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Anti-Predator Strategies of Cathemeral Primates: Dealing with Predators of the Day and the Night

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Introduction

The entire evolutionary history of the order Primates has occurred in ecological contexts where all primates, like all other animals (Vermeij, 1987; Endler, 1991, p. 176), are, at least, at risk of predation at some point in their lives (Hart & Sussman, 2005). These predator-prey ecological relationships can be conceived of as interspecific, asymmetric "attack-defense" arms races that give rise to diffuse coevolutionary effects (Dawkins & Krebs, 1979; Janzen, 1980). Predators and their prey exhibit asymmetric interactions because the selective pressure of predators on prey species is stronger than the selective pressure of prey species on their predators. The asymmetric nature of these relationships has been termed the "life-dinner principle" (Dawkins & Krebs, 1979): Failure on a predator's part means it has lost a meal, but failure on the prey's part dramatically increases its likelihood of being the meal (e.g., Terborgh, 1983; Vermeij, 1987; Lima & Dill, 1990; Endler, 1991, p. 176; Stanford, 2002).

Despite terminology in the literature such as "act of predation," or "predation event," predation is more accurately regarded as a sequence, or process, involving several stages, or phases, on the part of the predator: search/encounter/detection; identification/approach/pursuit; and, subjugation/consumption (Curio, 1976, p. 98; Taylor, 1984; Vermeij, 1987; Endler, 1991, p. 176). Because predation risk for any prey increases as the predation sequence proceeds from one stage to the next, and because many prey species are subject to predation by more than one predatory species, selection should be greatest for prey defenses that result in early detection of predators. While most predators hunt more than one prey type, predators will also often prey preferentially on the most common prey type(s), a form of frequency-dependent selection known as *apostatic selection* (Clarke, 1962; Maynard Smith, 1970; Curio, 1976, p. 98; Endler, 1991, p. 176). Thus, predators exert stronger selection pressure on individual prey species than any individual prey species can exert on its predators. The "life-dinner principle" and the asymmetric nature of predator-prey arms races mean that, in general, the prey tend to have the advantage in those particular arms races (Dawkins & Krebs, 1979).

Regardless of the advantage prey species might generally have in their arms races with predators, it is not immediately clear how those primate species that have adopted cathemerality deal with arms races with both diurnal or nocturnal predators (Kappeler & Erkert, 2003; Hill, 2006). Previously, I reviewed the effects of predators on the activity patterns of cathemeral lemurids and ceboids (Colquhoun, 2006). The present paper is the obverse of that earlier paper; here, I review the anti-predator behaviors of cathemeral lemurids and ceboids. Cathemeral primates hold some anti-predator strategies in common with diurnal primates (e.g., alarm calling and mobbing). But, in addition to discussing how cathemeral primates use their cathemerality as an anti-predator *strategy of temporal crypticity* (e.g., Wright, 1989, 1994, 1995, 1998, 1999; Wright et al., 1997; Donati et al., 1999; Curtis & Rasmussen, 2002; Colquhoun, 2006; Hill, 2006), I will show how cathemeral primates also make differential use of other behavioral and morphological anti-predator strategies (i.e., behavioral crypticity, social groups, "escape in size", and polymorphism) (Clarke, 1962; Terborgh, 1983; Endler, 1991, p. 176). While cathemeral primates are in arms races with the same types of major predators in both Madagascar and the Neotropics (i.e., carnivores, birds of prey, and constricting snakes), there is a non-convergence of the faunal communities in these two biogeographic regions (Terborgh & van Schaik, 1987; Kappeler & Ganzhorn, 1993; van Schaik & Kappeler, 1993, 1996; Kappeler & Heymann, 1996; Peres & Janson, 1999; Ganzhorn et al., 1999; Kappeler, 1999a, b; Hart, 2000; Colquhoun, 2006). Consequently, the anti-predator strategies of cathemeral lemurids exhibit different emphases from the anti-predator strategies emphasized by cathemeral ceboids. In particular, I propose that the sexual dichromatism that characterizes all species and subspecies of the lemurid genus *Eulemur* may represent a polymorphic anti-predator adaptation to apostatic selection. Thus, this paper will consider both proximate and ultimate anti-predator strategies of cathemeral primates.

Primate Cathemerality and Predation

The Taxonomic Distribution of Primate Cathemerality

Tattersall (1987, 2006) introduced the term "cathemeral" to describe the activity patterns of organisms in which equal or significant amounts of feeding and/or traveling occur "through the day"— that is, through the 24-hour cycle. Over the last 30 years, cathemeral activity has been reported in all species of the lemurid genus *Eulemur* (Colquhoun, 1993, 1997, 1998a; Overdorff & Rasmussen, 1995; Curtis, 1997; Donati et al., 1999; Wright, 1999; Curtis & Rasmussen, 2002; Kappeler & Erkert, 2003; Overdorff & Johnson, 2003; see, also, Table 7.1).

Considerable inter-species variability has also been noted in the cathemerality observed across the genus *Eulemur* (see Table 7.2). Cathemerality has also been reported or suggested for at least some populations of the other lemurid

TABLE 7.1. Taxa of the lemurid genus *Eulemur* for which cathemerality has been reported and the sites where that cathemeral activity was observed.

Lemur Taxon	Common Name	Site(s)	Reference(s)
Eulemur coronatus	crowned lemur	Ankarana; Mt. d'Ambre NP	Wilson et al., 1989; Freed,1996a, 1999
E. fulvus fulvus	brown lemur	Ampijoroa	Rasmussen, 1998a
E. (f.) albifrons	white-fronted brown lemur	Andranobe watershed	Vasey, 1997, 2000
E. f. mayottensis	Mayotte brown lemur	Mavingoni; Mayotte	Tattersall, 1977, 1979; Tarnaud, 2004
E. f. rufus	red-fronted, or rufous, brown lemur	Ranomafana NP; Kirindy Forest Antserananomby, Tongobato;	Overdorff, 1996; Donati et al., 1999; Kappeler & Erkert, 2003 Sussman, 1972
E. f. sanfordi	Sanford's brown lemur	Ankarana; Mt. d'Ambre NP	Wilson et al., 1989; Freed, 1996a, 1999
E. (f.) albocollaris	white-collared brown lemur	Andringitra NP	Johnson, 2002
E. macaco macaco	black lemur	Ambato Massif; Lokobe	Colquhoun, 1993, 1997, 1998a; Andrews & Birkinshaw, 1998
E. mongoz	mongoose lemur	Ampijoroa Anjouan; Moheli; Anjamena	Tattersall & Sussman, 1975; Sussman & Tattersall, 1976; Rasmussen, 1998b; Tattersall, 1976; Curtis & Zaramody, 1999; Curtis et al., 1999
E. rubriventer	red-bellied lemur	Ranomafana NP	Overdorff, 1988, 1996

genera besides *Eulemur* (see Table 7.3). Comparative assessment of lemur activity cycle data led Rasmussen (1999) and Curtis & Rasmussen (2002), to recognize three modes of cathemerality. Their "Pattern A" refers to the seasonal shifting from diurnal to nocturnal activity that has only been described in *Eulemur mongoz*. "Pattern B" involves a seasonal shift from diurnal activity to cathemerality, a pattern that has only been described in *E. fulvus fulvus*. "Pattern C" is the year-round cathemerality that has been described in most of the *Eulemur* taxa, as well as 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).

Comparative data raise questions concerning the activity patterns of the lesser bamboo lemur (*H. griseus*). In eastern Madagascar populations of the gray bamboo lemur (*H. griseus*) exhibiting either diurnality (Overdorff et al., 1997; Tan, 2000; Grassi, 2001) or largely nocturnal activity (Vasey, 1997, 2000) have been reported. At Ambato Massif, the western bamboo lemur (*H. g. occidentalis*) was observed to be diurnal (Colquhoun, 1993, 1998b). Such intraspecific variability in activity cycle is reminiscent of differing activity patterns reported for different populations of *Eulemur mongoz* (e.g., Tattersall, 1976) and the owl monkey

TABLE 7.2. Inter-species variability in cathemeral activity across the lemurid genus *Eulemur*.

Lemur Taxon	Cathemerality (Year-Round or Seasonal)	Nocturnal Activity Independent of Lunar Cycle?	References
Eulemur coronatus	Year-round	Yes	Wilson et al., 1989; Freed, 1996a, 1999
E. fulvus fulvus	Seasonal	No	Harrington, 1975; Rasmussen, 1998a
E. (f.) albifrons	Year-round;	No data	Vasey, 1997, 2000
E. f. mayottensis	Year-round	Yes	Tattersall, 1977, 1979; Tarnaud, 2004
E. f. rufus	Year-round;	No	Overdorff, 1996; Donati et al., 1999; Kappeler & Erkert, 2003
E. f. sanfordi	Year-round	No data	Freed, 1996a, 1999
E. (f). albocollaris	Year-round	No data	Johnson, 2002
E. macaco macaco	Year-round	No	Colquhoun, 1993, 1997, 1998a; Andrews & Birkinshaw, 1998
E. mongoz	Year-round;	Yes	Tattersall, 1976; Curtis, 1997; Curtis et al., 1999;
	seasonal		Curtis et al., 1999; Rasmussen, 1998a,b
E. rubriventer	Year-round	Yes	Overdorff, 1988, 1996

(*Aotus*, see below). Further comparative data are needed to clarify our understanding of *H. griseus* activity patterns (Tan, 2000; Mutschler & Tan, 2003). The remaining genera in the family Lemuridae, the ruffed lemurs (*Varecia*) and the ring-tailed lemur (*Lemur catta*), are usually considered to be strictly diurnal (Tattersall, 1982; Vasey, 2000, 2003; Jolly, 2003). But, there is a single report from Ranomafana National Park that the black and white ruffed lemur (*Varecia variegata*) exhibits cathemerality (Wright, 1999). Similarly, there is also a recent lone report of *L. catta* in Berenty Reserve being cathemeral (Traina, 2001). The extent to which these latter two taxa are indeed cathemeral deserves further attention in the field. In light of Wright's (1999) report, I include *V. variegata* in this review so as to provide as complete a reflection of the literature on primate cathemerality as possible; *L. catta* is the focus of another chapter (Gould & Sauther, this volume), and will not be considered further here.

In addition to most taxa in the family Lemuridae being cathemeral, cathemerality has also been reported in at least two genera of platyrrhine monkeys (see Table 7.3). The genus *Aotus* (variously known as the owl monkey, night monkey, or douroucouli) is usually noted for being the only nocturnal platyrrhine and the only nocturnal anthropoid (e.g., Moynihan, 1964, 1976; Thorington et al., 1976; Wright, 1978; Garcia & Braza, 1987; Kinzey, 1997). Yet, *Aotus* is also a cathemeral taxon because some populations exhibit diurnal activity (Rathbun & Gache, 1980). *Aotus azarai* in the Paraguayan Chaco has been reported as cathemeral (Wright, 1985, 1989, 1994). *Aotus azarai* in the eastern Argentinean Chaco has also been observed to be cathemeral (Fernandez-Duque & Bravo, 1997; Fernandez-Duque et al., 2001, 2002; Fernandez-Duque, 2003). Finally, the howler monkeys (*Alouatta*) are usually considered strictly diurnal (e.g., Kinzey, 1997). But, there are some data hinting that cathemerality may occasionally occur in the mantled howler monkey (*Alouatta palliata*) in Costa Rica (Glander, 1975) and the

TABLE 7.3. Other primate taxa besides *Eulemur* for which cathemerality has been reported or suggested.

Taxon	Common Name	Site(s)	Nature of Report and References
Hapalemur simus	greater bamboo lemur	Ranomafana NP	"… *H. simus* is cathemeral" "(Tan, 2000 p. iv)"
Hapalemur griseus alaotrensis	Lac Alaotra gentle lemur	Lac Alaotra	"… flexible 24-hour activity cycle… *H. g. alaoternsis* is cathemeral." (Mutschler et al., 1998, p. 329) "Night activity is substantial." (Mutschler, 2002, p.102)
H. griseus	lesser bamboo lemur	Andranobe	"*Hapalemur griseus* is largely nocturnal at Andranobe." (Vasey, 2000, p. 426)
		Ranomafana NP	"*H. griseus* are diurnal." (Overdorff et al., 1997, p. 217) "*H. griseus* and *H. aureus* are diurnal." (Tan, 2000) "*H. griseus* is strictly diurnal." (Grassi, 2001, p. 189)
Varecia variegata	black and white ruffed lemur	Ranomafana NP	"… *Varecia v. variegata* and *Hapalemur griseus alaotrensis* exhibit cathemeral behavior." (Wright, 1999, p. 45)
Lemur catta	ring-tailed lemur	Berenty Reserve	"… link between key sites in the home range of ringtailed lemurs and their day and night activity will be examined." (Traina, 2001, p. 188)
Aotus azarai	red-necked owl monkey	Paraguayan and Argentinean Chaco regions	See text
Alouatta palliata	mantled howler monkey	Hacienda La Pacifica, Guanacaste Prov., Costa Rica	"… traveling through the trees on several nights around midnight, and often began feeding well before dawn." (Glander, 1975, p. 41)
A. pigra	black howler monkey	Cayo District, Belize	"The group was found to become active and feed between three and five hours before sunrise" (Dahl & Hemingway 1988, p. 201)

black howler monkey (*A. pigra*) in Belize (Dahl & Hemingway, 1988). Because these reports are consistent with Tattersall's (1987) definition of cathemerality, and because other researchers (e.g., Kinzey, 1997) have cited these reports as suggesting howler monkey cathemerality, *A. palliata* and *A. pigra* are also included in this review. As with *Varecia* and *Lemur*, however, the aim of future fieldwork on *A. palliata* and *A. pigra* should be to seek to clarify the degree of cathemeral activity in these taxa.

Explaining Primate Cathemerality: Predation and Other Factors

In recent years, several authors have drawn attention to the fact that primate cathemerality is not a unitary phenomenon (Rasmussen, 1999; Curtis & Rasmussen, 2002; Mutschler, 2002; Overdorff & Johnson, 2003; Colquhoun, 2006; Tattersall, 2006). While considerations of primate cathemerality have often stressed single-cause explanations, it is apparent that a full understanding of primate cathemerality will show that both proximate and ultimate factors (Tinbergen, 1963) are involved in the variable and flexible activity patterns of cathemeral primates. Although proximate selective factors may be identified, it complicates matters that these factors do not necessarily provide an explanation for, nor give a reflection of, the ultimate factors that gave rise to cathemerality (Endler, 1986).

The range of possible factors that may contribute to a thorough explanatory model of primate cathemerality includes it being: an ancestral condition; a response to seasonality or availability of food resources; a mechanism for (or result of) reduction of interspecific competition; a response to precipitation, the lunar cycle, and/or ambient temperature, and an anti-predator strategy. Tattersall (1982) proposed that cathemerality represents the ancestral lemurid activity cycle. This is the view that has been taken in several reports of lemurid cathemerality (Overdorff & Rasmussen, 1995; Colquhoun, 1998a; Rasmussen, 1998a; Curtis & Rasmussen, 2002). A similar view was taken by Dahl & Hemingway (1988) in their preliminary report of cathemerality in *A. pigra*; they interpreted it as an activity pattern that provided a good degree of adaptability and considered it a characteristic that traced back to the earliest anthropoids. Engqvist & Richard (1991) suggested that cathemerality was a seasonal response to changes in food availability and/or quality. Some field data provide support for this interpretation (e.g., Overdorff, 1996). However, other field studies have produced results that are inconsistent with this ecologically-based explanation (e.g., Overdorff & Rasmussen, 1995; Colquhoun, 1998a; Kappeler & Erkert, 2003). But, as noted above, an absence of proximate evidence does not rule out seasonality of food resources as a possible ultimate cause of cathemerality. The recent extinctions of the diurnal “giant” lemurs were implicated by van Schaik & Kappeler (1993, 1996) as events that precipitated an “evolutionary disequilibrium.” By this model the cathemeral lemur species we observe today are in a transitional stage between nocturnality and diurnality, as they occupy econiches that opened up with the extinctions of the “giant” lemurs. This explanation is also problematic, however, as the retinal and optic foramina morphologies of lemurid species are not consistent with having been nocturnal until only 1,500–500 years ago (e.g., Martin, 1990; Colquhoun, 1998a; Kay & Kirk, 2000; Mutschler, 2002).

At present, the functional explanations most often invoked for the evolution of primate cathemerality focus on it being either a thermoregulatory strategy or a predator avoidance strategy. Thermoregulatory stress has been cited as a likely cause for cathemerality in several species: *Hapalemur griseus alaotrensis*

(Mutschler et al., 1997; Mutschler, 2002); *Eulemur mongoz* (Curtis et al., 1999); and *Aotus azarai* (Fernandez-Duque et al., 2002; Fernandez-Duque, 2003). Data correlating ambient temperature and activity patterns provide strong support for cathemerality in these species having a thermoregulatory basis. The predator avoidance function of cathemerality—a kind of concealment in time, or temporal crypticity—has been cited in regards to the activity cycles of many lemurids (Wright, 1995, 1998, 1999; Wright et al., 1997; Curtis & Rasmussen, 2002; Colquhoun, 2006), including: *Eulemur rubriventer* (Overdorff, 1988); *E. mongoz* (Curtis, 1997; Rasmussen, 1998b; Curtis et al., 1999), and *E. fulvus rufus* (Donati et al., 1999). Colquhoun (2006) proposed that *Eulemur* cathemerality might be an evolutionary stable strategy (ESS) to predation pressure from the fossa (*Cryptoprocta ferox*), a viverrid carnivoran that is also cathemeral and appears to be a lemur-hunting specialist (see also, Hart, 2000; Hart & Sussman, 2005; Hill, 2006). A release from the threat of diurnal raptor predation, together with the nocturnal threat posed by the great horned owl (*Bubo virginianus*), has been suggested as the reason for diurnal activity by *Aotus azarai* in the Paraguayan Chaco (Wright, 1985, 1989, 1994). While the literature on primate cathemerality has seen this consistent implication of predation as a causal factor, it seems an odd incongruity that over the last 20 years several major reviews of predation on primate species made no mention of primate cathemerality being a possible adaptive response to predation (Anderson, 1986; Cheney & Wrangham, 1987; Goodman et al., 1993; Isbell, 1994; Stanford, 2002; Goodman, 2003; Hart & Sussman, 2005).

Other Anti-Predator Strategies of Cathemeral Primates

Behavioral crypticity

Cathemeral primates tend to be relatively small-bodied (under about 2.5 kg), placing them at some risk of predation (Overdorff & Johnson, 2003). The largest primate species for which there are indications of cathemerality (but see above concerning uncertainties about that cathemerality) are the black and white ruffed lemur (*Varecia variegata*, at about 3.0 kg (Tattersall, 1982), and the howler monkeys, *Alouatta palliata* and *A. pigra*, averaging 6.4 kg (Kinzey, 1997). In some cathemeral primate species, the increased risk of predation that comes with small body size translates into cryptic behavior. Several cathemeral primate species also occur in small groups or family groups (Freed, 1999): *H. g. alaotrensis* (Mutschler et al., 1997; Mutschler, 2002); *E. rubriventer* (Overdorff, 1988, 1996); *E. mongoz* (Curtis, 1997; Curtis et al., 1999); and *Aotus azarai* (Rathbun & Gache, 1980; Wright, 1985, 1989, 1994; Stallings et al., 1989). By virtue of their size the small social groups of these species are less likely to be detected by predators. These species are also relatively cryptic when active. For example, at Ranomafana, Overdorff (1996) found that *E. rubriventer* (mean group size = 3 individuals), rested more, traveled less, and were less active at night than the sympatric rufous lemur (*E. f. rufus*), with their larger social groups (mean group size = 8 individuals). Grassi (2001) regards *H. griseus* at Ranomafana as an understory specialist whose ecology has been shaped by predator avoidance strategies. The resting sites used by *H. griseus* tend to be in dense vegetation tangles at a height of about 7 m (which Grassi interprets as an anti-raptor strategy), and sleeping sites are found above a height 15 m in large trees (which Grassi interprets as an anti-carnivore strategy). Grassi also reports that *H. griseus* has distinct alarm calls for snakes (Rakotodravony et al., 1998) and birds of prey; the response shown by group members to the latter call is to become quiet (an example of what Curio (1976, p. 98) terms "adaptive silence"), drop in height in the understory, and stay still (Grassi, 2001). Grassi concludes that *H. griseus* can distinguish between different types of predators and exhibit appropriate predator-specific behaviors.

Similarly, although *Aotus* is a powerful leaper and can move rapidly through the trees (Moynihan, 1964; see also Wright's (1984) observation of an *Aotus* male with an infant on its back narrowly escaping a pursuing, and possibly predatory, male *Cebus* monkey), *Aotus* lives in small family groups and utilizes cryptic sleeping sites in Peru, where they are nocturnal. In Paraguay, diurnal owl monkeys often sleep at night on open branches (Wright, 1985). Wright (1985, 1989, 1994) has interpreted the diurnal activity of *Aotus azarai* in the Paraguayan Chaco as the result of predation release from diurnal raptors, combined with the presence of the great horned owl (*B. virginianus*) as a nocturnal predation threat. However, Wright (1985) notes that while *B. virginianus* is large enough to prey on *Aotus*, it does not specialize on feeding on arboreal prey, unlike the harpy eagle (*Harpia harpyja*) and the Guiana crested eagle (*Morphnus guianensis*); rather, the great horned owl often catches its prey on the ground. Rathbun & Gache (1980, p. 213) describe what they term the "*Aotus* distress vocalization"—a "whoop, whoop, whoop"—but they provide no further information about this call, so the contexts of its use are unknown.

Other cathemeral primate species are not particularly cryptic, despite their relatively small body sizes. For example, when the black lemur (*E. macaco macaco*) is active at night, group progressions are quite noisy and groups often engage in nocturnal loud calling typical of inter-group encounters (Colquhoun, 1998a); the same is true of many nocturnal lemur species, which exhibit noisy behaviors and are highly vocal (e.g., Schulke, 2001). Black lemur resting sites, however, can be cryptic (e.g., dense liana tangles), especially in the dry season when activity levels are dramatically lower than in the wet season (Colquhoun, 1993, 1998a).

Social Groups—Safety in Numbers

Larger primate social groups are known to be better able to detect potential predators (e.g., Terborgh, 1983; van Schaik et al. 1983; Landeau & Terborgh, 1986; Hauser & Wrangham, 1990; Peres, 1993; Sauther, 2002; Hart & Sussman, 2005). Freed (1999) has presented comparative data on average group sizes in lemurid species which show that those species in the genus *Eulemur* that do not form family groups (i.e., *E. coronatus*, *E. fulvus*, and *E. macaco*) all have multi-male, multi-female social groups with group sizes that tend to range between 6–11 individuals. In two of these taxa, *E. macaco* (Colquhoun, 1998a) and *E. f. rufus* (Kappeler & Erkert, 2003), year-round cathemeral activity has been linked to the lunar cycle, with more nocturnal activity occurring on nights with bright moonlight.

Predator alarm calls are well developed in the *Eulemur* species that exhibit multi-male, multi-female social groups (see Table 7.4). In *E. coronatus*, Wilson et al., (1989) reported that detection of the fossa (*Cryptoprocta ferox*) was met with lemurs staring in the direction of the fossa and giving "grunt-shriek" alarm vocalizations; response to the fossa and the "grunt-shriek" vocalizations was to flee upwards. While Freed (1996a) reported often seeing fossas at night, he did not observe what response(s) fossas elicited in either *E. coronatus* or *E. f. sanfordi*. Freed does note, however, that while both lemurs would grunt occasionally on sighting the smaller Malagasy ring-tailed mongoose (*Galidia elegans*), neither gave distinct vocalizations or directed particular behaviors towards *Galidia*. Wilson et al. (1989) report that *E. coronatus* typically responded with evasive behavior on sighting large raptors, fleeing downwards rather than giving alarm vocalizations. Freed (1996a), however, describes both *E. coronatus* and *E. f. sanfordi* as giving loud and distinct vocalizations when either the Madagascar harrier hawk (*Polyboroides radiatus*), or the Madagascar buzzard (*Buteo brachypterus*) were sighted. But, Freed does not give further description of these distinctive vocalizations.

TABLE 7.4. Predator alarm responses of "safety in numbers" primate taxa that are, or may be, cathemeral.

Taxon	Terrestrial Predator alarm	Aerial Predator Alarm	Mobbing	References
Eulemur coronatus	grunt-shriek vocalization	no; loud and distinctive vocalizations	?	Wilson et al., 1989; Freed, 1996a
E. fulvus rufus	generalized alarm call	yes, directed at Madagascar harrier hawk	yes	Fichtel & Kappeler 2002; Fichtel & Hammerschmidt, 2002; Sussman, 1975, 1977; Karpanty & Grella, 2001
E. macaco macaco	generalized huff or hack alarm call	scream-whistle vocalization in response to Madagascar harrier hawk	yes, in response to large boa constrictors and harrier hawks	Colquhoun, 1993, 2001
Varecia variegata	anti-carnivore call	no;		Macedonia, 1990;
		yes, but not to all large raptors	?	Karpanty & Grella, 2001
Alouatta palliata	generalized roars, woofs and barks	generalized roars, woofs and barks	yes	Baldwin & Baldwin, 1976

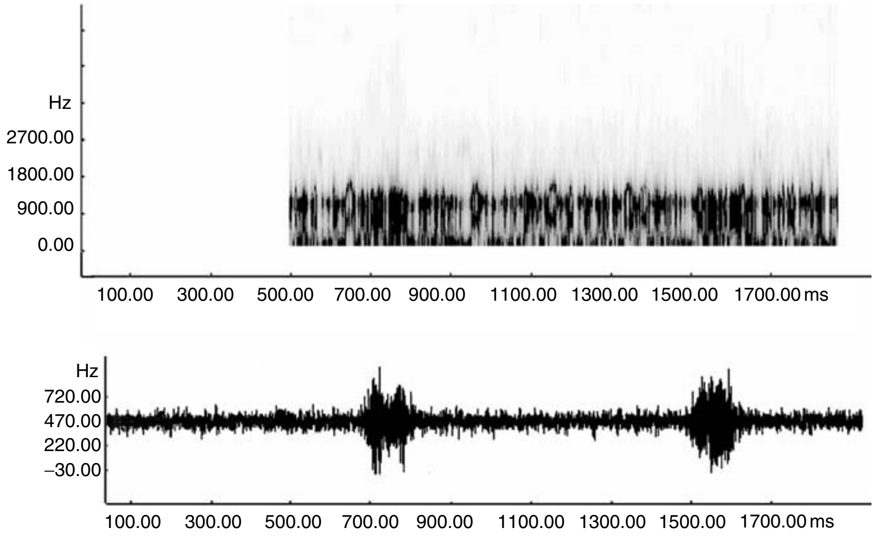

FIGURE 7.1. Spectrogram and waveform of black lemur "huff/hack" alarm vocalizations. The spectrogram of two closely-spaced calls is of poor quality due to load insect buzzing on the recording; regardless, two atonal pulses can discerned at around 700 ms and 1600 ms

Sussman (1975, 1977) reported that *Eulemur fulvus rufus*, *Lemur catta*, and *Propithecus verreauxi* would all move into very dense foliage and each give particular loud calls if a Madagascar harrier hawk was sighted overhead. All three species performed their calls in unison, and Sussman neither recorded the calls being given towards any other species of bird, nor towards the Madagascar fruit bat (*Pteropus rufus*—cf. *E. macaco*, below). Fichtel & Kappeler (2002) and Fichtel & Hammerschmidt (2002) report that at Kirindy Forest (western Madagascar), *E. f. rufus* exhibits a mixed alarm call system. Terrestrial predators (such as the fossa) are met with a generalized alarm call, while aerial predators (specifically, the Madagascar harrier hawk) elicit a specific alarm call. Fichtel & Kappeler (2002) noted that the ultimate cause for this predator alarm call variability is unclear, but they suggest that it might be explained by the so-called evolutionary disequilibrium hypothesis (van Schaik & Kappeler, 1993, 1996). But, in playback experiments at Ranomafana (southeastern Madagascar), Karpanty & Grella (2001) found that calls of the Madagascar serpent eagle (*Eutriorchis astur*), Henst's goshawk (*Accipiter henstii*), and the Madagascar harrier hawk, all elicited general predator alarm calls, dropping in the canopy, and fleeing from the source of the sound. However, none of the raptor calls was responded to by *E. f. rufus* with specific aerial predator alarm calls. Karpanty & Grella (2001) also report that the responses of *E. rubriventer* to the raptor call playbacks were similar to those of *E. f. rufus*.

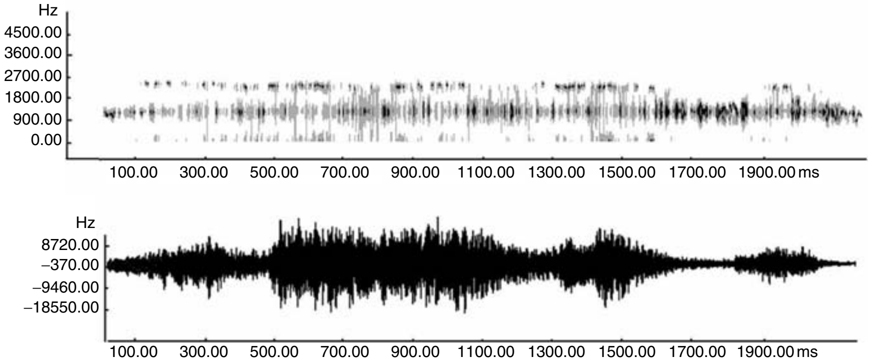

FIGURE 7.2. Spectrogram and waveform of black lemur "bark" vocalization

At Ambato Massif, Colquhoun (1993, 2001) documented a distinctive set of loud calls used by black lemurs (*E. macaco macaco*). Three distinct loud calls were noted. A short, sharp "huff" or "hack" vocalization (Figure 7.1) was heard fairly often in various situations where animals had been surprised or startled (e.g., by a falling tree branch, non-predatory birds suddenly taking flight, or the sudden appearance of humans and/or dogs). While local informants told of the fossa occurring at Ambato Massif, I never sighted a fossa. However, when a black lemur group sighted a domestic dog, they would give one or two "hack" vocalizations, and then move quickly and silently away from the dog. Most commonly heard was a generalized "loud call," or "bark" (Figure 7.2), that was given in many different situations, such as inter-group encounters, the sighting of small to mid-size raptors, and the "mobbing" of large boa constrictors (*Acrantophis madagascariensis*) (Colquhoun, 1993). The most distinctive loud call, the "scream-whistle" (Figure 7.3), was noted in only two particular types of situations. During the day it was invariably given upon sighting the Madagascar harrier hawk, the largest raptor species commonly seen at Ambato. Harrier hawks often circled overhead, not far above treetop level, and this would set off scream-whistle vocalizations from the lemurs, followed by urgent evasive behaviors (e.g., diving several meters down into the crowns of trees). On one occasion, as I observed a group of juvenile black lemurs playing on the ground in an open patch of disturbed, low-stature forest, a harrier hawk soared overhead. The juveniles scattered on the scream-whistle vocalization that ensued, leaping up into nearby saplings; one juvenile female, however, found herself closer to a dried palm frond on the ground and dove underneath it, lying flat against the forest floor. On another occasion, I observed a black lemur group mobbing, from below the forest canopy, a pair of Madagascar harrier hawks that were copulating on an exposed dead branch in the canopy. At the same time, the copulating harrier hawks were also mobbed and dive-bombed by a pair of crested drongos (*Dicrurus forficatus*); indeed, it appeared that the mobbing vocalizations of the drongos attracted the attention of the black lemurs and set them mobbing the harrier hawks as well (albeit from a safe distance and

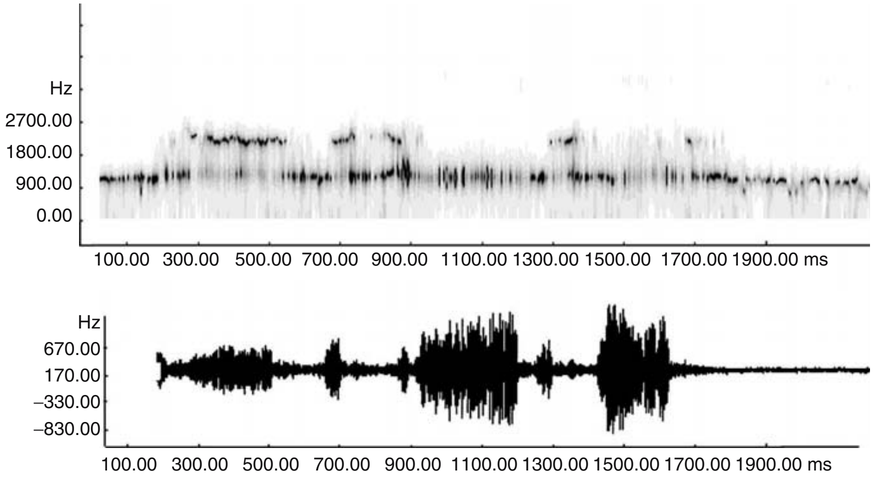

FIGURE 7.3. Spectrogram and waveform of black lemur "scream-whistle" vocalization

an unexposed position). But, I also recorded one occasion—on a brightly moonlit night—when a black lemur group was giving "scream-whistles" in response to swooping fruit bats (*Pteropus rufus*—a species with a similar wingspan to that of the Madagascar harrier hawk). "Scream-whistles" directed at fruit bats could be explained as due to young animals that 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. Rather than being a vocal signal solely symbolizing the harrier hawk, a more parsimonious explanation of the "scream-whistle" is that it carries ordinal information, signaling not just that something large has been sighted overhead but that something extremely large (and potentially dangerous) is overhead.

Black-and-white ruffed lemurs (*Varecia variegata*) have a variable, fission-fusion social community structure and organization (e.g., Freed, 1999; Vasey, 2005), but still give vocalizations in response to both raptors and carnivores (Table 7.4). Macedonia (1990) describes the vocal signal given by *Varecia* in response to sighting raptors as also occurring in other generalized, high-arousal contexts that don't involve predators. Thus, he suggests that this call does not represent either predator class or signal a situation requiring urgent response, but rather indicates an aggressive/defensive demeanor. By contrast, the anti-carnivore call of *Varecia* is interpreted by Macedonia as a high-urgency signal for the group to reaggregate. But, in the playback experiments of Karpanty & Grella (2001), only *Varecia*, along with the diurnal *Propithecus* (*diadema*) *edwardsi*, gave aerial alarm predator calls in response to the calls of the Madagascar serpent eagle and Henst's goshawk; interestingly, *Varecia* did not give aerial predator alarm calls in response to the Madagascar harrier hawk.

Both mantled howler monkeys (*Alouatta palliata*) and black howler monkeys (*A. pigra*) live in groups that exhibit variable social organization. Mantled howler monkeys are the smaller of the two species (females: 3.1–7.6 kg.; males: 4.5–9.8 kg; Ford & Davis, 1992); the multi-male, multi-female social groups vary widely in size, from 4–23 individuals (Kinzey, 1997). Black howler monkeys are larger (females: 6.4 kg; males: 11.35 kg; Ford & Davis, 1992), and tend to be found in smaller groups (4–10 individuals; Horwich & Lyon, 1990; Kinzey, 1997; Treves & Brandon, 2005); social organization may be either one male and multiple females, or one to four adult males and one to four adult females (Horwich & Lyon, 1990; Kinzey, 1997; Treves & Brandon, 2005).

An assortment of ecological data are consistent with the interpretation that *Alouatta palliata* seems to, at least in some contexts, use protection in numbers as an anti-predator strategy (see Table 7.4). Baldwin & Baldwin (1976) found that mantled howler monkeys gave “roar” vocalizations in response to “danger stimuli”, such as large birds, dogs, a fallen infant, proximity to humans, and gunfire. In some areas, howler monkeys “roar” at humans, in others they don’t, a function of whether or not humans are associated with danger. Where the stimuli are less intense or less dangerous, these same situations can also evoke “woofs” or “barks” from the monkeys. “Roars” do not necessarily function as an anti-predator strategy. While “roars” may interrupt the activities of some potential predators, or cause them to move off, “roars” can also have the reverse effect and attract potential predators (e.g., dogs and humans). Howler monkeys will “woof” when moving towards targets of group mobbing, but that they will “roar” when not moving towards the target; on this evidence, Baldwin & Baldwin (1976) suggest that “roars” may serve to signal avoidance or withdrawal responses, rather than an approach response. Terborgh (1983) noted that howler monkey groups spend much of their time resting on exposed perches in the forest canopy, making no efforts to be inconspicuous; he suggested that such behavior would seem to make it possible to detect predators at a distance. More recently, Gil-da-Costa et al. (2003) found that a safety in numbers response to “predator assessment” vocalizations by harpy eagles was critical in determining whether the harpy would attempt a predatory attack or not. When a mantled howler monkey group responded to the predator assessment calls of a harpy in a coordinated manner (i.e., vigilance by all group members, females collecting their infants and moving into dense foliage, males moving distally on canopy branches, often with alarm calls being given), the harpy either delayed its attack or moved off to seek other prey. If, however, a mantled howler monkey group was inattentive to the harpy’s “predator assessment” calls, or reacted in an unorganized and chaotic manner, the harpy would either attack or move closer (see, also, Gil-da-Costa, this volume).

“Escape in Size”

As several researchers have pointed out, in the life history course predation risk is greater for young individuals since they are potential prey for a larger range of predators; as individuals grow and mature, they often become “protected” from predation by certain predators simply because they are too big to be captured (e.g., Sauther, 1989; Endler, 1991, p. 176; Csermely, 1996). Because of the relatively small body size of most cathemeral lemurids and *Aotus*, adults are still potential prey for multiple predators. With an adult body weight of about 3 kg, *Varecia* is the largest of the lemurs for which there are indications of cathemerality. Even so, it is not so large that it cannot be preyed upon by the fossa (e.g., Britt et al., 2001, 2003). The playback results reported by Karpanty & Grella (2001) indicate that *Varecia* also regard large raptors as potential threats. Certainly, given that the Madagascar harrier hawk can capture sifakas that are heavier than adult *Varecia* (Karpanty & Goodman, 1999; Brockman, 2003), adult *Varecia* may fall prey to harrier hawks on occasion. However, it may be that adult *Varecia* have "escaped in size" from the majority of Madagascar's extant raptors.

Asensio and Gomez-Marin (2002) observed a group of four adult tayras (*Eira barbara*, Mustelidae) display aggressive behavior towards a group of mantled howler monkeys; two 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 never been observed; they, thus, conclude that unlike the jaguar (*Panthera onca*) and harpy eagle (Eason, 1989; Peres, 1990; Sherman, 1991; Peetz et al., 1992), the tayra is not a serious threat to the howler monkey (see also, Terborgh, 1983; cf. reports of observed unsuccessful attacks by *E. barbara* against, or anti-predator responses to *E. barbara* by, various callitrichid species: black-mantled tamarins (*Saguinus nigricollis*) (Izawa, 1978); buffy-headed marmosets (*Callithrix flaviceps*) (Ferrari & Lopes Ferrari, 1990); saddle-back and moustached tamarins (*S. fuscicollis* and *S. mystax*) (Peres, 1993); golden lion tamarins (*Leontopithecus rosalia*) (Stafford & Ferreira, 1995). In other words, it would seem that though the tayra appears to be a potential predator of small Neotropical primates (Colquhoun, 2006), *Alouatta* avoids threat from this particular predator on the basis of size.

Predator Confusion by Polymorphism

It is a notable fact that, although sexual dichromatism is rare across Order Primates, all taxa of the cathemeral genus *Eulemur* are, to one degree or another, sexually dichromatic (Tattersall, 1982; Mittermeier et al., 1994; Overdorff & Johnson, 2003). Clarke (1962) introduced the concept of apostatic polymorphisms, pointing out that such polymorphisms can be features that favor the prey in the arms races with their predators, especially if those predators employ a "search image" manner of hunting. If a particular predator species hunts a prey species in an apostatic manner (i.e., preying on the most commonly encountered form), a polymorphism in the preferred prey (i.e., dichromatism in the case of genus *Eulemur*), produces a selective advantage for those phenotypes that do not match the search image of their potential predators. Endler (1991, p. 176) subsequently expanded on the concept of apostatic selection (see also, e.g., Maynard Smith, 1970; Curio, 1976, p. 98), noting that polymorphisms in prey species produce what he termed "apparent rarity", reducing the predation risk per individual because the apostatic predator encounters two (or more) rarer prey forms as opposed to one common prey form. Further, the apparent rarity of the polymorphic prey may lead the apostatic predator to switch predation effort to an apparently more common monomorphic prey species. Finally, Endler (1991, p. 176) notes that a predator need not prey apostatically for polymorphism to be advantageous to a prey species. A predator may find itself confused by having to select among apparently different prey, particularly if the different morphs are seen at the same time by the predator (as would likely be the case when a *Eulemur* social group was encountered during the day by a raptor or a fossa). Functionally, this is the same effect achieved by mixed-species groups (see Landeau & Terborgh, 1986). Confusion or hesitation on the part of the predator could be the chance that the potential prey targets would need to elude the predator. Given that the relatively small-bodied *Eulemur* species are at risk of predation from both large raptors (Karpanty & Goodman, 1999; Karpanty & Grella, 2001; Karpanty, 2003; Colquhoun, 2006), and the cathemeral fossa (Hart, 2000; Goodman, 2003; Hart & Sussman, 2005; Colquhoun, 2006), if dichromatism lowers the probability of predation on individuals and/or increases the chances of eluding predatory attacks, it would certainly confer a selective advantage.

Discussion

In very broad terms, primate social organization has been characterized as enabling two general anti-predator strategies: (i) social groups that are relatively large and conspicuous, but that can detect, and even deter, potential predators; or (ii) social groups that are relatively small in size and primarily employ cryptic behaviors to avoid many potential predators (e.g., Cheney & Wrangham, 1987; Janson, 1998; Gautier et al., 1999). Among cathemeral primates, predator avoidance can be thought of as consisting of at least a two-track strategy that operates in parallel. One track centers on being cathemeral and exercising temporal crypticity (Donati et al., 1999; Colquhoun, 2006; Hill, 2006); the second track centers on the strong association between group size and whether a species practices behavioral crypticity or safety in numbers. Overall, family groups, or small groups, of cathemeral primates are more likely to be behaviorally cryptic. The association of relatively small body size (i.e., adult weight < 2.5 kg), small group size and crypticity (temporal, and in some cases behavioral) in some cathemeral lemurids accords well with the general pattern reported among small-bodied diurnal primates. For example, with average adult body weights ranging between 120–600 g (Ford & Davis, 1992; Kinzey, 1997), the New World callitrichids are the smallest anthropoids, and the cryptic nature of much of their behavior is well-documented (e.g., Izawa, 1978; Dawson, 1979; Sussman & Kinzey, 1984; Kinzey, 1997); their typical response to the threat of raptor predation is to rapidly seek the protective cover of thick vegetation, often dropping several meters in the forest canopy to do so, and then remain motionless as long as the raptor continues to be a threat (e.g., Ferrari & Lopes Ferrari, 1990; Heymann, 1990; Peres, 1993; Searcy & Caine, 2002).

This reaction to aerial predators is very similar to that described for *Hapalemur griseus* (Grassi, 2001).

But, while there may be a general association between small body size and cryptic behavior, particularly in response to raptors (e.g., Terborgh, 1983), other possibilities exist. That is, a range of anti-predator strategies across primate species in response to various predators is to be expected. For example, Terborgh (1983) notes that the squirrel monkey (*Saimiri sciureus*) employs a safety in numbers strategy, despite its relatively small body size. Similarly, Peres (1993) found that among Amazonian tamarins, the formation of large, stable mixed-species groups between *Saguinus fuscicollis* and one of its larger congeners (*S. mystax*, *S. imperator*, or *S. labiatus*) provided enhanced predator defense through safety in numbers for both species in the mixed-species groups, particularly for the smaller-bodied *S. fuscicollis* (see also Landeau & Terborgh, 1986). While at least some cathemeral lemurids also form mixed-species groups (i.e., crowned lemurs (*Eulemur* coronatus) and Sanford's brown lemurs (*E. fulvus sanfordi*) – Freed, 1996a, b), the relative predator defense benefits to each species are not clear at present. In some situations, even small-bodied primates will mob potential predators (e.g., marmosets mobbing scansorial carnivores: *Callithrix flaviceps* mobbing a tayra (Ferrari & Lopes Ferrari, 1990); *C. jacchus* mobbing a margay (*Felis wiedii*) (Passimani, 1995); or Coquerel's dwarf lemurs (*Mirza coquereli*) mobbing a boa constrictor (*Acrantophis madagascariensis*) (pers. obs.). Likewise, at Ambato Massif, family groups of *Hapalemur griseus occidentalis* traveling low in the forest occasionally encountered me as I observed one of my black lemur study groups; these chance encounters often resulted in the *Hapalemur* mobbing me (a potential terrestrial predator) at close range with staccato "ah-ah-ah-ah-ahhhhhh" vocalizations. Conversely, when faced with a formidable predator, even primates in relatively large social groups may opt for cryptic behavior (e.g., see the report by van Schaik & van Noordwijk (1989) of the responses of wild capuchin monkeys, *Cebus albifrons* and *C. apella*, to presentation of a harpy eagle (*Harpia harpyja*) model and harpy eagle vocal playbacks).

Cathemeral lemurid species that live in larger social groups are not necessarily behaviorally cryptic and seem to rely more on safety in numbers. Along with the strategy of safety in numbers in some cathemeral lemurids, well-developed predator alarm call systems also occur (Zuberbühler et al., 1999). These alarm call systems appear to be particularly fine-tuned to aerial predators; specific aerial predator calls in *Eulemur fulvus rufus* and *E. macaco* are associated with immediate evasive behaviors and the seeking of cover. By itself, however, group living may not be sufficient protection against attack from nocturnal (or cathemeral) predators (Peetz et al., 1992; Wright et al., 1997; Wright, 1998). Risk from nocturnal attack is especially high on moonless nights or nights with gusting winds, the noise of which provides an acoustic screen for a stalking predator (Terborgh, 1983; Bearder et al., 2002, 2006). Thus, living in multi-male, multi-female social groups combined with cathemerality may produce a heightened anti-predator strategy—that is, a two-track anti-predator strategy of safety in numbers coupled with predator avoidance through time (Donati et al., 1999; Colquhoun, 2006; Hill, 2006).

Apostatic selection is regarded as a commonly occurring predator-prey phenomenon (e.g., Hubbard et al., 1982; Endler, 1986; Gendron, 1987; Allen, 1988; but see, e.g., Sherratt & MacDougall, 1995, for conditions where anti-apostatic selection may occur). The selective advantage of polymorphism as an adaptation to (and even for) apostatic predation has been documented in studies of a wide range of non-primate taxa; e.g., "predation" of dichromatic bait by passerine birds (Allen & Clarke, 1968; Allen, 1972); predation of dimorphic bugs (*Sigara distincta*) by rudd (a fish, *Scardinius eryophthalmus*) (Elton & Greenwood, 1970); "predation" of dichromatic bait by Japanese quail (*Coturnix coturnix japonica*) (Cook & Miller, 1977); predation risk in normal and melanistic morphs of the adder (*Vipera berus*) (Andrén & Nilson, 1981); differential predation of the polymorphic aquatic isopod *Idotea baltica* by perch (*Perca fluviatilis*) (Jormalainen et al., 1995); "predation" of computer-generated polymorphic moth images by blue jays (*Cyanocitta cristata*) (Bond & Kamil, 2002); predation of mammal species by raptor species exhibiting plumage polymorphism (Roulin & Wink, 2004). The suggestion made here that the sexual dichromatism found across the cathemeral genus *Eulemur* is a polymorphic anti-predator strategy against apostatic predation is new, but it represents an extension of a well-established concept. While the concept of polymorphism as an adaptation to apostatic predation pressure has not heretofore been applied to nonhuman primates, there is no a priori reason why it could not be. Interestingly, in reviews of color polymorphisms in birds, Galeotti et al., (2002) and Galeotti & Rubolini (2004) found that the greatest expression of color polymorphism occurred in avian species that were active during both day and night (i.e., were cathemeral). These authors noted the selective importance of varying light levels affecting the detectability of the organisms and that this could be a key mechanism in maintaining color polymorphism.

Among primates, Bicca-Marques & Calegaro-Marques (1998) previously considered the evolution of sexual dichromatism in the black and gold howler monkey (*Alouatta caraya*). This species exhibits striking sexual dichromatism similar to that of *Eulemur macaco*: adult males are entirely black, while adult females are golden brown (see Rowe, 1996). Bicca-Marques & Calegaro-Marques found that despite the strong sexual dichromatism, as well as pronounced sexual dimorphism (adult males weigh 4.0–9.6 kg, adult females 3.8–5.4 kg) (Ford & Davis, 1992), there were no male-female differences in the thermoregulatory behavior of *A. caraya*. They thus concluded that sexual dichromatism in the black and gold howler monkey might better be explained as a result of sexual selection (their analysis did not include apostatic selection). Similarly, a thermoregulatory function would not seem to sufficiently explain the sexual dichromatism in *Eulemur* species. For example, the highly dichromatic black lemur (*E. macaco macaco*), showed no apparent sex differences in microhabitat preferences (Colquhoun, 1997).

Sexual selection was also the paradigm Cooper and Hosey (2003) employed to analyze sexual dichromatism in *Eulemur fulvus* subspecies, as well as *E.* (*f.*) *collaris* and *E.* (*f.*) *albocollaris*. Although their experimental results were consistent with the interpretation that sexual dichromatism in these *Eulemur* taxa was the evolutionary outcome of females exhibiting mating preference for brightly colored males, like Bicca-Marques & Calegaro-Marques (1998), Cooper & Hosey (2003) did not consider apostatic selection. Just as the evolution of cathemerality was likely influenced by multiple factors, (Tattersall, 2006) the same may be said of the evolution of sexual dichromatism. While it is worth noting that all *Eulemur* species exhibit strict seasonal breeding (e.g., Tattersall, 1982; Wright, 1999), both sexual selection and apostatic selection could drive the evolution of sexual dichromatism. Apostatic selection would favor sexual dichromatism outside the breeding season, and sexual selection could provide a breeding season advantage, thus enhancing the adaptive significance of this characteristic.

There are several aspects of the anti-predator behavior of cathemeral primates that deserve further research. Specifically, to test the possible impact of apostatic selection on the genus *Eulemur*, future field research on *Eulemur* species should pay attention to how the sexual dichromatism and the social organizations of these taxa may affect, or be affected by, ecological relationships with potential aerial and terrestrial predators (e.g., In any given lemur ecological community, does *Eulemur* represent the most numerous potential prey for these predators?). For *Eulemur* taxa to have possibly evolved sexual dichromatism as an adaptive anti-predator response to apostatic selection, one would have to predict that, in fact, *Eulemur* do represent a rather abundant potential prey pool for large raptors and the fossa. Detailed research on the predators of *Eulemur* taxa is also needed to augment the few available data and to try to establish how heavily different predatory species rely on these cathemeral lemurids (e.g., Do predators of *Eulemur* taxa prey on them in an apostatic fashion and, if so, which predators are responsible for any apostatic selective pressure?). On a more general level, additional field data on the activity patterns of *Varecia*, *Lemur catta*, *Alouatta palliata*, and *A. pigra* are needed to clarify the extent to which these taxa might be, or are, cathemeral. As is the case in general with studies of predation and predators, further data on the ecological interactions between the cathemeral primate species and their predators will allow us to better conceptualize and understand these predator-prey arms races and the processes involved therein.

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