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Predation and Cathemerality

Comparing the Impact of Predators on the Activity Patterns of Lemurids and Ceboids

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Key Words

Predation · Cathemerality · Lemurs · Madagascar · Owl monkey · Howler monkey · Neotropics · Activity patterns

Abstract

The removal, or absence, of predatory species could be a contributing proximate factor to the rise of primate cathemerality. But predators themselves can also be cathemeral, so cathemerality could well be an evolutionary stable strategy. From a comparative perspective, it appears that the effect of predatory species cannot provide a unitary explanation for cathemerality. Varying distributions and population densities of predators, especially raptors, may be key factors in owl monkey (*Aotus*) cathemerality, but temperature and lunar cycle variation have also been implicated. In Madagascar, while raptors are potential predators of lemur species, the cathemerality of *Eulemur* species coincides with that of the fossa (*Cryptoprocta ferox*), a major predatory threat to lemurs. Thus, lemurid cathemerality may be more parsimoniously explained as an evolutionary stable strategy.

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Introduction

Predation is widely regarded as a major force in shaping primate ecology and evolution [van Schaik and van Hooff, 1983; Andrewartha and Birch, 1984; Anderson, 1986; Cheney and Wrangham, 1987; Isbell, 1994; Stanford, 2002]. Consequently, much has been written about the potential influences of predation and predation risk on primate social behaviour [e.g. van Schaik, 1983; van Schaik and van Hooff, 1983; Anderson, 1986; Goodman et al., 1993; Isbell, 1994; Hill and Dunbar, 1998; Hill and Lee, 1998; Janson, 1998; Lima, 1998; Treves, 1999; Karpanty and Grella, 2001]. There has also been attention directed at how predation and predation risk

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may affect primate group progression and foraging behaviour [e.g. Lima and Dill, 1990; Wright, 1998; Boinski and Chapman, 2000; Miller, 2002; Sauther, 2002; Overdorff et al., 2002]. Yet, it has proven difficult to determine the extent to which predation and predation risk influence primate behaviour. Although detailed data on anti-predator behaviour are available for many non-human primate species, commensurate data on primate predators are not available. Indeed, detailed data on the predation of primates and on the predatory species themselves are notoriously difficult to obtain [but see Goodman et al., 1993]. Nonetheless, opinion is unanimous on the need for detailed studies of predators and predator-primate synecological relationships [Andrewartha and Birch, 1984; Anderson, 1986; Cheney and Wrangham, 1987; Isbell, 1994; Boinski and Chapman, 1995; Hart, 2000; Fernandez-Duque et al., 2001; Miller, 2002; Stanford, 2002; Zuberbuhler and Jenny, 2002; Goodman, 2003; Zuberbuhler, 2004].

The problem is the same when considering the interactions between predation and cathemerality – while the former has been linked to the latter in some studies of cathemeral primate species, the extent to which predation and predation risk may determine cathemerality remains unresolved. ‘Cathemeral’ is the term coined by Tattersall [1987] to describe the activity patterns of organisms that exhibit equal, or significant, amounts of feeding and/or travelling ‘through the day’ – that is, through the 24-hour cycle. Notwithstanding the lack of clarity concerning how cathemerality may be influenced by predation, cathemeral activity [sensu Tattersall, 1987] has now been reported in all species of the lemurid genus *Eulemur* [Overdorff and Rasmussen, 1995; Curtis, 1997; Wright, 1999; Donati et al., 1999; Curtis and Rasmussen, 2002; Kappeler and Erkert, 2003; Overdorff and Johnson, 2003] (table 1). Cathemerality has also been reported in at least some populations of the other members of the Lemuridae. Among the bamboo lemurs, both the Lac Alaotra gentle lemur (*Hapalemur griseus alaotrensis*) [Mutschler et al., 1998; Mutschler, 2002], and the greater bamboo lemur (*H. simus*) [Tan, 2000; Grassi, 2001], are reported to be cathemeral. However, the bamboo lemurs sympatric with *H. simus* in Ranomafana National Park, the lesser bamboo lemur (*H. g. griseus*) and the golden bamboo lemur (*H. aureus*), are both diurnal [Overdorff et al., 1997; Tan, 2000; Grassi, 2001]. There are also single reports of cathemeral activity in both the black and white ruffed lemur (*Varecia variegata variegata*), in Ranomafana National Park [Wright, 1999], and the ring-tailed lemur (*Lemur catta*), in Berenty Reserve [Traina, 2001]. In addition, cathemerality has been reported in two Neotropical anthropoid genera: *Aotus*, the owl monkey, and *Alouatta*, the howler monkey. *Aotus* in the Paraguayan Chaco have been reported as cathemeral [Wright, 1989, 1994; Kinzey, 1997]. Subsequently, *A. azarai* in the eastern Argentinean Chaco has also been observed to be cathemeral [Fernandez-Duque and Bravo, 1997; Fernandez-Duque et al., 2001, 2002; Fernandez-Duque, 2003]. Finally, there is one report, based on a brief study, that cathemerality occurs in the black howler monkey, *A. pigra*, and the mantled howler monkey, *A. palliata*, in Belize [Dahl and Hemingway, 1988].

Several ecological determinants have been suggested to account for the cathemerality observed across these species. In addition to cathemerality being seen as a means of avoiding predators and minimizing the risk of predation, cathemerality has also been interpreted as a response to seasonal food availability and quality; a means by which to avoid feeding competition; an activity pattern that facilitates

Table 1. Studies in which cathemerality in taxa of the lemurid genus *Eulemur* has been reported, and the sites where those studies were conducted

Lemur taxon	Common name	Sites	References
<i>Eulemur coronatus</i>	crowned lemur	Ankarana Mt. d'Ambre NP	Wilson et al., 1989 Freed, 1996
<i>E. fulvus fulvus</i>	brown lemur	Ampijoroa	Rasmussen, 1998a
<i>E. f. rufus</i>	red-fronted, or rufous, brown lemur	Antserananomby, Tongobato Ranomafana NP Kirindy Forest Kirindy Forest	Sussman, 1972 Overdorff, 1996 Donati et al., 1999 Kappeler and Erkert, 2003
<i>E. f. fulvus</i>	Mayotte brown lemur	Mavingoni Mayotte	Tattersall, 1977, 1979 Tarnaud, 2004
<i>E. f. sanfordi</i>	Sanford's brown lemur	Ankarana Mt. d'Ambre NP	Wilson et al., 1989 Freed, 1996
<i>E. (f.) albocollaris</i>	white-collared brown lemur	Andringitra NP	Johnson, 2002
<i>E. macaco macaco</i>	black lemur	Ambato Massif Lokobe	Colquhoun, 1993, 1998 Andrews and Birkinshaw, 1998
<i>E. mongoz</i>	mongoose lemur	Ampijoroa Ampijoroa Anjouan, Moheli Ampijoroa Anjamena Anjamena	Tattersall and Sussman, 1975 Sussman and Tattersall, 1976 Tattersall, 1976 Rasmussen, 1998b Curtis and Zaramody, 1999 Curtis et al., 1999
<i>E. rubriventer</i>	red-bellied lemur	Ranomafana NP	Overdorff, 1988, 1996

thermoregulation and minimizes the adverse effects of low ambient temperatures; a non-adaptive shift in activity pattern due to evolutionary disequilibrium, and an activity pattern that is an evolutionary stable strategy and is ancestral for both the Lemuridae and Ceboidea [Dahl and Hemingway, 1988; Overdorff, 1988, 1996; Engqvist and Richard, 1991; van Schaik and Kappeler, 1993; Colquhoun, 1993, 1998; Overdorff and Rasmussen, 1995; Rasmussen, 1998a, b; Andrews and Birkinshaw, 1998; Curtis and Zaramody, 1999; Curtis et al., 1999; Donati et al., 1999; Mittermeier et al., 1999; Wright, 1999; Curtis and Rasmussen, 2002; Mutschler, 2002; Fernandez-Duque et al., 2002; Kappeler and Erkert, 2003; Fernandez-Duque, 2003; Tarnaud, 2004]. In regard to the relationship between predation and cathemerality, it is interesting to note that several reviews of predation on primate species make no mention of primate cathemerality being a possible adaptive response to predation [Anderson, 1986; Goodman et al., 1993; Isbell, 1994; Stanford, 2002; Goodman, 2003]. Predation and predation risk have not been thoroughly considered to this point in efforts to gain a comprehensive understanding of cathemerality, de-

spite primate cathemerality frequently being interpreted as an activity pattern shaped by predation. Wright, however, has consistently drawn attention to the potential importance of cathemerality in predator avoidance, first in the case of the owl monkey [Wright, 1989, 1994], and more recently in the case of lemuriforms [Wright, 1995, 1998, 1999; Wright et al., 1997].

The purpose of this paper is to draw together for the first time the diverse literature concerning predation of cathemeral primate species and compare patterns of predation on cathemeral lemurids with patterns of predation on cathemeral ceboids. Although primates in both Madagascar and the Neotropics must deal with the same three classes of predators (carnivores, birds of prey and constricting snakes), the primate and predator communities in these two biogeographic regions are not convergent [Terborgh and van Schaik, 1987; Kappeler and Ganzhorn, 1993; Kappeler and Heymann, 1996; van Schaik and Kappeler, 1996; Peres and Janson, 1999; Ganzhorn et al., 1999; Kappeler, 1999a, b; Hart, 2000]. I will argue that in Madagascar, lemurid cathemerality may be due in large part to predation and the risk of predation by the fossa (*Cryptoprocta ferox*), a viverrid carnivoran. Predation and risk of predation by birds of prey on lemurids, while important, are secondary to the threat posed by the fossa. While carnivore species are much more numerous in the Neotropics than in Madagascar, none preys on primates to the same extent as the fossa. The predation–cathemerality link among ceboid populations is more likely affected by a release from predation by birds of prey. Constricting snakes in both biogeographic regions are known to prey on primates [Rakotondravony et al., 1998; Burney, 2002; Ferrari et al., 2004], but their possible impact on primate cathemerality is difficult to assess at this point. Human predation of cathemeral lemurids and ceboids will not be considered in this paper.

Predation of Cathemeral Lemurids

Carnivores

This review of the literature makes clear that the largest living carnivore on Madagascar, the fossa (*Cryptoprocta ferox*, Viverridae), is cathemeral [Kohncke and Leonhardt, 1986; Dollar et al., 1997], is a major cause of mortality in many lemur species and is widely regarded as a lemur-hunting specialist [Wilson et al., 1989; Goodman et al., 1993; Rasoloarison et al., 1995; Wright, 1995, 1998; Wright et al., 1997; Curtis et al., 1999; Hart, 2000; Britt et al., 2001, 2003; Goodman, 2003; Hawkins, 2003]. Table 2 lists the lemuriform species that have been reported to be preyed upon by *C. ferox*, and the activity patterns of those lemur species. As table 2 shows, cathemeral lemur species constitute a significant proportion of the lemur species that comprise *C. ferox* prey.

While the fossa will eat lemurs as small as *Microcebus* (30–70 g), and will dig sleeping or aestivating nocturnal lemur species out of their nests [Goodman et al., 1993; Rasoloarison et al., 1995], it is also capable of taking lemurs as large as *Propithecus diadema* (approximately 6,000 g) [Wright, 1995; Wright et al., 1997; Goodman, 2003]. A body weight of up to 12,000 g has been reported for the fossa [Albignac, 1970], but recent field data indicate an average adult body weight of 6,500–7,000 g (range = 5,500–8,600 g, with males tending to be larger than females). The fossa is thus capable of taking prey that weighs up to approximately 90% of its own

Table 2. Lemuriform species reported to have been preyed upon by *C. ferox*, the fossa

Lemur species	Body mass, g	Activity pattern	References
<i>Propithecus diadema candidus</i>	6,000	diurnal	Goodman et al., 1993
<i>P. d. edwardsi</i>	5,800	diurnal	Wright, 1995, 1998 Wright et al., 1997
<i>P. verreauxi verreauxi</i>	3,600	diurnal	Goodman et al., 1993 Rasoloarison et al., 1995
<i>P. tattersalli</i>	3,500	diurnal	Goodman, 2003
<i>Varecia variegata variegata</i>	3,000	diurnal/cathemeral (?)	Britt et al., 2001, 2003
<i>Haplemur simus</i>	2,600	cathemeral	Wright, 1995 Wright et al., 1997
<i>Eulemur fulvus fulvus</i>	2,600	cathemeral	Goodman et al. 1993
<i>E. f. rufus</i>	2,200–2,300	cathemeral	Rasoloarison et al., 1995 Wright, 1995 Wright et al., 1997
<i>E. f. albifrons</i>	2,300	cathemeral (?)	Britt et al., 2001
<i>E. rubriventer</i>	2,000	cathemeral	Overdorff and Strait, 1995 Wright, 1995 Wright et al., 1997
<i>E. coronatus</i>	2,000	cathemeral	Wilson et al., 1989
<i>E. mongoz</i>	2,000	cathemeral	Curtis et al., 1999
<i>Haplemur griseus</i>	800	diurnal/cathemeral (?)	Goodman, 2003
<i>Lepilemur mustelinus</i>	750	nocturnal	Rasoloarison et al., 1995 Goodman et al., 1997
<i>Phaner furcifer</i>	400	nocturnal	Rasoloarison et al., 1995
<i>Mirza coquereli</i>	360	nocturnal	Rasoloarison et al., 1995
<i>Cheirogaleus major</i>	300–400	nocturnal	Goodman et al., 1997 Goodman, 2003
<i>C. minor</i>	280	nocturnal	Rasoloarison et al., 1995
<i>Microcebus</i> spp.	30–70	nocturnal	Rasoloarison et al., 1995 Goodman, 2003

Body mass measures come from the references listed and from Tattersall [1982] and Mayor et al. [2004].

body weight [Hawkins, 2003]. A closer consideration of fossa morphology illuminates why it is such a formidable predator of lemurs.

Fossa morphology is often characterized as ‘cat-like’ (e.g. its dentition, Kohncke and Leonhardt [1986]). Indeed, Eisenberg [1981, p. 127] notes that *C. ferox* has converged with the Felidae in its dentition and skull morphology and states that, ‘*Cryptoprocta* stands as a classical case of convergent evolution’. Wozencroft [1989, p. 511] also remarks, ‘The fossa would make a good primitive cat on the basis solely of tooth structure...’. The carnassial upper and lower first molars are ‘cat-like’ [Kohncke and Leonhardt, 1986; Wright et al., 1997], and Nowak [1999] remarks that in its general appearance the fossa is very much like a large jaguarundi (*Felis yagouaroundi*) or a small cougar (*F. concolor*). *C. ferox* also has retractile claws and

large, fleshy paw pads which enable it to be extremely agile in an arboreal setting. In comparison to other viverrids and other arboreal carnivores, the morphology of *C. ferox* distinguishes it as a 'grasping species' [Laborde, 1986; Taylor, 1989; Veron, 1999]. Arboreal carnivores that are 'grasping species' tend to hunt by stealth [Taylor, 1989; Wright, 1995; Wright et al., 1997]. The fossa's abilities as a 'grasping' arboreal species includes the ability to perform 'vertical looping': besides being able to ascend a tree head first, it can rotate its ankles 180 degrees and descend a tree trunk head first [Laborde, 1986; Taylor, 1989; Hawkins, 2003]. Indeed, the arboreal agility of the fossa is reflected in it exhibiting forepaw dexterity that exceeds that of most felids [Iwaniuk et al., 2000]. Recently, analysis of subfossil remains from eleven sites across Madagascar led Goodman et al. [Goodman, 2003; Goodman et al., 2004] to conclude that there existed on Madagascar in the recent geological past a species of *Cryptoprocta* significantly larger than the living *C. ferox*. Goodman [2003] describes the large, extinct *C. spelea* as 'puma-like' and suggests that, although there is presently no direct subfossil evidence that this species fed on lemurs, its size would have made it a most formidable predator based on the behaviour of the extant *C. ferox*.

Although other extant Malagasy viverrids may also occasionally prey on lemurs (e.g. the ring-tailed mongoose, *Galidia elegans*, on *Cheirogaleus major* [Wright and Martin, 1995]), none pose the predation risk of *C. ferox*. The second largest viverrid endemic to Madagascar, the Malagasy striped civet (*Fossa fossana*), appears to be strictly nocturnal, weighs only about 1,500–2,000 g and has not been reported as a lemur predator [Wright, 1998; Nowak, 1999; Kerridge et al., 2003]. In contrast, lemurs can comprise up to 50–80% of the diet of the cathemeral fossa [Rasoloarison et al., 1995; Goodman, 2003; Hawkins, 2003]. At Kirindy Forest in western Madagascar, Rasoloarison et al. [1995, pp. 62–63] found that *C. ferox* preyed preferentially on larger lemur species (especially *P. verreauxi verreauxi*). Ganzhorn and Kappler [1996] report that *P. v. verreauxi* and other relatively large lemur species in Kirindy Forest may lose about one third of each year's birth cohort to fossa predation. In playback experiments at Berenty Reserve, southern Madagascar, Oda [1998] showed that *P. v. verreauxi* responded to the calls of *L. catta* given in response to the presence of *C. ferox*.

Rasoloarison et al. [1995, p. 62] found that a comparison of the lemur population densities in Kirindy Forest and the relative abundance of lemur species in the dry season diet of *C. ferox*, wherein lemurs comprised 57% of the vertebrate prey biomass, approached statistical significance (Kolmogorov-Smirnov test: $p = 0.05$). Goodman [2003] summarized comparative data based on scat analysis from several research sites that show considerable variation in the relative abundance of lemur species in the diet of *C. ferox*, ranging from a high of 81.6% of the vertebrate prey biomass at Kirindy Forest, to 30–40% of the vertebrate prey biomass at the high elevation sites of Montagne d'Ambre and Andringitra Massif [Goodman et al., 1997]. Given this seasonal and geographic variability, Goodman [2003] implies that labeling the fossa a 'lemur specialist' may be premature and suggests that to understand fossa ecology fully we still need to document better the compositions of local prey communities, track seasonal shifts in the availability of prey species and establish the range of variation in diet composition among individual *C. ferox*. In an exhaustive comparative review of primate predators, however, Hart [2000] concluded that the fossa is one of just four primate predators that are 'dedicated primate specialists',

the other three species being the leopard (*Panthera pardus*), harpy eagle (*Harpia harpyja*) and African crowned eagle (*Stephanoaetus coronatus*).

Birds of Prey

Several avian species have been identified as potential threats to lemurs. The largest extant raptor species in Madagascar, the Madagascar fish eagle (*Haliaeetus vociferoides*), has not been recorded attacking or preying on lemurs; as its common name suggests, its diet is chiefly fish [Langrand, 1990]. But the second largest raptor species, the Madagascar harrier hawk (*Polyboroides radiatus*), is known to prey on lemurs [Karpanty and Goodman, 1999; Thorstrom et al., 2003; Karpanty, 2003]; it has been observed to attack the black lemur (*Eulemur macaco macaco*) [Colquhoun, 1993] and Verreaux's sifaka (*P. v. verreauxi*) [Brockman, 2003]. Several diurnal and cathemeral lemur species react with alarm calls and evasive behaviour when a harrier hawk is sighted [Sussman, 1975, 1977; Harrington, 1975; Sauther, 1989; Wilson et al., 1989; Colquhoun, 1993; Goodman et al., 1993; Karpanty and Grella, 2001; Brockman, 2003; Karpanty, 2003]; this has been interpreted as evidence that *P. radiatus* is regarded by the lemurs as a potential predator. At Berenty Reserve, Karpanty and Goodman [1999] found that one pair of *P. radiatus* preyed heavily on Verreaux's sifaka during the courtship phase of the harrier hawk breeding season. This raises the possibility that Verreaux's sifaka, and perhaps other lemur species, may be seasonally preferred prey of *P. radiatus*. Indeed, Brockman [2003] suggests that Verreaux's sifaka is an important prey species of *P. radiatus*.

Besides *P. radiatus*, other raptors which elicit alarm calls from lemurs include the Madagascar buzzard (*Buteo brachypterus*), the black kite (*Milvus migrans*) and the rare Madagascar serpent eagle (*Eutriorchis astur*) [Sauther, 1989; Colquhoun, 1993; Goodman et al., 1993; Wright, 1998; Karpanty and Grella, 2001; Goodman, 2003; Karpanty, 2003]. Colquhoun [1993] observed a Frances' sparrowhawk (*Accipiter francesii*) swoop within striking distance of a pair of approximately 4-month-old black lemurs that were playing and grappling on a liana, well away from any adult animals. This unsuccessful attack was responded to by adult black lemurs in the social group with alarm 'hack' vocalizations. Another, larger, *Accipiter* species, Henst's goshawk (*A. henstii*) is known to prey on at least nine lemur taxa, including nocturnal, diurnal and cathemeral species: the rufous mouse lemur (*Microcebus rufus*), greater dwarf lemur (*C. major*), eastern woolly lemur (*Avahi laniger*), small-toothed sportive lemur (*Lepilemur microdon*), lesser bamboo lemur (*H. g. griseus*), rufous brown lemur (*E. fulvus rufus*), white-fronted brown lemur (*E. f. albifrons*), red-bellied lemur (*E. rubriventer*), and black and white ruffed lemur (*V. v. variegata*) [Goodman et al., 1998; Schwab, 1999; Karpanty, 2003]. In playback experiments at Ranomafana National Park, Karpanty and Grella [2001] found, perhaps surprisingly, that the most vigorous anti-predator behaviours of eight lemur species to the calls of *P. radiatus*, *E. astur* and *A. henstii* came in response to the calls of *A. henstii*. Karpanty [2003] showed, however, that lemurs comprise 23% of the diet, and 30.7% of the prey biomass, of *A. henstii*, while lemurs represented 13% of the diet, and 37.3% of the prey biomass, of the larger *Polyboroides radiatus*. Strigiform predators of lemurs include the barn owl (*Tyto alba*), the Madagascar red owl (*T. soumagnei*), and the Madagascar long-eared owl (*Asio madagascariensis*), all of which are known to prey on nocturnal lemur species [Goodman et al., 1993; Rasoloarison et al., 1995; Goodman and Thorstrom, 1998]. However, no strigiform species has been reported to

prey on cathemeral or diurnal lemur species [Wright, 1998; Thorstrom et al., 2003; but see Goodman et al., 1993 where a damaged lemur calcaneus recovered from a pellet of *A. madagascariensis* was identified as belonging to either the nocturnal *Avahi laniger* or the diurnal *H. griseus*].

Goodman [1994b] suggested that the anti-predator behaviour displayed by lemurs towards raptors is a behavioural artefact left over from earlier in the Holocene when larger, but now extinct, eagles (*Aquila* spp. and *Stephanoaetus mahery*) that preyed on lemurs were present on Madagascar [Goodman, 1994a; Goodman and Rakotozafy, 1995]. The size of these eagles, especially *S. mahery*, is consistent with them having been significant predators of a wide range of lemur species [Goodman, 2003; Simons et al., 2004]. The extinction of these eagles may, therefore, have been a major release from predation pressure for many lemur species [Goodman, 1994b]. Subsequently, Csermely [1996] questioned this interpretation and argued that the frequency of predation on lemurs by extant raptors could actually be quite high. In light of reports since his 1994b paper, Goodman [2003] stated that it is clear that several extant species of birds of prey on Madagascar are important predators of lemurs and that lemurs have not experienced a predation release due to an 'evolutionary disequilibrium' following the extinction of large Holocene eagles [see also Karpanty and Goodman, 1999; Karpanty, 2003]. The continuing predation threat posed by extant raptors is underscored by Fichtel and Kappeler [2002], who present data showing that both Verreaux's sifaka and red-fronted brown lemurs (*E. f. rufus*) have 'mixed' alarm call systems. That is, both *P. verreauxi* and *E. f. rufus* have specific calls for raptors, but use only generalized calls for terrestrial predators. Oda and Matsutaka [1996] showed in playback experiments that ring-tailed lemurs can perceive the difference between anti-predator calls given by *P. verreauxi* in response to aerial and terrestrial predators; *L. catta* reacts most strongly to the anti-raptor call of *P. verreauxi*. Black lemurs utilize at least three different alarm calls in response to different raptor species, including a specific 'scream-whistle' call made whenever the Madagascar harrier hawk is sighted overhead [Colquhoun, 1993, 1997, 2001]. Black lemurs also give the same 'scream-whistle' call at night in response to Madagascar fruit bats (*Pteropus rufus*) flying at tree-top level. 'Scream-whistles' directed at fruit bats could be explained as being due to young black lemurs who had not yet learned to reliably identify harrier hawks. This explanation is problematic, however, as no generalized use of 'scream-whistles' toward all large raptor species was ever heard. Thus, black lemurs appear to employ an ordinal scale alarm call system, wherein the 'scream-whistle' call indicates a 'very large thing' overhead, rather than specifically signaling the presence of a harrier hawk.

Constricting Snakes

It is an interesting bit of biogeography that species of the family Boidae are found in both Madagascar and South America. Madagascar is home to three boid species, two ground boas (*Acrantophis madagascariensis*, which can climb trees [pers. obs.], and *A. dumereli*), and a tree boa (*Sanzinia madagascariensis* = *Boa manditra*) [Raxworthy, 2003]. Raxworthy [2003] describes these three boids as being mostly nocturnal, but at Ambato Massif in northwestern Madagascar, I frequently observed *A. madagascariensis* to be active during the day; thus, this species may more accurately be described as cathemeral. Both *A. madagascariensis* and *S. madagascariensis* are known to at least occasionally prey on lemur species. Burney

[2002] gives a unique report of a very large *A. madagascariensis* attacking an adult female Coquerel's sifaka (*P. v. coquereli*). Burney saved the sifaka, but noted that the boa looked as if may have consumed the sifaka's infant. At Ambato Massif, I observed a black lemur group mob a large (approx. 2.5 m) *A. madagascariensis* that they had discovered resting on a tree branch about 2 m off the ground. None of the lemurs approached the snake any closer than about one metre. The mobbing behaviour continued for 15–20 min, at which point the lemur group moved from the area [Colquhoun, 1993]. The lesser bamboo lemur has been observed to be preyed upon by the Madagascar tree boa [Goodman et al., 1993; Rakotondravony et al., 1998; Goodman, 2003].

Although not a boid, the diurnal Malagasy giant hognose snake (*Leioheterodon madagascariensis*), which can be over 1.5 m in length, is reported to constrict large prey [Cadle, 2003]. Sauther [1989] reported that ring-tailed lemurs would give 'click' vocalizations (a sign of agitation) in the presence of *L. madagascariensis*. Similarly, on one occasion at Ambato Massif I observed a female black lemur to 'huff-grunt' (a sign of agitation) at a large (nearly 2 m) *L. madagascariensis* that slithered along the ground under the branch on which she was sitting. In a captive study, Bayart and Anthouard [1992] found that *E. m. macaco* responded to a presented boid snake (*Python molurus molurus*) with a mobbing display, while Mayotte brown lemurs (*E. f. fulvus*) were attentive to the snake but did not exhibit any sort of alarm reaction; these authors suggest that the absence of any potential snake predators on the island of Mayotte may explain this observation.

Predation of Cathemeral Ceboids

Carnivores

Compared to Madagascar, the Neotropics is home to a much more diverse array of potential primate predators. Several Neotropical felids are as large as, or larger than, *C. ferrox*, and are thus potential predators of primates (table 3). However, primates are not a main food item for any Neotropical felid species [Emmons, 1987, 1990; Wright, 1989, 1998; Hart, 2000]. Research by Emmons [1987] on the comparative feeding ecology of the ocelot (*F. pardalis*), puma (*F. concolor*) and jaguar (*P. onca*) at Cosha Cashu, Peru, revealed that primates and other arboreal mammals made up just 5–8% of the total diets of the ocelot and jaguar (as determined by analysis of scats); there were no signs of primates or other arboreal mammals in scats attributed to the puma. Comparative research by Facure and Giarretta [1996] on the predator community in a protected Atlantic forest in Espirito Santo State, southeastern Brazil, yielded similar data. Scats of the 6 felids, i.e. oncilla (*F. tigrina*), margay (*F. wiedii*), jaguarundi (*F. yagouaroundi*), ocelot, jaguar and puma, and 1 canid (the crab-eating fox, *Cerdocyon thous*), occurring at the site were examined; only 1 jaguar scat contained remains of the tufted capuchin (*Cebus apella*), representing 5.5% of prey occurrence in the jaguar diet.

Despite a lack of detailed dietary data on the Neotropical felids, interspecific comparisons suggest a pattern among species of opportunistic predation, while intraspecific comparisons between study sites suggest considerable dietary variation from region to region. Detailed field data on the margay are few [Eisenberg, 1989; Sunquist and Sunquist, 2002]. It has been reported to be primarily nocturnal [Em-

Table 3. Neotropical carnivores (Mustelidae and Felidae) that are potential, or known, primate predators

Carnivore species	Body mass, kg	Foraging habits	Vertical looping?	Confirmed primate predator?	References
Tayra (<i>Eira barbara</i>)	2.7–7.0	T/A	no	probably	see text
Margay (<i>Felis wiedii</i>)	3.0–9.0	A/T	yes	yes	Beebe, 1925 Emmons, 1990 de Oliveira, 1998b Nowak, 1999
Jaguarundi (<i>F. yagouaroundi</i>)	4.5–9.0	T/A (?)	no	yes	Emmons, 1990 McCarthy, 1992 Passamani, 1995 de Oliveira, 1998a
Ocelot (<i>F. pardalis</i>)	8.0–14.5	T/A (?)	no	yes	Sunquist and Sunquist, 2002 Emmons, 1987 Murray and Gardner, 1997
Puma (<i>F. concolor</i>)	29.0–120.0	T	no	no	Emmons, 1987 Sunquist and Sunquist, 2002
Jaguar (<i>Panthera onca</i>)	31.0–158.0	T/A	no	yes	Emmons, 1987 Seymour, 1989 Peetz et al., 1992

T = Terrestrial; A = arboreal. Vertical looping is the ability to rotate the ankles so that tree trunk descent can be made head first.

mons, 1990], but some diurnal activity was also reported by Azevedo [1996] during a brief study in disturbed Atlantic Forest in southeastern Brazil. The margay is reported to be an agile climber and, with broad, soft paws and mobile metatarsals, to forage extensively in trees [Nowak, 1999]. In addition to being much more arboreal than the ocelot [Redford and Eisenberg, 1992], the margay, like the fossa, can perform ‘vertical looping’ [Taylor, 1989; Emmons, 1990; Nowak, 1999]. This ability makes it unique among Neotropical felids. Recently, however, dietary data (again, analysis of scats) from a long-term study in Atlantic Forest in southeastern Brazil by Wang [2002] indicate a generalized feeding ecology for the margay; most prey species were nocturnal and 59.2% of the prey were terrestrial mammals. Arboreal mammals, terrestrial rodents, birds and reptiles have also been reported to be favoured prey of the margay [Mondolfi, 1986; Konecny, 1989; Facure and Giaretta, 1996; de Oliveira, 1998b]. Beebe [1925] provided an early report of margay predation on the wedge-capped capuchin (*C. nigrivittatus*), and de Oliveira [1998b] reports that captive margays in eastern Amazonia have been observed preying on golden-handed tamarins (*Saguinus midas niger*). Hart [2000] also counts the margay among the Neotropical felids that are primate predators. That there have not been more accounts of margay predation of primates could be because of its nocturnal foraging habits [Konecny, 1989; Emmons, 1990; Wang, 2002]. The margay ranges in weight from 3.0 to 9.0 kg [Emmons, 1990; de Oliveira, 1998b]; thus, the arboreal specializations of the margay certainly suggest that this felid would be a potential threat to small ceboids (a large margay would approach the average weight of the fossa). Passamani [1995] reports an observation of a group of common marmosets (*Callithrix*

jacchus), and a solitary male masked titi monkey (*Callicebus personatus personatus*), mobbing a margay. The mobbing behaviour of the marmosets involved moving towards the margay, which Passamani [1995] interpreted as serving both to advertise to the predator that it had been detected [see also Zuberbuhler et al., 1999]; cf. Stafford and Ferreira [1995], and to familiarize young with potential predators and their behaviour [see also Bartecki and Heymann, 1987].

Like the margay, the ocelot also has a high degree of forepaw dexterity and is a good climber [Iwaniuk et al., 2000]. While the ocelot is primarily nocturnal, diurnal activity is not uncommon [Sunquist et al., 1989; Emmons et al., 1989; Konecny, 1989; Murray and Gardner, 1997]. It is known to prey occasionally on ceboids [Emmons, 1987; Murray and Gardner, 1997; Hart, 2000]; however, the ocelot generally hunts and captures its mammalian prey on the ground [Bisbal, 1986; Emmons, 1990; Murray and Gardner, 1997]. Most prey of the ocelot are nocturnal, terrestrial and weigh less than a kilogram [Sunquist and Sunquist, 2002], but small mammal species larger than 3 kg and colubrid snakes can also figure prominently in the diet [Wang, 2002]. The cathemeral jaguarundi, although an agile climber [e.g., see McCarthy, 1992], also tends to forage on the ground [Emmons, 1990; Nowak, 1999; Sunquist and Sunquist, 2002]; it is reported to feed opportunistically on small rodents, birds, reptiles and occasionally fish [Bisbal, 1986; Konecny, 1989; Manzani and Monteiro Filho, 1989; McCarthy, 1992; Olmos, 1993; de Oliveira, 1998a]. Sunquist and Sunquist [2002] make reference to one report from Brazil of the stomach contents of a jaguarundi including the remains of a titi monkey (*Callicebus* sp.). The jaguar is also cathemeral [Emmons, 1987, 1990], has a high degree of forepaw dexterity [Iwaniuk et al., 2000], and is almost as arboreal as the leopard [Nowak, 1999; Hart, 2000]. However, hunting is done primarily at night and on the ground [Seymour, 1989]. In Venezuela, a subadult or young adult jaguar successfully preyed on 5 red howler monkeys (*A. seniculus*) from one social group over a period of 7 months [Peetz et al., 1992]. Seymour [1989] lists red howler monkeys and owl monkeys (*A. trivirgatus*) among the mammalian species in the diet of the jaguar. Emmons [1987] suggests that while the jaguar takes mammalian prey opportunistically [see also Olmos, 1993; Aranda and Sanchez-Cordero, 1996], it may be primarily adapted to preying on large reptiles (turtles, tortoises and caiman) [see also Sunquist and Sunquist, 2002]. Finally, while the puma is cathemeral and an agile climber [Seymour, 1989; Sunquist and Sunquist, 2002], it is a terrestrial forager [Emmons, 1990]. At Cosha Cashu, Peru, Emmons [1987] found that two large rodent species accounted for 60% of the puma diet: agouti (*Dasyprocta variegata*, 33%), and paca (*Agouti paca*, 27%). Olmos [1993] characterized the puma as an opportunistic predator in the caatinga of northeastern Brazil; elsewhere, the puma is reported to rely heavily on deer species [Aranda and Sanchez-Cordero, 1996; Nowak, 1999; Rau and Jimenez, 2002; Sunquist and Sunquist, 2002].

One other possible carnivoran predator of New World monkeys is the tayra (*Eira barbara*, Mustelidae). The tayra is cathemeral [Sunquist et al., 1989; Emmons, 1990; Presley, 2000], but its eyesight is reported to be poor [Defler, 1980]. The tayra is the only mustelid in the Neotropics that exhibits arboreality [Eisenberg, 1981], although progression is generally along the forest floor [Emmons, 1990]. There are several reports of close encounters between tayras and ceboids. In a study of the Panamanian tamarin (*S. geoffroyi*), Moynihan [1970, p. 4] relates a second-hand ac-

count of a tayra, 'carrying a dead tamarin in its mouth'. Galef et al. [1976] suggested that tayras might be important predators of callitrichids and small cebids, and Hernandez-Camacho and Cooper [1976] reported a tayra being observed in rapid pursuit of a troop of tufted capuchins (*C. apella*). Izawa [1978] described a foraging tayra coming dangerously close to a sleeping group of black-mantled tamarins (*S. nigricollis*), before it caught sight of the observer and withdrew. Defler [1980] observed a tayra attempt an arboreal pursuit of a white-fronted capuchin monkey (*C. albifrons*); although the capuchin threatened the tayra (i.e. showing canines, making stare threats, branch breaking and growling), it also easily leapt away from the tayra, which was described as being a clumsy climber. In contrast, Redford and Eisenberg [1992] describe the tayra as an excellent climber. Compared to the fossa and felids, however, the tayra has a relatively low degree of forepaw dexterity [Iwaniuk et al., 2000], so less agility in the trees might be expected. Defler [1980] concluded that tayras were only a minor threat to *Cebus* compared to predatory birds. Because tayras also eat fruit, Defler [1980] further suggested that interactions between tayras and white-fronted capuchins could actually come about due to feeding competition for fruit rather than predation attempts by tayras. Terborgh [1983] considered the tayra as being capable of occasionally ambushing ground-foraging *Cebus* or squirrel monkeys (*Saimiri* sp.), but also stated no such attacks had been witnessed. More recently, Phillips [1995] observed both white-faced capuchins (*C. capucinus*) and mantled howler monkeys on Barro Colorado Island give 'aggressive vocalizations' towards a tayra; the capuchins also threatened the tayra and lunged at it, while the howler monkeys remained high in emergent trees, vocalizing. Stafford and Ferreira [1995] described a group of seven reintroduced golden lion tamarins (*Leontopithecus rosalia*) suddenly reversing their direction of travel, scattering and beginning to alarm call following what was apparently an unsuccessful predation attempt by a tayra in the forest subcanopy (at a height of 3–5 m); the golden lion tamarins began alarm calling only after they had retreated to a distance of approximately 10 m from the tayra. Because the authors sighted the tayra only after the golden lion tamarins began fleeing, it was unclear to them whether the tayra had been lying in ambush, stalking the *L. rosalia*, or if it they had observed a chance encounter between the two species. Both the tayra and the golden lion tamarins left the area immediately after the encounter, but the golden lion tamarins continued their vocalizing for another 13 min. This report is significant because there has been concern among researchers about the risk of tayra predation of reintroduced *L. rosalia* [Fernandez-Duque, pers. comm.]. Asensio and Gomez-Marin [2002] observed a group of four adult tayras display aggressive behaviour towards a group of mantled howler monkeys; 2 adult female howler monkeys approached the tayras, causing the tayras to retreat. Asensio and Gomez-Marin [2002] also note that a successful predation of a primate by a tayra has not been observed (cf. Moynihan's [1970] second-hand account, above), and they conclude that unlike the jaguar and harpy eagle, the tayra is not a serious threat to the howler monkey [see also Terborgh, 1983].

Birds of Prey

Among the numerous raptor species of the Neotropics, at least 7 prey on, or occasionally attack, ceboids: the harpy eagle, the Guiana crested eagle (*Morphnus guianensis*), the black hawk-eagle (*Spizaetus tyrannus*), the ornate hawk-eagle (*S. ornatus*), the black-and-white hawk-eagle (*Spizastur melanoleucos*), the slate-

coloured hawk (*Leucoternis shistacea*), and the bicoloured hawk (*Accipiter bicolor*) [Hernandez-Camacho and Cooper, 1976; Terborgh, 1983; Robinson, 1994; Hart, 2000]. Notably, all these raptor species hunt by making long flights (>50 metres) through the forest as they attack their prey targets [Robinson, 1994]. Peres [1990] states that predation by the harpy eagle acts as a strong selective pressure on ceboid populations, and Hart [2000] lists the harpy eagle among the few primate predators that are 'dedicated primate specialists'. Ceboid species that are reported to be preyed upon by the harpy eagle include: squirrel monkeys (*Saimiri sciureus*), capuchins (*C. apella* and *C. albifrons*), sakis (*Pithecia pithecia*, *P. monachus*, *P. irrorata* and *P. albicans*), bearded sakis (*Chiropotes satanas* and *C. albinasus*), and red howler monkeys [Eason, 1989; Peres, 1990; Sherman, 1991]. The crested eagle (*M. guianensis*) has been observed preying on squirrel monkeys, dusky titi monkeys (*C. moloch*), white-faced sakis (*P. pithecia*), spider monkeys (*Ateles paniscus*), and infant moustached and saddle-backed tamarins (*S. mystax*, *S. fuscicollis*) [Terborgh, 1983; Robinson, 1994; Julliot, 1994; Gilbert, 2000; Vasquez and Heymann, 2001]. Additionally, there are also at least two strigiforms that are large enough regularly to be predatory threats to small ceboids (but see also Stafford and Ferreira [1995], where a burrowing owl (*Athene cunicularia*) was observed to opportunistically prey on a young common marmoset). In the Amazonian basin and the Argentinean Chaco, the spectacled owl (*Pulsatrix perspicillata*) is reported to be large enough to possibly take an adult owl monkey [Terborgh, 1983; Fernandez-Duque, 2003]. In the Paraguayan Chaco, the great horned owl (*Bubo virginianus*) is another possible predator of *Aotus*; the combination of the presence of the great horned owl together with the absence of large diurnal raptors in the Paraguayan Chaco has been suggested as the reason owl monkeys there are cathemeral [Wright, 1989, 1994; Kinzey, 1997; but see Fernandez-Duque et al., 2001, 2002, and Fernandez-Duque, 2003, where thermoregulation, not a release from the threat of raptor predation, is stressed in accounting for the cathemerality in *A. azarai* in the eastern Argentinean Chaco]. Fernandez-Duque [2003] reports attacks on *A. azarai* in the eastern Argentinean Chaco by the spectacled owl (*P. perspicillata*), and the bicoloured hawk. The attacks occurred at dawn and dusk, times at which the owl monkeys were most active, but Fernandez-Duque et al. [2001] suggest that systematic data on the ecology of the predator community of this region must be gathered before the presence or absence of particular predators can be used to explain *Aotus* cathemerality.

Constricting Snakes

Several reports have now been published regarding predation and predation attempts by constricting snakes, especially the boa constrictor (*Boa constrictor*) and the anaconda (*Eunectes murinus*), against both cebids and callitrichids [Chapman, 1986; Heymann, 1987; Tello et al., 2002; Perry et al., 2003; Ferrari et al., 2004]. Bartecki and Heymann [1987] observed a group of saddle-back tamarins (*S. fuscicollis nigrifrons*) mob a pair of Amazon tree boas (*Corallus enydris*); they suggested that mobbing achieved social transmission of information about potential predators [see also Passamani, 1995]. There is even an anecdotal account of a boa constrictor attempting to prey on the mantled howler monkey [Chapman, 1986]. To date, however, there is no report of any constricting snake attempting to prey on *Aotus*. So, while it is clear that small ceboids are subject to predator pressure from large con-

stricting snakes, there is presently no basis for assessing whether predation or the threat of predation by constricting snakes has played any role in determining the cathemerality of the owl monkey.

Discussion

Predation and a Comparative Assessment of Lemurid and Ceboid Cathemerality

This review is not sufficient to conclude definitively that predation and the threat of predation have caused cathemerality. But, looking at lemurid and ceboid cathemerality in a comparative light allows some clear distinctions to be drawn. In other words, cathemerality is not a unitary phenomenon.

In Madagascar, the cathemerality of the genus *Eulemur* and other members of the Lemuridae may be driven in large part by the predation threat posed by *C. fossa*. Although raptor predation is certainly an important factor in lemurid ecology [e.g. Karpanty and Goodman, 1999; Karpanty, 2003], the developing picture is that the fossa, a lemur-hunting specialist [Hart, 2000], is a much more formidable predator. This puts fossa-lemurid predator-prey relationships in a special class. Stanford [2002] remarked that few primate species are preyed upon by one predator the way chimpanzees (*Pan troglodytes*) prey on red colobus (*Procolobus badius*). Not reflected in this statement, however, are the fossa-lemurid predator-prey relationships. If a lemurid is pursued by an endemic carnivore, it must be the fossa – this is clearly the kind of singular predator-prey relationship to which Stanford [2002] was referring. If anything, carnivore predation pressure on lemurids would have been more severe in the past. The recently extinct, puma-like *C. spelea* would have been a fearsome predator; while it could have preyed on some of the large subfossil lemur species, it would certainly also have been capable of preying on lemurids [Wright, 1999; Goodman et al., 2004]. Such close ecological relationships provide the setting for the development of co-evolutionary adaptations [Andrewartha and Birch, 1984].

Recent genetic analysis indicates that whereas the lemuriforms are an ancient adaptive radiation, dating back some 66–62 million years ago, the endemic Malagasy carnivores represent a single adaptive radiation that arose from a colonization event between 24 and 18 million years ago [Yoder et al., 2003; Yoder and Flynn, 2003]. Since that time, the cathemeral fossa has departed from the ancestral nocturnality of carnivores [Veron et al., 2004]. There are two scenarios by which the derived activity pattern of the fossa could have evolved; neither of these scenarios relies on the ‘evolutionary disequilibrium’ model, whereby cathemerality among extant lemur species is interpreted as a transitional activity pattern between nocturnality and diurnality arising from the recent extinction of the ‘giant’ lemurs [van Schaik and Kappeler, 1993, 1996; cf. Heesy and Ross, 2001; Hill, 2006]. In the first scenario, it is possible that a cathemeral activity cycle was an adaptive response by the fossa to the existing, ancestral cathemeral activity patterns of its lemurid prey, as the activities of predators reflect those of their prey [Emmons, 1987; Zuberbuhler and Jenny, 2002; Curtis and Rasmussen, 2002]. If that transition occurred, it would have reinforced the adaptiveness of lemurid cathemerality and set in motion an evolutionary stable strategy between the predator and its prey. As Wright [1998] notes, primates can avoid predators either by concealment, or by early detection and flight.

However, Wright [1998] did not differentiate between the ways concealment could be achieved. Crypsis, either by colouration that provides camouflage, or by behavioural means (e.g. freezing), represents concealment in space; cathemerality by lemurs, as the potential prey of a powerful predator, represents concealment in time [see also Donati et al., 1999].

In the second scenario, lemurid cathemerality may have arisen in response to fossa cathemerality [see also Hill, 2006]. Both male and female fossas are sparsely distributed [Hawkins et al., 2002], with male home ranges being up to twice as large as those of females; Hawkins [2003] estimated the population density of *C. ferox* in Kirindy Forest to be one animal per 4 km². Despite low population densities, *C. ferox* would still be subject to the same climatic stresses of the austral winter that lemurs face. Like female lemurs, female fossas experience a brief annual oestrus. The mating season of *C. ferox* occurs between October and December, with gestation lasting 6–7 weeks [Hawkins et al., 2002; Hawkins, 2003]. Some aspects of the biology of *C. ferox* seem to be consistent with the energy frugality hypothesis that has been proposed to account for the combination of characteristics exhibited by lemurs (e.g. small group size, seasonal breeding, cathemerality), as either adaptations to conserve energy or adaptations to maximize the use of scarce resources [Wright, 1999]. The energy frugality hypothesis proposes that the breeding synchrony of lemur species both conserves the amounts of energy expended in reproduction and ensures that weaning coincides with peak levels of food availability and quality [Wright, 1999]. Mapping fossa seasonal reproduction on the reproductive patterns of lemur species reveals that the fossa birth period is centred on January, with the young being weaned at 4 months of age [Hawkins, 2003]. This time of weaning in the fossa coincides with a period in the yearly cycle when female lemurs are pregnant [Wright, 1999], and the activity levels of many species begin to decline markedly as the austral winter unfolds [e.g., see Colquhoun, 1998]. Thus, in this second scenario, fossa cathemerality may have evolved in response to seasonality of prey availability and the demands of having to feed newly weaned but still dependent offspring (the litters of 2–4 young stay with the female until they are about a year old [Hawkins, 2003]). Lemurids may have then responded to the fossa's activity pattern by adopting cathemeral activity patterns themselves (i.e. temporal crypticity – see above). An evolutionary stable strategy between predator and prey would also result from this scenario, although it involves the potential cost to cathemeral lemurs of increased exposure to diurnal raptors (this is not an element of the first scenario, where lemur cathemerality is interpreted as an ancestral condition). This cost of increased predation risk could be ameliorated by selection for fine-tuned diurnal raptor detection abilities. As this review has shown, specific raptor alarm calls and reactions are exhibited by many lemur species [Sauther, 1989; Colquhoun, 1993, 1997, 2001; Goodman et al., 1993; Csermely, 1996; Oda and Masataka, 1996; Wright, 1998; Karpanty and Grella, 2001; Fichtel and Kappeler, 2002; Karpanty, 2003].

In the Neotropics, the situation is rather different. While there are numerous felid species and the mustelid tayra, and some of these taxa prey on primates, none seems to be a primate-hunting specialist on par with the fossa [Hart, 2000]. The only carnivore that has been reported to prey on both *Aotus* and *Alouatta* is the jaguar [Seymour, 1989; Peetz et al., 1992], and then only opportunistically. But, when we consider the range of raptor species that prey on ceboids, it appears that avian predation is a greater threat to ceboids than is carnivoran predation. Indeed, the threat

of raptor predation may be great enough to outweigh any benefits from cathemerality, except under certain conditions [Hill, 2006]. Thus, the cathemerality of *Aotus* (and perhaps *Alouatta*), might better be linked to predation in terms of avoiding raptor predation. That is, where large monkey-eating raptors are absent, *Aotus* will adopt a cathemeral activity pattern and exhibit some degree of diurnal activity [Wright, 1989, 1994]. The reverse would be true for *Alouatta*; despite diurnal raptors, some degree of nocturnal activity would enable howler monkeys to forage at times when raptors would not be a threat. The relatively severe environments in which *Aotus* cathemerality occurs, however, means that the activity pattern might also be accounted for in terms of thermoregulatory maintenance and/or seasonality of food resources [Fernandez-Duque et al., 2001, 2002; Fernandez-Duque, 2003].

Both Madagascar and the Neotropics are home to several species of large constricting snakes. In both biogeographic regions, constricting snakes have been reported to at least occasionally prey on primates. At this time, however, it is not clear to what extent predation by constricting snakes (which, themselves, can be cathemeral) may have contributed to primate cathemerality, if at all.

The Special Case of Cryptoprocta – Is the Fossa an Imprudent Predator?

In an island ecosystem where primates predominate among the endemic mammalian fauna, it is not surprising that lemur-hunting specialist species like *C. fossa* and *C. spelea* could evolve on Madagascar. Wright et al. [1997] analyzed the impact of fossa predation on a population of Milne-Edward's sifaka (*P. d. edwardsi*) in Ranomafana National Park for which there were 10 years of data on behavioural ecology and demography. Wright et al. [1997] concluded that in addition to being a most formidable predator, the fossa hunted sifakas by stealth [see also Taylor, 1989], attacking them at night in their sleeping trees, and preferentially preyed on lactating females. By preying mostly on individuals that had the highest reproductive value, instead of young, aged or ill individuals, Wright et al. [1997] suggested that fossas were not being 'prudent predators' [Slobodkin, 1968, 1974; but see Wright, 1995, where it is suggested that the fossa may be an 'equal opportunity' predator, preying on all age-sex classes of prey species]. In a larger comparative context, there is good evidence that predators often prey on individuals that differ from the rest of their group [Curio, 1976]. While it would be of interest to know if fossa predation is regulating lemur population densities, Slobodkin's [1968, 1974] notion of 'prudent predation' was met with a good degree of criticism at the time because it was a concept that seemed to invoke group selectionism [Taylor, 1984]. Regardless, it might be premature to characterize fossa predation as 'imprudent'. Isbell [1994] notes that carnivore predation can often be episodic; individual carnivores may opportunistically and idiosyncratically take particular prey species at rates that depart from the average predation rates of those prey for their species [see also Taylor, 1984; Stafford and Ferreira, 1995; Goodman, 2003; cf. Slobodkin, 1968, 1974]. Since the report by Wright et al. [1997], patterns of fossa predation of ruffed lemurs (*V. v. variegata*) reintroduced to Betampona Reserve in northeastern Madagascar [Britt et al., 2001, 2003] provide clear evidence of episodic predation; Britt et al. suggested that one fossa was responsible for the deaths. Recently, a similar episodic bout of predation on diademed sifakas (*P. d. diadema*), apparently by one fossa, occurred in a forest fragment at Tsinjoarivo in eastern Madagascar [Irwin, pers. comm.]. The jaguar predation of 5 red howler monkeys from one social group reported by Peetz et al. [1992]

is another clear case of episodic predation. Predators, being opportunistic, may exploit particular predation tactics that work in a certain region or prey population, and keep exploiting those tactics as long as they prove successful. Thus, in order to clarify predation patterns and the impact predators have on prey populations, we come back to the point made earlier in this paper and echoed by many who study predation: we still require more detailed data on predatory species and their synecological relations with prey species [Andrewartha and Birch, 1984; Anderson, 1986; Cheney and Wrangham, 1987; Isbell, 1994; Boinski and Chapman, 1995; Hart, 2000; Fernandez-Duque et al., 2001; Miller, 2002; Stanford, 2002; Zuberbuhler and Jenny, 2002; Goodman, 2003; Zuberbuhler, 2004].

Directions for future research on the links between predators and cathemeral primates would include further fieldwork on those primate species for which we have only limited evidence of cathemerality (e.g. the ring-tailed lemur [Traina, 2001], black and white ruffed lemur [Wright, 1999], black howler monkey, and the mantled howler monkey [Dahl and Hemingway, 1988]). Additional information on these latter two taxa would be especially interesting because when Dahl and Hemingway [1988] initially reported cathemeral activity in *Alouatta*, they predicted that it was an ancient adaptation and one that would be found in many other New World anthropoids. This prediction has not yet been critically tested [but see Hill, 2006]. As for cathemerality in relation to predation, the relative impact of predation on lemur species that are seasonally cathemeral compared to those which exhibit year-round cathemerality [Curtis and Rasmussen, 2002], has not yet been fully determined. As Fernandez-Duque et al. [2001] and Goodman [2003] have both argued, a comprehensive understanding of the influence of predation on primate cathemerality will not come without a thorough assessment of the relative availability of prey for primate predators, as well as regional, seasonal and individual variation in prey selection by predators [e.g., see Karpanty and Goodman, 1999]. The differential responses of prey species to different predatory species must also be fully documented [e.g. Colquhoun, 1993, 1997, 2001; Karpanty, 2003]. Likewise, recognition of mutualistic interactions between prey species involving the recognition of the alarm calls of other species and the type of predator they signal [e.g. Oda and Masataka, 1996; Oda 1998] will allow us to assess more accurately predator impact on the primate species being preyed upon. It is certain that acquiring these data represents a massive research challenge. But, as data addressing these areas become available, our current conceptions of cathemerality in relation to predation will undoubtedly be tested and clarified.

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