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# PREDATION ON VERTEBRATES IN THE KIRINDY FOREST, WESTERN MADAGASCAR

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## INTRODUCTION

Predation plays a prominent role in concepts of community ecology and of the evolution of group size and social structure (Bertram 1978, Begon *et al.* 1990). Yet little quantitative information is available to assess the actual impact of predation on various prey species in the tropics (Emmons 1987, Struhsaker & Leakey 1990, Wright *et al.* 1994). Information is particularly scant for the island of Madagascar. Albignac (1973) reviewed what was then known about food composition of the Malagasy viverrids. Goodman *et al.* (1991; 1993a,b,c) and Goodman & Langrand (1993) summarized the available evidence for predation on lemurs across Madagascar and gave a number of examples of prey composition of the Barn Owl *(Tyto alba)* and the Madagascar Long-eared Owl *(Asio madagascariensis)* at various localities across the island. Here we would like to extend this comparative database on prey of the two owl species: *A. madagascariensis* in primary forest and *T. alba* in secondary vegetation formations, bordering the primary forest (Rasoloarison 1994). We also provide rhe first quantitative data on the food composition and prey selection of the Fossa *(Cryptoprocta ferox),* the largest extant viverrid of Madagascar (Rasolonandrasana 1994).

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## STUDY SITES AND METHODS

The studies were carried out on the west coast of Madagascar during the dry seasons in 1993 and 1994. Work in primary forest was carried out in the Kirindy Forest, within the forestry concession of the Centre de Formation Professionnelle Forestière de Morondava (CFPF) (20° 03'S, 44° 39'E) some 60 km north of Morondava, and in secondary forest and farmland around Marofandilia (20° 09'S, 44° 35'E), some 40 km north of Morondava. The primary and secondary forest ecosystems are described by Covi (1988) and von Schulthess (1990).

*A. madagascariensis* pellets were collected in primary forest under a roost bordering the river bed of the Kirindy River (plot CS6) in August 1993 and September 1994. *T. alba* pellets were obtained from secondary forest formations around Marofandilia under 4 different nests once per month in August 1993 and from October to December 1993.

For prey analysis of *C. ferox,* scats were collected in the CFPF forestry concession between mid-August and late November 1993. Searches for scats concentrated on an area of about 7 km$^2$ between plots N5 and CS7, covering the main logging trails. Based on density estimates by Albignac (1973) about 7 *C. ferox* should inhabit this area. 114 scats were collected over the 4 month period. Despite considerable effort, no scats were found in the same area after the onset of the rainy season between December 1993 and February 1994.

Teeth, bone fragments and fur isolated from the scats and pellets were used for determination of prey. Bones were removed after soaking the pellets and scats in water. Reference collections of the Laboratoire de Primatologie (Université d'Antananarivo) and the Parc Botanique et Zoologique de Tsimbazaza (Antananarivo, Madagascar) were used. In the case of owl pellets, paired bones of any taxon within a monthly sample were separated and the largest number of elements from either the left or the right side was considered the minimum number of individual (MNI) prey items.

For analyses of *C. ferox* scats, all samples collected per month over the whole CFPF forestry concession were pooled together. This procedure underestimates the actual number of prey items; however as long as nothing is known about the ranging pattern of *C. ferox* this conservative approach was favored.

## RESULTS

*Prey composition of Asio madagascariensis in primary forest.* In the lowland eastern rainforest, as well as in a dry deciduous forest of western Madagascar, pellets of *A. madagascariensis* contained remains of frogs, lizards, birds, terrestrial insectivores, bats, lemurs and rodents. *R. rattus* and *Microcebus* spp. were among the most important prey items. *A. madagascariensis* seem to rely on prey items below 100g, but occasionally catch larger birds or mammals up to medium-sized lemurs of 0.8kg (Goodman *et al.* 1991, 1993b).

The number of pellets from *A. madagascariensis* collected in the bed of the Kirindy River in primary dry deciduous forest was small (Table 1). Flooding of the river inhibited further collection of pellets. Neverrheless, the samples of two dry seasons confirm that large prey items up to the size of *Lepilemur mustelinus ruficaudatus* (body mass: 750 g) are taken and that *Microcebus* spp. (here *M. myoxinus* and *M. murinus*) play a prominent role in the diet of *A. madagascariensis.*

*Prey composition of* Tyto alba *in secondary vegetation.* Prey composition of *T. alba* was determined for four sites, all located in rather disturbed areas. Site 1 is located on the edge of a 12ha forest fragment surrounded by fields of corn and peanuts. Sites 2, 3 and 4 are in secondary forests also close to human habitations and agricultural fields.

At all sites *T. alba* feeds mainly on *R. rattus* and *M. musculus* (Table 2). The data at hand do not allow us to assess selection criteria based on prey size and abundance. They demonstrate, however, that *T. alba* hunts in all available habitats. The presence of *Micro-*

TABLE 1. Vertebrate remains identified from pellets of Asio madagascariensis. Calculations are based on analyses of 6 and 28 pellets collected in August 1993 and September 1994 respectively in the Kirindy Forest (from Rasoloarison 1994 and unpublished). *Microcebus* spp. consists of *M. murinus* and *M. myoxinus.* MNI = Minimum number of individuals.

| Species | Body mass (g) | 1993 MNI | 1993 % Prey biomass | 1994 MNI | 1994 % Prey biomass |
|---|---|---|---|---|---|
| AVES | | | | | |
| *Turnix nigricollis* | 69 | | | 1 | 2% |
| MAMMALIA | | | | | |
| RODENTIA | | | | | |
| *Rattus rattus* | 100 | 1 | 12% | 5 | 15% |
| *Eliurus myoxinus* | 82 | 1 | 8% | 5 | 12% |
| PRIMATES | | | | | |
| *Microcebus spp.* | 30/60 | 3 | 19% | 12 | 22% |
| *Cheirogaleus medius* | 280 | | | 2 | 17% |
| *Mirza coquereli* | 300 | | | 1 | 9% |
| *Lepilemur mustelinus* | 750 | 1 | 61% | 1 | 23% |
| Total: VERTEBRATA | | 6 | | 27 | |

TABLE 2. Vertebrate remains identified from pellets obtained below four *Tyto alba* roosts between August and December 1993 in secondary vegetation around Marofandilia (from Rasoloarison 1994, supplemented by identifications of *M. brevicaudata* by P. Jenkins).

| Taxa | Body mass (g) | Site 1 MNI | Site 2 MNI | Site 3 MNI | Site 4 MNI |
|---|---|---|---|---|---|
| AMPHIBIA | | | | | |
| small | 4 | 1 | 10 | | 1 |
| large | 9 | 14 | 7 | 5 | 2 |
| Total: AMPHIBIA | | 15 | 17 | 5 | 3 |
| REPTILIA | | | | | |
| small | 4 | 6 | 2 | 3 | 5 |
| large | 15 | 11 | 8 | 11 | 9 |
| Total: REPTILIA | | 17 | 10 | 14 | 14 |
| AVES | | | | | |
| *Gallus gallus* | 750 | 1 | | | |
| *Turnix nigricollis* | 69 | 3 | 4 | 2 | 1 |
| *Hypsipetes mad/sis* | 45 | | | 1 | |
| *Agapornis cana* | 30 | 3 | 2 | | |
| *Neomixis tenella* | 7 | | 3 | | 1 |
| *Newtonia brunneicauda* | 10 | 1 | | 3 | 3 |
| *cf. Saroglossa aurita* | 40 | | 1 | | |
| *Foudia mad/sis* | 17 | 10 | 6 | 5 | 4 |
| *Ploceus sakalava* | 24 | 2 | 1 | 1 | |
| Total: AVES | | 20 | 20 | 12 | 9 |
| MAMMALIA | | | | | |
| INSECTIVORA | | | | | |
| *Suncus mad/sis* | 2 | 30 | 31 | 36 | 40 |
| *Geogale aurita* | 7 | 7 | 12 | 6 | 8 |
| *Microgale brevicaudata* | 9 | | 1 | | 1 |
| CHIROPTERA | | | | | |
| *Mops condylura* | 44 | | 1 | | |
| PRIMATES | | | | | |
| *Microcebus murinus* | 60 | 1 | 1 | 3 | 2 |
| RODENTIA | | | | | |
| *Rattus rattus* | 100 | 49 | 61 | 36 | 38 |
| *Mus musculus* | 10 | 458 | 340 | 303 | 196 |
| Total: MAMMALIA | | 545 | 447 | 384 | 285 |
| Total: VERTEBRATA | | 597 | 494 | 415 | 311 |

*cebus* indicates hunting in the forest interior or along the forest edge, while *Rattus, Mus* and chicken are more likely to be caught around human habitations.

*Prey composition and selectivity of Cryptoprocta ferox in primary forest.* During the dry season lemurs are the most widely consumed prey in the diet of *C. ferox* in the Kirindy Forest (Table 3). They comprise more than half of the individual prey items and 57% of prey biomass.

Jumping rats *(Hypogeomys antimena)* also form a substantial part of the diet of *C. ferox*. This illustrates that *C. ferox* hunts in the trees as well as on the ground. Remnants of the aestivating tenrec *Echinops telfairi* and the lemur *Cheirogaleus medius* appeared in the scats long before the animals were observed in the forest. Thus *C. ferox* not only hunts active prey but also digs out hibernating animals. *Tenrec ecaudatus* was found in the November sample, during a period when it had already come out of aestivation.

Among the potential terrestrial prey species none of the smaller rodents known from the Kirindy Forest (*Macrotarsomys bastardi* and *Eliurus myoxinus*), with body mass of 0.03 and 0.08kg, appeared in the scats. In contrast, larger rodents, such as *Hypogeomys antimena* (body mass up to 1.3kg) and remnants of *Rattus rattus* (body mass 0.1kg) were found in the scats. Despite small sample size this preference for larger prey species is significant (Kolmogorov-Smirnov test: $P<0.01$; Fig. 1A).

The preference for larger prey items over smaller ones is confirmed by comparing lemur abundances in the Kirindy Forest and their contribution to the diet of *C. ferox* (Fig. 1B). In the case of lemurs the difference between the two distributions also approaches statistical significance (Kolmogorov-Smirnov test: $P=0.05$).

On the basis of the current data it appears that *C. ferox* exerts considerable predation pressure on the larger lemurs, especially *Propithecus verreauxi*. In the fol-

TABLE 3. Prey composition of *C. ferox* between August and November 1993 in the dry deciduous forest of Kirindy, based on analysis of 114 scats (from Rasolonandrasana 1994).

| Taxa | Body mass (g) | MNI | % Prey individuals | % Prey biomass |
|---|---|---|---|---|
| REPTILIA | | | | |
| Lacertilia | 15 | 1 | 2.7 | 0.0% |
| Ophidia (small) | 100 | 2 | 5.4 | 0.5% |
| Ophidia (large) | 300 | 2 | 5.4 | 1.5% |
| Total: REPTILIA | | 5 | 13.5 | 2.1% |
| AVES | | | | |
| *Leptosomus discolor* | 200 | 1 | 2.7 | 0.5% |
| Total: AVES | | 1 | 2.7 | 0.5% |
| MAMMALIA | | | | |
| INSECTIVORA | | | | |
| *Echinops telfairi* | 60 | 2 | 5.4 | 0.3% |
| *Tenrec ecaudatus* | 900 | 1 | 2.7 | 2.3% |
| RODENTIA | | | | |
| *Rattus rattus* | 100 | 1 | 2.7 | 0.3% |
| *Hypogeomys antimena* | 1100 | 4 | 10.8 | 11.1% |
| PRIMATES | | | | |
| *Microcebus* spp. | 60 | 1 | 2.7 | 0.2% |
| *Cheirogaleus medius* | 280 | 4 | 10.8 | 2.8% |
| *Mirza coquereli* | 360 | 2 | 5.4 | 1.8% |
| *Phaner furcifer* | 400 | 3 | 8.1 | 3.0% |
| *Lepilemur mustelinus* | 750 | 5 | 13.5 | 9.4% |
| *Eulemur fulvus rufus* | 2300 | 1 | 2.7 | 5.8% |
| *Propithecus v.verreauxi* | 3600 | 4 | 10.8 | 36.3% |
| ARTIODACTYLA | | | | |
| *Potamochoerus larvatus* | 8000 | 1 | 2.7 | 20.2% |
| CARNIVORA | | | | |
| *Mungotictis decemlineata* | 800 | 2 | 5.4 | 4.0% |
| Total: MAMMALIA | | 31 | | 97.4% |
| Total: VERTEBRATA | | 37 | | |

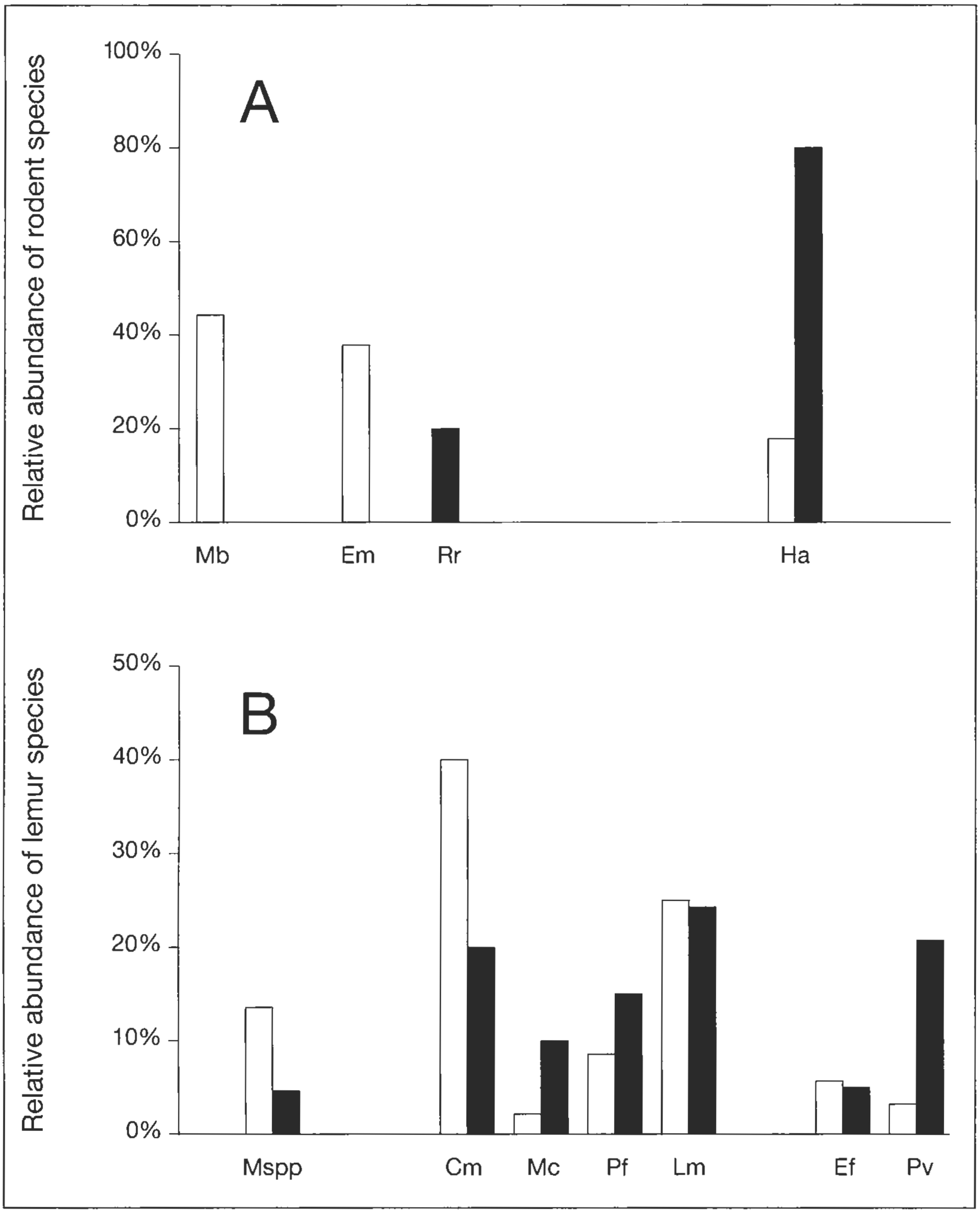


FIG 1. Comparison of the relative density of rodent (A) and lemur species (B) in the Kirindy Forest (grey bars) and their relative occurrence in the scats of *C. ferox* (black bars). Prey species are listed in ascending body mass along the x-axis. Data on prey composition and body mass can be found in Tables 1-3. Data on rodent abundances are from systematic trapping in N5 and CS7 during the dry season in June 1993. In each area 49 Sherman (7.7 x 7.7 x 30.5 cm) and 9 Tomahawk traps (18 x 18 x 50 cm) had been set for 4 nights (total 464 trapnights). Mb = *Macrotarsomys bastardi*, Em = *Eliurus myoxinus*, Rr = *Rattus rattus*, Ha = *Hypogeomys antimena*. Data on lemur density are based on repeated census walks between 1988 and 1994 throughout the area where scats were collected. Methodological details are given in Ganzhorn (1992). Mspp = *Microcebus myoxinus* and *M. murinus*, Cm = *Cheirogaleus medius*, Mc = *Mirza coquereli*, Pf = *Phaner furcifer*, Lm = *Lepilemur mustelinus ruficaudatus*, Ef = *Eulemur fulvus*, Pv = *Propithecus verreauxi*.

lowing assumptions we assess the predation pressure of *C. ferox* on *P. verreauxi*, the most important prey item in terms of biomass (Table 3):

1. The area between plots N5 and CS7 (about 7km$^2$) was thoroughly searched between August and November. During these four months remains of 4 *P. verreauxi* appeared in the scats. Extrapolating this number over the course of a year 12 individuals of *P. verreauxi* would be consumed.

2. The population density of *P. verreauxi* is about 30 individuals per km$^2$ across the searched area (Ganzhorn 1992).

3. Sex ratio, age structure and birth rate of *P. verreauxi* in the Kirindy forest are similar to demographic characteristics of this species in Beza Mahafaly. There, the sex ratio is about 1:1, about 80% of adult females are sexually active and birth rate is about 50% per year (Richard *et al.* 1991).

Thus the 7km$^2$ contain about 210 *P. verreauxi*, of which 105 are female, 84 of which are sexually active and give birth to 42 young each year. If *C. ferox* actually kill 12 *P. verreauxi* per year in this area, they remove about 29% of the yearly population growth. Since all the assumptions made here are conservative, the real predation pressure of *C. ferox* on *P. verreauxi* may actually be much higher.

Therefore, predation is not only important for the smaller species, such as *Microcebus* spp. (Goodman *et al.* 1993a,b,c), young animals (Sauther 1989), or acted only in the past (Goodman 1994a,b), but still is an active factor for various-sized animals in Malagasy ecosystems. Thus, the notion that reduced predation pressure on Madagascar would have allowed some ecological release of the prey fauna and the persistence of small social groups (e.g., van Schaik & van Hooff 1983, Ganzhorn 1988) needs revision.

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