Primate censuses indicated that group densities of potential prey varied nearly 30-fold, ranging from a high of

Table 1 Group densities, population densities, and group sizes of potential primate prey species at Ngogo

Species	Group density (groups/km^2)	Population density (individuals/km^2)	Mean group size (number of individuals)
Cercopithecus ascanius	5.06	162	32
Cercopithecus lhoesti	0.24	4	18
Cercopithecus mitis	0.18	3	15
Colobus guereza	0.36	4	11
Lophocebus albigena	2.10	38	18
Papio anubis	0.50	20	40
Piliocolobus badius	2.04	86	42

Table 2 Prey selection by crowned hawk-eagles

Species	Number of individuals
Primates	
Cercopithecus ascanius	36
Cercopithecus lhoesti	1
Cercopithecus mitis	0
Colobus guereza	4
Lophocebus albigena	2
Papio anubis	1
Piliocolobus badius	9
Unidentified Cercopithecinae	6
Unidentified Colobinae	3
Unindentified Cercopithecoidea	12
Non-primates	
Cephalophus sp.	4
Megachiroptera	1
Rodentia	1
Viverridae	3
Unidentified Mammalia	3
Bucerotidae	1
Unidentified Aves	3

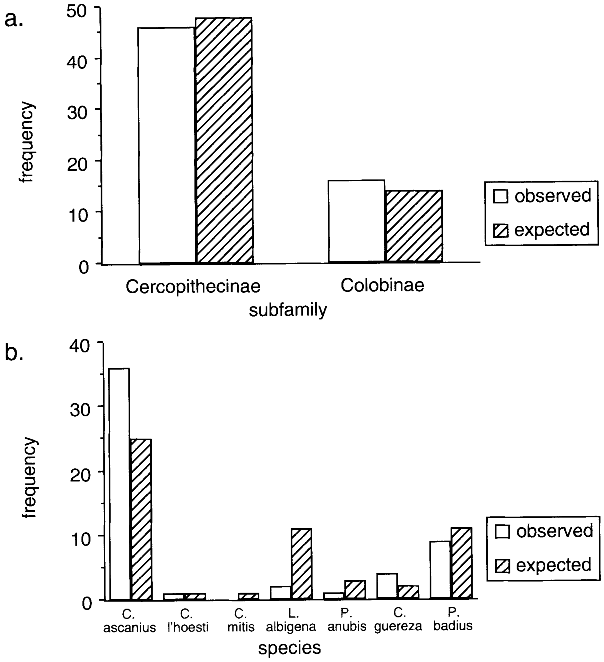

Fig. 1 Observed and expected numbers of primate prey, showing prey selection by subfamily (**a**) and by species (**b**). Expected values were generated based on the proportional representations of each subfamily and species in the forest as determined by censuses

over 5 groups per km^2 for redtail monkeys to a low of 0.18 groups per km^2 for blue monkeys (Table 1). Several mangabeys and red colobus monkeys reside at the Ngogo study site, with each species reaching densities of more than 2 groups per km^2. In contrast, baboons, black-and-white colobus, and l'Hoest's monkeys live at much lower densities, and as a result are not common potential prey items for crowned hawk-eagles at Ngogo.

Prey selection

Our searches yielded 390 prey items consisting of 470 skeletal elements. A minimum number of 85 individuals were represented in this sample (Table 2). We recovered 71 individuals under the first nest, while the second nest yielded 14 individuals. Three observed predation episodes, all on redtail monkeys, and two carcasses, one red colobus and one l'Hoest's monkey, formed the remainder of the prey sample (Table 2). All predation events and carcasses were witnessed and recovered within the hunting range of the first pair of eagles.

Primates composed the vast majority of all prey items (74/90=82%). Non-primate prey included other mammals such as duikers (*Cephalophus* sp.) and viverrids. Single bats, rodents, and hornbills were also present along with six other unidentified mammals and birds (Table 2).

Prey selection by primate subfamily and species

We were able to assign most of the primates in the sample of prey items to the level of subfamily (62/74=84%). Cercopithecines were taken more frequently than colobines (Fig. 1a), but the former outnumber the latter at Ngogo (Table 1). Thus, the disparity in offtake according to subfamily did not translate into a difference in observed and expected numbers of cercopithecine and colobine prey ($\chi^2=0.37$, 1 df, $P>0.70$; Fig. 1a).

We reliably classified prey items to species only in cases involving primates (Table 2). Redtail monkeys (*C. ascanius*) composed the majority of the primate prey (36/53=68%). Redtails were the most abundant primate numerically at the Ngogo study site (Table 1), but they were still preyed upon more often than expected on the basis their proportional representation in the forest (resampling test, $P<0.01$, 10,000 iterations; Fig. 1b). Red colobus monkeys (*P. badius*) were the next most frequently captured primate (9/53=17%). Red colobus were taken less frequently than expected by chance, though not significantly so (resampling test, $P>0.70$, 10,000 iterations; Fig. 1b). Four other primates, baboons (*P. anubis*), l'Hoest's monkey (*C. lhoesti*), black-and-white colobus (*C. guereza*), and mangabeys (*L. albigena*) were captured rarely. We recovered only two mangabeys, and they were taken much less frequently than expected given their proportional numbers in the forest (resampling test, $P<0.001$, 10,000 iterations; Fig. 1b). Baboons and l'Hoest's monkeys were represented by single individuals in our sample of prey items, while we recovered four black-and-white colobus. Observed numbers of kills for all three species did not show any marked departures from chance expectations (resampling tests, $P>0.15$ for all three comparisons, 10,000 iterations; Fig. 1b). Blue monkeys were not present in our sample of crowned-hawk eagle prey.

Age and sex classes of prey

We ascertained the age classes of primate prey in nearly all cases (73/74). Adults (38/73=52%) and non-adults (35/73=48%) were represented in roughly equal proportions. More non-adult primates (56%) reside in the population at Ngogo than adults (44%), and observed levels of predation on members of these two age classes did not differ from those expected on the basis of chance ($\chi^2=2.01$, 1 *df*, $P>0.10$; Fig. 2a).

We sexed all the adult primate prey in our sample. Males (20/38=53%) were represented slightly more often than females (18/38=47%). As is typically the case for primates in the wild (Mitani et al. 1996), females outnumber males at Ngogo. As a consequence, male primates were over-represented in the sample of prey items compared with females ($\chi^2=17.61$, 1 *df*, $P<0.001$; Fig. 2b).

Prey offtake

We recovered a minimum number of 63 primates within the hunting range of one eagle pair during the 37 months of study. The nests of the two eagle pairs were separated by approximately 2.2 km. Using this distance to derive the radius of the hunting range of each pair and assuming a circular territory, we estimated that each pair occupied an area of 3.8 km^2. This estimate is substantially smaller than the 10 km^2 figure previously employed by Struhsaker and Leakey (1990), who based their estimate on territories occupied by crowned hawk-eagles inhabiting more open habitats. Table 1 shows the population densities and group sizes of each potential primate prey species. Using these combined data, we estimate that approximately 2% of the total cercopithecoid primate population succumb to crowned hawk-eagle predation each year.

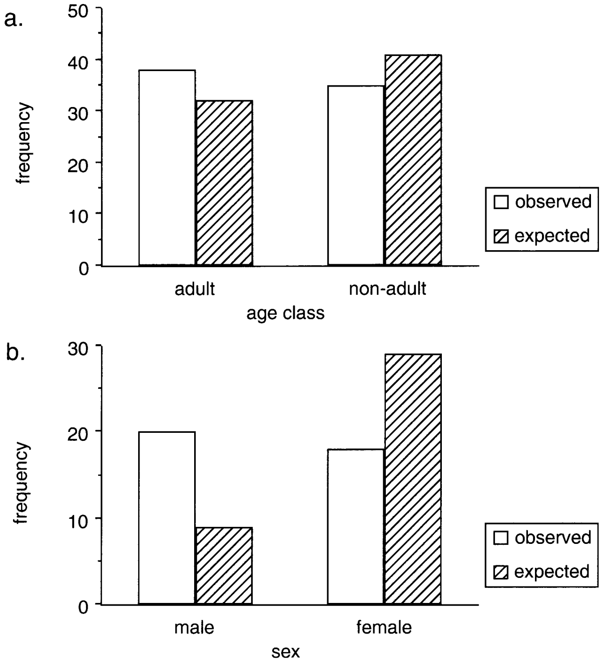

Fig. 2 Observed and expected numbers of adult and non-adult (**a**) and adult male and adult female (**b**) primate prey. Expected values were generated based on the proportional representations of each age and sex class in the forest as reported by Struhsaker and Leakey (1990)

Given the nature of our observations, our calculation for total primate prey offtake is likely to provide only a gross minimum estimate. Moreover, this estimate obscures variation in the types of primate taken and the impact eagle predation thus has on different species in the Ngogo community. Redtail monkeys were vastly over-represented in our sample of prey items, and further analysis reveals that 1% of their population was preyed upon by eagles each year.

Comparisons with other studies

Crowned hawk-eagles are important predators of primates in Kibale National Park. Based on the analysis of bones collected underneath the nests of two pairs of eagles at the Kanyawara study site in Kibale, Skorupa (1989) and Struhsaker and Leakey (1990) documented predation on six monkey species, including black-and-white colobus, blue monkeys, l'Hoest's monkey, mangabeys, red colobus, and redtail monkeys. Primates were the predominant prey of eagles at both nests. Moreover, predation appeared to be non-random, with eagles selectively choosing mangabeys and black-and-white colobus monkeys (Skorupa 1989; Struhsaker and Leakey 1990). Both studies showed a similar pattern of relatively low

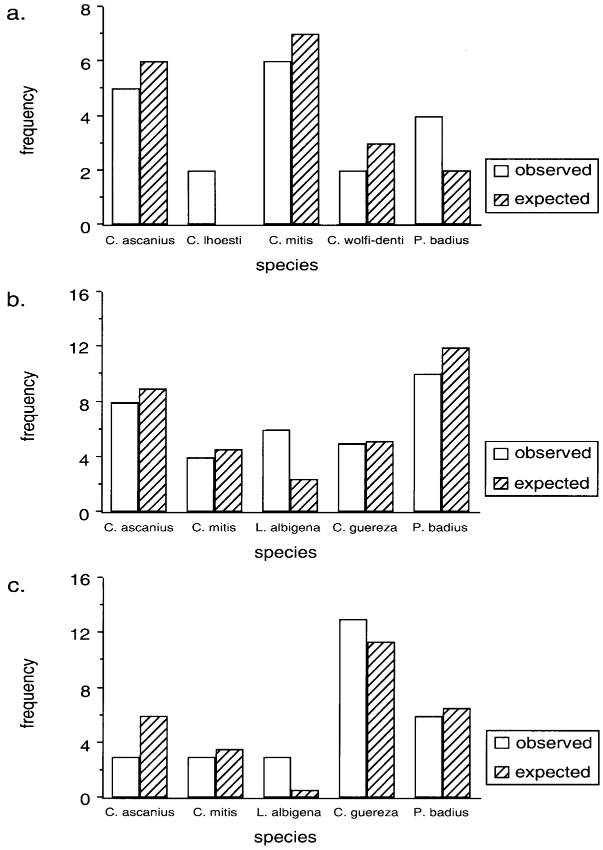

Fig. 3 Observed and expected numbers of primate prey selected at Ituri Forest (Hart et al. 1996) (**a**), from unlogged forest at the Kanyawara study site, Kibale Park (Struhsaker and Leakey 1990) (**b**), and from logged forest at the Kanyawara study site, Kibale Park (Skorupa 1989) (**c**). Expected values were generated based on the proportional representations of each species in the forest as determined by their group densities. **a** Group densities were based on data provided by Thomas (1991). **b** Group densities were taken from Struhsaker (1997) and Olupot et al. (1994). **c** Group densities were derived from combined group estimates of animals living in compartments 12–15 and 17 (Skorupa 1988 cited in Struhsaker 1997)

rates of predation on red colobus and redtails, leading Struhsaker and Leakey (1990) to propose that the frequent formation of mixed-species groups by these two species provides them protection against predatory attacks. Additional analyses suggested that, with the exception of red colobus, adult male monkeys were taken more often than other age-sex classes, and that total offtake was extremely low, typically only a fraction of 1% of the total primate population (Struhsaker and Leakey 1990).

Working in the nearby Ituri Forest, Democratic Republic of Congo, Hart and colleagues (1996) picked up carcasses from the forest floor that were known or inferred to have been preyed upon by crowned hawk-eagles. Using this technique, they documented crowned hawk-eagle predation on seven primate species, including blue monkeys, l'Hoest's monkey, mangabeys, red colobus, redtails, Wolf's guenon (*Cercopithecus wolfi*), and black-and-white colobus. As is the case at Kibale, primates were the most frequent prey item of crowned hawk-eagles in the Ituri Forest (21/24=88%). Hart and colleagues did not present the data needed to assess selection with respect to the age-sex classes of primate prey, but using observations made by Thomas (1991) at the same study site, selectivity with regard to species can be evaluated. Figure 3a shows that two species, l'Hoest's monkey and red colobus, were taken slightly more often than expected based on their proportional representations in the forest. The sample of Ituri prey items was relatively small and, as a consequence, the number of times each of these two species was captured did not depart significantly from chance expectation (resampling tests, $P>0.20$ for both comparisons, 10,000 iterations). Three other species, redtail monkeys, blue monkeys, and Wolf's guenon, were killed in numbers that did not deviate from those expected by chance (resampling tests, $P>0.40$ for all three comparisons, 10,000 iterations; Fig. 3a).

Comparing results regarding prey selectivity across studies is hindered by an important methodological difference. As in our analyses, prior studies have compared observed numbers of kills against those expected by chance to assess selectivity (Strusaker and Leakey 1990). Previous research, however, has derived chance expectations by assuming that eagles will make kills relative to the population densities of each prey species expressed in individuals per km^2 (Struhsaker and Leakey 1990). It is important to note in this context that monkey prey generally move in groups. Typical encounters thus involve eagles and groups of monkeys, suggesting that computations based on group densities, as employed here, represent a biologically more appropriate means to derive expected levels of predation. Re-analysis of the observations presented by both Skorupa (1989) and Struhsaker and Leakey (1990) using group densities to generate expected numbers of kills provides a very different picture of prey selection by crowned hawk-eagles at the Kanyawara study site. Mangabeys remain the lone species taken more often than expected by chance (resampling tests, $P\leq0.05$ for both comparisons, 10,000 iterations; Fig. 3b, c), while the selection bias against red colobus and redtails as prey disappears ($P>0.25$ for all four comparisons; Fig. 3b, c).

Discussion

The results presented here provide new insights into the predatory behavior of forest-dwelling crowned hawk-eagles. Primates compose the vast majority of all prey at the Ngogo study site. At Ngogo, eagles prey selectively on monkeys according to species and sex. One species, the redtail monkey, was taken significantly more often than expected by chance, while another, the mangabey, was captured less frequently than expected. Male primates were preyed upon more frequently than females. In contrast, there was no bias in the age of individuals that were killed: adults and non-adults were captured in numbers roughly equal to their proportional representations in the forest. Our observations further suggest that a non-trivial fraction of the entire primate population at Ngogo falls victim to crowned hawk-eagle predation.

The wide array of prey items recovered in our sample underscores the diversity of hunting styles employed by these raptors. Eagles appear to use stealth and surprise to capture arboreal monkeys, either by sitting and waiting in the canopy or swooping down from on high (Gautier-Hion and Tutin 1988; Cordeiro 1992; Maisels et al. 1993; our personal observations). Stealth and surprise are likely to play roles in successful predation on terrestrial duikers and volant hornbills, but are probably less important during hunts of nocturnal bats and viverrids, who may simply be picked off while they roost and sleep during daylight hours. Our record of a young baboon adds to an already long list of known prey items in the diet of crowned hawk-eagles living in Kibale Park (cf. Skorupa 1989; Struhsaker and Leakey 1990). That eagles prey upon primates as large as infant baboons and regularly capture other monkeys nearly three times their size, such as mangabeys and red colobus, highlights their formidable predatory skills, a fact reinforced through prior observations of them seizing bushbuck weighing up to 30 kg (Daneel 1979).

Considerable controversy has arisen regarding the role played by predation in affecting the social behavior and organization of non-human primates (Alexander 1974; Altmann 1974; Wrangham 1980; van Schaik 1983; Cheney and Wrangham 1987; Isbell 1994; Bshary and Noe 1997; Cowlishaw 1997; Hill and Lee 1998; Janson 1998). The persistence of this debate is largely due to a paucity of data on the phenomenon (see Introduction). By focusing on the activities of predators rather than their prey, we have been able to overcome some of the methodological problems associated with studying predation, and in the process, have assembled one of the largest datasets regarding predation on primates in the wild. These data add to a growing body of evidence that reveals the substantial impact of predation on the lives of primates. Our observations are of additional import insofar as they raise a cautionary flag with respect to the use of prior data employed in comparative analyses of predation on primates. Cheney and Wrangham (1987) originally assembled a now widely cited database of predation rates across primate species to explore the effects of predation on primate sociality. These data have been subsequently employed by others to investigate an array of related problems (e.g., Isbell 1994; Hill and Dunbar 1998). More recent attempts have been made to assay predation risk in a categorical fashion using characteristics of the local environment such as predator presence and density (e.g., Hill and Lee 1998). The results presented here and elsewhere (Mitani and Watts 1999; Watts and Mitani, in press), based on direct observations of predator behavior, are not entirely congruent with some of the figures for Kibale primates in the Cheney and Wrangham compilation, all of which were derived via indirect lines of evidence. Our observations are also not consistent with the assessment that Ngogo represents a “medium”-predation-risk environment (Appendix 1 in Hill and Lee 1998). As shown here, there is no substitute for direct observations, and in the absence of these, analyses based on limited and equivocal data will be of questionable utility.

Comparisons with other studies

Our observations of predation by crowned hawk-eagles reveal both similarities and differences to those reported by previous researchers. Primates are the most frequent prey item of the Ngogo eagles, composing 82% of their diet. This estimate approximates closely the 88% and 84% figures described from two additional nests within Kibale National Park (Skorupa 1989; Struhsaker and Leakey 1990). In contrast, crowned hawk-eagles living in open savannas and forest islands surrounded by grasslands and pastures prey on primates only infrequently, specializing instead on smaller, terrestrial prey items, such as hyrax and duiker (Brown 1976; Jarvis et al. 1980). Predatory behavior of eagles differs not only between habitats, but within similar environments as well. For example, redtail monkeys compose most of the prey items at Ngogo, while two colobines, black-and-white and red colobus, are the most frequently captured prey at Kanyawara, only 12 km to the northwest (Skorupa 1989; Struhsaker and Leakey 1990; Fig. 3). These between- and within-habitat differences in prey selection can be attributed in part to variations in prey availability. Primates live at much lower densities in open savannas and velds than in tropical forests, and this may account for the scarcity of monkeys in the diets of birds living in the former areas. Similarly, the high number of colobines taken at Kanyawara likely reflects their unusually high densities there (Struhsaker 1997). Alternatively, the selection bias toward redtails at Ngogo can be attributed to their relative abundance at this site (Table 1).

While differences in prey availability go a long way to explain some aspects of between-site differences in eagle predation at Kibale, why Kanyawara eagles selectively prey on mangabeys while Ngogo eagles choose redtails remains unclear. Here other factors related to predator and prey behavior are of probable importance. For example, these differences in prey selection may simply reflect inter-individual variation in the hunting behavior of eagle pairs. Few data presently exist to evaluate this hypothesis, although our limited sample is suggestive. Redtail monkeys composed 24 of 43 primate individuals (56%) identified to species level from the first nest, while these same monkeys constituted 9 of 10 primates (90%) from the second nest. Alternatively, the demographic structure of primates represents another source of variation that might affect the vulnerability of prey and hence influence the hunting success of eagle predators occupying different sites. For example, the large number of solitary male mangabeys at Kanyawara may form a population of animals particularly susceptible to predation (cf. Struhsaker and Leakey 1990). In contrast, the high density of redtails at Ngogo may preclude their ability to form mixed-species groups and thus increase their vulnerability to predatory attacks. Further study will be necessary to test these hypotheses. Specifically, larger samples of prey from multiple nesting pairs and direct observations of predatory attacks on monkeys in and out of mixed-species associations will help resolve these questions.

We suggest that additional differences in the hunting behavior of crowned hawk-eagles living within the Kibale National Park are more illusory than real. Struhsaker and Leakey (1990) reported that adult primates are especially susceptible to eagle predation at the nearby Kanyawara study site. In contrast, we did not detect any bias in the numbers of adult and non-adult individuals captured by eagles at Ngogo. We propose that these apparent discrepancies are largely due to important differences in sampling. During our 37-month study, we collected 425 skeletal items, representing 76 individuals at one nest. In contrast, Struhsaker and Leakey (1990) collected far fewer prey items under another nest over a similar period of time: only 108 bones from 37 individuals were recovered in 39 months (Leland and Struhsaker 1993). We suggest that our more intensive retrieval efforts resulted in a more representative sample of prey items, especially with respect to some of the smaller, less robust bones that will typically be derived from infants and juveniles. Two additional factors, one methodological, another empirical, cast doubt on the claim that eagles prey selectively on adult primates. First, bones of young individuals are more fragile and easily broken, crushed, and destroyed by eagle predators. Young prey will automatically be less easily detectable given our mode of sample collection. Second, studies of other predators consistently indicate that predators will selectively prey on the weakest and most vulnerable individuals in a population, individuals who are likely to be young rather than adults (e.g., Schaller 1972; Caro 1994).

Finally, our more intensive collection efforts combined with a smaller estimate of eagle hunting ranges also help to explain the discrepancies in prey offtake figures reported in this and earlier studies. Though our calculations provide only a gross minimum estimate of total prey offtake, they still represent a tenfold higher figure than that reported in a prior study at Kibale (Struhsaker and Leakey 1990). We regard the 2% total offtake figure computed here to be a more realistic estimate of the impact of crowned hawk-eagle predation on natural primate populations. Here too, further study will be necessary to ascertain the extent to which this can be generalized to other populations and to assess the long-term demographic and ecological consequences of crowned hawk-eagle predation.

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