Seasons of death: patterns of predation on wild lemurs and other fauna by endemic and introduced predators.

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Abstract

Introduced species can negatively impact endemic flora and fauna. Studies have primarily utilized camera trap observations and occupancy modelling to better clarify the presence/absence and temporal overlap of endemic and exotic predators. Longitudinal data from field research sites are important as they can provide a finer understanding of predator dynamics and their effects on endemic species. One such site is the Bezà Mahafaly Special Reserve, in southern Madagascar. Protected since the 1970s, the local human population around Bezà Mahafaly Special Reserve has greatly expanded, leading to habitat disturbance in the surrounding forests and increased contact between local wildlife, people and their livestock and dogs. Here we use a combination of scat sampling, field observations of successful and attempted predations, locations of scat samples with identifiable lemur remains, and camera trap data to better assess the predator ecology at Bezà Mahafaly Special Reserve. Our results indicate that forest cats (*Felis catus*), are effective predators of both adult and infant lemurs and appear to be a constant mammalian predator, utilizing mammal prey more than dogs. Dogs are both predators and scavengers of lemurs. Civets focus on small prey, such as insects and rodents as well as plant material. The fosa, *Cryptoprocta ferox*, are also present but may not hunt in the area continuously. The killing of an adult ring-tailed lemur by two men from outside the area indicate culturally imposed taboos against lemur killing may no longer be effective given that new arrivals may not share the same local cultural restrictions

Key words scat sampling, camera traps, Madagascar, conservation, Bezà Mahafaly Special Reserve, forest cat

Introduction

While rarely observed firsthand, predation on primates clearly is a key selective agent in their evolution (Isbell, 1994; Gursky and Nekaris, 2007). Meta-analysis of predation on primates living in Africa, Madagascar, Asia and the Neotropics indicate moderate levels of predation in Africa and Asia and heavy predation in the Neotropics and Madagascar, with primates being a generalist prey that are taken across all body masses, habitats and include both nocturnal and diurnal species (Hart, 2007). Anthropogenic effects of hunting by humans (Koné et al., 2023) as well as introduced non-endemic predators such as dogs are an additional pressure on extant primates globally (Cuozzo et al., 2022; Waters et al., 2023). Free-ranging domestic cats are generalist predators, will use a variety of wild prey (Lepczyk et al., 2023) and have been associated with 26% of global animal extinctions (Doherty et al., 2016), While there are few published studies, free-ranging domestic cat also prey on primates (e.g., Duarte and Young, 2010). On islands of the world, introduced animals have had dramatic effects on native fauna. For example, the native forest birds of Guam have been decimated through egg exploitation by the introduced brown tree snake (*Boiga irregularis*) (Savidge, 1987), and feral dogs have long been known to prey upon marine iguanas in the Galapagos Islands (Kruuk and Snell, 1987). As humans and lemurs are increasingly pushed into direct contact, assessing the threat of introduced animals is becoming of critical importance for lemur conservation, especially in the few remaining areas of intact primary vegetation.

For almost two millennia, human activity has dramatically impacted the environment of Madagascar, leading to habitat loss, fragmentation, and species' extinction. In a deadly combination with climatic change (Virah-Swamy et al., 2010), such

anthropogenic stressors have resulted in Madagascar's faunal diversity being radically reduced, with the elimination of endemic megafauna such as the giant lemurs (Burney et al., 2004), as well as their likely predator, the giant fosa, *Cryptoprocta spelea* (Goodman et al., 2004; Meador et al., 2017). While many smaller (less than 10kg), species of lemurs and their predators still exist, (e.g., the smaller fosa, *Cryptoprocta ferox*), the extinction of megafauna has likely altered current community dynamics compared to the past (Razafindratsima et al., 2013).

Previous research clearly illustrates that predation by a wide range of endemic Malagasy vertebrates including raptors and endemic carnivores (i.e., the fosa, *Cryptoprocta ferox*) affect lemur ecology and behavior (Goodman, 2003; Dollar et al., 2007; Gould and Sauther, 2007; Karpanty and Wright, 2007; Scheumann et al., 2007; (Bonadonna et al., 2024). Introduced species have the potential to negatively impact Madagascar's endemic flora and fauna, with assessments indicating that more introduced predators may outnumber endemic species in some areas of Madagascar (e.g., Gerber et al., 2012). Studies have primarily utilized camera trap observations and occupancy modelling to better clarify the presence/absence and temporal overlap of endemic and exotic predators as well as patterns of exotic predator expansion colonization and its effects on endemic predator communities (Farris et al., 2015, 2016, 2017; Gerber, 2012). Many of these studies focus on the singular endemic mammalian predator, the fosa, *Cryptoprocta ferox* (common name follows Duckworth et al., 2014), with camera trap data used to understand how fosa occupancy patterns are affected by habitat alteration and disturbance and the presence of exotic species (Merson et al, 2019). Research on the fosa include assessing this species' food habits via scat (Wright, 1998; Dollar, 2007; Hawkins and Racey, 2008), analyses of kill sites (Irwin et al, 2009) and behavioral

124 adaptation to this predator by lemur prey (Wright, 1998; Bonadonna et al., 2024) and by
125 the fosa itself (Lührs and Dammhahn, 2010). The impact of domestic carnivores (i.e.,
126 dogs, *Canis lupus familiaris* and cats, *Felis catus*) and other introduced predators (the
127 Indian civet, *Viverricula indica*), on Madagascar's lemurs has not been systematically
128 assessed, and has received only cursory attention in the literature (e.g., Goodman, 2003;
129 Gould and Sauther, 2007; Karpanty and Wright, 2007).

130
131 Longitudinal data from field research sites are important as they can provide a finer
132 understanding of predator dynamics and their effects on endemic species. One such
133 site is the Bezà Mahafaly Special Reserve. Protected since the 1970s (Sussman et al.,
134 2012), the local human population (villagers in the Commune of Anzakazombalala)
135 around the Bezà Mahafaly Special Reserve has greatly expanded from 8,090 in 1993 to
136 over 20,000 in 2009, leading to habitat disturbance in the surrounding forests and
137 increased contact between local wildlife, people and their livestock and dogs
138 (Ranaivonasy et al., 2016). While both endemic and exotic predators are having a
139 noticeable impact on lemur behavioral ecology at this site (e.g., Bolt et al., 2015),
140 studies of the predator impact of non-endemic species at Bezà Mahafaly Special
141 Reserve have been primarily anecdotal, based on reactions of potential prey to predator
142 presence (e.g., Sauther, 1989; Gould and Sauther, 2007) or assessed from presumed
143 felid damage on skeletal remains (Brockman et al. 2008). Here we use a variety of
144 approaches: scat sampling (June 2008-July 2009), field observations of successful and
145 attempted predations (2004-2009), locations of scat samples with identifiable lemur
146 remains (June 2008-July 2009), and camera trap data June 2008-July 2009), to
147 describe the overall patterns of mammalian predator ecology at the Bezà Mahafaly

Special Reserve and to compare potential predators (domestic dog, forest cat, civet) to assess their predation behavior.

Methods

STUDY SITE

The Bezà Mahafaly Special Reserve (hereafter BMSR) is in the Spiny Thicket Ecoregion of southwestern Madagascar (23°30'S, 44°40'E), and is characterized by a highly seasonal climate, with brief rainy seasons and prolonged dry seasons (Sussman et al., 2012). The reserve comprises two non-continuous parcels. Parcel 1 is a fenced 80ha section of a Malagasy dry deciduous forest dominated by *Tamarindius indica* along the ephemeral Sakamena River (Sussman et al., 2012). It is divided into marked transects with trails intersecting to form 100 x 100m squares. Parcel 2 is a 520ha xerophytic spiny forest. There are several villages nearby each parcel (Sussman et al., 2012). Four lemur species reside at BMSR, the diurnal Verreaux's sifaka, *Propithecus verreauxi* (Richard et al., 1991) and the cathemeral (LaFleur et al., 2014), ring-tailed lemur, *Lemur catta*, (Sauther,1992), and two nocturnal species, the white-footed sportive lemur, *Lepilemur leucopus* (Nash, 1998) and the reddish-gray mouse lemur, *Microcebus griseorufus* (Cuozzo et al, 2013; Rasoazanabary, 2004). Potential known mammalian predators of lemurs at BMSR include introduced species: domestic dogs (*Canis lupus familiaris*), "forest cats" descended from domestic cats from the Arabian Sea region and who live full time in the forest (*Felis catus*, Sauther et al., 2020), which weigh 3.24 kg (adult, n = 1), at the reserve (Sauther, Cuozzo unpublished data), the small Indian civet, *Viverricula indica* which weigh 2.46 kg (adult, n = 1) at the reserve (Sauther, Cuozzo unpublished data), and the endemic fosa, *Cryptoprocta ferox* which

weigh 7-14 kg at other sites (Dollar et al., 2007). BMSR also contains raptors including the Madagascar harrier hawk (*Polyboroides radiatus*), the Madagascar buzzard (*Buteo brachypterus*) and snakes such as the Madagascar tree boa constrictor (*Boa mandtria*) and the Madagascar giant hognose snake (*Leioheterodon madagascariensis*) all of which are potential predators (Sauther, 1989). Raptor predation at BMSR is supported by eye-witness accounts of a young *L. catta* being predated by a Madagascan harrier hawk (Ratsirarson, 1985) and the presence of mouse lemur remains in Barn Owl (*Tyto alba*) pellets (Goodman et al., 2007) which has also been observed at sites near BMSR (Rasoma and Goodman, 2007). Since 1995 BMSR has employed the Bezà Mahafaly Ecological Monitoring Team which is comprised of individuals from local villages. This team carries out surveys, collects systematic ecological data, and are formally trained under the Monitoring Team Program (https://campuspress.yale.edu/bezamahafaly/environmental-monitoring-program/environmental-monitoring-at-beza/). When lemur remains are found they are collected and become part of the BMSR osteological collection.

SCAT SAMPLING

All data were collected in Parcel I at BMSR. From June to July 2008, five of us carried out an intensive daily survey of terrestrial mammalian scat samples along and within 1m of each side of all marked trails (6.5 km), collecting a total of 30 scat samples (19 forest cat, 0 civet, 11 dog). From August 2008 to July 2009 identifiable terrestrial mammalian scat samples (n = 24, 16 forest cat, 6 civet, 3 dog) were also collected during weekly surveys along all marked trails by Jacky Youssouf and the Bezà Mahafaly Monitoring Team for a total of 54 scat samples (34 forest cat, 6 civet, 14 dog). Species were

197 determined based on morphology (Zuercher, G. L. et al. 2003; Prugh and Ritland 2005),
198 and by verification by the monitoring team who are well versed in such identification. We
199 identified scat samples by exotic predator type (e.g., felid, canid, viverrid). Most felid
200 samples were not buried. General locations on the trail system were noted for each
201 sample (see Table 1). For the June to August 2008 samples, estimated age of scat was
202 based on freshness. It should be noted that the physical features of the terrain
203 throughout the reserve are similar in that the whole area is very flat, so this helped limit
204 variation in predator scat detection in the different areas. In addition, all known
205 predators commonly use the trails to move throughout the reserve (Figure 1). Scats
206 from the year-long sample period from identified predator species were collected
207 throughout two seasons, Wet and Dry, at BMSR (Wet season samples = 11, Dry
208 season samples = 43). Wet was classified as November to April while Dry constituted
209 May through October as determined by documented local weather patterns including
210 rainfall at BMSR (Sussman et al., 2012). Each scat sample was given an identification
211 number and wrapped in tinfoil with a desiccant pack for storage and transportation and
212 the identification number was entered into a Microsoft® Excel spreadsheet.

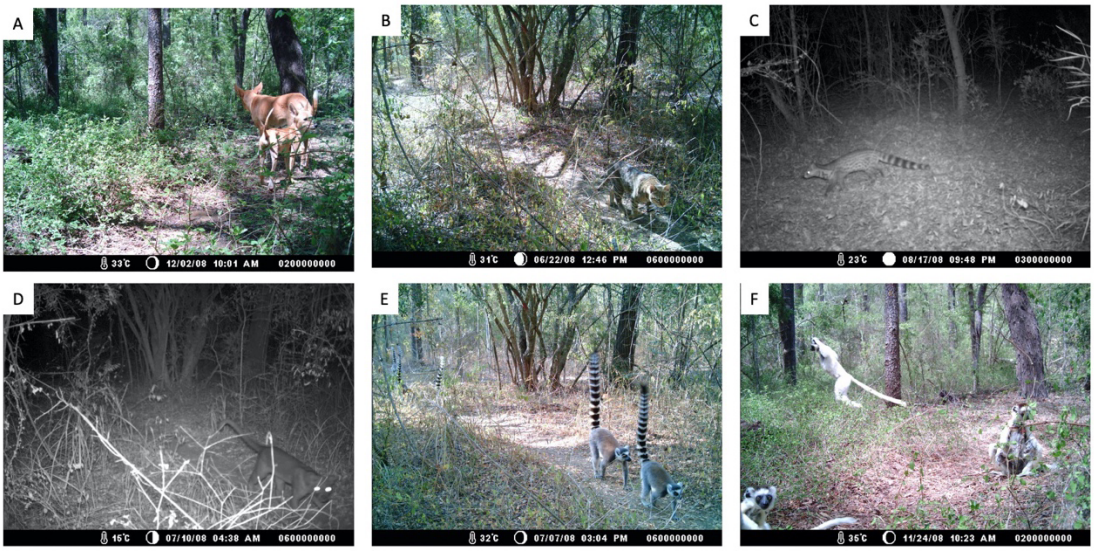

Figure 1. Camera trap pictures of the various exotic, endemic predators and large lemurs at the Bezà Mahafaly Special Reserve, Madagascar. A. Domestic Dog and puppy, *Canis lupus familiaris,* B. Forest cat *Felis catus,* C. The small Indian civet, *Viverricula indica,* D. The fosa, *Cryptoprocta ferox,* E. The ring-tailed lemur, *Lemur catta*, F. Verreaux's sifaka, *Propithecus verreauxi.*

SAMPLE PREPARATION

Once samples were visually identified as to the species of origin, a small, dime-sized, section was removed with a razor blade and set aside in a clear plastic dish for dissection. The dish with the sample was placed under a stereoscopic dissecting microscope where dissection was performed using tweezers and dental picks. Large identifiable items were placed in a separate plastic bag and catalogued by major types; fur = mammalian prey, bone = vertebrate prey, insect chitin = arthropod prey, scales=reptilian prey, leaves, seeds = plants, feathers = avian prey. Felids can incorporate their own hair into scats from self-grooming. However, samples scored as containing fur consisted of large mats of hair and/or fur and skin and were unlikely to be from self-grooming. Most bone material was too fragmentary to determine prey species

but, in several cases, whole body parts were identifiable (e.g., eye, phalange). Lab implements were disinfected between each sample using 91% isopropyl alcohol and commercially available first aid alcohol swabs. Identified remains by general category (e.g., bone, scale etc.) were entered into a Microsoft® Excel spreadsheet using a simple "present/absent" value for each scat sample since individual scats commonly contained more than one prey category.

PREDATED REMAINS

Predated remains were discovered either by us during lemur follows as part of our ongoing research (June to August 2003 – 2009) or by the ecological monitoring team, who monitored all lemur troops monthly across each year (2004-2009). The location of remains were noted and unprepared specimens were then collected and buried for a year to allow natural processes to deflesh soft tissue. Remains were numbered and included as part of the onsite Beza Mahafaly Osteological collection. Observations of predation attempts, and events were also noted during ongoing research.

CAMERA TRAP DATA

From June 2008 to July 2009 (14 months), nine camera traps (Moultrie I40 Digital Game Camera, Moultrie, Calera Alabama) were placed along trails throughout BMSR to cover all parts of the reserve. These trails were established during the development of BMSR and were commonly used by lemurs, dogs, forest cats and local villagers. Camera traps were set to capture images across a 24-hour period. Each was set to capture three consecutive images and, as there could be multiple images of one camera trap capture event, we only counted the first camera trap picture for each predator or lemur. In most cases the predator or lemur did not stay near the camera trap

for more than a few seconds. We thus separated all events by at least 10 minutes to avoid multiple counts of single events. The number of camera trap days per camera trap ranged from 237 to 340 days. Some feral dogs live within the reserve, and as villagers and their dogs commonly moved through the reserve, only dogs without humans were counted. We determined percentage predator abundance for each camera trap by taking the number of photos of each predator, divided by total number of camera trap days containing predator or lemur images for each camera trap times 100.

ANALYSES

We used the Pearson chi-square test for independence to determine if there were seasonal (wet, dry) differences in the expected/observed counts of food categories (vertebrate bone and/or fur, insect chitin, plant materials, bird feathers) within all scat samples of all species combined and whether expected/observed counts of food categories present in each species' scat samples differed among species (forest cat, domestic dog, civet). We used the Fisher's Exact Test for comparisons if 20% or more of cells had expected counts less than 5. Camera trap quantitative data (the number of photos for each species by trap days for each species) were not normally distributed so we performed a logarithmic transformation prior to analyses to ensure normality. Here the predictor was camera trap location, and the response variable was species. We compared there number of species' images across camera trap months (14 months x nine camera traps = 126 camera trap months). A one-way ANOVA was used to assess if each predator species and lemur images (ring-tailed lemurs and sifaka combined) were captured more on some camera traps versus others and we used the all-pairs Tukey HSD post hoc test to assess which comparisons were significant. Using a

bivariate fit line regression to fit our regression models, we determined whether images of any species of predators were significantly correlated with each other as well as whether any predator species images were significantly correlated with lemur images. We used an F Ratio as our test statistic to evaluate the effectiveness of the models and RSquare values to provide the proportion of variation explained by the models. Significance was set at $p \leq 0.05$. All statistical analyses were performed using JMP® Pro 16.0 (JMP Statistical Discovery LLC 2022).

Results

Scat Samples

Scats with evidence of mammalian consumption (containing vertebrate bone and/or hair) showed no difference in expected relative to observed counts by season (X^2 (1, 54) = 2.75, p = 0.10). For both insect chitin and plants, scat counts with evidence of consumption were greater than expected in the wet versus the dry season (insect chitin: X^2 (1, 54) = 7.55, p = 0.006; plants: X^2 (1, 54) = 7.02, p = 0.008). There were no other seasonal differences [reptile scales: X^2 (1, 54) = 0.12, p = 0.73; bird feathers: X^2 (1, 54) = .12, p = 0.73, Figure 2].

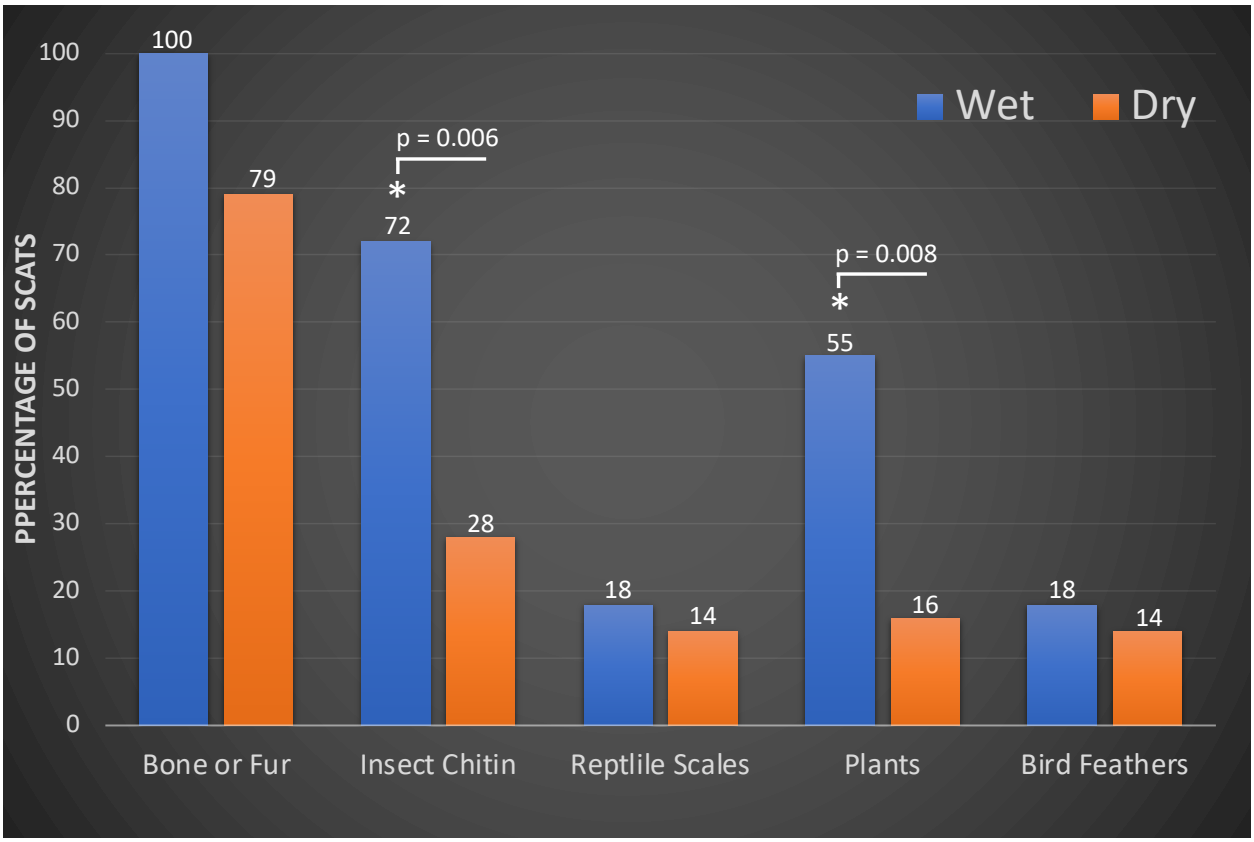

Figure 2. Percentage of scats from all species combined containing food item by season. * are observed counts greater than expected for food items during the wet season.

For scats containing different food items, none of the analyses violated the 20% rule so Chi-Square results are presented. Forest cats had a higher than expected count of scats containing mammalian bone or fur compared to dogs [X^2 (1, 48) = 3.73, p = 0.05]. There were no differences between civets and forest cats [X^2 (1, 40) = 0.78, p = 0.38)] or civets and dogs (X^2 (1, 20) = 2.86, p = 0.09) in expected compared to observed counts for samples containing either bone or fur. Civets had a greater than expected count of scats containing insect chitin compared to forest cats [X^2 (1, 40) = 7.80, p = 0.005] and dogs [X^2 (1, 20) = 15.92, p = 6.613e5]. Forest cats also had a greater than expected count of scats with insect chitin compared to dogs [X^2 (1, 48) = 4.64 p = 0.03]. A greater than expected count of civet scats also contained plants compared to both

cats [X^2 (1, 40) = 12.81, p = 0.0003] and dogs [X^2 (1, 20) = 6.71, p = 0.009]. There were no differences in expected compared to observed counts relative to reptile scales [forest cats versus dogs X^2 (1, 48) = 0.52, p = 0.47, forest cats versus civets: X^2 (1, 40) = 1.23, p = 0.27, dogs versus civets: X^2 (1, 20) = 2.26 p = 0.13] or bird feathers [forest cats versus dogs: X^2 (1, 48) = 0.001, p = 0.97, forest cats versus civets: X^2 (1, 40) = 0.02, p = 0.90, dogs versus civets: X^2 (1, 20) = 0.02, p = 0.89, Figure 3].

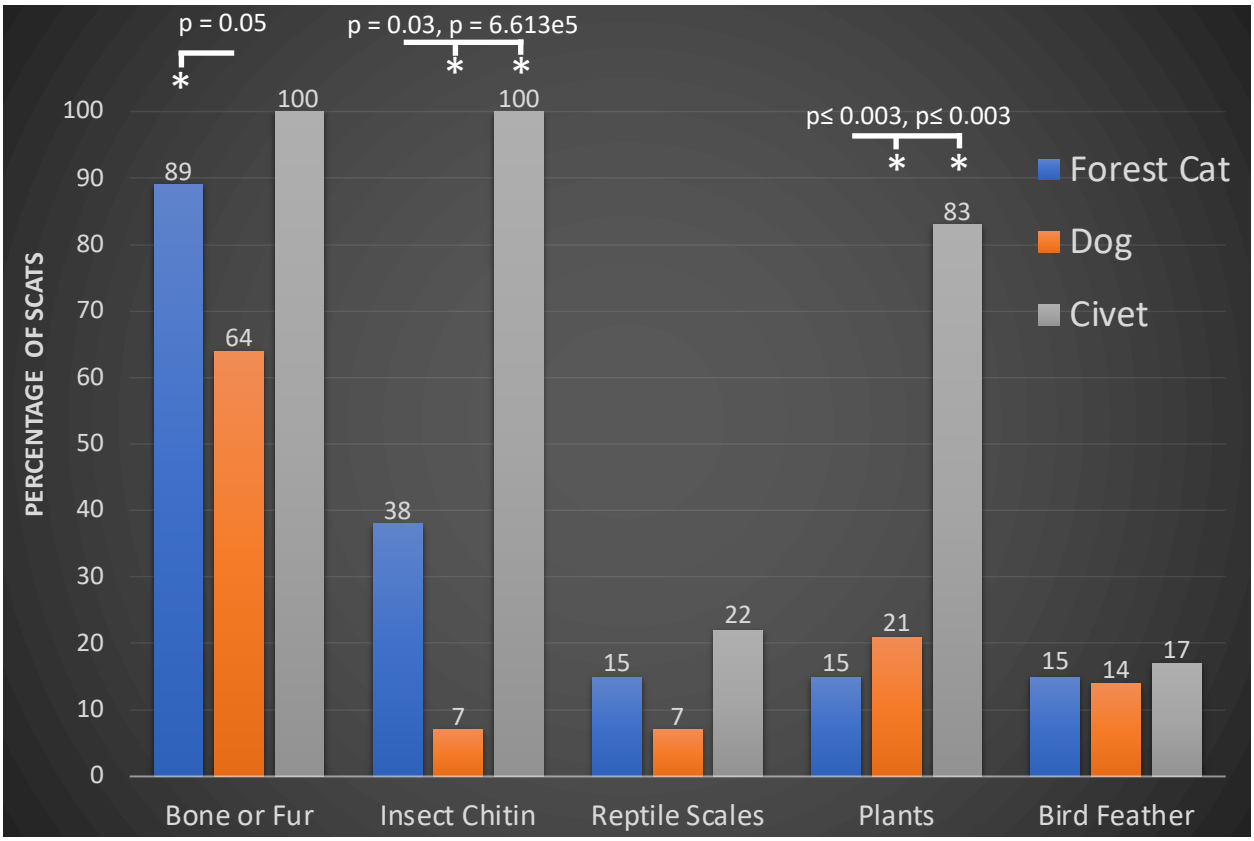

Figure 3. Percentage of scats containing food item by exotic predator. * are observed counts greater than expected for food items for a species.

In addition to these general food items, from the scats collected from June to July 2008 we retrieved several intact body parts from the scats that included the hallux and proximal phalange of a *Lepilemur leucopus* (Table 1, sample 1, Figure 4A), a *L. catta* phalange and distal hallux (Table 1, sample 25), and, remarkably, the Personal Identification Transponder (Trovan Ltd., Melton, North Ferriby), of a ring-tailed lemur,

male #151 (Table 1, sample 5) (Figure 4). This adult male was first collared by our research team in 2003, was recaptured one more time in 2004 weighing 2.32kg, and was never seen again. From the scats collected from August 2008 to June 2009 insect remains included beetles and especially cockroaches. While bone remains were primarily fragmented, one civet scat sample included a rat mandible (*Rattus rattus*), and one contained bone material from a small rodent, either the non-endemic house mouse (*Mus musculus*) or the endemic dormouse tufted tailed rat (*Eliurus myoxinus*). Seven forest cat samples also contained lemur material that included the unfused epiphysis of an infant ring-tailed lemur (*L. catta*).

Figure 4. Lemur body parts and Personal Identification Transponder found in scats. A. Sample number 1 –see Table 1. *Lepilemur leucopus* proximal phalange and distal hallux. B. Sample number 25 – see Table 1. *Lemur catta* distal hallux. C. Sample number 5 – see Table 1. Personal Identification Transponder (Trovan ID-100), of Male *Lemur catta* 151, (Photos by Michelle Sauther).

345 Table 1. Remains found in scat specimens sampled between June and July 2008 at
346 Bezà Mahafaly Special Reserve.

Date	Species	Scat Sample Number	Estimated Age	Location	Comments
6.19.08	Felid	1	3-4 days	Blue II: Between Black and Red West	Light grey fur, primate phalange (lepilemur hallux), two unidentifiable bone fragments.
6.19.08	Canid	2	2-3 days	In camp: Near blue WWF vehicle	Piece of a feather, seven bone fragments, large but not identifiable.
6.21.08	Canid	3	3-4 days	Blue III: Between Yellow West and Orange West	Plant material only.
6.21.08	Canid	4	4-5 days	Blue III: Between fence and Blue West	No bone or hair recovered.
6.21.08	Felid	5	2-3 days	Blue II: Between Yellow West and Orange West	Light gray/brown finely textured hair; Personal identification transponder for *Lemur catta* #0006206E4E Male 151, feathers-white fragments; two bone fragments, identified as avian as bone is hollow.
6.21.08	Canid	6	4-5 days	Blue II: Between Red West and Black	No bone, hair or teeth recovered.
6.25.08	Canid	7	4-5 days	Yellow East, South of reserve camp	35 bone pieces/fragments recovered and a *Lemur catta* distal hallux (big toe). Found near predated remains of female *Lemur catta* #271.
6.25.08	Felid	8	3-4 days	Blue III: Between Black and Center	Light brown/gray finely textured hair.
6.25.08	Canid	9	3-4 days	Blue III: Between Black and Center	No hair, bone or teeth recovered.
6.25.08	Felid	10	4-5 days	Black: Between Blue II and Blue I	Light brown/gray finely textured fur.
6.27.08	Canid	11	5-6 days	On Sakamena River near location of Lemur #271.	Light white hair coarsely textured thick hair (goat?), two bone fragments, distal end of humerus; one unidentified bone fragment, suspected eyeball (small, lemur sized). Found near *Lemur catta* #271.
6.28.08	Canid	12	1 day	Road to camp: Betioky	No bone, hair or teeth recovered
6.29.08	Canid	13	4-5 days	Southern extension of the reserve	16 bone fragments; brown-reddish finely textured fur, several of the bone fragments are substantially sized.
6.29.08	Felid	14	4-5 days	Southern extension of the reserve	Light gray-brown fur; bird quills, bird feathers, insect parts.
6.29.08	Felid	15	3-4 days	Southern extension of the reserve	Light grey - brown fur, one small eyeball (lemur?).
7.01.08	Felid	16	3-4 days	Road to Betioky	Mixes of dark brown and light brown fur, three bone fragments.

7.01.08	Felid	17	3-4 days	Pink I East: Between Green and Blue East	Suspected goat hair: large amount of white thick coarse fur, 25 bone fragments.
7.01.08	Felid	18	7-8 days	Pink I East: Between Yellow East and Orange East	27 bone fragments, distal phalange, possibly sifaka.
7.01.08	Felid	19	3-4 days	Pink I East: Between Orange East and Red East	Light gray/brown fur, finely textured, 17 bone fragments, three vertebrae, 1 scapula.
7.02.08	Felid	20	4-5 days	No data.	Suspected lemur hair.
7.04.08	Felid	21	less than 24 hours	South of the reserve road; just southwest of River Trail	Buried and found near recently killed lemur (#212, male ring-tailed lemur), contains light gray fur and reptile skin. Subsequent DNA analysis (Tkach and Ness, unpublished data) indicate forest cat.
7.06.08	Felid	22		Near bageda field South of Road; extension of Green East and Yellow East	Large amount of light brown fur, one *Lemur catta* toe, 2 caudal vertebrae, rodent humerus, 16 bone fragments.
7.08.08	Felid	23		Near bageda field	Light gray and finely textured hair, 1 bone fragment, six bird quills.
7.13.08	Felid	24		Blue II: Between Black and Center	More than 40 fragments, two rodent incisors, two rodent jaws, two rodent rami, one rodent maxilla, 1 distal humerus, rodent phalanges, tail.
7.13.08	Felid	25		Black: Between Blue I and Blue II	Bone and hair; fine light fur; *Lemur catta* phalange, *Lemur catta* distal hallux, 11 total bone fragments, four vertebrae
7.13.08	Felid	26		Black: Between blue II and blue I	Light brown, finely textured hair that appears to be lemur hair; one small piece of bone with connective tissue.
7.13.08	Felid	27			Bird quills and insect parts: fine light gray hair; feathers and quills, four bone fragments.
7.13.08	Felid	28			Insect parts.
7.13.08	Canid	29	3-4 days	Reserve Road	Nine bone fragments
713.08	Canid	30	3-4 days	Reserve Road	30 bone fragments, two bone fragments.

Lemur successful and attempted predations

Table 2 provides a summary of thirteen predation remains or events across six years at BMSR (Figures 4-5, see supplementary Table 1 for complete descriptions of each event). In 2004 there was one predated remain found. For 2005 there were no predated

remains found. In 2006 there were two predation attempts, both by dogs. In 2007 there were again no predated remains found. In 2008 there was an increase in predations with a total of six remains (three *P. verreauxi* and three *L. catta* individuals) found within a 22-day period. Of these, five show a pattern suggesting either fosa or forest cat predation and one indicating dog predation or perhaps scavenging. In 2009 there were two predations, one was an eyewitness account, and the other was a freshly killed sifaka with an eyewitness observing a forest cat running from the site.

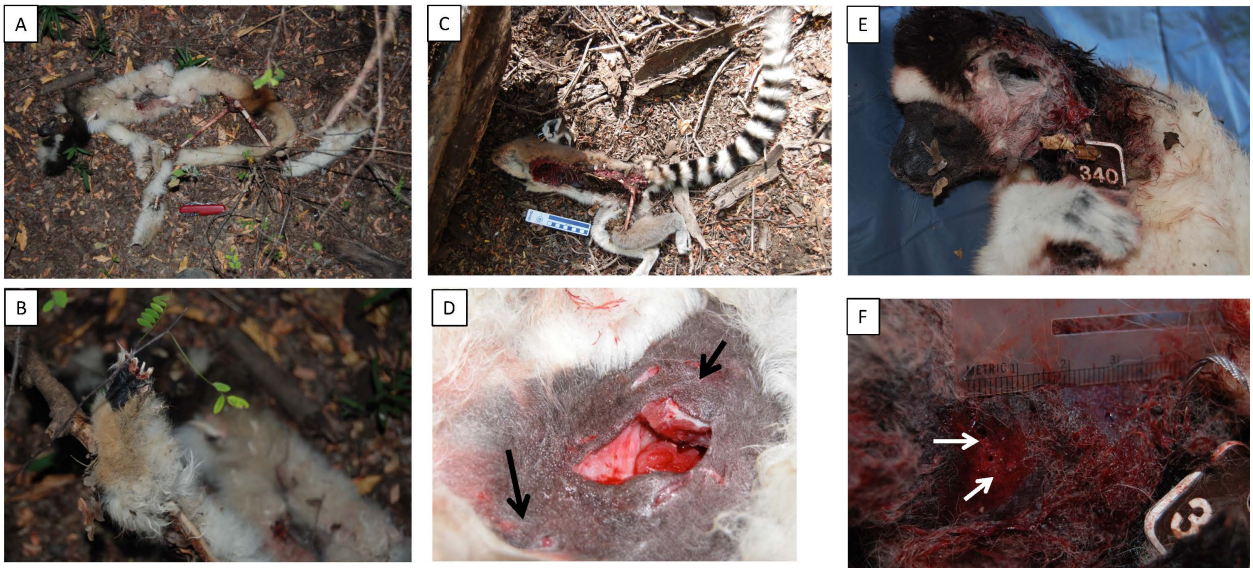

Figure 5. A. Adult *Propithecus verreauxi* (unknown individual). Muscles have been stripped from both thighs and the body cavity has been opened. B. All the phalanges on this individual's left foot have been consumed (see Table 2, predation #7). C. Predated remains of adult male *Lemur catta* animal #212, July 4, 2008 (See Table 2, predation #8). As in *Propithecus verreauxi* the muscles have been stripped from left thighs, body cavity opened, the abdominal and thoracic organs are missing, and the intestines are intact and have been removed from the body. D. Closeup of a wound from a dog attack on an adult *Propithecus verreauxi* #94. Clear upper and lower bite marks on the upper right thigh by all teeth including the canines (arrows), can be seen (see Table 2, supplementary Table 1, predation attempt #4). This sifaka was released and was able to climb after veterinarian intervention. E. Predated remains of adult male *Propithecus verreauxi,* animal #340. We observed a forest cat running away from the group of sifaka F. The animal likely died from severe blood loss from the severed right jugular vein and carotid artery (arrows), (See Table 2 and supplementary Table 1, predation #13). (Photos by Michelle Sauther).

Table 2. Lemur successful and attempted predations at Bezà Mahafaly in 2006, 2008 and 2009. For a complete description see supplementary Table 1.

1. *Lemur catta* adult, unknown individual, and sex. July 14th, 2004. Yellow West, below Blue I. Remains indicate fosa or cat predation.
2. *Lemur catta* adult female. March 2006. Killed by a dog.
3. *Lemur catta,* juvenile. June 23, 2006 (Supplementary Figure 1A). Red West, Blue II. Juvenile *Lemur catta* with broken lower jaw resulting from a dog attack. Individual disappears several days later.
4. *Propithecus verreauxi* #94, adult male. July 27th, 2006 (Figure 5D). Green East, Pink 3. This individual is found alive by members of the BMSR monitoring team and had severe injuries indicative of a dog attack.
5. *Propithecus verreauxi*, adult #367. Found June 25, 2008 (Supplementary Figure 1C). Near Green East North of Pink 3. Remains indicate fosa or cat predation.
6. *Lemur catta*, young adult female #271, 2.8 years old. Found July 2, 2008. (Supplementary Figures 1D-E) Outside eastern part of reserve, southeast of camp. Remains consistent with dog scavenging or predation.
7. *Propithecus verreauxi*, adult uncollared. Found July 2, 2008 (Supplementary Figure 1B). Outside western part of reserve, south of road. Remains indicate fosa or cat predation.
8. *Lemur catta,* adult male # 212. Found July 4, 2008 (Figure 5C, supplementary figure 2 A-D). Outside eastern part of reserve, northwest of camp. Remains and fecal DNA indicate cat predation.
9. *Lemur catta*, adult female #232. Found July 14, 2008. Outside western part of reserve, south of road. Remains indicate fosa or cat predation.
10. *Propithecus verreauxi*, adult #153. Found July 19, 2008. Yellow East above Pink 2. Unknown predator.
11. *Lemur catta*, adult male, uncollared. January 14, 2009. Located at Fihamy Be, outside of the reserve, East of Sakamena River, 800 m east of camp, outside Parcel 1. Individual killed by two unidentified men.
12. *Lemur catta,* juvenile, uncollared. June 26th, 2009. Green (East) 20 meters south of Pink1 (S23.65219 E044.63289 +/- 2.9m). Cat predation.
13. *Propithecus verreauxi*, adult male #340, 11 years old. July 21, 2009 (Figure 5E, F). Blue I between Black and Center Trail. Cat predation. See necropsy report, Supplementary data.

Locations of successful and attempted predations and scat samples with identifiable lemur remains

Based on location, most predation events and attempts occurred near the southern part of the reserve above and below the road and the northeastern part of the reserve near

the Sakamena River (Figure 6).

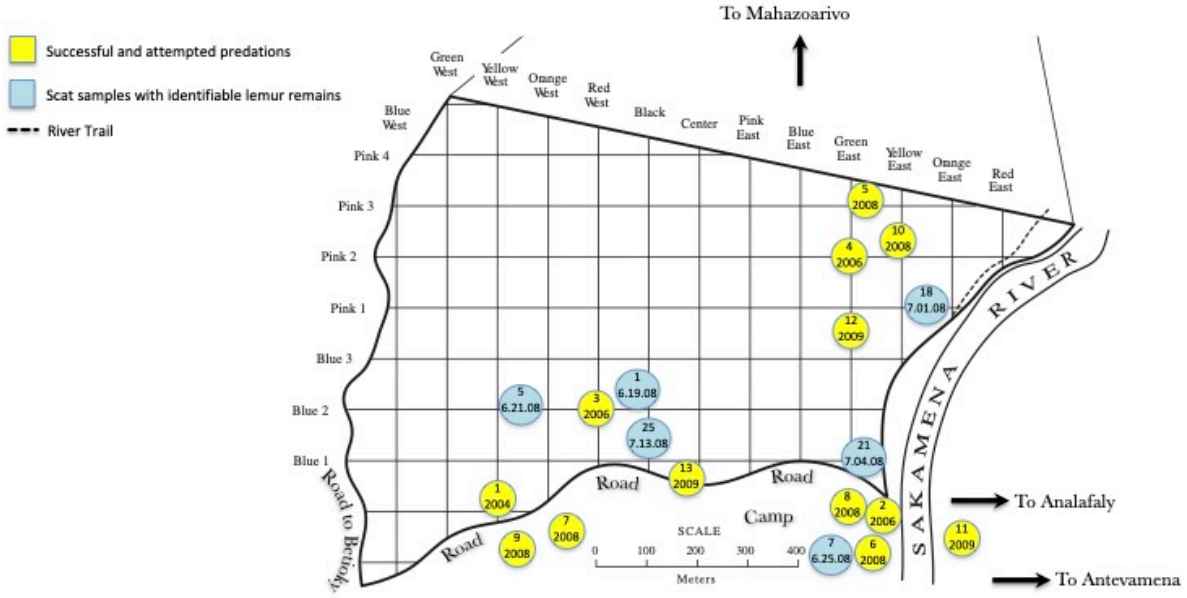

Fig. 6. Map of the Bezà Mahafaly Special Reserve showing locations of scat samples containing lemur remains from June 2008 to August 2008 (blue circles, numbers and dates, see Table 1 for a description of each sample), and attempted or successful predations from June 2006 to June 2009 (yellow circles, numbers and years, see Table 2 and supplemental Table 2 for a description of each predation).

Camera trap results

Camera trap pictures documented the presence of forest cat, (*Felis catus* n = 149 images, day = 92, night = 57*)* domestic dog (*Canis lupus familiaris* n =142 images, day = 90, night =52*)*, and civet (*Viverricula indica* n = 28, day = 1, night = 27). All the images of cats depicted the typical forest cat coloration (wildtype mackerel tabby coat color; Sauther et al., 2020, Figure 1B). A total of 388 images were of lemurs, either Verreaux's sifaka, *P. verreauxi,* or ring-tailed lemur, *L. catta* (we did not separate the two species in our analysis). While *L. catta* is cathemeral at a variety of locations (LaFleur et al., 2014), all these images were triggered during the day. Figure 7 shows the predator and lemur abundance by camera trap location. Comparisons of predator images by camera trap

location across all camera trap months revealed no effect of camera trap location on camera trap images for dogs [n = 142 images across 47 camera trap months, ANOVA: $F_{8,38}$ = 1.49, p = 0.19) or civets [n = 28 images across 17 camera trap months, ANOVA: $F_{5,11}$= 1.46, p = 0.19]. Lemur images varied by camera trap [n = 388 images across 85 camera trap months, ANOVA: $F_{8,76}$ = 2.02, p = 0.05], with more lemur images on Camera Trap 6 compared to Camera Trap 2 [p = 0.02]. Forest cat images also varied by camera trap location [n = 149 images across 55 camera trap months, ANOVA: $F_{8,46}$ = 4.04, p = 0.001 with more images on Camera Trap 9 than Camera Trap 1, 2 or 4 (9,1 p = 0.02, 9,2 p = 0.02, 9,4 p = 0.02). On June 10, 2008, a single camera trap picture of *Cryptoprocta ferox* (fosa) was taken (Figure 1D) on Camera Trap 6, which was located at the intersection of Red West and Blue I trails.

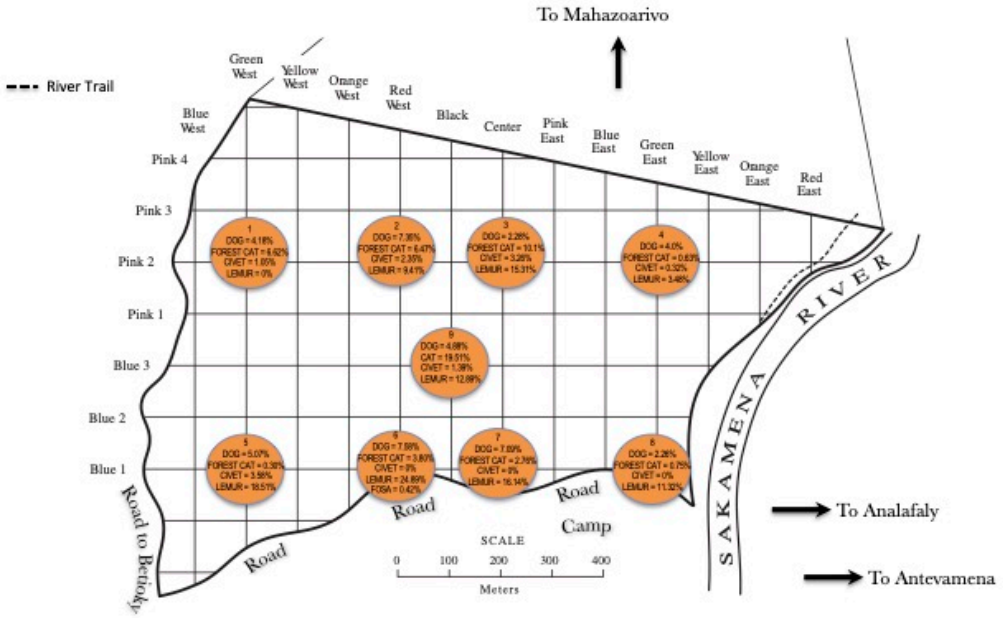

Fig 7. Location of camera traps within the Bezà Mahafaly Special Reserve and relative predator and lemur abundance by camera trap location. Abundance = Number of photos of predators per camera trap divided by total number of camera trap days for each camera trap x 100.

Results of bivariate fit regressions comparing images of pairs of species are presented

421 in Table 3. We found a positive correlation between dog images and lemur images for
422 Camera Trap 2 and 5, dog and forest cat images for Camera Trap 1, dog and civet
423 images for Camera Trap 2. Forest cat images were positively correlated with lemur
424 images on Camera Trap 6 and civet images were positively correlated with Camera
425 Trap 2. We found no other significant correlations, but for many camera traps there
426 were not enough images to compare.

427
428 Table 3. Bivariate Fit Regression Results Comparing Images of Pairs of Species. ND =
429 not enough observations to compare, (n ≤ 2 observations).

Dog/Lemur

Trap Number	Number of Observations	RSquare	Slope	DF	Error	F Ratio	P value
1	4	0.45	0.40	1	2	1.69	0.32
2	6	0.79	0.86	1	4	14.92	**0.02**
3	2	nd	nd	nd	nd	nd	nd
4	4	0.62	1.45	1	2	3.22	0.21
5	8	0.56	0.44	1	6	7.62	**0.04**
6	4	0.17	0.59	1	2	0.42	0.58
7	6	0.74	0.58	1	4	11.43	0.03
8	4	0.55	0.44	1	2	2.34	0.26
9	3	0.08	0.33	1	1	0.09	0.81

Dog/Forest Cat

Trap Number		RSquare	Slope	DF	Error	F Ratio	P value
1	4	0.95	2.97	1	2	36.47	**0.03**
2	8	0.02	0.15	1	6	0.14	0.72
3	2	nd	nd	nd	nd	nd	nd
4	2	nd	nd	nd	nd	nd	nd
5	1	nd	nd	nd	nd	nd	nd
6	2	nd	nd	nd	nd	nd	nd
7	2	nd	nd	nd	nd	nd	nd
8	1	nd	nd	nd	nd	nd	nd
9	2	nd	nd	nd	nd	nd	nd

Dog/Civet

Trap Number		RSquare	Slope	DF	Error	F Ratio	P value
1	0	nd	nd	nd	nd	nd	nd

2	5	0.97	2.09	1	3	80.07	**0.003**
3	2	nd	nd	nd	nd	nd	nd
4	1	nd	nd	nd	nd	nd	nd
5	0	nd	nd	nd	nd	nd	nd
6	0	nd	nd	nd	nd	nd	nd
7	0	nd	nd	nd	nd	nd	nd
8	0	nd	nd	nd	nd	nd	nd
1	0	nd	nd	nd	nd	nd	nd

Forest Cat/Lemur

Trap Number		RSquare	Slope	DF	Error	F Ratio	P value
1	9	0.04	-0.17	1	7	0.35	0.57
2	7	0.17	0.37	1	5	1.04	0.35
3	10	0.08	0.19	1	8	0.72	0.42
4	2	nd	nd	nd	nd	nd	nd
5	2	nd	nd	nd	nd	nd	nd
6	4	0.94	1.18	1	2	34.05	**0.03**
7	4	0.30	0.58	1	2	0.85	0.45
8	1	nd	nd	nd	nd	nd	nd
9	8	0.14	0.27	1	6	0.96	0.36

Forest Cat/Civet

Trap Number		RSquare	Slope	DF	Error	F Ratio	P value
1	1	nd	nd	nd	nd	nd	nd
2	4	0.09	0.36	1	2	0.20	0.70
3	5	0.48	-0.91	1	3	2.78	0.19
4	0	nd	nd	nd	nd	nd	nd
5	0	nd	nd	nd	nd	nd	nd
6	0	nd	nd	nd	nd	nd	nd
7	0	nd	nd	nd	nd	nd	nd
8	0	nd	nd	nd	nd	nd	nd
9	3	0.58	0.69	1	1	1.41	0.45

Civet/Lemur

Trap Number		RSquare	Slope	DF	Error	F Ratio	P value
1	1	nd	nd	nd	nd	nd	nd
2	6	0.68	0.35	1	4	8.42	**0.04**
3	5	0.25	-0.30	1	3	0.99	0.39
4	1	nd	nd	nd	nd	nd	nd
5	1	nd	nd	nd	nd	nd	nd
6	0	nd	nd	nd	nd	nd	nd
7	0	nd	nd	nd	nd	nd	nd

8	0	nd	nd	nd	nd	nd	nd
9	3	0.22	-0.58	1	1	0.28	0.69

Discussion

Using multiple measures of predation (scat sampling, field observations of successful and attempted predations, locations of scat samples with identifiable lemur remains, and camera trap data), we demonstrate that exotic predators at the Bezà Mahafaly Special Reserve have a demonstrable impact on local fauna. Vertebrate prey, including lemurs, are predated on all year long, while insects show a seasonal pattern, with higher use in the wet versus the dry season. Forest cat predation of mammals is greater than dog predation. Eyewitness accounts verify that forest cats can take prey as large as an adult sifaka and that human predation on lemurs occurs at BMSR.

SCAT SAMPLES

While scat sampling is commonly used to determine predator diets (Wilson and Delahay, 2001), has been used to understand fosa diet (e.g., Dollar, 2007; Hawkins and Racey, 2008), and is particularly useful in assessing effects of invasive predators (Wysong et al., 2019), we could find no published research using scat sampling to understand lemur predation by exotic predators in Madagascar. With regards to scat samples, our study was limited in that that we were not able to carry out DNA analyses except on one sample, and we could not establish specific prey species from most hair and bone fragments. Nevertheless, exotic predator scat indicates a constant use of mammalian prey throughout the year, irrespective of season at BMSR. Greater use of insect prey and plants during the wet season likely reflects the greater seasonality of food resources at the research site during that season (Sussman et al., 2012). Forest

cats appear to be a constant mammalian predator, utilizing mammal prey more than dogs. The numerous forest cat scat samples containing distal phalanges and hallux may link to actual predation remains also missing distal phalanges and hallux, indicating forest cats may also scavenge remains (Figure 5A, 5B; Supplementary Table 2). Based on the few civet scat samples, this species also appear to consistently use mammalian prey and while they may focus on rodents and especially insect prey, they can also be predators of smaller lemurs, as they have been observed predating an infant *L. catta* at BMSR (Goodman et al., 2007).

LEMUR SUCCESSFUL AND ATTEMPTED PREDATIONS

Both ring-tailed lemurs, *Lemur catta*, and Verreaux's sifaka, *Propithecus verreauxi*, are clearly important prey for the larger exotic predators at BMSR. Ring-tailed lemurs have several antipredator calls (Sauther 1989), as do Verreaux's sifaka (Fichtel and Kappeler 2002) and both species exhibit referential signalling (Sauther, 1989; Pereira and Macedonia, 1991; Fichtel, 2004). At BMSR Verreaux's sifaka are especially vigilant and more arboreal when dogs are present (Chen-Kraus et al., 2022). Nevertheless, these large-bodied lemurs at BMSR may be especially prone to predation. Ring-tailed lemurs are known to be semi-terrestrial (Sauther et al., 1999) and Verreaux's sifaka at BMSR also commonly forage (Brockman et al., 2008) and even travel on the ground using the established trail system (Sauther, pers. obs.). We might posit that predators should affect these lemur's terrestriality, but a meta-analysis of 47 arboreal diurnal primates did not find the presence of predator to be a predictive factor overall as there was much variability both within and between primate species (Eppley et al., 2022). At BMSR the lemurs use ground resources such as herbaceous plants and the ripe fruits of a key

480 food resource, *Tamarindus indica*, which they forage for both in the trees and on the
481 ground (Sauther and Cuozzo, 2009; Richard et al., 2016), and thus must trade-off
482 between foraging and predation pressure. Overall, likely predation by fosa on these
483 species is not absent at BMSR (contra Kappeler and Fichtel, 2022) and the combined
484 predation by dogs, forest cats, fosa and even civets should have a significant effect on
485 their demography. Our results indicate a preference for lemur prey during the dry
486 season (May through October), which has been observed at other sites where the
487 predator has been documented as fosa (Wright et al., 1997, Patel, 2005; Irwin et al.,
488 2009). BMSR is a very seasonal habitat with a strict dry season of reduced food
489 availability and a wet season with high food availability (Sauther and Cuozzo 2009). As
490 such, it is possible that *L. catta* and *P. verreauxi* are bolder (e.g. need stronger cues)
491 during the dry season when resources are scarce and may thus be more susceptible to
492 predation (Ehlman et al., 2019).
493 *Fosa predator behavior*
494 Fosa are relatively large predators, with adult males weighing between 8.1 and 12 kg
495 (Albignac 1973; Dollar 1999) and are often noted as “lemur specialists” although they
496 use a wide variety of prey, including domestic chickens (Dollar et al., 2007; Racey et al.,
497 2008). Remains at BMSR indicate fosa and forest cat are both stalk-and-ambush
498 predators, subduing prey by suffocation and/or exsanguination. Fosa at other Malagasy
499 sites characteristically open the body cavity and eat the internal organs (*Propithecus*
500 *edwardsi* at Ranomafana: Wright et al., 1997, Irwin et al., 2009; *Varecia variegata* at
501 Torotorofotsy: Sefczek et al., 2018), although there are no reports of the muscles being
502 eaten. At Betampona researchers observed numerous fosa predation attempts on
503 diademed sifakas (*Propithecus diadema)* and found one set of remains they attributed

504 to fosa predation, and in this case the bones of the lower legs were missing and
505 assumed consumed (Bonadonna et al., 2024). At Tsimanompetsotsa adult ring-tailed
506 lemur remains have been found in both fosa and forest cat scat and the eviscerated
507 remains of an infant missing its ventral torso and internal organs and exhibiting two
508 puncture wounds on the neck have been documented (LaFleur et al., 2014). Along the
509 Onilahy River, near BMSR an eviscerated adult *V. verreauxi* was found missing the
510 heart and liver (Rasoanindrainy 1985). At BMSR, between 1984-1988 one sifaka was
511 found eviscerated, with the contents of the thoracic cavity missing, suggesting fosa
512 predation (Richard et al., 1991). At BMSR we also confirm this pattern, with the lemur's
513 body cavity opened, intestines removed and found nearby, the internal organs missing,
514 and the muscles of the thigh and lower leg missing.
515 The number of predated remains were also much greater during June-July 2008 (six
516 events) compared to June-July 2004 (one event), June-July 2006 (two events), June-
517 July 2007 (zero events) and June-July 2009 (two events). Thus, the highest number of
518 predation events was during the period where the presence of fosa (*Cryptoprocta ferox*)
519 was documented for the first time in over fifteen years. The last time this endemic
520 predator was seen at BMSR was in 1993 and fosa have been assumed to be rare or no
521 longer persist in the area (Brockman et al., 2008). However, our informal conversation
522 in 2008 with a local villager indicates fosa are frequently found along an escarpment
523 about 10 km from BMSR and that their presence in the area is well known, but that they
524 have large home ranges (contra Brockman et al., 2008). In 2011 a fosa was also
525 encountered on Red West Trail by a researcher at BMSR (Kyleen Breslin, pers. com).
526 As in this study, lemur kills by fosa at Ranomafana also occurred during a short period,
527 with the fosa killing nine Milne-Edward's sifaka (*Propithecus diadema edwardsi)* across

the territory of four groups from mid-July to mid-September 1994, which was also during the dry season. Based on their results it appears fosa can take up to a year to return to a site. This endemic carnivore has a very large home range in fragmented habitats such as Ankarafantsika National Park which may reflect lower prey availability and the need for larger home ranges to acquire enough food resources (Wyza et al., 2020). Given the fragmented nature of the area surround BMSR (Sussman et al., 2012) we posit that the higher than usual documented predation in 2008 was caused at least in part by fosa being present, but that this predator may not be continuously in the area. Thus, fosa remain an important potential predator at BMSR but their large ranges may result in periodic episodes of lemur predation rather than continuous predation by dogs, foresdt cats and perhaps civets.

Forest cat predator behavior

Our results provide the first eyewitness evidence that forest cats can and do take adult sifaka at BMSR. Before our research, one eye-witness account of forest cat predation has been documented, when a forest cat was seen carrying a dead infant ring-tailed lemur in its mouth (Ratsirarson et al., 2001). There has also been one instance at BMSR where *L. catta* bones and fur were found at the entrance of a forest cat's shelter (Goodman et al., 1993). In 1988 the body of a male ring-tailed lemur (#7) was found with puncture wounds at the base of the skull, indicative of either fosa or forest cat predation (Sauther 1989). Previous research noted several instances where forest cats were observed stalking Verreaux's sifaka at BMSR (which has also been witnessed by members of our research team) and used the BMSR osteological collection to argue

552 forest cat predation on Verreaux's sifaka, stating that fosa were rare or perhaps
553 extirpated from BMSR (Brockman et al., 2008). Our camera trap evidence of fosa in
554 2008 and an eyewitness account of fosa at BMSR in 2011 complicate this somewhat as
555 it indicates that fosa were still present at BMSR at least recently. While fosa have much
556 longer and broader canines, data we collected from three BMSR forest cats in 2008
557 show considerable overlap in distance between maxillary canine tips in both species
558 compared to our measurements of fosa museum specimens [Distance between
559 maxillary canines at tips: Forest cats, Juvenile male 15.62mm, Young female 14.74mm,
560 Adult male 16.30mm; Fosa museum measurements, Juvenile 10.02mm (23090 AMNH),
561 Adult 15.93mm (100463 AMNH), Adult male 17.8mm (BMNH 1937.11.16.1.), Adult Male
562 19.89mm (BMNH 7.19.12)]. As such, understanding patterns of predation based on the
563 BMSR osteological collection must also include the possibility of fosa predation.
564
565 In addition to smaller fauna such as mice and use of plants, insects and birds as dietary
566 items, forest cat predation at BMSR also includes both infant ring-tailed lemurs, but also
567 adult sifaka and potentially adult ring-tailed lemurs. Based on forest cat scats, the
568 phalanges of lepilemurs, sifaka and ring-tailed lemurs could indicate scavenging
569 behavior. The predator of the adult *Lemur catta* male, #212 is potentially a forest cat as
570 fresh buried cat scat attributable to domestic cat were found near the body. Burying scat
571 is a common behavior in domestic and feral cats but is rare in wildcats, *Felis silvestris*
572 (Piñeiro and Barja, 2015), and is not associated with either wild or zoo fosa (Gerber,
573 pers. com.; Beth Jo Schoeberl pers.com.). Based on three individuals, BMSR adult
574 forest cats are larger than adult *L. catta* and *P. verreauxi* (young adult = 3.24kg, juvenile
575 male = 1.84kg, juvenile female = 1.7kg; Sauther, unpublished data) and can weigh an

576 average of 5.5kg at other sites (Brockman et al. 2008), while BMSR adult ring-tailed
577 lemurs and sifaka weigh an average of 2.2 (Miller et al., 2007) and 2.8 kg (Richard et
578 al., 2002), respectively. Forest cats at Andranomena Special Reserve can take lemur
579 prey as large as *Eulemur rufus* which range from 1.7 to 2.1 kg (Steffens et al., 2020;
580 Merson et al., 2019) and, as noted above, have been previously observed to predate
581 infant ring-tailed lemurs at BMSR (Ratsirarson et a. 2001). Based on the osteological
582 collection at BMSR there is also circumstantial evidence of forest cat predation, (e.g.,
583 Brockman et al., 2008), but there is little data available relative to actual predation by
584 cats at other sites (e.g., LaFleur, et al., 2014, Merson et al., 2019). Studies of the
585 relationship between fosa occupancy and exotics at Ankarafantsika National Park and
586 Andranomena Special Reserve document a considerable negative association between
587 fosa and cats *Felis sp.* but not dogs (Merson et al., 2019), and it is possible that
588 resource competition by forest cats may also be playing a role in fosa presence at
589 BMSR.
590
591 *Dog Predator Behavior*
592 During our research, solitary dogs occurred within BMSR and were even seen in packs,
593 as well as mothers and young, indicating that some are free-roaming and that they are
594 not only in the forest due to accompanying livestock and humans (contra Chen-Kraus,
595 2022). Given the pattern of wounding on the sifaka (Table 2, predation event #4, Figure
596 5D, supplementary table 1,), our results indicate that when dogs attack large lemurs in
597 the reserve, they do so in a typical manner for domestic dogs, e.g., attack the
598 hindquarters and abdomen (Izabela et al., 2016), while small lemurs, such as infant
599 ring-tailed lemurs, are grabbed by the head. The processing of prey appears different,

600 as predated remains of the young adult female ring-tailed lemur #271 involved chewing
601 the entire skull and bones, with little skeletal material remaining. Dog scat near the
602 predated remains included many pieces of bone and even a ring-tailed lemur distal
603 hallux (see Table 2, scat #7). It is thus difficult to assess if this was predation or
604 scavenging of an already deceased individual. As dogs are not obligate carnivores, like
605 the forest cats, they can subsist on a broader range of food types, and even scavenge,
606 which is reflected in this study given the number of scat samples containing many bone
607 fragments as well as plant material and feathers (Figure 3). Interview data indicate that
608 while owned dogs do indeed kill endemic wildlife such as tenrecs near Andasibe-
609 Mantadia and Ranomafana National Parks, no lemurs were reported killed, which may
610 reflect under-reporting due to the potential negative consequences (Merz et al., 2021).
611 Historically dogs may not have relied on forest bushmeat (Hixon et al., 2021). There is
612 conflicting data regarding the effect of dogs on fosa presence. As noted above, at
613 Ankarafantsika National Park and Andranomena Special Reserve dogs did not impact
614 fosa presence (Merson et al., 2019). However, capture rates of fosa at Ankarafantsika
615 National Park were lower in areas with dogs (Barcala 2009). At Ranomafana National
616 Park fosa declined relative to dog presence (Farris et al., 2015).

617 *Civet predator behavior*

618 Based on our results, civet predation at BMSR focuses on small mammalian prey and
619 insects. We found no direct evidence of lemur predation. However, M. Enafa, a member
620 of the ecological monitoring team, was an eyewitness to a civet predation on a young *L.*
621 *catta* in 1993. Here the civet was lying low on the ground near a *L. catta* troop, waving
622 its striped tail which is like that of *L. catta*. The civet grabbed the young lemur when it
623 came over to investigate (In Goodman et al., 1993).

Location of lemur remains

Successful and attempted predations and scat samples with identifiable lemur remains occur primarily near and just outside the southern edge of the reserve which coincide with the main road, and the eastern edge of the reserve which is along the ephemeral Sakamena River (Figure 6). The northeast part of the reserve abuts what was then unprotected habitat and is relatively near the village of Mahazoarivo. There were also a high number of remains found along and just outside the southern portion of the reserve near the road to Analafaly and Antevamena. In general, these are high traffic areas as people with or without dogs and livestock travel along the roads and the mainly dry, seasonal Sakamena River, as well as the Red West trail, which is heavily used by villagers, their dogs and livestock to travel from Mahazoarivo to the main road below the reserve (upublished data). Of note, the remains of the unidentified ring-tailed lemur killed by two men from outside the area were found near the roads to Analafaly and Antevamena. The Mahafaly peoples who live around BMSR have taboos, called *fady* against harming lemurs, which are seen as ancestors, and lemurs at BMSR have traditionally had a culturally protected status (Loudon et al., 2006). However, individuals moving into the area from other cultural groups for which bushmeat hunting of lemurs is not *fady* may not share the same cultural restrictions (LaFleur et al., 2018). Location of remains also tended to be near lemur “hot spots” based on the high presence of camera trap pictures of lemurs around and on Red West Trail, which is where our single picture of fosa is also located.

CAMERA TRAP DATA

Forest cats showed a higher abundance in some areas, being seen more often on

Camera Trap 9, located in the center of the reserve (Figure 7). This may be the center of their range as forest cat pictures with young have also been seen here. As noted above, the Red West Trail (Fig 7) is heavily used by villagers, their dogs and livestock. Lemurs were seen more often on camera traps located on this trail (Camera Trap 6) and our sole picture of a fosa was also on this camera trap. A fosa was also encountered on Red West Trail by a researcher in 2011 (Kyleen Breslin, pers. com.). In addition, both dog and civet images were positively correlated with lemur images on Camera Trap 2 and forest cat images were also positively correlated with Camera Trap 6, all on Red West Trail, suggesting that dogs, cats, civets and potentially fosa may be attracted to areas where lemurs are more likely to be found. While all *L. catta* pictures were taken during the day, previous research at BMSR has noted anti-predator calls at night (Sauther, 1998) and when *Tamarindus indica* fruit is plentiful, *L. catta* at BMSR will also forage for ripe fruit in the trees at night during a full moon (Sauther, pers obs). The lack of nocturnal images suggests these lemurs do not travel on the ground at night, which is also the case at Tsimanompetsotsa where *L. catta* is cathemeral (LaFleur et al., 2014).

SIGNIFICANCE OF STUDY TO CONSERVATION

Lemur conservation threats have tended to focus on loss of habitat caused by anthropogenic effects such as deforestation (Reed and Bidner, 2004), but other pressures are also important. Lemur hunting by humans is clearly a very major threat (e.g., Patel et al., 2005) and, as noted here, hunting by introduced domestic species, e.g. feral dogs and forest cats, is also a mounting problem likely to be exacerbated as humans and lemurs come into closer contact. It is critical to develop methodology for monitoring

672 and assessing ongoing patterns and impact. Such data are rarely available when
673 developing models of lemur population viability, and understanding this type of predator
674 pressure is critical for establishing accurate future trends, since most lemur habitats have
675 or will eventually contain both "natural" and human induced impacts. There are also
676 ecological ramifications. As some lemurs, e.g. *L. catta*, are highly terrestrial they may be
677 more susceptible to feral dog and cat predation. In addition, if exotic animals such as
678 dogs and specifically forest cats, are filling the niche of original endemic mammalian
679 predators such as the fosa, *Cryptoprocta ferox* this might reduce the effectiveness of
680 existing lemur anti-predator behavior (Ehlman et al., 2019), as fosa are solitary often
681 crepuscular hunters (Dollar et al. 2007), but forest cats and dogs are active day and night
682 and dogs may hunt in pairs or packs both day and night (Sauther, pers. obs). Given the
683 critical nature of feral dog and forest cat predation on lemurs, it is essential that we
684 develop a better understanding of the types, distribution and abundance of introduced
685 predators. The first step is to determine the source and severity of the problem, and to
686 develop a working template for assessing this in the field, as we have done here. Such
687 data will form the basis for effective wildlife management plans, including how to
688 successfully reduce the negative impact of introduced predators while at the same time
689 being cognizant of local cultural views.
690
691 CONCLUSIONS
692 Understanding the interplay of exotic and endemic predators creates a complicated
693 picture. Clearly forest cats and dogs are important and lethal predators at BMSR. Fosa
694 are not extirpated from the area but may have large ranges and therefore pose less of a
695 continuous threat compared to forest cats and even feral dogs who live in or next to the

forest. Nevertheless, when they do visit the area there can be a synergistic effect with predator behaviors of exotic species resulting in peaks of lemur predations that could have serious conservation and demographic implications. Evidence of human predation is low but not completely absent and may reflect different cultural norms of people moving into the area. Scat sampling of exotic predators is one way to expand our understanding of their impact on lemur populations and long-term studies with multiple assessments of predation can provide a clearer understanding of how non-endemic and endemic predators affect endangered species survival.

Acknowledgements

We thank Elahavelo Efitroarane, Enafa, Efitiria and Edouard (members of the Bezà Mahafaly Special Reserve Ecological Monitoring Team) and the many field and laboratory assistants, veterinary personnel, and Malagasy colleagues who have aided our work in Madagascar from 2003 to 2012. We especially thank Dr. Joel Ratsirarson and Dr. Jeannin Ranaivonosy, for their assistance and support. We also thank Madagascar National Parks (MNP, formally ANGAP) for permission to work at Beza Mahafaly, and especially Andry Randrianandrasana. We thank two anonymous reviewers for their comments which substantially improved the manuscript. Thanks also to Nando Grow and Sharon Gursky and for inviting us to participate in this special volume.

Statement of Ethics

This project received approval by and followed standard animal handling guidelines and protocols of the Institutional Animal Care and Use Committee the University of Colorado. All data were collected in Madagascar with the approval of MNP

(Madagascar National Parks, formerly known as ANGAP, Association Nationale pour la Gestion des Aires Protégés), the body governing research in Madagascar's protected areas and with CITES approval (05US040035/9). Additionally, all research was conducted in compliance with the American Society of Primatologists' Principles for the Ethical Treatment of non-Human Primates.

Conflict of interest

The authors have no conflicts of interest to declare.

Funding Sources

Our work in Madagascar has been supported by Primate Conservation Inc., The International Primatological Society, Sigma Xi, The Explorer's Club, The St. Louis Zoo (FRC 06-1), The University of Colorado-Boulder (IGP and CRCW), The National Geographic Society, the American Society of Primatologists, The Lindbergh Fund, and the National Science Foundation (BCS 0922465) and DDIG (BCS 0851761).

Author contributions

MLS organized and wrote the manuscript. All authors conceived the research and provided input on the manuscript. MS and JN prepared and analyzed the scat specimens. IAJY and JN collected scat specimens. IAJY collected camera trap data. SL provided veterinary analyses and the necropsy reports.

Data availability

All data used in this research are available upon request to the corresponding author.

Supplementary material

Supplementary materials are available online.

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SUPPLEMENTAL MATERIALS

Supplementary Table 1. Lemur successful and attempted predations at Bezà Mahafaly in 2006, 2008 and 2009.

1. *Lemur catta* adult, unknown individual, and sex. July 14th, 2004. Yellow West, below Blue I. Primarily intact with remnant intestines separate from body and muscles of both femurs missing. Remains indicate fosa or cat predation.
2. *Lemur catta* adult female. March 2006. Killed by a dog (IAJY, pers. com).
3. *Lemur catta,* juvenile, June 23, 2006 (Supplementary Figure 1A). Red West, Blue II. JM comes upon the event due to hearing alarm calls. Going to the area of the calls, he finds a dog has pinned a young individual (probably best described as a young juvenile since this would have occurred during the dry season) to the ground. He chases the dog away. Once the dog left, the juvenile then climbs back into the tree where it then attempts to approach an individual who JM assumes is its mother. This is when it becomes apparent that the individual has serious damage to its jaw, which was broken and bent down vertically. The other individual seems a hesitant to approach the injured juvenile. She does not run down to pick it up or comfort it like one often sees when an infant falls from tree. Most of the other animals in the group have left during or immediately after the attack. The infant survives for almost a week after the attack and then disappears.
4. *Propithecus verreauxi* #94, adult male. July 27th, 2006 (Figure 5D). Green East, Pink 3. This individual is found alive by members of the BMSR monitoring team. The sifaka has severe injuries indicative of a dog attack that include massive bites and muscle damage to the lower right leg and the upper right thigh as well as back of the upper left arm. Project veterinarians attempt to close numerous wounds and after several days the individual is released, where it is able to climb into a tree. It is not clear if this individual survived as it was not seen by our team again in 2006.
5. *Propithecus verreauxi*, adult #367. Found June 25, 2008 (Supplementary Figure 1C). Near Green East North of Pink 3. Muscles have been stripped from both thighs, body cavity has been opened, stomach and intestines are present but have been removed from the

body cavity. Remains indicate fosa or cat predation.
6. *Lemur catta*, young adult female #271, 2.8 years old. Found July 2, 2008. (Supplementary Figures 1D-E) Outside eastern part of reserve, southeast of camp. This individual had previously survived a perforated bowel with a diverticulum in 2007 (Moresco et al., 2012). Massive trauma to the face, missing left orbit and maxilla, areas appear crushed, disarticulated lower jaw. Only the rib cage, skull, mandible, hair, and small bone remnants remain. Feeding style suggests a canid but it is unclear whether a dog was the predator or subsequent scavenger of the remains.
7. *Propithecus verreauxi*, adult uncollared. Found July 2, 2008 (Supplementary Figure 1B). Outside western part of reserve, south of road. Muscles have been stripped from both thighs and the body cavity has been opened. All the phalanges on the individual's left foot have been consumed. Remains indicate fosa or cat predation.
8. *Lemur catta,* adult male # 212. Found July 4, 2008 (Figure 5C, supplementary figure 2 A-D). Outside eastern part of reserve, northwest of camp. Orange troop is giving click-click and yap alarm call (Sauther, 1989), which attracts the research team. ML finds the lemur's body. Remains are fresh with no evidence of rigor mortis. Muscles have been stripped from left thighs, body cavity opened, the abdominal and thoracic organs are missing, and the stomach and intestines are intact and have been removed from the body. Injuries around the neck, esophagus and trachea analyzed by SL, the research project veterinarian are consistent with a bite from a carnivore, with puncture by canines and pressure from incisors. Enafa, a member of the Ecological Monitoring Team, notes a dirt mound near the body and from this a large, fresh (12 cm long) buried scat sample is found (Figure 7 B). He states it is an "ampaha" or forest cat. Subsequent DNA analysis indicates it is likely from a cat, (Tkach and Ness, 99-100% match, unpublished data). See necropsy report, Supplementary data.
9. *Lemur catta*, adult female #232. Found July 14, 2008. Outside western part of reserve, south of road. Muscles have been stripped from left hind thigh and lower leg and body cavity opened and internal organs are missing. In addition, phalanges of this individual's right foot have been consumed. Remains indicate fosa or cat predation.
10. *Propithecus verreauxi*, adult #153. Found July 19, 2008. Yellow East above Pink 2. Remains include intact skull and articulated mandible, hair, and long bones. Unknown predator.
11. *Lemur catta*, adult male, uncollared. January 14, 2009. Individual killed by two unidentified men. Back of skull crushed, left tibia and fibula chopped at midsection, splinters of bone of tibia. Located at Fihamy Be, outside of the reserve, East of Sakamena River, 800 m east of camp,

outside Parcel 1.
12. *Lemur catta,* juvenile, uncollared. June 26th, 2009 found by TO. The juvenile (sex unknown) ring-tailed lemur was a member of an uncollared group (UG125) that resides north of Blue-III and Green (East) in Parcel I of the Beza Mahafaly Special Reserve. The observation was made at Green (East) 20 meters south of Pink1 (S23.65219 E044.63289 +/- 2.9m) on 26 June 2009 at 11:25 am while following a study group (Green) that was foraging on the ground (eating termite soil) approximately 30 meters from the uncollared group. The UG125 group members (approximately 7) were spread throughout the understory trees and along the ground. Ground cover was not dense and very little foliage was present in the herb layer of the forest floor. At least one subadult animal (approximately 21 months of age) was sitting on the ground on the trail and several other adult individuals were foraging on the ground. The juvenile was observed to descend a large tamarind tree to its base where 3 adult lemurs were foraging on fallen tamarind fruits. While surveying the group's composition a loud squealing was heard and the foraging animals fled the ground into nearby trees. We then observed a medium-sized cat (estimated at 3 kg based on the size of female wildcats measured by Luke Dollar) holding the juvenile to ground by the back of the neck until it stopped struggling (approximately 5 seconds). The cat then saw us and quickly carried the dead lemur by the back of the neck (like a kitten) to the trail (2 meters away) and moved away rapidly north along Green (East) for 10 meters and then ran west into the underbrush. Only once the cat was 20 meters away did the lemurs begin to alarm call (the whap – whap – whap vocalization with growling/croaking) and move high into the trees. Until this moment the rest of the group members were silent and immobile. After the predation event was over, we inspected the kill site and found small amounts of blood, but not enough to indicate exsanguination as a primary cause of death.
13. *Propithecus verreauxi*, adult male #340, 11 years old. July 21, 2009 (Figure 8). Blue I between Black and Center Trail. At 11:30 AM MLS hears sifaka alarm calling in Parcel 1. She approaches the group and witnesses a forest cat running into the bushes in the Beza Mahafaly Special Reserve near the Blue I trail, between the Black trail and the Center trail. A group of sifaka in the area are alarm calling and a dead sifaka is found ~2 meters south of the Blue I trail. The body is warm with no evidence of rigor mortis and there is a large amount of blood staining around the head and neck. With the permission of Youssouf Jacky, the Beza representative of the University of Antananarivo, the sifaka carcass is moved to camp for a gross postmortem examination by xxx, the project veterinarian. The sifaka is in lean body condition at the time of its death. Other than this, there is no gross evidence of underlying

pathology that would have contributed to its death by predation. The animal likely died from severe blood loss from the severed right jugular vein and carotid artery but may have also died from trauma to the back of the head and base of neck, with both brain and spinal damage possible. The pattern of the punctures on the neck suggest that the maxillary canines and incisors of the cat punctured the more dorsal aspects of the sifaka's neck, while the mandibular canines and incisors punctured the more ventral aspects of the neck. See necropsy report, Supplementary data.

Folia Primatologica

Seasons of death: patterns of predation on wild lemurs and other fauna by endemic and introduced predators using multiple methods of assessment.

Scott Larsen

Supplementary material

Gross Necropsy Report 1. 4 July 2008. *Lemur catta,* ring-tailed lemur #212. Scott Larsen, Project Veterinarian.

Examined is the body of an adult male ring-tailed lemur, with a black collar and 212 ID tag. A Trovan microchip transponder was located: 00-0663-E82E. The body was found approximately 15 meters to the south of the road that forms the southern border of the Beza Mahafaly Special Reserve. The body was located at 11:45 AM; at that time there was no evidence of rigor mortis, but small fly larvae were evident in the oral cavity and in the exposed thoracic cavity. The head was thrown back in an opisthotonic posture. At 1:20 PM, rigor mortis was evident.

The lemur appears to be in fair body condition; however much of the musculature of the body wall and back are missing and minimal fat is evident in the remaining tissues. There is abundant infraorbital fat. All thoracic and abdominal viscera have been removed and are missing. Some feces containing *Enterospermum* seeds, is present in the caudal abdomen.

There is a large gaping wound on the ventral abdomen and much of the skin, hair, and musculature of the ventral abdomen is missing. Multiple ribs are broken and the caudoventral aspect of the rib cage is removed and missing. The last six ribs on the left and last five ribs on the right are broken, approximately in the region of the costochondral junctions. There is a 7 cm longitudinal full-thickness skin tear on the right aspect of the ventral abdomen with evidence of bruising. There is moderate subcutaneous and muscular hemorrhage that extends from rib 4 to rib 10 on the right side and corresponds to the large skin tear. The gaping abdominal wound extends to the level of the anus and to the left rear leg. The penis, testicles, and all surrounding soft tissue are removed and missing. Ribs 1-5 on both sides were cut and removed in order to examine the cranial thorax and remove the trachea and esophagus. There is a linear longitudinal area of hemorrhage along the right dorsal aspect of the caudal lumbar vertebrae, but this hemorrhage is confined to the superficial fascia and the underlying muscles do not appear to be affected. Although the transponder was detected by a scan, there was no evidence of injury to

the dorsal musculoskeletal system in the cervicothoracic region, so this area was not dissected, and the microchip was not retrieved.

There is moderate hemorrhage in the cranial aspect of the thorax, but it cannot be determined if this was antemortem or postmortem pooling of blood. The trachea and esophagus are transected at the cranial aspect of the thorax. There is nothing within the esophageal lumen and no lesions are found in the trachea. A focal area of hemorrhage is present on the ventral base of the larynx. Dissection of the larynx reveals moderate serosanguinous material in the lumen, but no further evidence of trauma.

There is hemorrhage in the left axillary area congealed in the region of the left axillary lymph node. There is also subcutaneous hemorrhage just cranial to the right shoulder. The musculature of the left rear femur is missing, although the femur itself is intact. The skin and fur are present on the left rear leg below the level of the knee. The right rear leg is intact, but the medioproximal aspect is covered with feces containing *Enterospermum* seeds.

The surface of the tongue is covered with small, rice-grain-size fly larvae. The molariform teeth and incisors show moderate wear. No external wounds are evident on the head, but reflection of the skin reveals hemorrhage in the region of the left cheek. There are two focal areas of hemorrhage on the left cheek – one area in the musculature at the ventral base of the ramus of the mandible and another area 18 mm dorsally, at the juncture of the masseter muscles and the salivary glands. There is associated hemorrhage and bruising on the medial aspect of the skin in this region. The bruising is most intense in two focal areas, 18 mm apart, with a linear connecting area of less intense bruising. These injuries are most consistent with a bite from a carnivore, with puncture by canines and pressure from incisors. There is coagulated blood coming from the left nostril but there is no outward evidence of trauma or fracture of the nose.

Conclusions

The injuries sustained appear to be most consistent with an attack by a felid, presumably an ampaha. The wounds on the head are compatible with a felid bite. The longitudinal lacerations on the ventral abdomen may have been a result of injuries from claws, also consistent with a felid. The abdominal and thoracic organs are missing, and there is a large gaping wound with tissues missing on the ventral abdomen, so it is difficult to surmise the extent of internal injuries. The animal may have died from the trauma to the larynx and associated fluid accumulation, but the damage to this area does not appear extensive enough to be the cause of death. The lungs, and half of the trachea, are not present to look for fluid accumulation. There is minimal trauma of the skeletal system, with only fractures of the ribs. Death may have been a result of abdominal injuries and/or injury to the large vessels of the left leg.

Gross Necropsy Report 2. 21 July 2009. Verreaux's sifaka, *Propithecus verreauxi* 340. Scott Larsen, Project Veterinarian.

The necropsy was started at approximately 14:00 and rigor mortis had begun to set in. The animal was identified with collar #340 as an 11-year-old male. It weighed 2.28 kg and no subcutaneous, visceral, or retro-orbital fat. On reflection of the thoracic skin, the ribs were very prominent with decreased muscle mass. When the skin of the abdomen was reflected, the abdominal musculature was thin, and the tip of the cecum could be seen before making an

incision in the abdominal muscles and entering the peritoneum. The diaphragm musculature was also thin.

The hair and skin around the right side of the head, neck and craniodorsal thorax were stained with blood. There is a small amount of blood staining on hair of the right rear leg. There were two large punctures (4 x 2 mm and 2 x 2 mm) in the skin at the base of the right mandible on the neck, two smaller punctures (1 x 1 mm) in the skin, mid-cervical on the right dorsal aspect of the neck, and a large puncture (0.5 mm x 1.5 mm) slightly left of midline cranial cervical on the dorsum. There was another large puncture (1.5 mm x 1.5 mm) just to the left of the trachea, mid-cervical. The distance between the two large punctures on the mandible is ~ 4mm and the distance to the large puncture from these to the puncture left of the trachea is ~ 2.7 cm. Several punctures are found on the right side of the neck and the dorsal aspect of the neck near the base of the skull. When the skin was removed, from the head, neck, and cranial thorax, there was severe hemorrhage around the caudal third of the skull, with severe disruption and hemorrhage of the dorsal and right lateral neck musculature, particularly cranially where the spine connects with the skull. Hemorrhage extended from the caudal third of the skull to the cranial thorax at the point of the scapulae. There was increased laxity to the right of the occipto-atlas junction. No fractures of the skull or spine were found; however, dissection of these structures was limited in order to limit artifactual changes for any skeletal preparation. The right jugular vein was severed and macerated as was the right carotid artery. There were focal, ~3 cm x 3 cm areas of hemorrhage bilateral on the surface of the thoracic cavity. There was a much smaller (~1 cm x 1 cm) focal area of associated hemorrhage on the skin of the right side of the thorax, but no associated skin hemorrhage on the left side of the thorax. There appear to be four pinpoint punctures associated with the skin hemorrhage on the right, but no such punctures on the left side of the thorax. For body lengths: from last rib to caudal pelvis = 15 cm; pelvis = 2.3 cm; caudal pelvis to cranial thorax = 31 cm; and from first rib to last rib = 14 cm.

Several thin white nematodes were found in the peritoneal cavity, most of which were adhering to the abdominal peritoneum or the surface of abdominal organs. It is presumed that these were *Paulianfilaria* nematodes. Several specimens were preserved intact in formalin and in 90% isopropyl alcohol.

The muscles of the jaw were in rigor mortis and the mouth was not opened so as not to damage the skull or the teeth. From limited evaluation, the dental wear appeared to be moderate, with no broken canines and an intact tooth comb. At the end of the necropsy (~16:00) fly larvae were evident in the oral cavity. The esophagus was empty, and no lesions were found. The stomach was very full of homogenous green chewed plant material and weighed > 250g (maximum of gram scale); no lesions on the luminal surface of the stomach were found; however, the lining of the stomach was separating from the stomach wall postmortem. The small intestine (245 cm) had liquid ingesta with gas; no intestinal lesions were found. The large intestine was 320 cm and had no visible abnormalities on the visceral or luminal surface. There was voluminous stool in the large intestine and cecum, with abundant fecal pellets in the ascending and descending colon. On cut section, the luminal surface of the cecum, large intestine, and colon appeared normal. The liver (66.4 g) appeared normal, and no abnormalities were found on cut-section. The gall bladder appeared normal. The spleen was 100 x 6 mm. It had three large, smooth, purple nodules on the lateral surface (12 x 6 mm, 10 x 5 mm, and 8 x 4 mm).

There was a small amount of ingesta in the glottis, but no food material was found in the trachea, bronchi, or on cut-section of the lungs. The right lungs were very firm and congested throughout while the left lungs were only congested in the medial third. No distinct lesions were found in the pulmonary parenchyma or on cut surface of the trachea or bronchi. No abnormalities were found in the heart or greater vessels. The inguinal lymph nodes appeared normal. The urinary bladder was empty and small; no abnormalities were found on the peritoneal or luminal bladder surface. Two tubular structures were observed on either side of the bladder and are presumed to be accessory sex glands. The kidneys appeared normal, with no abnormalities on cut surface. The left kidney weighed 5.6 g (3.2 cm long) and the right kidney weighed 5.3 g.

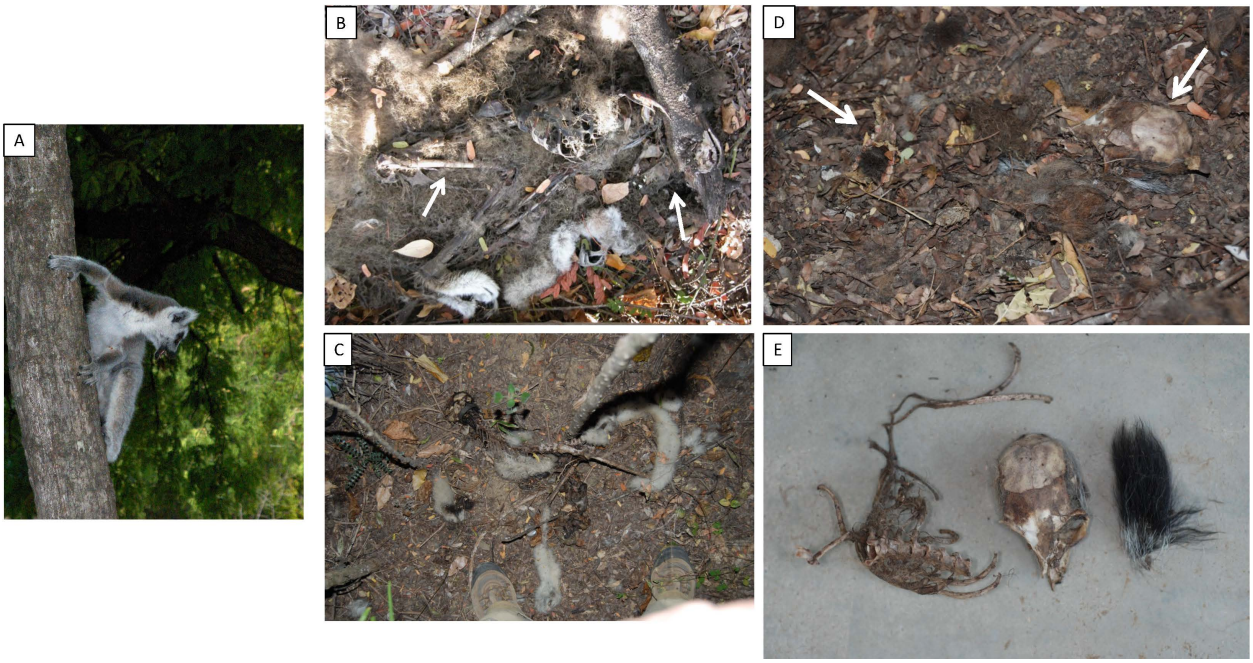
To preserve the skeleton, the brain was not removed and examined. The skeleton was left as intact as possible and returned to Jacky.

Samples in formalin included inguinal lymph nodes, thymus, tongue, trachea, esophagus, eye, liver, gall bladder, skeletal muscle (semitendinosus/semimembranosus mm), testicle, both kidneys, urinary bladder, ureter, bulbourethral glands, spleen, pancreas, stomach, cecum, colon, jejunum, ileum, duodenum, both lungs, and heart.

Complete histopathologic evaluation of these tissues by a veterinary pathologist with experience with non-human primates, particularly prosimians, is highly recommended.

Preliminary Conclusions

The sifaka was in lean body condition at the time of its death. Other than this, there was no gross evidence of underlying pathology that would have contributed to its death by predation. The animal likely died from severe blood loss from the severed right jugular vein and carotid artery but may have also died from trauma to the back of the head and base of neck, with both brain and spinal damage possible. The pattern of the punctures on the neck suggest that the maxillary canines and incisors of the cat punctured the more dorsal aspects of the sifaka's neck, while the mandibular canines and incisors punctured the more ventral aspects of the neck.



Supplementary Figure 1. A. Juvenile *Lemur catta* with broken lower jaw resulting from a dog attack (see Table 2 and Supplemental Table 1, predation attempt #3) (Photo by James B. Millette). B. Adult *Lemur catta*. Skull (arrow) and body intact with intestines removed from body and thigh muscles also missing (arrow) (see Table 2, predation #1). C. Adult *Propithecus verreauxi,* individual #367. Intestines have been pulled outside of the body; internal organs and thigh muscles also removed (see Table 2 and Supplemental Table 1, predation #5). D. Young adult female *Lemur catta*, individual #271. Massive trauma to the face and jaw (white arrows) (see Table 2 and Supplemental Table 1, predation #6). E. Only the rib cage, skull, mandible, hair, and small bone remnants of this individual remains).

Supplementary Figure 2. Predated remains of adult male *Lemur catta* animal #212, July 4, 2008 (see Table 2 and Supplemental Table 1, predation #8). A. Muscles have been stripped from left thighs, body cavity opened, the abdominal and thoracic organs are missing, and the intestines are intact and have been removed from the body. B. A large (12 cm long) buried scat sample is found near the remains that is subsequently identified as *Felis catus*, based on DNA analysis. C. Injuries around the neck, esophagus and trachea analyzed by Dr. Scott Larsen, the research project veterinarian is consistent with a bite from a carnivore, with puncture by canines and pressure from incisors (arrows). D. Skull of forest cat fit puncture wounds at the neck, but as noted in the text, this does not by itself rule out fosa predation by a younger individual. (Photos by Michelle Sauther).