


Cryptoprocta spelea (Carnivora: Eupleridae): What Did It Eat and How Do We Know?

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Abstract The extent to which Madagascar's Holocene extinct lemurs fell victim to nonhuman predators is poorly understood. Madagascar's Holocene predator guild included several now-extinct species, i.e., crocodiles, carnivorans, and raptors. Here we focus on mammalian carnivory, specifically the roles of *Cryptoprocta spelea* and its still-extant but smaller-bodied sister taxon, *C. ferox*, the fosa. *Cryptoprocta spelea* was the largest carnivoran on Madagascar during the Quaternary. We ask whether some extinct lemurs exceeded the upper prey-size limits of *C. spelea*. We use univariate and multivariate phylogenetic generalized least squares regression models to re-evaluate the likely body mass of *C. spelea*. Next, we compare characteristics of the forelimb bones of *C. ferox* and *C. spelea* to those of other stealth predators specializing on small, mixed, and large-bodied prey. Finally, we examine humeri, femora, crania, and mandibles of extinct lemurs from six sites in four ecoregions of Madagascar to identify damage likely made by predators. We test the relative prevalence of

carnivory by mammals, raptors, and crocodiles at different sites and ecoregions. Our data reveal that crocodiles, raptors, and the largest of Madagascar's mammalian predators, *C. spelea*, all preyed on large lemurs. *Cryptoprocta* opportunistically consumed lemurs weighing up to ~85 kg. Its forelimb anatomy would have facilitated predation on large-bodied prey. Social hunting may have also enhanced the ability of *C. spelea* to capture large, arboreal primates. *Cryptoprocta* carnivory is well represented at cave and riverine sites and less prevalent at lake and marsh sites, where crocodylian predation dominates.

Keywords Fosa · *Cryptoprocta* · Extinct lemurs · Madagascar · Extinction · Eupleridae · Predator

Introduction

Cryptoprocta spelea was the largest Holocene carnivoran on the island of Madagascar. It became extinct sometime during the past 2000 years, leaving its sister taxon, *C. ferox*, as the largest of the remaining endemic Madagascan carnivorans. Male and female *C. ferox* overlap in body mass but show some sexual dimorphism, and there is considerable interpopulation variation, so that adult body mass of *C. ferox* ranges from 5.5 to 9.9 kg (Goodman 2012). Past reconstructions of the mean body mass of *C. spelea* have differed considerably, from not much more than 10 kg (Goodman and Jungers 2014) to around 20 kg (based on regressions published by Van Valkenburgh 1990), the latter being over twice the body size of living *C. ferox*. *Cryptoprocta ferox* regularly kill prey that match or exceed their body size (Goodman et al. 1997, 2004; Britt et al. 2001; Dollar et al. 2007), and it is likely that *C. spelea* would have done the same, but whether it also killed much larger now-extinct lemurs has remained uncertain

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(Goodman and Jungers 2014). The largest of the extinct lemurs may have weighed over 150 kg, and several others weighed around 50 kg or more. Other formidable megafaunal predators, including a now-extinct crocodile (*Voay robustus*) (Grandidier and Vaillant 1872; Brochu 2007), may have competed with *C. spelea*, perhaps more successfully killing larger lemurs. Living crocodiles routinely attack and kill large mammals (Baquedano et al. 2012). Goodman and coworkers (Goodman 1994a, b; Goodman and Rakotozafy 1995; Goodman and Jungers 2014; Goodman and Muldoon 2016) have also identified three species of extinct raptors (two *Aquila*, or “true” eagle species, and a crowned eagle, *Stephanoaetus mahery*) that would have been capable of preying on the now-extinct lemurs.

We reconstruct the role of *Cryptoprocta* as a possible predator of large-bodied lemurs by combining an analysis of the size and morphology of its forelimb bones with an analysis of predator traces on the bones of extinct lemurs. First, we establish the contemporaneity of subfossil *Cryptoprocta* and extinct lemurs by examining the geographic distribution of *Cryptoprocta* and its radiocarbon records. We then ask whether the forelimb structure of *C. spelea* conforms to expectations for small-, mixed-, or large-prey hunting by predators that depend on stealth ambush methods. We use univariate and multivariate phylogenetic generalized least squares (PGLS) models to reconstruct the body size of *C. spelea*, and test the notion that *Cryptoprocta* targeted only prey animals at the low end of the megafaunal range in body size by examining the predation traces on the bones of the extinct lemurs themselves. We test the hypothesis that *Cryptoprocta* was an opportunistic hunter by examining the correspondence between the size of its selected prey and the size of individuals that we take to represent the populations of available prey animals at particular sites – i.e., those that do not show predation traces. Finally, we determine the relative prevalence of carnivoran predation on animals of different body sizes, in different ecoregions, and at sites of different types (marsh or lake, cave, and flood plain).

Materials and Methods

JCR collected metric data on 75 postcranial bones of subfossil *C. spelea* and *C. ferox* (including 17 humeri, 25 femora, 17 radii, and 16 ulnae; see Online Resource 1), as well as on miscellaneous fragmentary skulls, a complete skull of a *C. spelea* from Bevoha (uncatalogued) and a complete skull of a modern *C. ferox*, AM 240 (AM = Académie Malgache). Both of the complete skulls were previously illustrated (Lamberton 1939). Radiocarbon dates for subfossil *Cryptoprocta* have been published, but, as pointed out by Goodman and Jungers (2014), the species identifications of radiocarbon-dated individuals have been uncertain. Therefore,

we verified the species for each of the previously-dated long bones of *Cryptoprocta*. This information allowed us to evaluate sympatry in time as well as space.

Long bone measurements were used to reconstruct the body mass of subfossil *Cryptoprocta* and indices were calculated to assess forelimb function, following Meachen-Samuels and Van Valkenburgh (2009) (Table 1). Meachen-Samuels and Van Valkenburgh (2009) devised forelimb skeletal indices to distinguish felids concentrating on small prey from those targeting prey of mixed sizes and those specialized to bring down large prey. Following Carbone et al. (2007), we classified “small-prey specialists” as species targeting prey smaller than themselves, “large-prey specialists” as those targeting prey larger than themselves, and “mixed-prey specialists” as opportunists that regularly target either. Despite being distantly related to cryptoproctids (family Eupleridae), felids make an excellent reference population for cryptoproctids because, like

Table 1 Postcranial measurements taken and indices calculated

Measurement (mm) or Index
Humeral length
Humeral midshaft circumference
Humeral midshaft transverse diameter
Humeral midshaft anteroposterior diameter
Femoral length
Femoral midshaft circumference
Femoral midshaft transverse diameter
Femoral midshaft anteroposterior diameter
Radial length
Ulnar length (olecranon tip to distal styloid)
Humeral biepicondylar breadth
Humeral distal articular breadth
Length of the ulnar olecranon process
Radial midshaft diameter
Mediolateral diameter of distal radial articular facet
Anteroposterior diameter of distal radial articular facet
Brachial Index (BI): radial length / humeral length
Humeral Robustness Index (HRI): humeral midshaft transverse diameter / humeral length
Humeral Epicondylar Index (HEI): humeral biepicondylar breadth / humeral length
Humeral Condylar Index (HCI): humeral distal articular breadth / humeral length
Olecranon Index (OI): length of olecranon process / (ulnar length – length of olecranon process)
Radial Robustness Index (RRI): radial midshaft diameter / radial length
Radial Articular Index (RAI): mediolateral diameter distal radial articular facet / radial length
Radial Distal Articular Area Index (RAA): (mediolateral diameter of the distal radial articular facet x anteroposterior diameter of the distal radial articular facet) ⁵ / radial length

Indices follow Meachen-Samuels and Van Valkenburgh (2009)

Cryptoprocta, they are generally hypercarnivorous ambush hunters, and many are arboreal or semi-arboreal. Genetic research confirms that *Cryptoprocta* belongs to the Feliformia clade of the order Carnivora (Yoder et al. 2003; Eizirik and Murphy 2009), and morphological research confirms that *Cryptoprocta* is cat-like in cranial as well as postcranial traits (e.g., Legendre and Roth 1988; Véron 1995).

To identify predator traces on subfossil lemur bones, one of us (LRM) examined bones of extant prey animals with confirmed predator identification, and studied the literature on predator behavior and bone modification (Table 2; Online Resource 1). Particularly relevant for this study were modern cryptoproct kills of *Propithecus diadema* from an eastern Madagascar rainforest, Tsinjoarivo; they were identified as such either because *C. ferox* was sighted near the cadaver and bone damage was consistent with carnivoran predation, or because they were collected from areas with scat of *C. ferox*. These specimens were initially described by Irwin et al. (2009) and are maintained in the Sadabe osteological collection (sadabe.org). They were examined here to further document the taphonomic signature of *Cryptoprocta* and to confirm that *Cryptoprocta* prey exhibit a generalized carnivoran taphonomic signature with tooth pits, punctures, and scores as described by Lyman (1994). Recovered elements ranged from complete bones with very little damage to small fragments from *C. ferox* scat.

To estimate the body mass of *C. spelea*, we used a comparative database comprising measurements of humeri and femora of 1000 individuals belonging to 98 extant mammalian species (Godfrey et al. 1995). For each species, mean values for each measurement were entered into predictive equations. We used both univariate and multivariate phylogenetic generalized least squares (PGLS) models to regress humeral and femoral measurements against body mass in our comparative sample. PGLS models incorporate phylogenetic information by modifying the regression's error term. This is accomplished via weighting each individual species' residual value by its branch length. We used the maximum likelihood estimate of Pagel's lambda (λ ; Pagel 1999) as a branch length transformation to best fit the evolution of our traits on the set of phylogenetic trees of all extant mammals from Faurby and Svenning (2015). These represent the 1000 most likely trees from the posterior distribution of the heuristic-hierarchical Bayesian analysis used by the authors. In order to account for possible effects of minor differences in tree typology, we ran all of our analyses on the full set of phylogenies. First, all data were log transformed using the natural logarithm. Individual regressions of each measurement against body mass were performed across all phylogenies. The coefficients from each of these regressions were used to estimate the body mass of *C. spelea*. We then used the three variables (midshaft transverse femoral diameter, midshaft

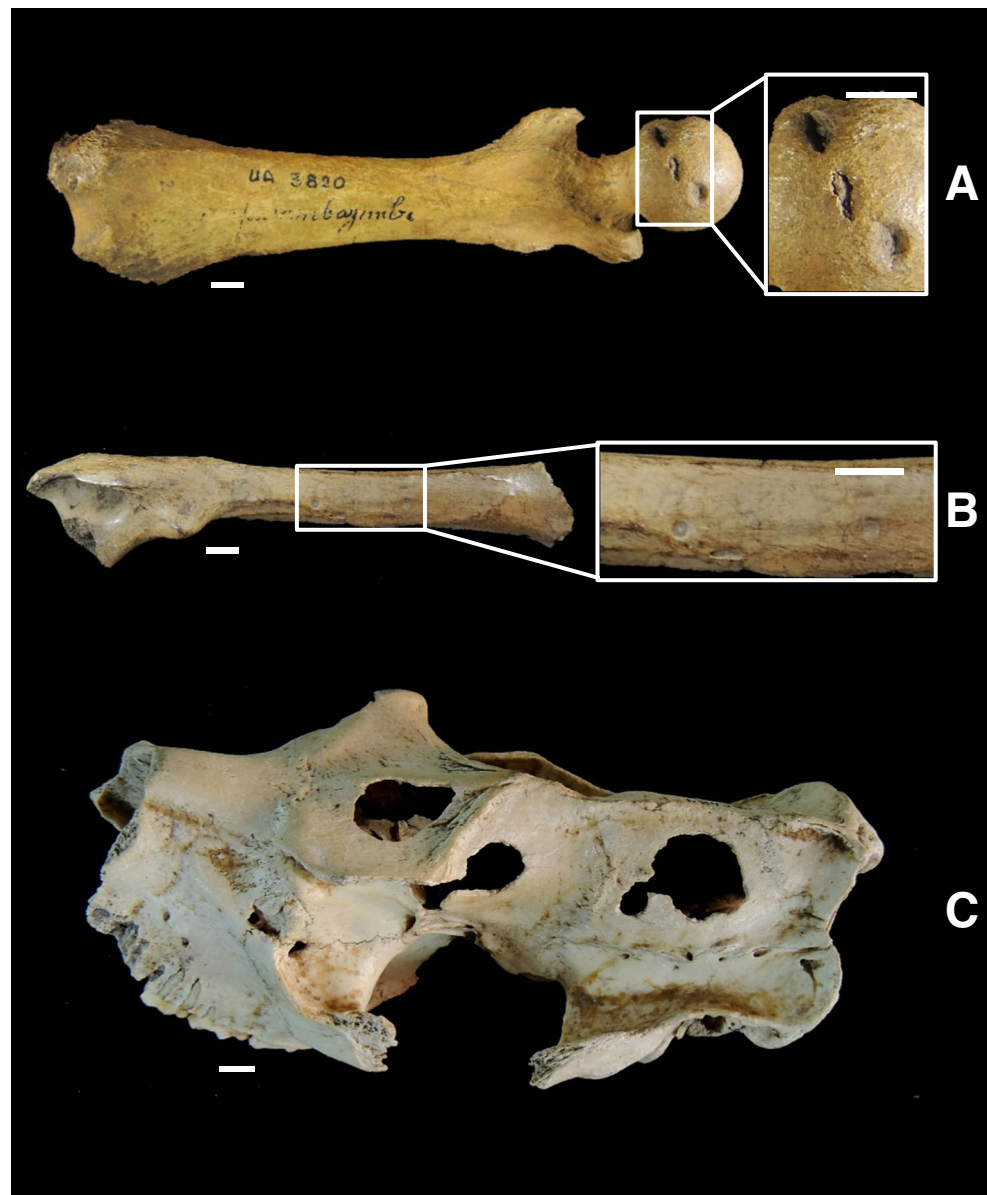
transverse humeral diameter, and midshaft humeral circumference) that showed average R^2 values above 0.85 and regressed them against body mass in a multiple PGLS, once more across all 1000 phylogenies. We used the resultant coefficients to estimate the body mass of *C. spelea*. All PGLS analyses were performed in the R statistical environment (R Core Team 2014) using the “caper” package (Orme et al. 2013).

Finally, one of us (LRM) examined 1141 elements (humeri, femora, crania, and mandibles) representing 15 species of extinct lemurs from six subfossil sites in the collection at the University of Antananarivo, Laboratory of Primatology (Online Resource 1). Site types were lake or marsh (Beloha Anavoaha, Ampasambazimba, and Manombo Toliara), cave (Ankarana and Grotte d'Ankazoabo), and riverine flood plain (Tsirave). Ecoregions sampled were the Spiny Thicket (i.e., Beloha Anavoaha, Grotte d'Ankazoabo, and Manombo Toliara), Succulent Woodland (i.e., Tsirave), Central Highland (i.e., Ampasambazimba), and Dry Deciduous Forest (i.e., Ankarana). All specimens were photographed and examined with a 10 \times hand lens. Surface damage (specifically the presence of tooth marks, beak marks, claw marks, and chemical alteration resulting from digestion) was recorded. Marks made by teeth, beaks, and claws included pits, punctures, scores, and furrows (Binford 1981; Selvaggio 1994). We used the shape of tooth pits or punctures, the abundance of each type of tooth mark, tooth mark placement, breakage patterns, and evidence of digestion to diagnose predator type as detailed in Table 2 (see also Figs. 1 and 2). Bones of extinct lemurs were classified as either showing no evidence of predation or as showing diagnostic evidence of predator damage by birds, crocodiles, or carnivorans. Bones with non-diagnostic evidence of predation (i.e., 28 of the total 1141 specimens examined) were coded as “unknown” and excluded from statistical analyses. Human modification (cut or chop marks characteristic of knife or machete damage) was noted, but for our purposes here, bones showing these marks were included in the “no predation” category, as no avian, carnivoran, or crocodylian damage was identified on them. To assess prey size upper limits for carnivoran predation, we examined the relative prevalence of three size groups of extinct lemurs: (1) roughly equal to or smaller than *C. spelea* (i.e., *Mesopropithecus* and *Pachylemur*), (2) larger than *C. spelea* but not more than about twice its size (i.e., *Archaeolemur* spp.), and (3) more than twice the mass of *C. spelea* (i.e., *Hadropithecus*, *Palaeopropithecus*, *Megaladapis*, and *Archaeoindris*); mass estimates for extinct lemurs were derived from Jungers et al. (2008). We also used humeral and femoral midshaft measurements of predators and preyed individuals to directly assess predator-prey size relationships. All of these lemurs are larger than *C. ferox* and most are larger than *C. spelea*. We used standard statistical tools (chi square, Analysis of Variance, and correlation) to analyze the predation data.

Table 2 Diagnostic marks left by crocodiles, raptors, and *Cryptoprocta* on the bones of prey

Predator	Kill behavior & processing characteristics	Expected damage on bones	Sources
Crocodile	Ambush predators attacking the heads or legs of unsuspecting animals. Animals are subdued and drowned, then forcefully dismembered. Whole animals or animal parts may be swallowed. Crocodiles do not chew bone.	Tooth pits/punctures (approximately 10% bisected), scores and furrows. Punctures are often large, with a high density of scores and furrows, diagnostic hook scores. Digestion results in erosion of dental enamel and cortical bone. Bone fractures/crushing is common. Digested bone is characterized by surface etching, corrosive pitting, foramen enlargement, polishing, and cupules. Cortical bone may be slimmed. Teeth may have eroded enamel, or may lack enamel entirely.	Fisher 1981; Njau and Blumenschine 2006; Esteban-Nadal et al. 2010; Cohen 2013; Drumheller and Brochu 2014
Raptor	Avian predators attacking the heads, necks, and backs of large animals. Prey are dismembered and portions transported to the nest where they are consumed. Bones may be discarded beneath the nest.	Raptor beaks frequently puncture thin bones and may be used to access the brain cavity by creating keyhole or v-shaped, “can opener” perforations in the cranial vault, often through the base of the skull. Depressed flaps of bone are common along preserved edges of can-opener edges. Small, v-shaped nicks from the tips of talons are common on the frontal, orbits, palate, sphenoid, maxilla, and parietals. Long bones are modified by the raptor’s beak, resulting in damaged epiphyses and splintered distal ends of bones. Small talon scratches frequently surround punctured areas, sometimes in groups of three. Crania, hind-limb elements, and scapulae are the elements most likely to be recovered.	Sanders et al. 2003; McGraw 2006; Kerley and Slaght 2013; McGraw and Berger 2013; Muldoon et al. 2017
<i>Cryptoprocta</i>	When engaged in solitary hunting, fosa ambush and subdue sleeping animals with bite to face/cranium/neck. Prey is eviscerated, then the face and limbs are consumed over several feeding bouts.	Punctures and scoring on the neurocranium and destruction of facial bones, especially the frontal, maxillae, zygomatic, and orbital bones, are common, as is crushing of the gonial angle of the mandible. Pits, punctures, scores, and crenulation of edges/ends of scapulae, iliac blades, ribs, and long bones. Long bone epiphyses exhibit a range of damage, from minimal tooth markings to complete destruction. Diaphyses sometimes exhibit fractures, apparently produced to expose and provide access to the marrow cavity. Pits or punctures may be paired, with intercanine distances characteristic of species (e.g., 28–30 mm maxillary intercanine distance in the case of <i>Cryptoprocta spelea</i>).	Wright et al. 1997, Wright 1998; Patel 2005; Irwin et al. 2009; Muldoon et al. 2017

Fig. 1 Comparison of crocodile, *Cryptoprocta*, and avian predation damage on bones of extinct lemurs. **A.** Anterior aspect of the femur (UA 3820) of a *Palaeopropithecus maximus* from Ampasambazimba. Crocodile tooth marks on femoral head (inset) and on the medial edge of the patellar groove. **B.** Posterior aspect of femur (UA 1161) of an *Archaeolemur edwardsi* from Ampasambazimba with evidence of *Cryptoprocta* predation. Paired canine tooth pits (inset) are visible on the midshaft. Proximal and distal ends exhibit crenulated edges resulting from gnawing. Tooth pits are 27 mm apart as measured from the center of each pit. **C.** Cranium (UA 5484) of *Megaladapis madagascariensis* from Beloha Anavoaha with characteristic evidence of avian predation including “keyhole” damage resulting from accessing the braincase using talons and/or beak. Scale = 1 cm



The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Results

Predator Distribution and Morphometrics

While it is clear that *C. spelea*, like *C. ferox*, once occurred in all sampled ecoregions (Fig. 3, Table 3), the former is best represented in the arid southwest (Spiny Thicket ecoregion). The genus *Cryptoprocta* was present at each of the six subfossil lemur sites that we examined, although not all sites have both species represented. The ranges for radiocarbon dates

overlap for the two species, but in the Spiny Thicket ecoregion where both are well represented, overlap is minimal; dates for *C. ferox* (1790–560 Cal BP, or calibrated years before present) are generally younger than those for *C. spelea* (3720–1740 Cal BP). The mean radiocarbon ages for the two species are statistically indistinguishable (1868.6 ± 819.6 Cal BP for *C. ferox* and 2305 ± 839.8 Cal BP for *C. spelea*) ($t = -0.77$, $df = 8$, NS) (Table 4). Two-thirds of all calibrated radiocarbon dates for both species fall in the past 2000 years. However, the most recent radiocarbon date for subfossil *C. spelea* is 1740 Cal BP (Grotte d’Ankazoabo, southwest), while that for *C. ferox* is 560 Cal BP (Ankilitelo, west).

The two species of *Cryptoprocta* are distinguishable by size and other morphological characteristics (Fig. 4) (Goodman et al. 2004). Our measurements affirm earlier



Fig. 2 Comparison of femur of recent *Propithecus diadema* (TFFP-003) from Tsinjoarivo (A) damaged by *Cryptoprocta ferox* and femur of sub-fossil *Pachylemur insignis* (UA 3096) from Tsirave (B) with *Cryptoprocta* damage. Note the damage to the proximal and distal ends of the bone,

with crenulated edges resulting from gnawing/chewing. Both elements exhibit complete destruction of the greater trochanter and distal femur, with the femoral head also destroyed in the subfossil specimen. Scale = 1 cm

reports (e.g., Lamberton 1939; Goodman et al. 2004) that skull length is approximately 20% greater in *C. spelea* (152.7 mm) than *C. ferox* (125.2 mm). The differences in maxillary and mandibular bicanine distances (tip to tip) are closer to 15%. Our means for maxillary intercanine distance (tip to tip) are 28.8 mm for *C. spelea* and 25.3 mm for *C. ferox*.



Fig. 3 Map showing the geographic distribution of *Cryptoprocta spelea*

Our regression analyses yielded a “best” estimate for body mass of *C. spelea* of 12.6 kg. Despite our relatively large sample size, we were unable to estimate lambda properly on some of the phylogenies for some of our variables. Iterations that included models that could not be estimated were discarded, which still allowed us to run individual PGLS models on 797 of the phylogenies and on 991 phylogenies for the multiple PGLS. This discrepancy results from difficulties in estimating λ for one of our variables in particular (the midshaft anteroposterior diameter of the humerus), which tended to optimize at λ values of 0, indicating little to no phylogenetic signal in this trait. All other variables showed strong phylogenetic signal ($\lambda > 0.7$). The differences in *C. spelea* body mass estimates from the two sets of analyses, however, are minimal. Averaging all the estimates from the individual PGLS regressions produced a mean of 12.3 kg. Averaging all the estimates from the multiple PGLS regressions produced a mean of 12.6 kg.

The values that *C. ferox* and *C. spelea* display for forelimb indices that, in felids, distinguish mixed or large-prey specialists from small prey specialists, suggest that cryptoprocts are well adapted for mixed or large prey consumption (Table 5). Like felid mixed and large-prey ambush specialists, both species of *Cryptoprocta* have short forearms, relatively large distal radial articular surfaces, high humeral and radial robustness, relatively long olecranon processes, and relatively broad distal humeri. *Cryptoprocta spelea* differs significantly from *C. ferox* in having more robust humeri (HRI) and radii (RRI) and relatively longer ulnar olecranon processes (OI) (Table 5).

Bone Modification by Predators

Fourteen species of extinct lemurs are represented by five or more bones (i.e., humeri, femora, crania, and/or mandibles) from one or more of the six sites that we sampled. Of these, ten

Table 3 Geographic distribution of subfossil *Cryptoprocta* spp

Site	<i>C. ferox</i>	<i>C. spelea</i>	Ecoregion	Data source (museum) ³
Ampasambazimba	X ¹	--	CH ²	UA
Andrahomana	--	X	ST	MNHN
Andranoboka	X	--	DDF	DLC
Ankarana	X	X	DDF	UA
Grotte d’Ankazoabo	--	X	ST	UA
Antsirabe	X	X	CH	UA
Ankilitelo	X	--	ST	DLC
Beavoaha	X	X	ST	UA
Beloha Anavoha	X	X	ST	UA
Belo-sur-mer	--	X	DDF	UA
Bemafandry	--	X	ST	UA
Taolambiby	X	X	ST	UA, OXUM
Lakaton’ny akanga	--	X	DDF	UA
Lelia	X	--	ST	AMNH
Manombo-Toliara	X	--	ST	UA, MNHN
Mitoho and Malaza Manga Caves, Tsimanampetsotsa	--	X	ST	Rosenberger-Godfrey expeditions 2014–2016
Tsiandroina	--	X	ST	UA
Tsirave	X	--	SW	UA

¹ X = present; -- = absent. ² CH: Central Highlands; DDF: Dry deciduous forest; ST: Spiny thicket; SW: Succulent woodland. ³ UA = Université d’Antananarivo; OXUM = Oxford Museum of Natural History; DLC = Duke Lemur Center; MNHN = Muséum National d’Histoire Naturelle, Paris; AMNH = American Museum of Natural History

species showed evidence of carnivoran predation (Table 6). The estimated body size range of extinct lemur prey with carnivoran damage on the bones is 11.3–85.1 kg. Some of these animals were clearly considerably larger in body size than *C. spelea*.

When measurements of bones of extinct lemur prey of *Cryptoprocta*, raptors, and *Voay* are directly compared, the crocodile-predated specimens are always larger (sometimes significantly so) than those preyed upon by carnivorans or raptors (Table 7). At Tsirave, a flood plain site in the

Table 4 Radiocarbon-dated specimens of subfossil *Cryptoprocta*, with species identifications

Species	Bone and specimen number	Lab number	Source	Site and ecoregion	Mean calibrated age in years BP
<i>C. ferox</i>	Femur UA 10546	CAMS 142629	Crowley 2010	Manombo Toliara, ST	1355 ± 45
<i>C. ferox</i>	Humerus UA 10549	CAMS 142872	Crowley 2010	Manombo Toliara, ST	1790 ± 80
<i>C. ferox</i>	Tibia UA 10547	CAMS 142804	Crowley 2010	Manombo Toliara, ST	1450 ± 80
<i>C. ferox</i>	Humerus UA 10571	CAMS 142720	Crowley 2010	Tsirave, SW	2555 ± 185
<i>C. ferox</i>	Humerus UA 10570	CAMS 142880	Crowley 2010	Tsirave, SW	2500 ± 170
<i>C. ferox</i>	DLC-uncat	Beta-201844	Muldoon et al. 2009	Ankilitelo, ST	560 ± 60
<i>C. ferox</i>	Tibia UA-uncat	CAMS 143075	Crowley 2010	Ampasambazimba, CH	2870 ± 90
<i>C. spelea</i>	Femur UA 10556	CAMS 143077	Crowley 2010	Grotte d’Ankazoabo, ST	1740 ± 120
<i>C. spelea</i>	Humerus UA 10544	CAMS 142720	Crowley 2010	Taolambiby, ST	1905 ± 75
<i>C. spelea</i>	Femur UA 10543	CAMS 143062	Crowley 2010	Taolambiby, ST	3270 ± 100

Lab acronyms: CAMS = Center for Accelerator Mass Spectrometry at the Lawrence Livermore National Laboratory; Beta = Beta Analytic

Fig. 4 Comparison of skulls of *Cryptoprocta spelea* (from Bevoha, UA uncatalogued) (A) and *C. ferox* (modern, AM 240) (B). Scale = 1 cm



Succulent Woodland ecoregion, *Cryptoprocta* consumed mainly *Pachylemur insignis*, a relatively small-bodied extinct lemur that is well represented at this site (Table 8). While *Cryptoprocta* predation is present at all site types, its prevalence is lowest at lake and marsh sites, where crocodile kills are very common. Bones with evidence of *Cryptoprocta* predation are most likely to be found in caves (where avian predation is also high) and flood plain deposits (where crocodylian predation can be even more prevalent).

Because so many bones with carnivoran damage are *Pachylemur*, a lemur that lies on the lower end of the spectrum of body masses of extinct lemurs, one might infer that *Cryptoprocta* preferred prey smaller than or equal to its own body size. However, there is strong evidence that predation of extinct lemurs by *Cryptoprocta* was opportunistic and minimally constrained by prey body size. Across our six sampled sites, there is a significant positive correlation between the size of “available” extinct lemur prey (i.e., assessed by measuring extinct lemur humeri and femora with no predator damage at each site) and the size of humeri and femora at the same sites with carnivoran modification (Table 9; $r = 0.86$, $P = 0.007$). The largest-bodied lemur preyed upon by *Cryptoprocta* was *Megaladapis edwardsi* (ca. 85 kg), which was sympatric with the smaller-bodied *M. madagascariensis* (ca. 45 kg). If we control for ecoregion and genus, and compare the relative

frequencies of *M. edwardsi* and *M. madagascariensis* preyed upon by *Cryptoprocta* in southwestern Madagascar, where the two species of *Megaladapis* are sympatric, we find little evidence of prey size selectivity. Nine *M. edwardsi* and six *M. madagascariensis* bones show signs of cryptoproct predation in the southwest. These proportions are not significantly different from the proportions of “available” *M. edwardsi* and *M. madagascariensis* at these sites.

Evidence of differences in the niche structures of crocodiles, raptors, and cryptoprocts appears when all sites are considered. Table 10 shows a chi square test of differences in extinct lemur prey frequencies by predator type across all ecoregions. The smallest-bodied extinct lemurs, *Pachylemur* and *Mesopropithecus*, show less crocodylian predation than “expected,” while lemurs weighing 30 kg or more show higher frequencies of crocodylian predation than expected. Mid-sized extinct lemurs, *Archaeolemur* spp., have equal observed and expected frequencies of crocodylian predation. In contrast, both avian and carnivoran predation evince the opposite pattern, with larger-bodied extinct lemurs exhibiting frequencies that are lower than expected (especially for raptors) and smaller-bodied species exhibiting frequencies that are higher than expected. Mid-sized extinct lemurs exhibit different signals for carnivorans and raptors.

Table 5 Comparison of forelimb indices of *Cryptoprocta* with those of felids targeting small, mixed, and large prey

Index	Felid small prey specialists	Felid mixed prey consumers	Felid large prey specialists	<i>Cryptoprocta ferox</i> (N)	<i>Cryptoprocta spelea</i> (N)	Sig. of diff. betw. cryptoproct species
BI	0.902	0.901	0.881	0.773 (7)	0.740**	--
HRI*	0.066	0.071	0.080	0.087 (9)	0.103 (7)	$P = 0.001$
HEI*	0.188	0.202	0.231	0.243 (8)	0.249 (7)	NS
HCI*	0.128	0.138	0.158	0.175 (8)	0.180 (7)	NS
OI*	0.139	0.153	0.196	0.182 (9)	0.207 (6)	$P < 0.001$
RRI*	0.063	0.071	0.091	0.083 (9)	0.097 (8)	$P < 0.001$
RAI†	0.105	0.111	0.139	0.148 (8)	0.151 (7)	NS
RAA†	0.088	0.092	0.111	0.129 (8)	0.130 (8)	NS

Felid data from Meachen-Samuels and Van Valkenburgh (2009)

*For felids, Small < Mixed < Large; †For felids, Small & Mixed < Large

**Calculated as sample “mean radius length ÷ mean humerus length” because there are no associated humeri and radii available for analysis

Discussion

This is the first comprehensive study that combines data from subfossil *Cryptoprocta* and predation traces on the bones of extinct lemurs to evaluate the role of the largest-bodied carnivoran in Madagascar’s recent predator guild. Some researchers have argued that many of the extinct lemurs may have exceeded the upper size limits for prey of *Cryptoprocta* and raptors, and that, whereas crocodiles would have been sufficiently large to kill extinct lemurs, arboreality may have rendered lemurs invulnerable to crocodiles (Goodman and Jungers 2014). Furthermore, it has been argued that *C. spelea* was more robust and less arboreal than *C. ferox* (Goodman and Jungers 2014), and therefore may have targeted the more terrestrial of the subfossil lemurs who also happened to have been at or near the low end of the megafaunal size range.

This study demonstrates that large-bodied arboreal lemurs were indeed prey of *Cryptoprocta*. Indeed, we found traces of crocodile and raptor predation, as well as carnivoran predation on large-bodied, now-extinct lemurs. Our predator trace data show that *Cryptoprocta* was an opportunistic hunter capable of taking down animals up to 80–85 kg, but that the relatively small-bodied *Pachylemur* was heavily preyed upon by *Cryptoprocta* at Tsirave where *Pachylemur* was abundant. In effect, *C. spelea* was almost certainly a “mixed-prey” specialist, capable of considerable flexibility in the size of targeted species. This is consistent with the variability in diet observed in modern *C. ferox*; living cryptoproctos have been reported to consume everything from invertebrates to the largest living lemurs (Goodman et al. 1997; Dollar 2006). Only one extinct lemur species probably exceeded the upper prey size limit for *Cryptoprocta* – the 160 kg *Archaeoindris fontoynontii*. Unfortunately, we cannot test the vulnerability of

Archaeoindris directly with predator trace data because subfossil samples of *A. fontoynontii* are rare. Bones belonging to only a few individuals are known, and no postcranial bone shows evidence of predation of any sort.

We see little evidence that *C. spelea* was more terrestrial than *C. ferox*. *Cryptoprocta ferox* is comfortable hunting on the ground and in trees. It is a capable arboreal ambush hunter, with retractable claws and mobile ankle joints. Its skeletal adaptations are typical for arboreal or semi-arboreal carnivorans (see, for example, Laborde 1986), and *C. spelea* exhibits very similar skeletal features. For example, the greater tuberosity of the proximal humerus does not greatly exceed the height of the humeral head and the medial epicondyle of the distal humerus resembles that of semi-arboreal animals in size and orientation. The medial epicondyle is the site of attachment of the extrinsic digital flexor muscles, and an excellent indicator of whether, as in most terrestrial species, the forearm is habitually pronated, or, as in more arboreal animals, it shows a wide rotatory range.

Skeletal proportions (e.g., short hands and radii relative to total forelimb length, short feet relative to total hind limb length, proportions of the elements of the hand and foot) similarly align both species of *Cryptoprocta* with arboreal quadrupeds. Total limb length (relative to body mass or trunk length) can distinguish terrestrial from arboreal quadrupeds. Elongated limbs occur in more terrestrial quadrupeds where they function to increase ground speed, while shorter limbs help arboreal quadrupeds maintain balance on precarious supports. In particular, the brachial index is a good indicator of arboreality in quadrupedal animals (Laborde 1986): while suspensory animals may have high brachial indices, arboreal quadrupeds do not. Low brachial indices are particularly advantageous in keeping the body well balanced and nearer to the branch supports. Our brachial index values for *C. ferox*

Table 6 Comparison of body mass estimates and of means for humeral and femoral metric data collected on *Cryptoprocta spelea* and its large lemur prey

Trait	<i>Cryptoprocta spelea</i>	<i>Mesopropithecus globiceps</i>	<i>Pachylemur insignis</i>	<i>Pachylemur julnyi</i>	<i>Archaeolemur majori</i>	<i>Archaeolemur edwardsi</i>	<i>Hadropithecus stenognathus</i>	<i>Palaeopropithecus ingens</i>	<i>Megaladapis madagascariensis</i>	<i>Megaladapis granditieri</i>	<i>Megaladapis edwardsi</i>
Estimated body mass (kg)*	12.6	11.3	11.5	13.4	18.2	26.5	35.4	41.5	46.5	74.3	85.1
Humeral midshaft circum. (mm)	42.3	40.0	33.6	--	36.0	--	--	51.0	62.0	--	--
Humeral midshaft transverse (mm)	14.5	10.9	9.9	--	10.1	--	--	14.6	20.4	--	--
Humeral midshaft A-P (mm)	15.0	11.5	10.3	--	11.2	--	--	15.8	17.5	--	--
Femoral midshaft circum. (mm)	39.7	--	42.4	43.0	46.0	50.0	62.0	--	59.8	62.0	80.3
Femoral midshaft transverse (mm)	12.8	--	13.3	13.3	15.4	16.4	21.5	--	23.0	22.9	29.8
Femoral midshaft A-P (mm)	12.6	--	11.5	11.3	12.1	13.6	15.9	--	13.5	14.9	18.0

*Body mass estimates for extinct lemurs taken from Jungers et al. (2008)

Table 7 Comparison of metric data for the prey of *Cryptoprocta*, crocodiles, and birds

Trait (mm)	<i>Cryptoprocta</i> -predated extinct lemurs N, Mean (mm) \pm SD	Crocodile-predated extinct lemurs N, Mean (mm) \pm SD	Avian-predated extinct lemurs N, Mean (mm) \pm SD	F	df (between and within groups)	sig.
Humeral midshaft circumference	9, 38.4 \pm 9.7	51, 53.4 \pm 14.1	2, 41.0 \pm 12.7	5.25	2, 59	$P < 0.01$
Humeral midshaft transverse diameter	10, 12.2 \pm 4.5	51, 16.4 \pm 4.8	1, 9.8	4.00	2, 59	$P < 0.05$
Humeral midshaft anteroposterior diameter	9, 11.4 \pm 2.6	51, 16.8 \pm 4.8	1, 9.8	6.18	2, 58	$P < 0.01$
Femoral midshaft circumference	37, 50.9 \pm 12.2	73, 55.2 \pm 15.7	5, 45.4 \pm 4.2	1.92	2, 112	NS
Femoral midshaft transverse diameter	37, 17.2 \pm 5.5	73, 19.5 \pm 7.1	5, 13.8 \pm 1.0	2.86	2, 112	$P = 0.06$
Femoral midshaft anteroposterior diameter	37, 13.0 \pm 2.4	73, 13.7 \pm 3.3	5, 12.8 \pm 2.0	0.80	2, 112	NS

match those of Laborde (1986), and our estimate for *C. spelea* is lower yet, indicating that this animal was an adept arboreal quadruped.

Forelimb robustness has been invoked as evidence of greater terrestriality in *C. spelea* than *C. ferox*. We would argue that high humeral and radial bone robustness is related not to increased terrestriality in *C. spelea* but to greater force transmission through the forelimbs in subduing prey. Feliform stealth hunters often use their forelimbs (especially their forearms) in subduing their victims prior to delivering the killing bite. Among felids, forelimb robustness has been shown to increase as a function of relative prey size (Meachen-Samuels and Van Valkenburgh 2009). Values for the humeral robustness index (HRI) and radial robustness index (RRI) are significantly higher in felid large prey specialists than in mixed prey specialists, and significantly higher in mixed prey specialists than in small prey specialists (Meachen-Samuels and Van Valkenburgh 2009). Cryptoproct values for these indices fall at the high end of the felid spectrum, and are significantly higher in *C. spelea* than *C. ferox*. The olecranon index (OI), an indicator of mechanical advantage of the triceps muscle in subduing prey, gives the same signal. This index distinguishes small-, mixed-, and large-prey specialists among felids; cryptoproct values fall at the upper end of the felid distribution; and *C. spelea* has a significantly higher mean value than does *C. ferox*. The larger species thus appears to have had greater capacity for killing large prey than its smaller-bodied congener. Large articular surfaces also help to distribute more substantial loads, and both species of *Cryptoprocta* have very high values (exceeding the felid range) for indices reflecting the relative size of the distal articular surfaces of the humerus (HCI) and radius (RAI and RAA). Low values for the brachial index (discussed above in relation to stabilization and balance in arboreal settings) also function to increase the mechanical advantage of the forelimbs in subduing prey. We conclude that, like *C. ferox*, *C. spelea* was a powerful stealth hunter.

Our estimated body mass for *C. spelea* (12.6 kg) falls within the range of previously published estimates. Goodman and Jungers (2014) estimated the body mass of *C. spelea* as 10–15 kg based on its being 30% larger in certain linear dimensions than *C. ferox*. Anderson et al. (1985) provided body mass estimates for *C. spelea* of 13.7 \pm 0.7 kg based on a femoral length regression and 14.7 \pm 1.6 kg based on a humeral length regression. Robert Dewar (cited by Burness et al. 2001 as pers. commun.) estimated its body mass at 17 kg (method not specified). Wroe et al. (2004) reported a body mass of 20 kg based on Van Valkenburgh's (1990) skull length regression for carnivorans. These estimates suggest that *C. spelea* may have weighed up to twice what modern adult *C. ferox* typically weigh.

That *C. spelea* targeted extinct arboreal lemurs is not surprising, given the preference by its sister taxon *C. ferox* for lemurs (Rasolonandrasana 1994; Wright et al. 1997; Karpanty and Wright 2007; Hawkins and Racey 2008; Irwin et al. 2009). However, the fact that extinct lemurs as large as three times its body mass (or larger) were victims of *Cryptoprocta* is surprising, particularly for a semi-arboreal predator. While, in general, larger-bodied carnivorans are more likely to target prey surpassing their own body mass than smaller-bodied predators (Carbone et al. 1999), *C. spelea* weighed less than 20 kg, and hunting in precarious arboreal settings cannot have been easy; hunting very large lemurs in such settings was likely dangerous. Furthermore, while pack hunting enables predators of any size (e.g., dholes, which are comparable in body mass to the larger-bodied cryptoproct) to target much larger-bodied prey species, arboreal, feliform carnivorans are rarely pack hunters.

Several factors may have facilitated large-prey hunting in *C. spelea*. Surprise (stealth) attack was certainly important. Specializations of the forelimb for large-prey hunting were surely important, and we have documented these specializations in *C. spelea* as well as *C. ferox* here. The ability to hunt

Table 8 Chi square tests of differences in the relative frequencies of avian, mammalian, and crocodylian predation on extinct lemurs by prey size, ecoregion, genus, site, and site type

H ₀ : Differences in the frequency of avian, mammalian and crocodylian predation are not influenced by:	Chi square, df, sig	Observations
Prey size	26.2, 4, $P < 0.001$	Null hypothesis rejected. Around 48% of extinct lemur prey consumed by <i>Cryptoprocta</i> are species less than or equal to <i>C. spelea</i> in mass.
Ecoregion	49.2, 6, $P < 0.001$	Null hypothesis rejected. <i>Cryptoprocta</i> predation is exceptionally high in the Succulent Woodlands.
Genus	41.7, 10, $P < 0.001$	Null hypothesis rejected. <i>Cryptoprocta</i> predation on <i>Pachylemur</i> is exceptionally high.
Site	57.8, 10, $P < 0.001$	Null hypothesis rejected. <i>Cryptoprocta</i> predation is exceptionally high at Tsirave and lower than expected at Ampasambazimba.
Site type (lake or marsh, cave, flood plain)	47.3, 4, $P < 0.001$	Null hypothesis rejected. Cave sites show a mix of avian and carnivoran predation (50% each) and no crocodylian predation. Crocodylian predation dominates at lake or marsh sites (77.7%), followed by carnivoran predation (16.8%), and avian predation (5.6%). At Tsirave, a flood plain site, crocodylian (46.1%) and carnivoran (35.4.0%) predation dominate, and avian predation is relatively low (18.5%).

diurnal prey species at night was likely important; most of the larger-bodied extinct lemurs were likely diurnal (Jungers et al. 2002) and living *C. ferox* often target sleeping lemurs (Irwin et al. 2009). Finally, while living *Cryptoprocta* are generally solitary hunters, there is increasing evidence that they will use communal hunting to take down relatively large-bodied living lemurs (Lührs and Dammhahn 2010; Lührs and Kappeler 2013; Lührs et al. 2013). Indeed, Goodman and Jungers (2014) have posited communal hunting for *C. spelea*.

Recent research has further revealed interesting variation in body size and sexual dimorphism in *C. ferox*. Lührs and Kappeler (2013) have found that in Kirindy forest there are two morphotypes of males: smaller males (7.3 kg) who are roughly the same size as females, and larger males (9.6 kg). Lührs and Kappeler (2013) reported long-term associations between dyads or triads of males. Animals in dyads/triads tend

to be larger and hunt cooperatively, taking relatively larger prey, notably *Propithecus* (Lührs and Dammhahn 2010; Lührs et al. 2013; Lührs and Kappeler 2013). Solitary males are relatively smaller in size. Lührs and Kappeler (2013) hypothesized that selection favors large size for animals in associations because associations increase hunting success.

We cannot completely rule out the possibility that the tooth marks observed on extinct lemur bones result from scavenging. Various researchers have examined bone modifications in an attempt to determine whether predators or scavengers are responsible for marks (Binford 1981; Bunn 1982; Shipman 1983; Behrensmeyer 1978), but this work remains debated. Furthermore, at least in the predator types of concern here, acts of scavenging have been reported in closely related predators. Rotten chicken has been used successfully as a lure to attract *C. ferox* into

Table 9 Comparison (for study sites) of metric data on “available” extinct lemurs and *Cryptoprocta*-predated individuals

Site	Bone measured (N)	Mean midshaft circumference (means and standard deviations in mm) of bones of:	
		“Available” extinct lemur prey at site	<i>Cryptoprocta</i> -predated extinct lemurs at site
Grotte d’Ankazoabo	Humerus (3)	49.0 ± 8.9	42.0 --
Beloha Anavoha	Humerus (76)	55.8 ± 17.6	62.0 --
Tsirave	Humerus (104)	38.1 ± 3.7	34.6 ± 3.8
Ampasambazimba	Femur (101)	53.6 ± 14.6	47.6 ± 8.8
Ankarana	Femur (19)	54.7 ± 7.7	53.0 ± 2.7
Beloha Anavoha	Femur (121)	59.8 ± 16.7	62.3 ± 13.9
Manombo Toliara	Femur (40)	49.0 ± 11.8	56.8 ± 14.3
Tsirave	Femur (118)	42.1 ± 4.8	42.4 ± 2.9

$$r = 0.86 \quad P = 0.007, \quad N = 8$$

Table 10 Predator niche differentiation across all sites

Predator type	<i>Pachylemur</i> and <i>Mesopropithecus</i> (relatively small prey) Obs. (Exp.)	<i>Archaeolemur</i> (mid-sized prey) Obs. (Exp.)	<i>Hadropithecus</i> , <i>Palaeopropithecus</i> , and <i>Megaladapis</i> (relatively large prey) Obs. (Exp.)	Totals
Avian	13 (8.5)	11 (6.7)	3 (11.8)	27
Carnivoran	28 (18.3)	11 (14.4)	19 (25.3)	58
Crocodylian	39 (53.2)	41 (41.9)	89 (73.9)	169
Totals	80	63	111	254

Chi-square = 26.2, df = 4, $P < 0.001$

traps for the purpose of research (Hawkins and Racey 2005), captive *Stephanoaetus* have been fed harvested rats and rabbits, and captive *Crocodylus niloticus* have been fed butchered farm animals including suids and bovids (Baquedano et al. 2012). Despite the maintenance of these predators in captivity as forced scavengers, these animals are all known to be predators in their natural habitats where scavenging is probably rare. It is unlikely that much if any of the bone modification attributable to each of these predator types results from scavenging.

Our data support separate species status for *C. spelea* and *C. ferox*. When Guillaume Grandidier (1902) first described bones of a large cryptoproct from Andrahomana cave in southeastern Madagascar, he considered it a new variety of the living species of cryptoproct, and he named it *C. ferox* var. *spelea*, a view endorsed most recently by Köhncke and Leonhardt (1986). Petit (1935), Lamberton (1939), and Goodman et al. (2004) defended its status as a distinct species. The strongest arguments that can be made in defense of separate species status are that the two differ in morphology (our data confirm that *C. spelea* has a significantly lower brachial index, significantly higher humeral robustness, and significantly higher olecranon index) and show no overlap in body size. Body size differences cannot be attributed to sexual dimorphism (Goodman et al. 2004), as they well exceed differences between modern male and female *C. ferox* (Goodman et al. 2004; Dollar 2006). Subfossil sites with single species representation do not show size bimodality. Extended contemporaneity with sympatry would bolster the argument for separate species status, but the radiocarbon dates collected thus far are of little help as samples for *C. spelea* are too few. All radiocarbon dates available for *C. spelea* are from the Spiny Thicket, and they show only marginal temporal overlap with *C. ferox* from the same ecoregion. However, both species also occur at some subfossil sites in the north and Central Highlands, so temporal overlap is likely.

Finally, our data have taphonomic implications. Site bias in the subfossil representation of mammalian carnivory exists, and can be easily understood within a taphonomic context. While we can expect to see evidence of *Cryptoprocta* predation at all site types, their numbers are higher than “expected”

at cave and riverine sites and lower than “expected” at lake and marsh sites, where crocodylian predation dominates. This is unsurprising because crocodiles are known to drown their prey and may not consume entire cadavers. Crocodile predation is also common, although lower than “expected,” at Tsirave (our only sampled flood plain site); we found no evidence of crocodile predation at cave sites. In absolute frequency, predation by raptors is poorly represented in our samples, but it followed the same pattern as did predation by cryptoprocts, with frequencies higher than “expected” at cave and riverine sites and lower than “expected” at lake and marsh sites.

Conclusion

This study confirms that *C. spelea* is morphologically distinct from the extant *C. ferox*. Using PGLS regressions based on long-bone measurements, we determine that, at an estimated 12.6 kg, *C. spelea* falls far from the mean and outside the body mass range of extant *Cryptoprocta*. Skeletal evidence indicates that *C. spelea* lived in all ecoregions sampled here (Central Highlands, Dry Deciduous Forest, Spiny Thicket, and Succulent Woodland). *Cryptoprocta* predation is least common at lake and marsh sites, although it occurs everywhere. Radiocarbon dates show temporal overlap of the two species; those for *C. spelea* range from 3270 ± 100 Cal BP to 1740 ± 120 Cal BP, while those for *C. ferox* range from 2870 ± 90 Cal BP to 560 ± 60 Cal BP.

There is spatial and temporal overlap between *C. spelea* and *C. ferox*, although dates for the latter are more recent than those for the former in the Spiny Thicket ecoregion. Social hunting may have enabled *Cryptoprocta* to target successfully the extinct lemurs, but forelimb morphology indicates that this was a capable predator specializing in relatively large-bodied prey species. Taphonomic evidence suggests that *C. spelea* was capable of preying on some of the largest of the extinct lemurs although there is also strong evidence for opportunistic hunting. We found evidence of *Cryptoprocta* predation in all well represented species of extinct lemurs.

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