

Spatial and temporal variability in predation on rainforest primates: do forest fragmentation and predation act synergistically?

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Abstract

Predation is a constant risk for most primates, impacting demography, population dynamics, activity patterns and social behaviour. Data are limited on both the rates of predation and its spatial and temporal variability. We present long-term observations of *Cryptoprocta ferox* predation on rainforest sifakas in Madagascar, *Propithecus diadema* at Tsinjoarivo (22 group years) and *Propithecus edwardsi* at Ranomafana (73 group years), derived from intensive observations based on ongoing behavioural studies. Average per capita offtake rates are relatively low (0.06–0.07), but temporal variability is high (kills are clumped in time). This is consistent with *Cryptoprocta* ecology; individual home ranges are much larger than sifaka ranges, and individuals may hunt in a subsection of their range until prey density is decreased, then move on. These results have broad implications. First, in terms of the evolution of anti-predator strategies, it now becomes important to ask: (1) whether average or peak predation rates determine the strength of selection and (2) whether antipredator strategies (e.g. vigilance, sleeping site selection) fluctuate interannually, reflecting recent experience. Second, in terms of population ecology, *Cryptoprocta* may have disproportionately large impacts on the (small) sifaka groups, even driving groups to extinction (as observed at both sites). Third, the disappearance of groups has important implications for conservation. When this happens in continuous forest (as at Ranomafana), home ranges will likely be re-filled over time, whereas in isolated forest fragments (as at Tsinjoarivo), recolonization is less likely. Thus, conservation planners should consider predation as a potentially important proximate cause of extirpation in fragmented landscapes, even when resource density and quality could otherwise sustain populations. Considering the effects of predation can be useful in (1) decisions regarding the allocation of limited conservation resources, including which landscapes to invest resources in and (2) investigating ways to increase resilience of prey species.

Introduction

Predation is a constant risk for most primates and is fundamental in shaping demography, population dynamics, activity patterns and social behaviour (Isbell, 1994; Miller & Treves, 2007). However, our understanding of this pressure remains limited because large sample sizes of predation events are extremely hard to collect. Observations based on studies of prey give a biased view of predator ecology (Dollar, Ganzhorn & Goodman, 2007), yet long-term quantitative studies of predators are logistically difficult, and diet

reconstructions are usually based on indirect methods such as scat analysis. Long-term studies of predation on primates are rare, and mostly focus on non-forest species (Isbell, 1990). There are therefore few predation data for forest-dwelling primates (e.g. offtake rates, prey preferences, spatial and temporal variability of hunting) with which to model and understand the demographic impacts of predators on their prey (Janson, 1998).

One aspect of predation that remains largely unexplored is predators' responses to habitat loss and fragmentation – an interaction that is increasingly important given

anthropogenic impacts on natural habitats (Laurance, 1999; Dufils, 2003). Forest loss and fragmentation threaten vertebrate populations by altering abiotic conditions (Murcia, 1995; Fahrig, 2003), constraining dispersal (Smith & Batzli, 2006), altering population genetics (Gaines *et al.*, 1997) and magnifying the effects of demographic and environmental stochasticity (Lande, 1998). However, additional indirect threats may impact species' persistence in forest fragments (Turner, 1996). These include changes in the abundance or behaviour of a second species with which the first shares a trophic relationship (i.e. predation). Thus, in some cases prey may experience reduced predation risk (e.g. when predators are extirpated), while in others predation risk may increase due to altered predator density or behaviour. Finally, other aspects of predation may change, including its temporal and spatial distribution.

For animals isolated in fragments, natural or invasive predators can be major causes of declines and extirpations (Crooks & Soulé, 1999). This is unstudied in most systems. One exception is nest predation in birds: egg predation rates in real or artificial nests can be easily quantified across edge-interior transects, among different-sized fragments and among more- or less-fragmented landscapes. Although much variation exists among studies, meta-analyses have shown a trend towards increased nest predation at edges (Batáry & Báldi, 2004), in smaller patches and in more fragmented landscapes (Stephens *et al.*, 2003).

The fosa *Cryptoprocta ferox* (Eupleridae) is the largest Malagasy carnivore. It measures 1.4 m total length, and weighs 6.75 kg in Madagascar's western dry forests (Hawkins, 2003; Hawkins & Racey, 2005), and 8–12 kg in eastern rainforests (L. Dollar, pers. comm., 2006). It is forest-dependent (and thus endangered; Dollar, 2000) and well-adapted for arboreal locomotion (Laborde, 1986). Its diet includes most lemur genera, rodents, insectivores, small carnivores, an artiodactyl (*Potamochoerus*), birds and invertebrates (Rasoloarison *et al.*, 1995; Goodman, Langrand & Rasolonandrasana, 1997; Wright, Heckscher & Dunham, 1997; Hawkins, 2003). Although it is well-documented that *Cryptoprocta* consumes lemurs, few long-term offtake data are available. It is therefore hard to quantify its demographic impact on lemurs, and harder still to understand and contextualize lemurs' behavioural and life history-based responses. Given *Cryptoprocta*'s broad diet (it is not normally a lemur specialist; Dollar *et al.*, 2007), one might expect pressure on lemur populations to be manageable. However, considering the rapid anthropogenic alterations of Malagasy forests and the high percentage of lemur species that are endangered (Dufils, 2003; Mittermeier *et al.*, 2006), the potential of *Cryptoprocta* predation (albeit a pre-existing, natural process) to cause lemur extinction or extirpation in human-altered landscapes urgently needs to be understood.

Predation by *Cryptoprocta* on sifakas (lemurs of the genus *Propithecus*, 4–7 kg; Richard, 2003) is ubiquitous throughout Madagascar (Goodman, 2003), having been recorded for *Propithecus edwardsi* (Wright *et al.*, 1997), *Propithecus diadema* (Powzyk, 1997), *Propithecus candidus*

(Patel, 2005), *Propithecus perrieri* (Mayor & Lehman, 1999), *Propithecus tattersalli* (Goodman, 2003) and species of the smaller, western *Propithecus verreauxi* group (Richard, 1978; Rasoloarison *et al.*, 1995; Goodman, 2003). *Propithecus verreauxi* makes up a large proportion of the diet at Kirindy (36.3% of prey biomass; Rasoloarison *et al.*, 1995), but similar quantitative studies have not been undertaken for rainforest sifakas (*P. candidus*, *P. diadema* and *P. edwardsi*). There are, however, two reasons to suspect lower predation rates for rainforest species: their larger body size and lower population densities (Irwin, 2006b). In general, dry forest sifakas are consumed by *Cryptoprocta*, raptors and invasive predators including wildcats (Brockman *et al.*, 2008), while *Cryptoprocta* thus far seems to be the sole predator of rainforest sifakas (Karpanty & Wright, 2006).

Most of what is known about *Cryptoprocta* predation on rainforest sifakas comes from the ongoing study of Milne-Edwards Sifaka (*P. edwardsi*) at Ranomafana National Park. Wright *et al.* (1997) and Wright (1998) described several *Cryptoprocta* predation events, documenting one kill in 1990 and four in 1994 (spread over three groups, targeted successively over 43 days). These data suggest that predation exerts an important demographic pressure, but groups persisted, due to (1) long return times, and (2) the fact that groups tend to lose only one individual when a *Cryptoprocta* is active in the area. Here we present longer-term documentation of *Cryptoprocta* predation in the Ranomafana population (five groups, 1986–2007), and six diademed sifaka (*P. diadema*) groups at Tsinjoarivo.

Materials and methods

Ranomafana

Ranomafana National Park (43 500 ha) is located in south-eastern Madagascar (21°16'S, 47°20'E; 600–1400 m; Fig. 1), and has been described previously (Wright, 1995). Four *P. edwardsi* groups (Fig. 2) were continuously monitored in selectively logged (1986–1989) continuous rainforest at the Talatakely research site: TALA1 and TALA2 since January 1986, TALA3 since January 1991 and TALA4 since January 1996 (Pochron & Wright, 2003; Pochron, Tucker & Wright, 2004). Group SAKA1 at the Sakaroa site (mixture of recovering disturbed and secondary forest west of and contiguous with Talatakely) was monitored since 2007. Data are presented up to December 2007. Most animals were captured (following Glander *et al.*, 1992) and collared; all animals were individually known. All groups occupy continuous submontane rainforest within Ranomafana National Park and have contiguous home ranges (c. 50 ha per group).

Tsinjoarivo

Tsinjoarivo Forest (19°41'S, 47°48'E; 1400–1650 m; Fig. 1) is a high-altitude rainforest in eastern Madagascar. Its legal status is 'Classified Forest' and as such it has little legal protection; consequently the western half of the forest is

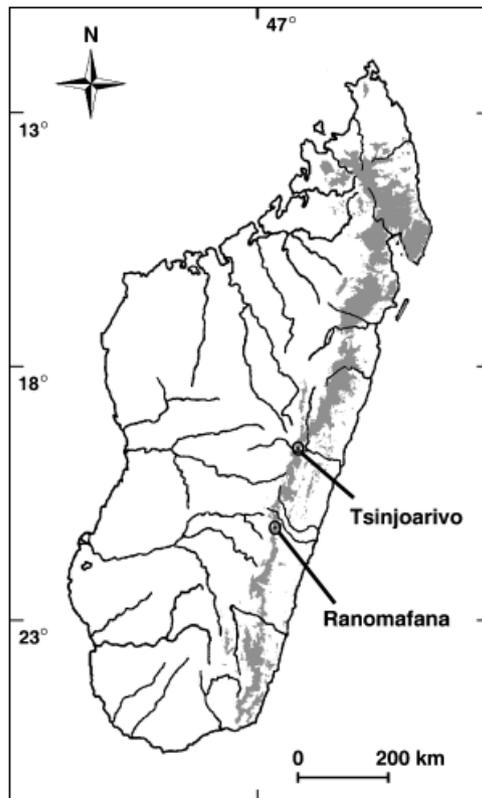


Figure 1 Location of study sites.

fragmented and degraded (details in Irwin, 2006a). Data were collected since October 2002, and are presented up to December 2007. During 2003, we followed four *P. diadema* groups (Fig. 2) for 6–11 days per month (6–21 focal animal-days per group). Since January 2004, all groups were recontacted monthly or bimonthly (except January–June 2004, in which no demographic changes occurred). Groups CONT1 and CONT2 are located in intact, undisturbed forest (Vatateza: 19°43.25'S, 47°51.41'E; 1396 m) and four others, FRAG1, FRAG2, FRAG3 and FRAG4 were located in disturbed, fragmented forest (Mahatsinjo: 19°40.94'S, 47°45.46'E; 1590 m). Most animals were captured (following Glander *et al.*, 1992) and collared; all animals were individually recognizable. CONT groups have larger home ranges (72–79 ha); FRAG groups have smaller ranges of 20–50 ha (Irwin, 2008a).

Documenting *Cryptoprocta* predation

All *Cryptoprocta* kill sites detected were photographed, and skeletal remains were collected when found. At Tsinjoarivo, nine *Cryptoprocta* scats found near one kill site (MAHA1: TP) were processed by soaking and washing through a sieve; skeletal remains were identified and tallied, with the largest number of elements from the right or left side yielding the minimum number of individuals (following Goodman *et al.*,

1997). Scats from Ranomafana have been analysed previously (Wright *et al.*, 1997).

'Confirmed' kills include only those with remains consistent with *Cryptoprocta* predation, infants that disappeared when their mothers were killed, or when there was strong circumstantial evidence (e.g. *Cryptoprocta* sightings within a day of disappearance, injuries to other group members). 'Suspected' kills include: (1) juveniles that disappeared well before dispersal age, or (2) unexplained disappearances when *Cryptoprocta* was known to be active in the area. To avoid ambiguity, analyses include only confirmed kills.

Results

Ranomafana

Seventeen confirmed *Cryptoprocta* kills (14 events) were documented, corresponding to an annual 23.3% chance of each group losing an animal, and an annual 5.7% chance of any individual being killed (Tables 1 and 2; Fig. 3). Kills occurred in somewhat discrete time periods: one in 1990, four in 1994, one each year from 2001–2005, four in 2006 and three in 2007. The gap between 1995 and 2000 is conspicuous; no predation events were detected during this 6-year interval despite continuous monitoring (~20 days per group per month).

We calculated the 13 'interarrival times' (number of days between successive predation events: mean = 470.2, SD = 702.9), and compared this distribution to a randomly generated distribution (14 events placed on random days, with replacement, over a 22-year period; 500 replicates). Only 6.4% of distributions had a standard deviation greater than the observed standard deviation. Though not statistically significant at $\alpha = 0.05$, this suggests temporal clumping: if one event is likely to be closely followed by another, more extreme short and long intervals are expected, causing a higher standard deviation. Additionally, within each period of *Cryptoprocta* activity, kills tended to be distributed among *Propithecus* groups: in 1994, four kills were shared across the three groups studied at that time, and in 2006–2007 seven kills were shared across four groups.

The predation events showed strong seasonality, with 13 of 14 occurring between April and October (Fig. 4). This distribution is significantly different from random (Rayleigh test: $r = 0.52$, $P = 0.02$; mean vector direction = 173°/July).

Predation appeared to contribute to group extinctions. TALA2 suffered two predation events in 2004–2005, and its two remaining members emigrated to Sakaroa. Group TALA3 experienced at least one kill in 2006 and two in 2007, disappearing in February 2007 after the breeding female was killed (it is unknown if the other three animals emigrated or were also killed).

Tsinjoarivo

Four confirmed *Cryptoprocta* predation events were documented, all at the fragmented site. This corresponds to an annual 18.2% chance of each group losing an animal, and



Figure 2 *Cryptoprocta ferox* (top, photo <http://www.nickgarbutt.com>), *Propithecus diadema* (bottom left, photo M. Irwin), and *Propithecus edwardsi* (bottom right, photo J. Jernvall).

an annual 7.3% chance of any individual being killed (Tables 1 and 3; Fig. 3). Offtake rates are higher in fragments than in continuous forest, but it is unclear whether this is an effect of low sample size.

Table 1 Summary statistics for predation rates: *Propithecus edwardsi* and *Ranomafana* and *Propithecus diadema* at Tsinjoarivo

Site:	Group-years	# kills	# events	Average annual offtake rate (per group)	Average annual offtake rate (per capita)
Ranomafana	73	17	14	0.233	0.057
Tsinjoarivo	22	4	3	0.182	0.073
Tsinjoarivo CONT	10	0	0	0	0
Tsinjoarivo FRAG	12	4	3	0.333	0.133

Data presented through December 2007.

Until 2004, *C. ferox* was thought to be absent within the forest fragments (local farmers typically know when *Cryptoprocta* are present because of predation on livestock). This predator presumably existed before human settlement, but had not been detected by locals for at least 10 years. A carnivore survey in November–December 2002 failed to locate *Cryptoprocta* within the fragments despite its presence in nearby continuous forest (Vatateza; L. Dollar, unpubl. data).

Between June 2004 and March 2005, four of five individuals in FRAG1 were killed by *Cryptoprocta* (Table 1). In two cases (subadult females), bones, stomach/intestine, hair and scats were found; in a third case (adult female) only stomach/intestine remains and hair remained. The fourth individual (infant) disappeared at the same time as its mother. All scats were characteristic of *Cryptoprocta* (large size, high hair and bone content, jointed appearance with twisted hair joining segments, pointed tip and musky, fish-like smell) and distinct from that of dogs or other carnivores (Hawkins, 2003). The only animal that survived was the adult male (BG). After the first three kills, BG lived with his

Table 2 Details of 14 predation events for *Propithecus edwardsi* in Ranomafana National Park

Animal ID	Age and sex/group size	Details of predation/disappearance	Remains
TALA II: Red-Red	Adult Male/4	Killed 31 July 1990	Stomach, intestines, hair and tibiae found on ground the morning after kill; 2 months later, collar and damaged femora found a few hundred metres from kill site
TALA III: Blue-Yellow and infant	16-year-old female and 1 month old infant/5	Killed 1 August 1994	Hair, near-complete skeleton, collar, hair remnants; infant corpse not found, but presumed eaten as too young to survive alone
TALA II: PYI	1-year-old female/4	Killed 6 September 1994	Eviscerated cadaver found at base of sleep tree by research team at 06:35 AM; <i>Cryptoprocta</i> seen at kill site at 08:15 AM
TALA I: Brown (BB)	3-year-old female/6	Corpse found 12 September 1994	Partially consumed corpse: bones, hair, stomach, intestines and organs
TALA II: TU	3-year-old male/4	Killed May 2001	Decomposed corpse
TALA I: Red	26-year-old male/4	Last seen 19 July 2002	Remains found
TALA I Purple-Silver	3-year-old male/4	Killed 15 May 2003	Bones, including skull with punctures
TALA II: Pink male	28-year-old male/4	Disappeared 19 July 2004; remains found in September 2004	Bones
TALA II: Radio-Silver	Adult female/4	Killed 25 May 2005	Hair, bone fragments and radiocollar
TALA I: Brown	3-year-old female/4	Last seen 29 May 2006	Long bones and hair
TALA III: No Collar	3 year old male/5	Killed 20 August 2006	Corpse found 10 m from sleep tree on ground
TALA IV: Green-Silver and infant	26-year-old female/7	Disappeared, last seen 11 September 2006; <i>Cryptoprocta</i> seen at river night before disappearance	No remains found
TALA III: Blue-Blue and infant	30-year-old female/4	Killed 30 January 2007	Eviscerated cadaver found; 7-month-old infant not found but presumed killed in the attack
SAKA I: Radio-Male	Young adult male/4	Killed 26 April 2007	Radiocollar with bones, hair and skull with puncture

Adjacent groups at Talataky have been studied for 20 years (TALA Groups I and II), 16 years (TALA Group III) and 11 years (TALA Group IV); an additional group at Sakaraoa has been censused for 4 years and followed since 2007 (SAKA I).

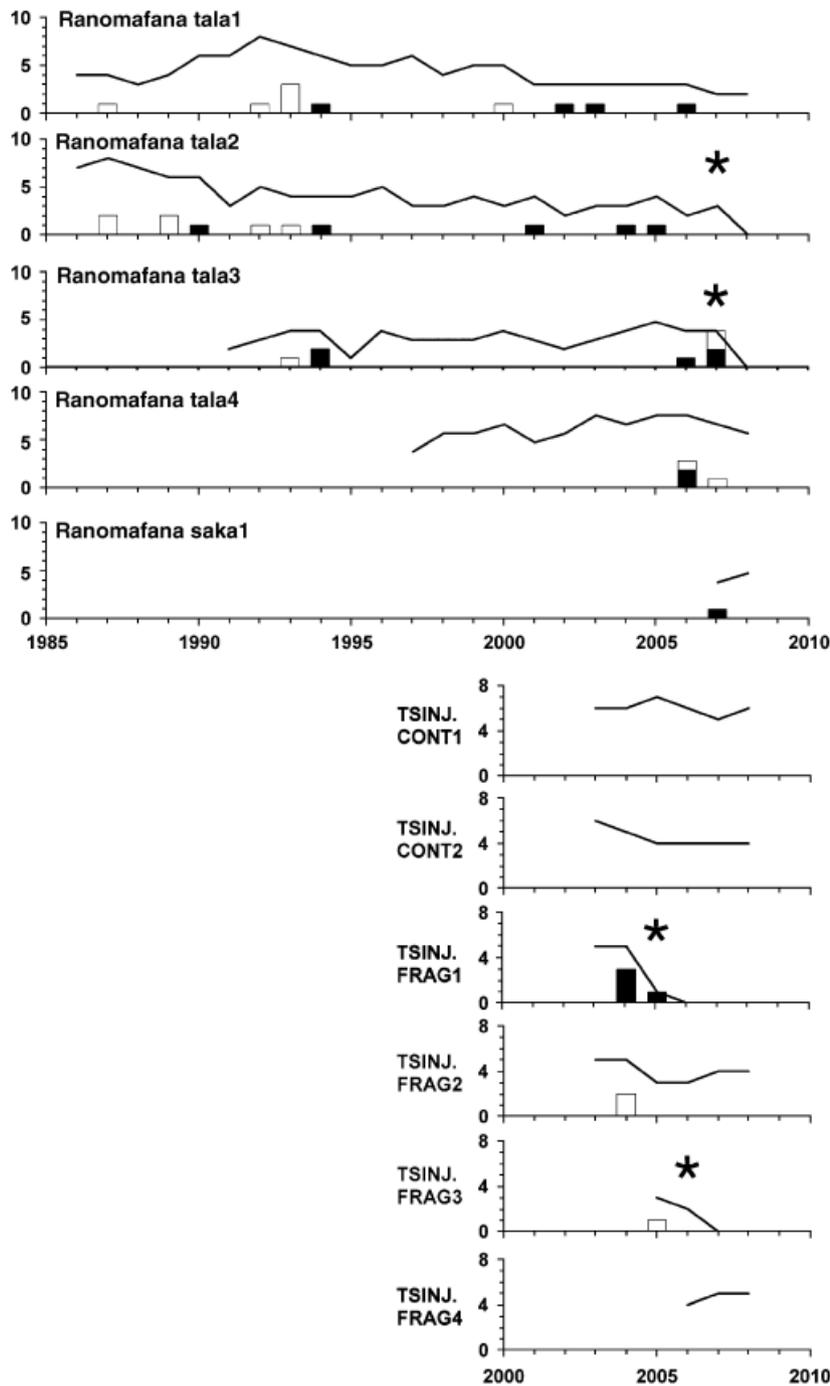


Figure 3 Temporal distribution of confirmed (black bars) and suspected (white bars) *Cryptoprocta* predation events across *Propithecus* groups at Ranomafana and Tsinjoarivo. Line represents group size in each year on 1 January, X-axis represents number of animals, asterisks indicate group extinction events.

subadult daughter (PB) for c. 1 month, then disappeared for 2 weeks and was seen c. 4 km to the north-east. After returning for 1 week, he was then seen c. 4 km to the south-east. Finally, he returned briefly and then emigrated permanently (PB lived alone until she was killed by *Cryptoprocta* in March 2005). He later settled in a group within semi-

fragmented forest 2 km to the east. This dispersal was the first recorded instance of *P. diadema* at Tsinjoarivo crossing between fragments.

Three animals in neighbouring groups also disappeared during the *Cryptoprocta* activity in FRAG1. One subadult female in FRAG2 was of dispersal age (5 years), thus her

disappearance may be due to dispersal. However, one juvenile male in FRAG2 (disappeared July–August 2004, age 3 years) and one juvenile female in FRAG3 (disappeared July–August 2005, age 2 years) disappeared before typical dispersal age (Wright, 1995; M. T. Irwin & J.-L. Raharison, unpubl. data.), and were likely preyed upon (FRAG2 and FRAG3 ranges are within 1 km of FRAG1).

Analysis of the nine scats recovered from the 24 August 2004 kill site revealed exclusively primate bones among the identifiable elements. The MNI was 9, with 1 *P. diadema*, 1 *Eulemur fulvus* and 7 *Lepilemur mustelinus*/*Avahi laniger* (similar-sized and indistinguishable based on recovered elements).

Osteological and soft tissue observations

The near-complete (PB) and fragmentary (TP) skeletons from Tsinjoarivo exhibited trauma consistent with *Cryptoprocta* kills described by Wright *et al.* (1997) (Fig. 5). The

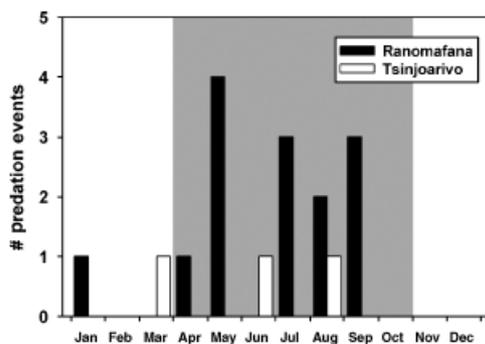


Figure 4 Seasonal distribution of 14 predation events at Ranomafana and three events at Tsinjoarivo. Shaded region represents dry season (typically <200 mm rainfall per month; Irwin 2006a, Ranomafana National Park records).

cranium of PB shows major damage to the left side, including two punctures in the parietal bone (distance between punctures is 23.9 mm, consistent with *Cryptoprocta* maxillary bicanine distance), fractures near the parietal–temporal junction, and destruction of the zygomatic arch and lateral orbit margin. This trauma is consistent with a surprise attack on a sleeping sifaka with its head down. Indeed, local residents relate that *Cryptoprocta*'s first attack on domestic animals usually involves a bite to the cranium. Both hemi-mandibles show crushing of the gonial angle, consistent with a bite to the neck (presumably following the initial attack). Finally, most ribs show damaged and frayed distal ends, consistent with evisceration. Similar osteological traces are found at Ranomafana (showing a killing bite to the neck and/or cranium, as evidenced by canine punctures to the lower mandible or braincase).

Combined evidence from osteological remains and cadavers reveals typical patterns of consumption. First, sifakas are eviscerated (damaging rib ends), with inner organs removed and apparently consumed; Wright *et al.* (1997) documented cadavers missing heart, lungs, spleen and liver. Intestines are piled to one side, uneaten. Next (on the second day), limb muscles are consumed and long bone ends gnawed. Long bones are sometimes broken around mid-shaft, as if to extract marrow. Finally, only stomach, intestines, fur and bone fragments remain. On several occasions at both Ranomafana and Tsinjoarivo, remains were found in two locations – the first directly under the sleep tree, and the second in a more hidden location several meters away. This suggests that *Cryptoprocta* begins consumption at the kill site but later moves the cadaver (possibly at daybreak).

Discussion

Physical evidence at Tsinjoarivo sifaka kill sites was consistent with *Cryptoprocta* predation at Ranomafana (Wright

Table 3 Details of disappearance and predation events for *Propithecus diadema* group FRAG1 at Tsinjoarivo

Animal ID	Age and sex/group	Details of predation/disappearance	Remains
FRAG1: Radio	Adult female/5	Remains found 26 June 2004, on resuming fieldwork after a 6-month break. This animal was sighted by locals < 1 month previously.	Radiocollar, hair remnants, partially decomposed stomach/intestines
FRAG1: INF	Infant (born June 2003)/5	Disappeared at same time as Radio. Presumed dead as young of this species do not emigrate until 4–5 years Wright (1995).	No discernable remains
FRAG1: Tartan-Purple (TP)	Subadult female (born June 1999/2000)/3	Remains found 24 August 2004	Hair, several damaged long bones, collar, stomach/intestines, <i>Cryptoprocta ferox</i> scats
FRAG1: Pink-Blue (PB)	Subadult female (born June 2001)/1	Remains found 25 March 2005. Local resident heard loud, unusual <i>Propithecus diadema</i> vocalizations (including bark alarm) at c. 9–10 PM of an unknown day in 'mid-March' near kill location	Hair, near-complete skeleton, collar and hair remnants
FRAG1: Black-Gold (BG)	Adult male/2	First prolonged absence from forest fragment: 15–28 September 2004; disappeared 6 October 2004. Sighted and recognized by locals in other (unconnected) forest fragments. During 2005 settled in semi-fragmented forest 2 km to the east	N/A



Figure 5 Osteological remains from PB kill site at Tsinjoarivo (scales in cm). Top, left side of cranium showing correspondence of punctures with maxillary bicanine difference of a *Cryptoprocta ferox* skull found in continuous forest at Tsinjoarivo (Vatateza). Middle, hemimandibles showing damage at gonial angle. Bottom, ribs showing damage to distal ends.

et al., 1997). Thus, *Cryptoprocta* is the only confirmed sifaka predator at Tsinjoarivo, though other potential predators include raptors (especially for immatures) and wildcats (not yet reported from Tsinjoarivo). Below, we combine observations from Ranomafana and Tsinjoarivo in attempting to understand the effects of *Cryptoprocta* predation on sifakas.

At Ranomafana, *Cryptoprocta* predation occurred within all five contiguous *Propithecus* groups. Kills tended to be temporally clumped, with clusters of activity interspersed

with long breaks including one 6-year absence (1995–2000), but in other periods were more evenly spaced (2001–2005). When multiple kills occurred within a short time, they were spread among neighbouring groups, meaning that a maximum of one to two individuals was taken per group per year (occasionally additional events were suspected). Overall, therefore, individual groups tend to receive a lower impact. However, it does appear that *Cryptoprocta* predation can contribute to group extinctions, with two groups disappearing in 2007 largely due to predation.

The 14 predation events at Ranomafana were concentrated in the dry season (April–October); there are several possible reasons for this seasonality. First, *Cryptoprocta* may be prey-switching (Goodman, O'Connor & Langrand, 1993; Dollar *et al.*, 2007): other prey species are less active (reptiles, amphibians and birds) or hibernating (tenrecs, dwarf lemurs) during the dry season (Schmid & Stephenson, 2003). Second, sifakas experience low density of preferred foods during the dry season (Hemingway, 1998; Wright *et al.*, 2005; Irwin, 2008b) and lose mass (Wright *et al.*, 2005); thus they may be less vigilant, or less able to escape predator attacks. Finally, some rainforest trees and plants shed leaves during this season (D. Turk, unpubl. data, 1995), possibly causing altered visibility; this might favour the predator or the prey, depending on hunting strategies.

Although observations at Tsinjoarivo are less extensive, predation seems to be temporally and spatially clumped. All confirmed and suspected events occurred within three groups at one site (within a 2-km radius), in a 1-year period (2004–2005). Both continuous forest groups had no kills over 6 years (*Cryptoprocta* occurs in the vicinity of all groups). Confirmed predation occurred only in one group (FRAG1), but was intense and caused the group's extirpation, with four of five animals killed within 10 months.

Temporal clumping of kills within a local area is consistent with *Cryptoprocta* ecology. *Cryptoprocta* have low density (0.26 individuals km⁻²) and large home ranges (10–30 km²) in dry forests (Hawkins & Racey, 2005), and might be expected to have larger ranges in rainforest, due to the lower density of lemurs and other prey (e.g. Irwin, 2006b). Indeed, preliminary density estimates at Ranomafana based on camera trapping are low (0.1675 ± 0.064 individuals km⁻²) (S. Karpanty, B. Gerber, M. Kotschwar & C. Crawford, unpubl. data). Thus, *Cryptoprocta* ranges may be many times larger than sifaka ranges (20–80 ha; Pochron *et al.*, 2004; Irwin, 2008a), meaning that one *Cryptoprocta* range could contain hundreds of sifaka groups. Since hunting depresses local prey biomass, *Cryptoprocta* might respond by moving nomadically: hunting in a subset of its range until it becomes unprofitable, then moving on (Wright *et al.*, 1997). While hunting in a given area, it might be adaptive to spread kills among groups, to avoid the heightened behavioural defences (e.g. increased vigilance, altering sleep site selection) that may occur after kills.

Temporal and spatial heterogeneity in predation has several implications for understanding and managing primate populations. In terms of the evolution of anti-predator strategies, it becomes important to ask: (1) whether average

or peak predation rates determine the strength of selection, and (2) whether antipredator strategies (e.g. vigilance, sleeping site selection) fluctuate interannually, reflecting recent experience. In terms of ecology and management, it is important to ask whether predation pulses have different impacts on primate demography than would evenly spaced hunting, and whether the impact can be heightened in forest fragments.

First, constrained predator ranging in fragments may increase the initial demographic impact on primate groups. Predators in continuous landscapes may increase hunting efficiency by spreading their impact among neighbouring groups, especially if prey respond behaviourally to recent kills. However, fragmentation may constrain predator ranging: in terms of optimal foraging theory (Stephens & Krebs, 1986) the cost of moving between patches is increased. Thus, predators in small fragments may drive prey density lower than in continuous habitat, causing predation to be *more* temporally and spatially clumped. Primate groups in fragments may therefore go longer without predation, only to have the predation events be more devastating. Our observations show that predation can be a proximate cause of group extinctions in intact and fragmented forest; testing whether extinctions are more likely in fragments will require more data.

Second, consequences may be longer-lasting in fragments. Ranomafana groups have been lost, but as they are contiguous, it is likely that empty ranges can be re-colonized relatively easily. In fragments, as at Tsinjoarivo, re-colonization may be limited when dispersers are reluctant to cross matrix, and may be further limited by primates' sociality; dispersers seek to join conspecifics or pre-existing social groups (Reed & Dobson, 1993) and thus may pass up on unoccupied, but otherwise suitable, fragments. Such extirpations may therefore be a major driver of regional population size, especially for long-lived species (i.e. strong persistence potential) that are reluctant to cross matrix (i.e. low probability of re-colonizing). At Tsinjoarivo, the group that disappeared (FRAG1) was the sole occupant of a 24 ha fragment; its range remains unoccupied as of July 2008, 3 years after its disappearance (the fragment's size and quality remain relatively unchanged).

It is also interesting to note that the Tsinjoarivo *Cryptoprocta* scats suggest an extreme specialization on primates (100% of identifiable elements), though the sample is small (nine scats from one kill site). This runs contrary to *Cryptoprocta* diet elsewhere, with primates constituting 4–54% of prey items and 25–82% of prey biomass (Rasoloarison *et al.*, 1995; Goodman *et al.*, 1997; Goodman, 2003; Hawkins, 2003), and suggests that the consumption of primates (relative to other prey) increases in fragments.

There are several possible reasons for this. First, primate density may be elevated. Like other primates (especially folivores; Johns & Skorupa, 1987; Onderdonk & Chapman, 2000) sifakas in disturbed fragments at Tsinjoarivo exist at higher densities than in nearby continuous forest (Irwin, 2008a). Second, density of other prey may be reduced. Third, habitat structure may affect hunting success: frag-

ments have smaller trees, with lower, discontinuous canopies and well-developed understories (Irwin, 2006a); this (plus the barrier of the forest edge) may reduce escape routes. Fourth, some primates (e.g. *Lepilemur*) preferentially sleep in tree holes (Rasoloharijaona, Randrianambinana & Zimmerman, 2008); the lack of large trees may reduce the availability of holes and increase predation risk (we have observed *Lepilemur* sleeping in the open in Tsinjoarivo fragments; M. T. Irwin & J.-L. Raharison, unpubl. data). Finally, the absence of predation over long periods may cause behavioural responses to atrophy, to the extent that these are learned and/or reinforced by experience.

At present, there are few comparable data by which to evaluate the generality of the patterns reported here. Although many researchers have censused primates and other mammals in fragments, few have undertaken ecological study and monitoring (for exceptions see: Estrada *et al.*, 1999; Tutin, 1999; Onderdonk & Chapman, 2000). In the only comparable study of which we are aware, Peetz, Norconk & Kinzey (1992) documented demographic changes in a howler monkey *Alouatta seniculus* group stranded on a 70 ha island created following the construction of a hydroelectric dam. Over 7 months, five of six animals were consumed by jaguar *Panthera onca* – a similar scenario to group FRAG1 at Tsinjoarivo.

In summary, if forest fragmentation and predation act synergistically through altering predator ranging and diet, several conservation implications become evident. First, primates may decline in fragmented landscapes despite having the ecological capacity to survive on available resources. This may proceed as a 'ratchet' effect: successive local extinctions in fragments, not followed by re-colonization. Second, species most at risk will likely be those with slow reproductive rates and low colonization ability, and those that form social groups. Finally, planners should be wary of the stochastic nature of predation and its potential for quickly decimating groups, even when short-term surveys show stable or increasing populations.

It is important, however, to clarify that while predation can be a *proximate* cause of extinction, forest fragmentation remains the *ultimate* cause. Removing predators from fragments would only be a short-term solution, unnecessarily disturbing the ecosystem further without guaranteeing the prey's survival. Indeed, many fragments may not be viable habitat for primate species, regardless of predator impact. We are not advocating predator removal. Rather, we are suggesting that a greater understanding of predation pressure across habitats is needed, including baseline offtake rates, spatial and temporal heterogeneity, and differences in population resilience and antipredator behaviours. These data will help in (1) promoting better-informed allocation of limited conservation resources, including which landscapes to invest resources in and (2) investigating ways to increase viability of prey species, such as creating or maintaining connectivity to provide routes for re-colonization of empty habitat (and, in extreme situations, translocation).

The results presented here underscore the pressing need for conservation of relatively large, unbroken forest tracts in

Madagascar and elsewhere, to preserve functioning ecological communities. However, failing this, studies of predator ranging and behaviour and predator–prey interactions in intact and fragmented forest will assist in the management of human-dominated landscapes, and increase our capacity to preserve species and ecological processes within them.

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