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Evidence of Invasive *Felis silvestris* Predation on *Propithecus verreauxi* at Beza Mahafaly Special Reserve, Madagascar

Diane K. Brockman · Laurie R. Godfrey · Luke J. Dollar · Joelisoa Ratsirarson

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Abstract Increasing evidence supports the idea that endemic avian and mammalian predators have profoundly impacted primate populations in Madagascar (Goodman, S. M. Predation on lemurs. In S. M. Goodman, & J. P. Benstead (Eds.), *The natural history of Madagascar* (pp. 1221–1228). Chicago: University of Chicago Press, (2003).). The role in regulating lemur populations of the 3 introduced mammalian carnivorans —small Indian civets (*Viverricula indica*, Desmarest 1804), domestic dogs (*Canis lupus familiaris*, Linnaeus 1758), and invasive wildcats (*Felis silvestris*, Schreber 1775)— is less clear, but recent evidence suggests that the latter 2 are becoming important predators of diurnal lemurs. We report evidence for invasive wildcat predation on sifaka (*Propithecus verreauxi verreauxi*) in Parcel 1 at Beza Mahafaly Special Reserve, Madagascar, including skeletal remains of apparent *Propithecus* sifaka victims, observations of wildcat predatory behavior, and behavioral responses of the lemurs in the presence of wildcats.

Keywords behavior · Beza Mahafaly Special Reserve · *Felis sylvestris* · predation · *Propithecus verreauxi* · skeletal remains

D. K. Brockman (✉)
Department of Anthropology, University of North Carolina at Charlotte, Charlotte, NC 28223, USA
e-mail: dkbrockm@uncc.edu

L. R. Godfrey
Department of Anthropology, University of Massachusetts, Amherst, Amherst, MA 01003, USA

L. J. Dollar
Department of Biology, Pfeiffer University, Misenheimer, NC 28109, USA

J. Ratsirarson
ESSA, Département Eaux et Forêts, BP 175, Université d'Antananarivo (101), Antananarivo, Madagascar

Introduction

The impact of predation pressure on the evolutionary history of lemurs was once contentious, but increasing evidence, both direct and indirect, supports the idea that avian and mammalian predators, including carnivorans introduced to Madagascar in recent times (Goodman 2003; Gould and Sauther 2007), profoundly impact lemur populations. *Cryptoprocta ferox* (7–14 kg) is the predominant mammalian predator of large-bodied (3–4 kg) lemurs, e.g., *Propithecus*, and though observations of predation by *Cryptoprocta* on diurnal lemurs are infrequent (Wright 1998), indirect evidence derived from their prey remains, prey composition in scats, and behavioral/vocal responses to potential carnivoran predators suggests that *Cryptoprocta* plays an important role in regulating populations of *Propithecus* in both dry (Kirindy CFPF: Dollar *et al.* 2007; Ganzhorn and Kappeler 1996; Rasoloarison *et al.* 1995) and rain forest (Ranomafana National Park, Wright 1998) habitats.

The role in regulating lemur populations of the 3 introduced mammalian carnivorans —small Indian civets (*Viverricula indica*, Desmarest 1804), domestic dogs (*Canis lupus familiaris*, Linnaeus 1758), and wildcats (*Felis silvestris*, Schreber 1775)— is less clear, but recent evidence (Dollar *et al.* 2007; Gould and Sauther 2007; Sauther and Cuozzo 2005) suggests that domestic dogs and wildcats are becoming increasingly important predators of diurnal lemurs. We report evidence for invasive wildcat predation on *Propithecus verreauxi verreauxi* in Parcel 1 at Beza Mahafaly Special Reserve (BMSR), Madagascar, including skeletal remains of apparent lemur victims, observations of wildcat predatory behavior, and behavioral responses of *Propithecus* in their presence. Among the potential predators of *Propithecus* at BMSR (Table I), the Madagascar harrier hawk (*Polyboroides radiata*), *Cryptoprocta ferox*, and *Canis lupus familiaris* are the only ones reported on the basis of observed predation attempts (Brockman 2003), prey remains

Table I Behavioral and vocal responses of *Propithecus verreauxi verreauxi* to predators/potential predators at Beza Mahafaly Special Reserve, Madagascar

Predators[a]/ potential predators	Common name	Behavioral response	Vocal response
Polyboroides radiatus[a]	Madagascar harrier hawk	Drop lower in the canopy and toward the center of the tree; visually scan upward; mobbing	Roaring bark
Buteo brachypterus	Madagascar buzzard	Approach nesting pair (~8 m)	None
Cryptoprocta ferox	Fossa	No observations	No observations
Canis lupus familiaris[a]	Domestic dog	Move up in the canopy; visually scan downward	Roaring bark
Felis silvestris	Wildcat	Move up in the canopy; visually scan downward	Silence → continuous si-faking
Acrantophis dumerili	Dumeril's ground boa	Visually scan downward	None

[a] Observed predation attempts.

(Richard *et al.* 2002), and more recently, observed injuries (Sauther and Cuozzo, *pers. comm.*). In rain forest habitats, harrier hawks have also taken smaller lemurs, including *Microcebus* and *Cheirogaleus* (Ranomafana National Park, Karpanty and Wright 2007). Brockman observed domestic dogs stalking *Propithecus* at BMSR, but the predation attempts were not successful (Brockman, *unpub. data*). However, since October 2005, 4 lemurs have sustained serious injuries from attacks by dogs (Sauther and Cuozzo, *pers. comm.*). Further evidence that dogs have played an important role in the lives of *Propithecus* at the site derives from the distinct and stereotypic responses *Propithecus* exhibit toward the predators, including avoidance, mobbing, and predator roars (Table I).

Dollar has studied wildcats in the dry forests of Ankarafantsika National Park, Madagascar, since 1999. His studies of activity patterns and ranging indicate that wildcats tend to inhabit fringe areas between secondary or degraded forests and savannas (Dollar *et al.* 2007). Most bouts of ranging tend to occur on a crepuscular or nocturnal basis, but occasional diurnal bouts also occur (Dollar, *unpub. data*). The numbers of understory bird and small rodent censuses in areas of known wildcat activity tend to be lower in Ankarafantsika than in areas outside the hunting grounds. The potential of wildcats to prey upon diurnal and nocturnal lemurs, particularly when the lemurs spend significant time on the ground, is considerable (Dollar *et al.* 2007).

Wildcats are distinguishable from domestic cats via their ranging habits, pelage patterns, and overall size. Wildcats Dollar captured and radiocollared near Ankarafantsika ranged on the edges of savannas, regularly penetrating <500 m into transitional forest. Only when crossing forested areas to distant savannas would wildcats range deeply into forested areas or near villages (Dollar, *unpub. data*). In contrast, researchers have not captured or phototrapped domestic cats far beyond the fringes or clearings of rural villages and towns in and around Ankarafantsika. Whereas current research on wildcats in Africa and Europe leaves little doubt that interbreeding between domestic and wildcat populations occurs (Daniels *et al.* 1998), differences in their ranging behavior in Madagascar would operate to segregate the stocks.

Anatomically, invasive wildcats are easily distinguishable from domestic cats. The pelage of wildcats in and around Ankarafantsika and BMSR is a brown and gray tabby pattern, whereas domestic cats may have a wider range of coat patterns and are often non-tabby coated. There are also morphometric differences. In a comparison of anesthetized live domestic cats and wildcats around Ankarafantsika, wildcats are uniformly larger. They also exhibit notable sexual dimorphism, with males almost twice as large as females (Table II).

Materials and Methods

Study Site and Subjects

BMSR is in the Spiny Forest Ecoregion in southwest Madagascar. The climate is semiarid with highly seasonal patterns of rainfall and temperature. The area receives an average 700 mm of rain annually, most of it during the austral summer months of

Table II Mean values for morphometric comparisons of adult domestic cats ($n=18$) and wildcats ($n=12$) in and near Ankarafantsika National Park, a northwestern dry forest in Madagascar

	Mass (kg)	Body length (cm)	Upper canine length (mm)	Forelimb length (cm)	Hindlimb length (cm)
Domestic cat males	3.6	54.7	10.5	22.5	31.1
Domestic cat females	2.5	42.7	8.0	17.0	22.0
Wildcat males	5.5	63.6	12.3	31.2	35.1
Wildcat females	2.9	52.6	9.9	27.1	32.1

Measurements were taken by LJD on live specimens of both sexes.

October–March, while the austral winter months receive little or no rain (Ratsirarson 2003). Austral summer temperatures typically reach 42°C during the day and fall to 21°C at night, and austral winter temperatures range from a high of 36°C to a low of 3°C during the day and night, respectively (Richard *et al.* 1991). BMSR, 35 km northeast of Betioky-Sud, measures 600 ha and is subdivided into 2 noncontiguous protected parcels of land: Parcel 1 (80 ha) and Parcel 2 (520 ha).

Long-term studies of demography, ecology, and behavior of *Propithecus* began in 1984 (Brockman 1994, 1999; Brockman and Whitten 1996; Brockman *et al.* 1998, 2001; Kubzdela 1997; Ranarivelo 1993; Richard *et al.* 1991, 1993, 2000, 2002) and were focused on populations living in Parcel 1. The parcel comprises a diversity of microhabitats, ranging from riverine gallery forests bordering the Sakamena River in the east to grassy xeric forests in the west. *Tamarindicus indica* dominates the eastern portion of the reserve while species of Euphorbiaceae and Didiereaceae augment in abundance with increasing distance from the river. The area is protected by a barbed wire fence, which usually prevents incursions by local herds of zebu cattle and goats, but allows free movement of indigenous fauna in and out of the forest bordering the reserve. It has a 100×100 m grid system of contiguous forest plots (Fig. 1).

The study population of *Propithecus* comprises *ca*. 275 marked individuals living in 32 core social groups. Their 4–6 ha overlapping home ranges are confined within the boundaries of Parcel 1. Members of the population are monomorphic in body and canine size, averaging 2.8 kg, though there is considerable seasonal variation in body mass between the sexes (Godfrey *et al.* 2002; Lawler *et al.* 2005; Richard *et al.* 2000). At BMSR most females conceive during the January–March austral summer, birth *ca.* 164 d later during the late June–late August austral winter, and wean their infants coincident with the onset of the November spring rains when weaning foods are just becoming available and infants are moving independently (Brockman and van Schaik 2005). Five- to 8-mo-old juveniles (*ca.* 1.5 kg) are particularly vulnerable then as they continue developing their arboreal locomotor skills (Lawler 2006).

At BMSR, *Propithecus* are targeted, balanced feeders (Yamashita 2002, p. 1044), consuming the leaves, fruit, flowers, and buds of various trees, e.g., *Tamarindus, Dichrostachys* sp., *Grewia* sp., *Euphorbia* sp., *Acacia* sp., and shrubs, e.g., *Metaporana* sp., according to seasonal availability (Yamashita 2002). During the wet season, and occasionally during the dry season when it rains, *Propithecus* consume succulent grasses and young leaves of herbs, e.g., *Ruellia anaticollis* (Fig. 2)

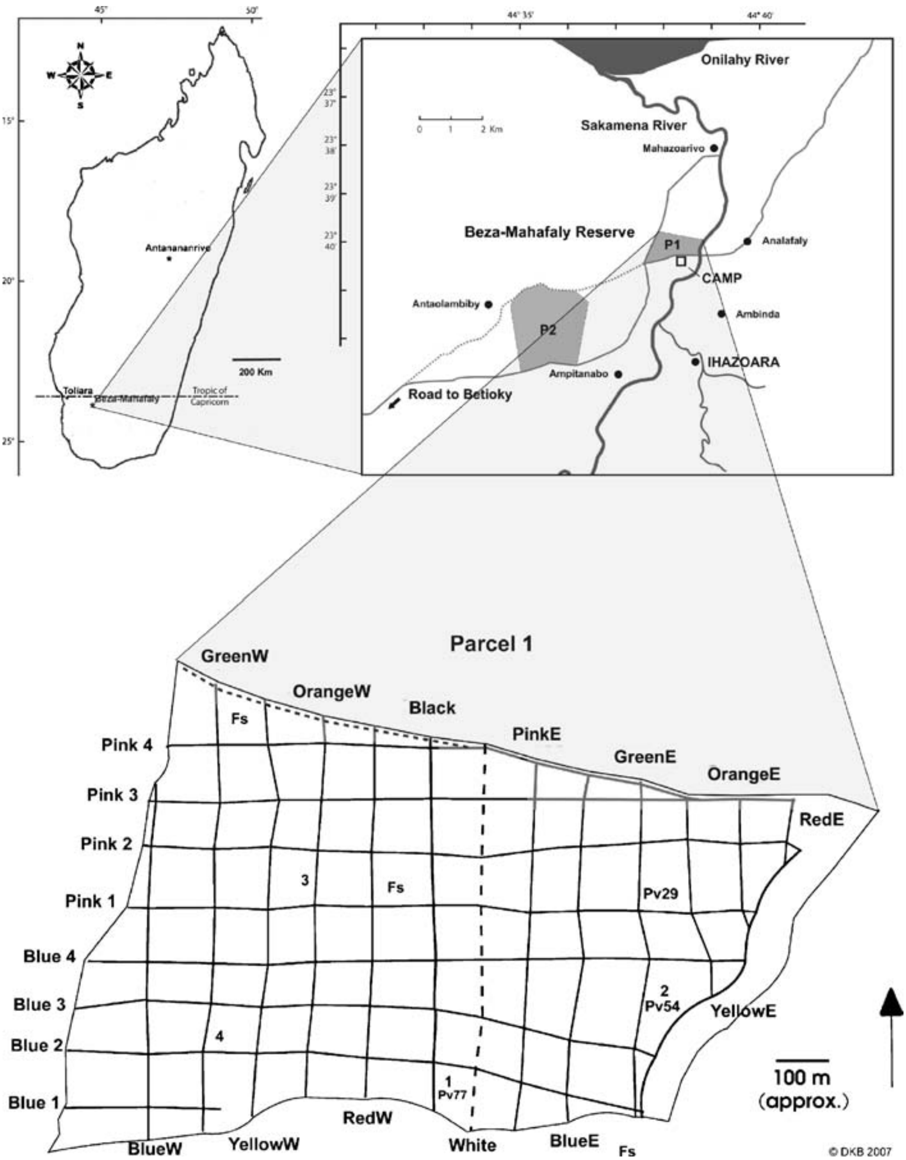

Fig. 1 Site location for Beza Mahafaly Special Reserve, Madagascar, with map of Parcel 1 showing locations of wildcat sightings (numbers), and the remains of *Propithecus* (BMOC no.) and wildcats (Fs). (Modified from maps drawn by Diane K. Brockman, Darren Godfrey, and Robert Dewar.).

and vines growing on the ground along with unripe fruits (*Tamarindus*) and berries (*Azima*) accessible in the trees (Brockman and Ratsirarison, *unpub. data*). Whereas *Propithecus* are typically arboreal, Brockman nevertheless frequently observed them coming to the ground in Parcel 1 during both the dry and wet seasons. During the 1990–1992 drought, Brockman also observed resident *Propithecus* in the shady eastern part of

Fig. 2 BMSR *Propithecus verreauxi verreauxi* lying on the ground prone, feeding on *Ruellia anaticollis*, Benoist (Acanthaceae). (Photo by Diane K. Brockman).

Parcel 1 resting at the base of trees, assuming a tree-hugging position for 1–2 h when summer temperatures reached *ca.* 47°C (Brockman, *unpubl. data*).

Data Collection

Beginning in 1985, researchers fairly regularly collected and labeled skeletal remains of *Propithecus*, invasive wildcats, and other fauna encountered within or near the periphery of Parcel 1. Godfrey catalogued the resulting Beza Mahafaly Osteological Collection (BMOC, housed at the museum of BMSR) and established a protocol for adding new skeletal materials. Beginning in 2001, we asked guides and researchers to follow the protocol in collecting new skeletal materials, and collection became more regularized and systematic.

Godfrey examined each of the crania and mandibles of *Propithecus* in the collection for signs of scavenging or predation. Postmortem rodent damage tends to have a characteristic pattern: the tooth marks are elongated and roughly parallel, though they can assume a fan-shaped pattern. They occur on the thinnest, blade-like bones, such as the gonial angle of the mandible or the blade of the scapula. Shredding or fraying invariably occurs along the edge of the bone. Perimortem damage by carnivorans is very different: there may be crushing and deformation or breakage of the bone but the edge is not frayed. Puncture wounds with hinged fractures and adhering flakes may be present on the top and the back of the skull. A portion of the skull, i.e., the rostrum, the base, and back of the neurocranium, may be missing. Fresh bone deforms in a manner that dried bone cannot without splintering or cracking; therefore it is usually easy to identify perimortem damage to a skeleton.

Godfrey used dental macrowear analysis to age skulls that could not be matched with field numbers. Our comparative database comprises >400 casts of the teeth of *Propithecus* at BMSR that were captured, tagged, and recaptured beginning in 1984 (Godfrey *et al.* 2002). Richard and colleagues (2000) took molds of the upper dentition of *Propithecus verreauxi verreauxi* from anesthetized individuals shortly after their capture. They dried the teeth with canned air and also cleaned them with a small tooth brush if necessary and then made molds using Cuttersil Light Body Impression Material, which is fast drying and of low viscosity. Once they mixed the material, held in place by a preformed dental tray, with a universal hardener, they quickly and firmly placed it on the upper dentition of the subject. The molds hardened in <2 min and then they carefully removed them from the subjects' mouths. Richard and colleagues made casts using Epotek (Epoxy Technology, Inc., Billerica, MA), a slow-drying, high-precision clear epoxy, that they poured into the molds and placed in a vacuum chamber to extract bubbles that tend to form at the tips of the teeth. They allowed casts to cure for 24–48 h in the molds before removing them.

We know the ages of most of the captured individuals that were born in 1984 or later, i.e., after the initiation of the *Propithecus* field project at BMSR. Using molds of their teeth, we could document ranges of dental wear variation for individuals of any given age. Owing to the repeated recapture of some individuals, we could also quantify dental wear for known age intervals. We could then use variation in the degree of tooth wear to estimate ages of individuals lacking birth records, including all individuals born before 1984.

To age individual skulls or jaws in the BMOC, Godfrey molded their teeth and compared the resulting casts directly to those of known-aged individuals from the same population, paying special attention to the wear facets on the upper canine and the first and second molars. She assessed age on the basis of the closest match. She used other criteria (specifically, the stage of eruption of the deciduous and permanent teeth) to age immature individuals, as the dental eruption schedules for *Propithecus* are known (Godfrey *et al.* 2001b, 2004). Then, using Godfrey's age estimates, Brockman searched the BMSR database on *Propithecus* for possible victims that disappeared at the specified ages. In each case, Brockman was able to narrow the possibilities to 1 or a few individuals.

Brockman conducted behavioral observations during studies of reproduction (1990–92; Brockman 1994) and male dispersal (1998–2005; Brockman *et al.* 2001) in *Propithecus* occupying Parcel 1, coinciding with their December–February breeding and late June through August birth seasons, respectively. She collected data opportunistically on the location and behavior of invasive wildcats and the responses of *Propithecus* to their presence during all-day follows of selected sifaka focal groups.

Results

Skeletal Evidence

We and our Malagasy colleagues found skeletal remains of wildcats in and near the BMSR in Parcel 1 on July 13 (west of Yellow West and north of Pink 4) and August 12, 1994 (22 m east of Red West and 28 m north of Pink 1), and southeast of Parcel 1 near the Sakamena River on June 20, 2003. The wildcat is well known to the local people, who call it the *piso an'ala* or *ampaha.* An adult wildcat skull is slightly larger than that of an adult *Propithecus* (Fig. 3).

We judged 8 individual *Propithecus* to show skeletal evidence of carnivoran predation, 4 definitively so. Predation by wildcats is our preferred explanation because the skulls bear puncture wounds that can accommodate the upper canines of a wildcat, and because the pattern of punctures on the posterior portion of the neurocranium signals a nonfrontal mode of attack (stalk-ambush) that is character-

Fig. 3 Comparison of skulls of *Propithecus verreauxi verreauxi* (BMOC 052) and *Felis silvestris* in the collections of the Beza Mahafaly museum. Note that the wildcat skull is larger than that of an adult sifaka.

istic of invasive wildcats. None of the 4 skulls of *Propithecus* had an associated collar. We do not describe an additional 4 individuals (BMOC 111, 126, 129, and 133) lacking puncture wounds on the top or back of the skull, but with a similar pattern of destruction of the back and the base of the cranium, because evidence of wildcat involvement is equivocal. More detailed descriptions follow of 4 apparent victims of wildcat predation:

1. BMOC 029 is a skull and mandible (without postcranial skeleton) of a young individual found in July 2000 along the eastern border of Parcel 1, between Green East and the Sakamena River and south of Pink 2 (Fig. 1). It has 4 puncture wounds on the top and back of the skull but an intact basicranium. The rostrum is missing. We could easily determine its biological age at death because it was not dentally mature. Its cranial capacity is full adult size; its metopic suture is open: and, its mandibular corpus is only three-fourths of expected full-adult height. On the mandible, the caniniform premolar is almost fully erupted. It is the last mandibular tooth to come into full occlusion in *Propithecus* (Godfrey, *unpub. data*). The upper permanent canine is not yet erupted; the deciduous canine is still in place. All of the other teeth are permanent and in full occlusion. This state of craniofacial and dental development is typical of individuals that have been weaned and are therefore independent foragers, but are ≤9 mo. Generally, in this species of *Propithecus*, the permanent upper canines emerge at 8 mo or shortly thereafter and the last maxillary teeth erupt (Godfrey *et al.* 2004; Godfrey, *unpub. data*). On the basis of our age estimate of *ca*. 8–9 mo and the locality data, we believe the victim was a Vavy Masiaka infant born on July 31, 1999 and not seen during the July–August 2000 census. If indeed the individual was 8 mo old at death and born at the end of July 1999, then we can deduce death in late March or early April (and certainly not later than early May) 2000 (Table III).
2. BMOC 052 is a skull without mandible or postcrania; its recovery date and locality were lost or never recorded. There are 4 puncture holes, with adhering flakes, on the top and back of the neurocranium (Fig. 4a): one in the occiput, just above the nuchal crest; 2 in the parietal bones (lateral to the temporal lines, that on the right is a double puncture, i.e., the predator's canine was retracted and reinserted adjacent to the first puncture); and another on the right side just above the posterior root of the

Table III *Propithecus verreauxi verreauxi* candidate victims of wildcat predation

Skeletal remains	Est. age	Candidate victims by group	Age	Date last seen	Date not seen
BMOC 029	8–9 mo	Vavy Masiaka infant b. July 31, 1999	~8 mo	July 31, 1999	July–Aug. 2000
BMOC 052	8–9 yr	Vaovao F193	8 yr	July–Aug. 2000	Jan.–Mar. 2001
		Vahiny M9040	8 yr	July–Aug. 2000	Sept.–Dec. 2000
		Andref2 M9132	6 yr	Jan. 1999	July 1999
BMOC 054	>25 yr	Vaovao F20	28.5 yr	Jan.–Mar. 2001	July 2001
		Fety F95	23 yr	July 2000	Nov. 2000
		Vavygoa F172	20 yr	Dec. 1999	Feb. 2000
BMOC 077	<25 yr, ~20 yr	Disrat M258	21 yr	July 1999	July–Aug. 2000
		Disrat F247	19 yr	Dec. 1999	July 2000
		Didy F170	>15 yr	Jan.–Mar. 2001	July 2001

zygomatic process, superior to the external auditory meatus (Fig. 4b). The superior margin of the zygomatic arch in this region has associated damage. The base of the cranium is damaged and most of the occipital bone below the nuchal crest is missing. There is no additional damage to either zygomatic arch, or to the front of the skull, palate, or rostrum. From its state of dental wear, we inferred an age of *ca.* 8 or 9 yr for the individual; we also know that it died sometime before the austral winter of 2001, when we catalogued it. Only 3 individuals match the description: a female (F193) from Vaovao, a male (M9040) from Vahiny, and a male (M9132) from Andref2 (Table III). The latter was only 6 yr old when he disappeared; the former 2 are the more likely victims.

3. BMOC 054 is a skull and mandible, without a postcranial skeleton, of a much older individual, again lacking locality data. Multiple puncture wounds occur on the right side of the skull (Fig. 5a), and the gonial angle of the right hemimandible is deformed in a manner suggesting carnassial crushing (Fig. 5b). The back of the neurocranium and the rostrum are destroyed. We estimate the age of the individual at death as >25 yr from its extremely worn teeth. There are 3 possible candidates in the age group that disappeared before 2001, when we catalogued the individual: a female (F20) from Vaovao (most likely candidate), a female (F95) from Fety, and a female (F172) from Vavygoa (Table III).
4. BMOC 077 is a skull and mandible, without postcranial skeleton, collected on August 7, 2001, 10 m north of the gate and east of Black (Fig. 1). Both the skull and mandible had suffered extensive damage. The gonial angle on the right and the entire left ramus had been chewed. Much of the back of the neurocranium is missing. There are chew marks surrounding the nasal aperture. The zygomae are missing on both sides, and parts of the orbits are also missing. Two puncture holes on the top of the skull match the distance between the upper canines of a wildcat (Fig. 6). We deduced the probable identity of the victim from locality data, the state of wear on the teeth (heavy but not as heavy as that of BMOC 054), and field records of *Propithecus* that disappeared from the region proximate to discovery of the skull. Two individuals best match this description: a male (M258) belonging to Disrat and a female (F247) also from Disrat. A third possible candidate is a female from Didy (F170; Table III).

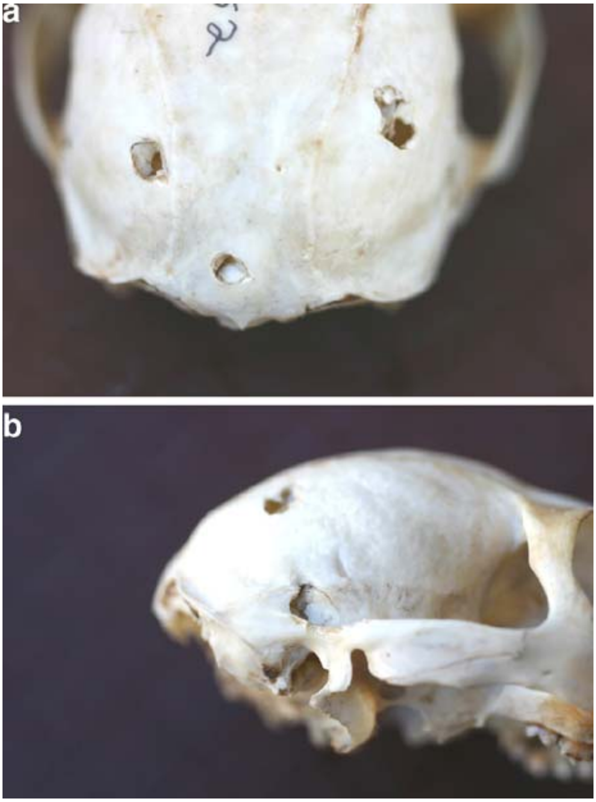

Fig. 4 **(a)** Posterior portion of the neurocranium of BMOC 052, showing puncture wounds. **(b)** Lateral view of the posterior portion of the skull of BMOC 052, showing a puncture wound superior to the external auditory meatus.

Behavioral Evidence

Brockman observed single wildcats on 4 occasions, twice in the breeding and birth seasons of *Propithecus* at BMSR. The locations of the sightings are indicated by numbers on Fig. 1 and the descriptions are from Brockman's field books.

Sighting 1 occurred November 16, 1990 as Brockman was entering the parcel to census *Propithecus*. Brockman observed a cat-sized individual darting from west to east across Black trail 15 m north of the gate leading into the parcel. The cat was in view for *ca*. 5–10 s before disappearing into the dry scrub vegetation. It was larger than a domestic house cat, e.g. *ca.* 4–5 kg, and had long pointed ears, a pronounced muzzle, a long, tapering tail, and a brownish multicolored coat with dark spotted stripes down the back. Brockman estimated the individual to be an adult based on size and coat coloration, the latter being distinct from the yellow coat immature wildcats exhibit (Ratsirarson, *unpub. data*).

Sighting 2 occurred during Brockman's all-day follows of Vavy Masiaka, which comprised 2 adult females and 3 adult males. At 0935 h on December 9, 1990, Brockman observed the focal female, followed by group members, hopping along the ground in a clearing east of Green and south of Blue 3

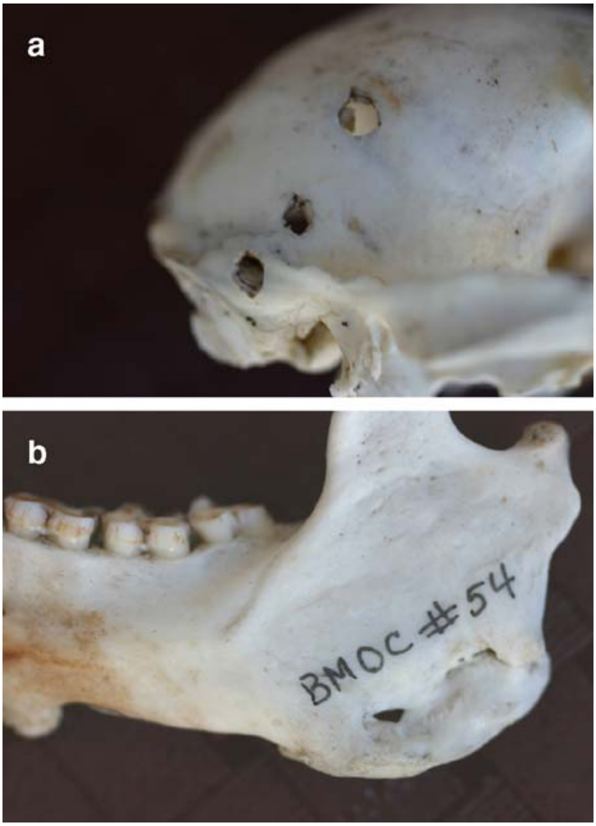

Fig. 5 **(a)** Lateral view of the neurocranium of BMOC 054, showing puncture wounds. **(b)** Lateral view of hemimandible of BMOC 054, showing evidence of crushing by carnassials, and resulting deformation of the gonial region.

when a large-eared fox-like animal darted past. All of the group members leaped into the trees. It was cat-sized but taller and thicker in the middle.

Sighting 3 occurred during Brockman's all-day follows of Borety, comprising 2 adult females and 4 adult males. At 1347 h on August 2, 2005, Borety was resting *ca.* 7 m up in a tree 2 m west of Orange West when suddenly they became alert and silently stared at the ground in the direction of nearby rustling. Brockman immediately followed their gaze and observed a wildcat leaping over a rotting log in a pounce *ca*. 3 m away. Startled, the cat subsequently darted north on Orange West and disappeared. Male 387 continued to scan the ground in the direction of the wildcat for 10 min, after which Borety members resumed feeding on dense thickets of vines on the ground. The wildcat had large ears, a broad face, a multicolored coat, and spotted dark stripes extending from head to tail.

Sighting 4 occurred during Brockman's all-day follows of Fotaka, comprising 3 adult females, 5 resident adult males, an immigrant male and the female yearling born in 2004. At 0938 h on August 13, 2005 Fotaka was feeding on flowers of *Acacia ca.* 5 m from the ground when they immediately stopped feeding and began to defecate and to si-fak en masse while

Fig. 6 Superior view of the skull of BMOC 077, with Beza Mahafaly wildcat, showing fit of wildcat's upper canines into the puncture wounds on the skull of the *Propithecus*.

staring at the ground. Continual si-fak vocalizations (*ca.* 1.5/s) persisted for *ca.* 10 min. Brockman followed their gaze and saw a wildcat sunning on the ground under a bush on Blue 1, east of Green (Fig. 7). The wildcat was largely gray-brown with darker spotted stripes along the back, like those of individuals at Ankarafantsika. The cat appeared longer than a domestic cat. Between 0950 h and 1030 h Fotaka resumed feeding while drifting slowly east away from the cat's location. At 1045 h a focal male suddenly ceased feeding and began si-faking while staring west down Blue 1. He was immediately joined by the remaining Fotaka members, which began a chorus of si-faking. Brockman followed their gaze and observed the wildcat *ca.* 12 m away strolling unhurried along Green West north of Blue 1. By 1050 h all si-faking had stopped, though the male continued to scan northwest in the direction of the wildcat.

Discussion and Conclusions

Wildcats (4–5 kg) are opportunistic, cryptic solitary hunters. Their stalk-and-ambush hunting tactics allow them to kill surprisingly large-bodied prey. Whereas their

Fig. 7 Wildcat at Beza Mahafaly Special Reserve. (Photo by Diane K. Brockman, August 13, 2005).

primary prey are rodents, birds, small reptiles, and amphibians, their preferred prey varies according to a number of factors; e.g., in parts of Europe, wild rabbits (*Oryctolagus cuniculus*, which can be >3 kg) are preferred prey (Lozano *et al.* 2006; Malo *et al.* 2004).

The BMSR *Propithecus* that were apparent victims of wildcat predation range from *ca*. 8 mo to >25 yr, and some seem to have been in their prime. Full adult *Propithecus* normally weigh less than wildcats (mean mass of adult candidate victims: 2.68 kg±0.34 SD, range: 3.0–2.0 kg, n=7). However, the masses do not reflect perimortem masses because we did not weigh them just before their disappearance.

Little is known about reproduction in wildcats at BMSR and whether or not predation risk for lemurs might increase when females have dependent young. In this regard, Ratsirarson observed a litter of 5 kittens in November 2004 in a hole in a sasavy tree (*Salvadora angustifolia*, Salvadoraceae) on the ground. His earlier sighting (November 1999) of a wildcat carrying an infant *Lemur* in its mouth (Ratsirarson *et al.* 2001), and subsequent sightings, suggest that wildcats may be more active during the day, when they have litters.

The inference that wildcats very recently emerged as a major predator of *Propithecus* at BMSR derives from the fact that most —if not all— of the victims in our report died since 2000 (Table III). Researchers have observed invasive carnivorans, including wildcats, within the BMSR since 1986, and as recently as 2006 (Table IV). In contrast, whereas fossa were present within the reserve at its inception, the last sighting of a *Cryptoprocta ferox* within the reserve was on November 23, 1993 (in Parcel 1, an individual moving quietly west at Green West × 28 m north of Pink 1; Kubzdela, *pers. comm.*). People in nearby villages do not speak of their presence, and guides and researchers have not seen fossa within the

Table IV Sightings and activities of invasive predators in Beza Mahafaly Special Reserve, Madagascar

Species	First sighted (reference)	Activity/ context	Last sighted (reference)	Activity/ context
Cryptoprocta ferox	March, 1986 (Ratsirarson, 1987)	Moving on the ground	November, 1993 (Kubzdela, *pers. comm.*)	Moving on the ground
Felis silvestris	December, 1986 (Ratsirarson *et al.*, 2001)	Moving on the ground	November, 2006 (Jacky-Youssouf, *pers. comm.*)	Moving on the ground
Canis lupus familiaris	January 1992 (Brockman notebooks)	Moving toward *Propithecus* focal group	August, 2006 (Richard, *unpub. data*)	Attacks on *Propithecus* and *Lemur*

reserve despite nearly constant ongoing field research there. Whereas the negative evidence does not prove local extirpation, it suggests that the fossa population may be on the decline in the region, if it even persists there at all.

Behavioral evidence supports the idea that invasive carnivorans may be important predators of *Propithecus* today. *Propithecus* foraging on the ground respond to the presence of terrestrial predators by moving quickly into the trees. Responses to terrestrial predators of *Propithecus* in the trees include moving up and scanning downward while emitting low-intensity si-faks in reaction to wildcats or high-intensity roaring barks in reaction to dogs. Behavioral responses associated with aerial predators include moving down into dense foliage, scanning upward, and mobbing, while emitting roaring barks (Table I). The results accord with those obtained on *Propithecus* in other spiny forest habitats such as Kirindy, where they direct growls to both aerial (*Polyboroides*) and terrestrial predators (*Cryptoprocta*, *Canis*), but direct roars solely at the aerial predators (Fichtel and Kappeler, 2002). Thus *Propithecus* appear to have developed antipredator strategies that reduce the risk of being attacked and that are specific to the perceptual abilities and hunting styles of terrestrial and aerial predators (Scheumann *et al.* 2007).

Because systematic collection of skeletal materials at BMSR is a recent phenomenon, we are not able to access accurately trends in mortality in the population. Nevertheless, it is clear that *Propithecus* are falling victim to a mammalian predator and that *Cryptoprocta* are rare in or absent from the region (Jacky-Youssouf, *pers. comm.*). Long-term demographic data indicate the population of *Propithecus* continues to experience a 2% decline per year for reasons that are not clear (Lawler and Caswell 2007).

Whereas wildcats are not endemic to Madagascar, no one knows exactly when they were introduced. They were on Madagascar from at least the 17th century (Saca or chat sauvage: Flacourt 1661). Allibert *et al.* (1989) reported them at Dembeni on Mayotte during the 9th century.

Endemic *Cryptoprocta ferox* (fossa) are considerably heavier than wildcats. At 7–14 kg, fossa are formidable predators of *Propithecus* (Dollar *et al.* 2007; Ganzhorn and Kappeler 1996; Wright 1998; Wright *et al.* 1997). *Cryptoprocta* are the main predator of *Propithecus* in Ankarafantsika National Park, where the incidence of them taking *Propithecus* increases as the dry season progresses and prey items that are at other times more readily available are less frequent (Dollar *et al.* 2007).

Cryptoprocta take *Propithecus* arboreally, an action that entails a high risk of injury and tenuous guarantee of payoff. It is noteworthy that dry-forest *Cryptoprocta* take them more often in the dry season than at any other time. Though wildcats are not as agile in trees as *Cryptoprocta* are, cats in general have at least semiarboreal abilities, particularly in pursuit of prey. *Propithecus* inhabiting the fenced areas of BMSR appear to be more terrestrial than *Propithecus* are in other parts of Madagascar, and thus likely more vulnerable to predation by wildcats.

Cryptoprocta spp. were once common in Beza Mahafaly. Indeed the large-bodied form (now-extinct *Cryptoprocta spelea*; Goodman *et al.* 2004) occurs in abundance at a nearby subfossil site, Taolambiby (Godfrey *et al.* 2001a; Walker 1967). On the basis of skull length, *Cryptoprocta spelea* weighed *ca*. ≥20 kg (Wroe *et al.* 2004). Researchers have not radiocarbon-dated skeletal remains of *Cryptoprocta spelea* at Taolambiby, but dates on other subfossils from Taolambiby range from *ca*. 2700 BP to historic (Burney *et al.* 2004), confirming the recent age of the deposits and thus supporting a relatively recent occurrence of *C. spelea* in the area. Its smaller-bodied relative, the fossa (*Cryptoprocta ferox*), is common today in the forests north of Beza Mahafaly, such as Kirindy.

Other potential mammalian carnivorans at BMSR capable of preying upon lemurs are feral domestic dogs and small Indian civet. Brockman observed Malagasy feral dogs hunting alone and in packs in Parcel 1, and since October 2005, serious attacks and fatal injuries to *Propithecus* and/or *Lemur* linked to feral dogs have occurred (Sauther and Cuozzo, *pers. comm*.; Richard, *pers. comm*.). Dogs typically leave little skeletal evidence of predation and few remains of scavenged items, regardless whether victims are large- (such as *Propithecus*) or small-bodied. Further, even when they leave skeletal remains, their processing of scavenged or captured prey leaves unquestionable evidence as to the agent (Dollar, *unpub. data*). Small Indian civets are scavengers, but are not notable predators on prey their size or larger (Ewer 1973). While *Viverricula* may be able to take smaller lemurs, they are relatively incapable of climbing and do not have the dentition to prey upon larger lemurs (Dollar *et al.* 2007). In the absence of *Cryptoprocta*, wildcats and dogs are the most capable and largest mammalian predators likely to take larger lemurs. Frequent terrestriality of BMSR *Propithecus* during the dry season, the apparent reduction in population size or indeed complete disappearance of *Cryptoprocta* from BMSR, and behavioral and skeletal data combine to demonstrate that wildcats are active predators of *Propithecus* at BMSR.

In conclusion, it appears that, with the gradual extirpation and extinction of the larger endemic bird and mammalian carnivores on Madagascar, the role of introduced carnivorans in controlling lemur populations may be expanding. Researchers are only beginning to study the relative importance of predation on lemurs by the remaining endemic and invasive carnivorans in Madagascar. Such research is imperative for small reserves such as Beza Mahafaly because carnivoran predation eliminates lemur species from small forest fragments within a very short time (Irwin 2006). It is imperative that we understand better the predation threats that lemurs face, from both endemic and invasive species.

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