

# Why Be Diurnal? Or, Why Not Be Cathemeral?

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## Key Words

Cathemerality · Day length · Predation · Thermoregulation · Seasonality · Behavioural flexibility · *Papio hamadryas ursinus*

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## Abstract

As a behavioural strategy, cathemerality is thought to confer considerable advantages by allowing animals to extend activity flexibly into either the diurnal or nocturnal phase in response to the prevailing ecological conditions. Factors such as temperature, access to food sources and minimising the risk of predation are all thought to be important in promoting cathemerality, although previous studies have produced inconsistent results. This paper adopts a different approach by first asking whether an obligate diurnal species, the chacma baboon (*Papio hamadryas ursinus*), exhibits seasonal variation in behavioural flexibility in response to annual cycles of day length. While short day lengths are an important constraint on the activity of the baboons at De Hoop Nature Reserve, South Africa, long summer days permit considerable flexibility in thermoregulatory response, diet selection and patterns of habitat choice. Given that baboons adapt flexibly in response to a relaxation of time constraints, the question thus arises as to why diurnal and nocturnal primates do not adopt cathemeral activity patterns when time is constrained? For baboons, the costs of predation appear to prohibit exploitation of the nocturnal phase and it is likely that such constraints are true of most primates. It thus follows that Madagascar's predatory environment must in some way permit or select for a cathemeral lifestyle. The importance of the predation by fossa (*Cryptoprocta ferax*) on the evolution of cathemerality is discussed.

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0015–5713/06/0772–0072\$23.50/0

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## Introduction

It has become increasingly clear that the traditional classifications of diurnal and nocturnal are insufficient to describe the activity patterns of certain primate species [Tattersall, 1982; Curtis and Rasmussen, 2002]. A number of primates regularly exploit both the diurnal and nocturnal niche, and Tattersall [1987] coined the term *cathemeral* to describe species exhibiting significant amounts of activity during both the light and dark phases of the 24-hour cycle. Among the lemurs of Madagascar, two genera, *Eulemur* and *Haplemur*, which together comprise at least eight species, exhibit cathemeral activity patterns [van Schaik and Kappeler, 1996; Wright, 1999; Curtis and Rasmussen, 2002], and diurnal activity has been regularly reported for certain populations of the usually nocturnal Neotropical owl monkeys, *Aotus* spp. [Wright, 1989; Fernandez-Duque, 2003].

The question of which factors favoured the evolution of cathemerality has generated considerable debate [Tattersall, 1982; van Schaik and Kappeler, 1996; Curtis et al., 1999; Curtis and Rasmussen, 2002, 2006; Kappeler and Erkert, 2003]. It is clear, however, that a key benefit to cathemerality is that it is a highly flexible strategy that allows differential movement into either the diurnal or nocturnal niche in response to a variety of selective pressures. Given that cathemerality is such a successful behavioural pattern in the Malagasy lemurs across the many different climatic zones of Madagascar, the question arises as to why this activity pattern is not more widespread amongst primates [Curtis et al., 1999]?

This paper will address this question by first asking whether day length, or the need to restrict activity to a single phase of the light-dark cycle, does indeed represent a constraint for obligate diurnal or nocturnal species. Kappeler and Erkert [2003] found that for cathemeral redfronted lemurs (*Eulemur fulvus fulvus*) day length was an important determinant of activity patterns; total and diurnal activity increased during the long days of the austral summer, with nocturnal activity increasing during the longer nights of the cool season. Similar relationships were reported by Curtis et al. [1999] for the mongoose lemur (*Eulemur mongoz*). These results suggest that for cathemeral species, activity levels in each phase may be linked to the duration of that phase. Similar relationships appear to hold for diurnal species. Hill et al. [2003, 2004a] showed that the activity patterns of chacma baboons (*Papio hamadryas ursinus*) at De Hoop Nature Reserve, South Africa, were closely linked to day length. Day length showed substantial seasonal variation at this site and the baboons experienced significant constraints on behaviour during the short winter days, with levels of all activities reduced during this period. Furthermore, since baboons must live in social contexts that allow them to survive when ecological constraints are most severe, day length may be important in understanding cross-population variation; the bottleneck created by short day lengths in certain months may account for the smaller group sizes observed in non-equatorial populations [Hill et al., 2003].

### *Prediction 1*

*Day length is an ecological factor constraining behavioural and social flexibility in chacma baboons.*

If baboons are living in social group sizes that allow them to balance their time budgets when day lengths are short, then an obvious implication is that during the summer months, when day lengths are significantly longer, the animals will have

‘excess’ or ‘spare’ time that could be used strategically to permit greater flexibility in conducting certain activities [Hill et al., 2003]. If one of the primary benefits of cathemerality is its inherent flexibility, then examining how a baboon population responds to varying day length, and thus varying opportunity for behavioural flexibility across an annual cycle, should provide insights into the factors favouring cathemerality. This paper will address this possibility within the De Hoop baboon population through an examination of some of the proposed factors accounting for the evolution of cathemerality.

Previous studies have suggested three primary explanations for the evolutionary advantages of cathemerality: (1) thermoregulatory benefits, (2) nutritional benefits, and (3) reduced predation pressure. A number of studies of lemurs have addressed each of these factors, although in many the support has been equivocal. Below, some of the relevant literature is reviewed to generate predictions as to how baboons under a varying day length regime should respond to each of these factors when conditions permit greater behavioural flexibility.

#### *Prediction 2*

*The baboons at De Hoop should exhibit pronounced thermoregulatory responses during only the long summer day lengths.*

In relation to thermoregulation, previous studies have suggested that cathemerality might reduce the costs of thermoregulation during the hot season if animals shift activity to the cooler, nocturnal phase [Engqvist and Richard, 1991; Curtis et al., 1999]. Alternatively, increased nocturnal activity may also be a response to low nighttime temperature during the cool season, since activity is an obvious mechanism for increasing body temperature [Overdorff and Rasmussen, 1995; Donati et al., 1999]. Although published patterns of cathemeral activity in relation to thermoregulatory benefits are far from consistent, and are probably insufficient for thermoregulation to represent the general selective advantage for the evolution of cathemerality [Kappeler and Erkert, 2003], temperature is nevertheless an important ecological constraint. Previous analyses have indicated that the baboons at De Hoop engage in more sedentary activities as perceived environmental temperature increases [Hill et al., 2004b; Hill, 2005, 2006]. Interestingly, however, such responses to high temperatures are not a consistent feature of all baboon populations, despite higher mean annual temperatures at other sites [Stelzner, 1988; Brain and Mitchell, 1999; Pochron, 2000]. The explanation for these differences appears to relate to the greater behavioural flexibility afforded to the De Hoop baboons by longer summer day lengths when temperatures are also high [Hill, 2005]. If this is the case, we would expect to see such a marked thermoregulatory response during only the summer months; baboons should be constrained from responding to high environmental temperatures during short days since there is likely to be insufficient time left over from foraging.

#### *Prediction 3*

*The baboons at De Hoop should utilise long day lengths to permit greater foraging and dietary flexibility.*

Cathemeral activity may also afford nutritional benefits. For example, cathemerality may allow animals to reduce the intensity of interspecific food competition through temporal avoidance of competitors [Kappeler and Erkert, 2003]. Alternatively, extending activity into both the diurnal and nocturnal phase may allow ani-

mals to switch to a high-fibre diet and increase feeding time when food is scarce [Engqvist and Richard, 1991] or exploit temporally limited resources [Sussman and Tattersall, 1976]. In general, there has been little support for a foraging advantage to cathemerality [Colquhoun, 1998; Curtis et al., 1999] and Kappeler and Erkert [2003] concluded that improved food availability is not the primary proximate or ultimate determinant of cathemeral activity. It is important to remember, however, that patterns of diet choice and diet composition can be complex to analyse, particularly when species composition and intake rates are so difficult to observe during the nocturnal phase, and diet selection may also be confounded by factors such as predation risk or interspecific competition. As a consequence, while animals are anticipated to forage so as to maximise their rate of nutrient intake [Schoener, 1971], they could switch to a risk minimising strategy at certain times of year. Such inter-relationships are inherently difficult to separate, particularly where dietary data are incomplete, and this could account for a lack of published evidence. Since baboon diets are easier to observe, and predation risk is less seasonal, an analysis of diet selection by the De Hoop baboons in relation to extended activity periods should provide greater insights into how additional time can be utilised for increased dietary flexibility.

#### *Prediction 4*

*Long day lengths should be used to permit greater flexibility in response to predation risk by the baboons at De Hoop.*

Predation risk is the final factor proposed to favour the evolution of cathemerality. Colquhoun [2006] has argued that cathemerality may be a specific response to the predation risk posed by the cathemeral fossa (*Cryptoprocta ferox*). Observations that cathemeral lemurs feed more in the exposed canopy at night have also been interpreted as a response to reduced nocturnal predation risk [Curtis et al., 1999; Donati et al., 1999], although as Kappeler and Erkert [2003] point out, these observations may be as easily explained by the greater light availability in these areas, or possibly result from daytime thermoregulatory responses [Andrews and Birkinshaw, 1998]. In general, predation has proved to be difficult to quantify and study, although evidence from baboons confirms its importance. Cowlshaw [1997] found that high predation risk habitats were utilised only for feeding by baboons at Tsao-bis, Namibia, with the majority of non-feeding activity occurring in higher-visibility, lower-risk habitats. Furthermore, habitat use was influenced by group size, with smaller groups spending proportionately less time in the high-risk habitats. Similar patterns have been observed for the baboons at De Hoop [Hill, 1999], and patterns of individual vigilance behaviour in the two populations are also explained by similar rules [Hill and Cowlshaw, 2002]. The possibility exists, therefore, that baboons may show a flexible response to predation risk with animals becoming more risk sensitive when additional time is available during the long summer days.

This paper initially addresses Prediction 1 and the question of whether day length represents a constraint on the behaviour patterns of the diurnal chacma baboon. Having illustrated that short winter days are indeed an ecological constraint on activity, the question of whether long summer days may be used strategically to permit behavioural flexibility is addressed through an examination of Predictions 2–4. Since the baboons at De Hoop appear to behave flexibly in response to thermoregulation, diet and predation risk, the question of why activity is confined to the diurnal phase during the short winter months is discussed.

**Table 1.** Results of linear regression analysis of mean monthly day length against levels of activity (in hours per day) each month

Behaviour	r <sup>2</sup>	F <sub>(1, 8)</sub>	p
Foraging	0.607	12.3	<0.01
Non-foraging	0.966	228.6	<0.001
Feed	0.124	1.1	n.s.
Move	0.119	1.1	n.s.
Groom	0.808	33.7	<0.001
Rest	0.923	96.2	<0.001

## Methods

The data presented here derive from the study of a single troop of chacma baboons (*Papio hamadryas ursinus*) at De Hoop Nature Reserve, Western Cape Province, South Africa. The troop (VT) ranged in size from 40 to 44 individuals over the course of the 10-month study (March to December 1997). Data were collected by means of instantaneous scan samples [Crook and Aldrich-Blake, 1968; Altmann, 1974] at 30-min intervals with information on identity, activity, food item consumed and habitat type recorded for each individual in the scan. The data presented here are from 1,535 scans, resulting in 10,269 point samples over the course of the study.

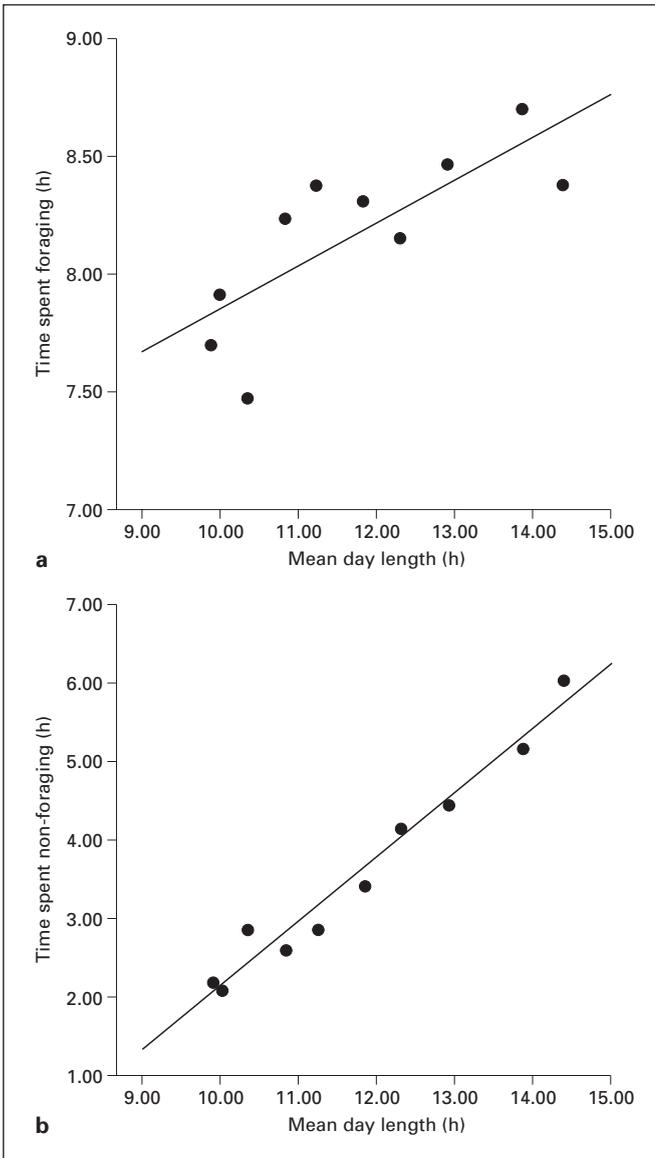
De Hoop is a coastal reserve and the vegetation is dominated by fynbos, a unique and diverse vegetation type comprising 80% of the Cape Floral kingdom [Cowling and Richardson, 1995]. The reserve has a Mediterranean climate: annual rainfall during the study year was 395 mm, with mean shade temperatures of 17.4°C. Due to its southerly latitude, De Hoop is highly seasonal, with substantial variation in both rainfall and temperature. More importantly, De Hoop experiences the largest range of day length variation (9.8–14.2 h) in sub-Saharan Africa, making this the ideal test population for examining the benefits of behavioural flexibility on primate activity. More detailed information on the ecology of the reserve and data collection methods are given in Hill [1999]. Specific information relating to temperature indices and analyses of thermoregulatory constraints is given in Hill et al. [2004b] and Hill [2005, 2006], while issues relating to day length variation and seasonal analyses of behaviour are discussed in Hill et al. [2003, 2004a].

In order to assess the importance of day length on behavioural flexibility, behavioural patterns are compared under conditions of long and short days. Data for short days are for 3 winter months (June to August), while those for long days are for the 3 months with the longest day lengths (October to December). Mean day length under the short day condition is 10¼ h, with a mean day length of 13¾ h for the long day months. The activity period in the summer months is thus extended by 3½ h, and this additional time should offer the opportunity for behavioural flexibility by the baboons at this time of year.

## Results

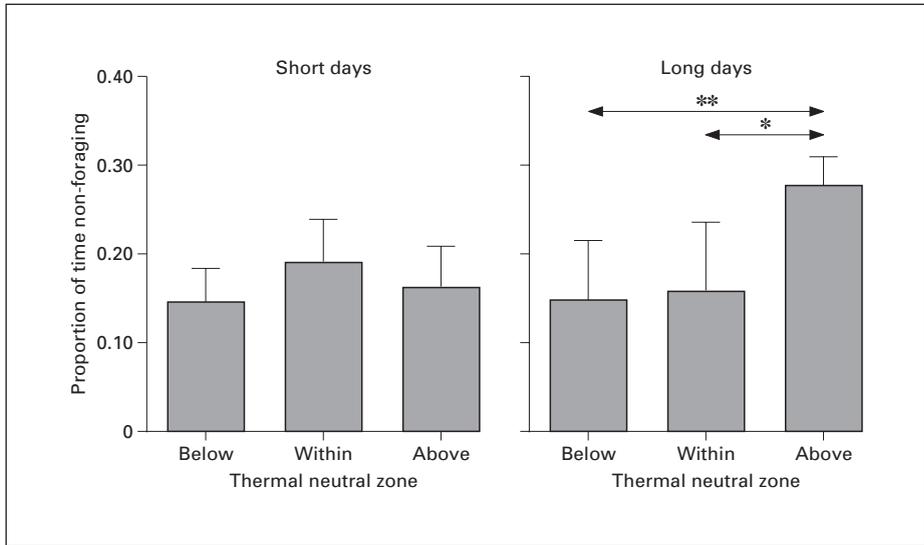
### *Is Day Length an Ecological Constraint?*

Table 1 displays the relationships between mean monthly day length and activity levels (in hours: see Hill et al. [2004a]) for foraging (feeding plus moving) and non-foraging (grooming plus resting) behaviour, and the four major behavioural cat-



**Fig. 1.** The relationship between mean monthly day length and the number of hours per day spent in foraging (a) and non-foraging (b) activity.

egories individually. Both foraging and non-foraging activities are significant positive functions of day length (fig. 1), and these relationships hold true for grooming and resting behaviour alone. Although, superficially, the result is an obvious one, the baboons spend more time engaged in a particular behaviour when there is more time available, there is no a priori reason to predict that behaviour should increase lin-

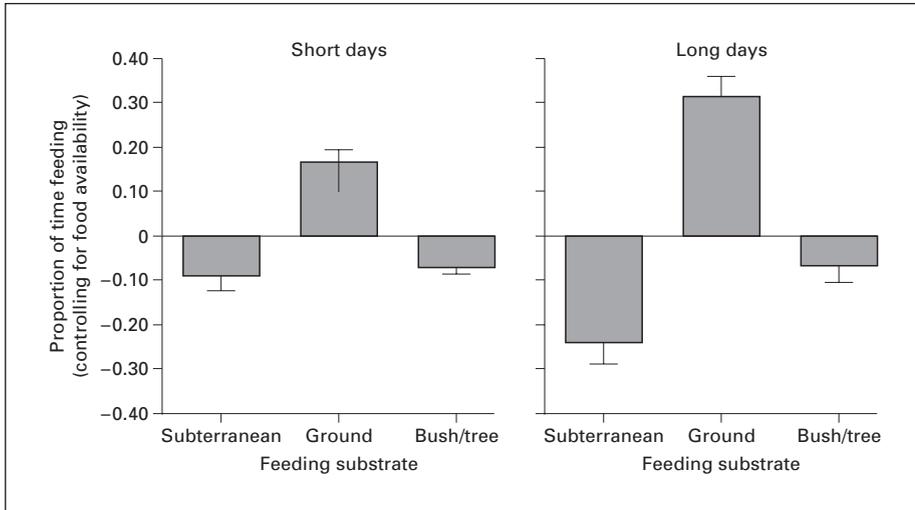


**Fig. 2.** Proportion of time spent non-foraging over the midday period (10:30–16:30) under short day lengths and long day lengths for perceived environmental temperature values below, within and above the approximate thermal neutral zone for baboons. Horizontal lines reflect significant post-hoc comparisons (Scheffé: \*\*  $p < 0.001$ ; \*  $p < 0.02$ ).

early with day length. Indeed, these relationships indicate that the animals are not spending as much time as they would like in a particular behaviour when day lengths are short. This confirms that day length is indeed an ecological constraint. The fact that the relationship does not hold true for feeding and moving when considered alone almost certainly reflects the confounding effects of differential monthly food availability (see Hill et al. [2003] for relationships controlling for climatic variation). Nevertheless, given that total foraging time is constrained by day length it is clear that day length is an important constraint on behavioural patterns each month.

#### *Do Long Day Lengths Permit Behavioural Flexibility in Relation to Thermoregulation?*

Previous analyses have indicated that the baboons at De Hoop respond to high temperatures by engaging in more sedentary activities (mostly resting and grooming: Hill et al. [2003]; Hill [2005, 2006]). Figure 2 displays the proportion of time spent in non-foraging behaviour for perceived environmental temperatures below, within and above the approximate thermal neutral zone for baboons. The results presented here are restricted to the midday period (10:30–16:30) since not only are thermal constraints likely to be most significant during this period [Wheeler, 1994], but this also controls for possible time-of-day effects (high levels of resting and grooming on sleeping sites at dawn and dusk may result in an apparent association of these activities with low temperatures [Hill, 2005]). Under long days, significant differences exist in levels of non-foraging behaviour across the three thermal neutral zone categories (ANOVA:  $F_{(2, 44)} = 7.27$ ,  $p = 0.002$ ). Post-hoc comparisons reveal that it is



**Fig. 3.** Residual proportion of time spent foraging from the subterranean, ground and bush/tree levels, controlling for food availability in each layer, under short day lengths and long day lengths.

the ‘above’ category that differs significantly from the other two. This relationship is primarily due to an increase in resting as temperatures increase ( $F_{(2, 42)} = 4.93$ ,  $p < 0.02$ ), with a concomitant decline in feeding under conditions of thermal stress ( $F_{(2, 42)} = 3.56$ ,  $p < 0.05$ ). As a consequence, these results mimic the relationships for this population as a whole [Hill, 2006]. No significant differences exist between the thermal neutral zone categories in non-foraging under short days ( $F_{(2, 46)} = 1.23$ , n.s.) nor for resting ( $F_{(2, 46)} = 0.72$ , n.s.) or feeding ( $F_{(2, 46)} = 1.42$ , n.s.) alone. Increasing day length thus provides the opportunity for behavioural flexibility in thermoregulatory responses.

*Do Long Day Lengths Permit Behavioural Flexibility in Relation to Foraging and Diet Choice?*

In order to assess the importance of day length variation on foraging, patterns of diet choice were classified on the basis of three broad categories; subterranean, ground and bush/tree level food items. Figure 3 displays the mean proportion of diet selected by individuals from each of the substrate levels, controlling for the proportion of time predicted on the basis of food availability each month in each substrate level. It is clear that similar patterns of diet choice exist under conditions of both long and short days. Subterranean and bush/tree food items are generally under-represented in the diet, with ground level items consumed at levels greater than predicted on the basis of food availability. Nevertheless, significant differences exist between the long and short days in the proportion of subterranean foods ( $t$  test:  $t = 4.59$ , d.f. = 31,  $p < 0.0001$ ) and ground level items ( $t = -4.77$ , d.f. = 31,  $p < 0.0001$ ) in the diet. No differences exist in the proportion of bush/tree level food items ( $t = -0.15$ , d.f. = 31, n.s.). Because the different substrate levels are associated with different food types (ta-

**Table 2.** Percentage representation of food types in the diet of individuals feeding from the bush/tree, ground and subterranean substrate levels

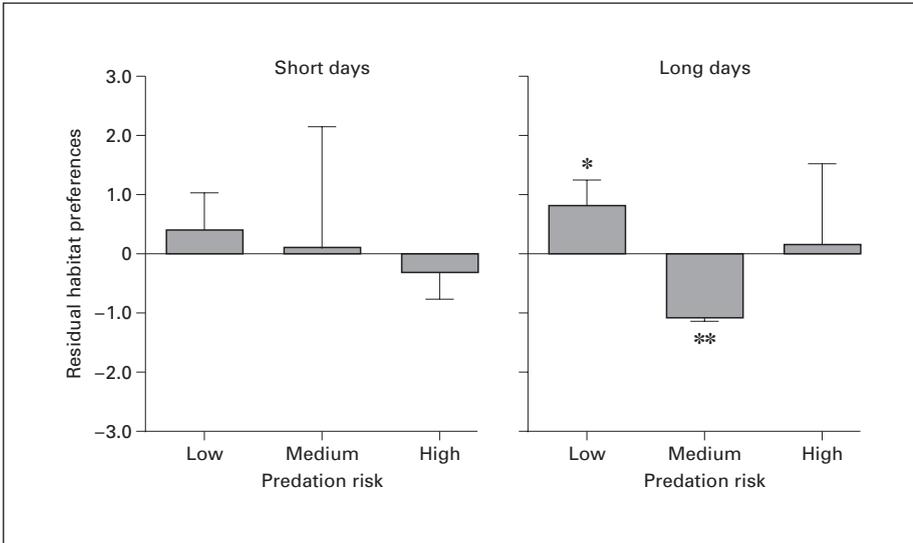
Feeding Level	Food type					
	fruits	seeds	flowers	leaves	roots	bulbs/corms
Bush/Tree	25.1	70.1	4.5	0.1	–	–
Ground	22.8	14.7	9.9	46.1	0.1	0.1
Subterranean	–	–	–	–	87.3	12.7

ble 2), the increase in food items from the ground layer during the long summer months may be due to the baboons selecting for increased dietary diversity. Table 2 clearly illustrates that the ground layer offers the greatest range of food types and should thus offer the greatest opportunity for diet selection. Increased dietary diversity has been reported in response to increased food availability at Amboseli, Kenya [Post, 1982], suggesting that when choice is available baboons select for diversity. Alternatively, it may simply be that when sufficient time is available, the baboons avoid the energetic and time costs of excavating subterranean food items [Whiten et al., 1990], and instead focus on items more easily harvested (which are likely to come from the ground layer). Either way, the results suggest that the additional time available in the summer months is being utilised as part of a more flexible foraging strategy.

*Do Long Day Lengths Permit Behavioural Flexibility in Relation to Predation Risk?*

Previous analyses of the patterns of habitat choice in baboons have indicated that high-risk habitats are used less frequently than predicted on the basis of food availability, and this trade-off is influenced by group size [Cowlshaw, 1997]. At De Hoop, only the smallest study group (ST: size range 17–21 individuals) was observed to trade-off food availability with predation risk (this troop is not included in the analyses presented here). It was concluded that the largest group (VT) was unable to respond to predation risk due to foraging constraints [Hill, 1999]. The possibility exists, however, that subtle trade-offs with predation risk are made by the largest study group during the long summer days.

Habitat preferences each month were determined on the basis of Krebs' Electivity Index [Krebs, 1989]. Under conditions of both long and short days, habitat preferences were a strong positive factor of habitat food availability (short days:  $r^2 = 0.247$ ,  $F_{(1, 16)} = 5.25$ ,  $p < 0.05$ ; long days:  $r^2 = 0.427$ ,  $F_{(1, 16)} = 11.93$ ,  $p = 0.003$ ). The residuals from these relationships can be used to control for differential food availability each month and figure 4 displays the mean residual habitat preferences for low-, medium-, and high-risk habitats [Hill, 1999]. For short days, the residuals show no significant differences on the basis of predation risk (1-sample t test: low-risk:  $t = 1.558$ , d.f. = 5, n.s.; medium-risk:  $t = 0.105$ , d.f. = 5, n.s.; high risk:  $t = -2.004$ , d.f. = 5, n.s.), indicating that habitats are selected purely on the basis of food availability. When day lengths are longer, however, significant differences emerge in the response to predation risk. The baboons show a significant preference for foraging



**Fig. 4.** Residual proportion of time spent in low, medium and high predation risk habitats, controlling for food availability in each habitat, under short day lengths and long day lengths. Asterisks indicate significant differences from the proportion of time in habitat predicted by food availability (\*\*  $p < 0.001$ ; \*  $p < 0.005$ ).

in low-risk habitats ( $t = 4.817$ ,  $d.f. = 5$ ,  $p < 0.005$ ), with medium-risk habitats significantly avoided ( $t = -44.036$ ,  $d.f. = 5$ ,  $p < 0.001$ ). Interestingly, high-risk habitats appear to be utilised exactly as predicted on the basis of food availability ( $t = 0.293$ ,  $d.f. = 5$ ,  $n.s.$ ). Thus, while there is evidence that the baboons prefer low risk habitats when day lengths are sufficiently long to permit foraging flexibility, it is the medium-rather than high-risk habitats that are underutilised. One possible explanation is that one of the high-risk habitats (climax fynbos) surrounds a number of sleeping sites, and although it is low in food availability, it must nevertheless be utilised by the baboons on their foraging pathways. A second issue, however, is that with all of these analyses, it is impossible to consider one factor in isolation. Previous analyses have indicated that baboons respond to high midday temperatures by seeking shade in safe habitats (mostly cliffs: Hill [2006]). Since the medium-risk habitats at De Hoop offer no shade, thermoregulation, as much as predation risk may be important in decisions about habitat utilisation. Thus, while long day lengths may permit behavioural flexibility to predation risk, other factors, including food availability and thermoregulation, are undoubtedly important.

## Discussion

By inhabiting a highly seasonal environment, the baboons at De Hoop experience variable time constraints across the annual cycle. Short days represent a behavioural bottleneck that restricts levels of activity during these months. Since animals

must live in social contexts that allow them to pass through these bottlenecks without significant foraging and reproductive constraints, however, months with longer days provide access to additional time that can be utilised strategically to permit behavioural flexibility in relation to a number of ecological and social factors. The analyses presented here illustrate that baboons can utilise long day lengths for more flexible thermoregulatory, foraging and antipredation strategies. While a detailed discussion of these relationships is not the focus of this paper, it is clear that they provide general support for primates behaving flexibly when environmental conditions permit. This confirms that temperature, diet and predation could all be important factors driving the evolution of cathemerality. Nevertheless, some of the results, in particular those for habitat choice and predation risk, are difficult to interpret in isolation. Since high temperatures, high food availability and long day lengths are all associated with the summer months a level of interdependence in patterns of behaviour is inevitable. To fully explore these factors in future, therefore, and to also assess the importance of such factors in cathemeral systems, will ultimately require multivariate analysis on large and complete datasets in order to tease the different factors apart.

If extended activity periods can be used strategically for more flexible activity patterns, the question arises as to why the De Hoop baboons do not extend their activity period into the nocturnal phase during the winter months when day lengths are short? Furthermore, for baboons in equatorial populations, the question could similarly be asked as to why these animals do not extend their activity periods during times of low food availability or high thermoregulatory stress, and this question could equally be extended to most primates. Although certain nocturnal primates may exhibit diurnal activity in response to specific ecological conditions [Bearder, 1987], cathemerality appears to be predominantly the preserve of a few lemur species and owl monkeys. Since cathemerality is not an unusual activity pattern across mammals [Curtis and Rasmussen, 2006], the question arises as to why is it so rare among primates. Why are not more primates cathemeral?

The answer appears to be a straightforward one: predation. In relation to baboons, Cowlshaw [1994] reviewed the available literature and concluded that leopards (*Panthera pardus*) were the principal predator, with lions (*Panthera leo*) representing the secondary threat. Although diurnal predation represented the rule for lions, leopards were predominantly nocturnal predators and were generally the more successful hunters. For leopards, nocturnal attacks were significantly more likely to be successful and this result is particularly interesting given that all of these attacks were on sleeping sites that baboons had selected for their properties as predator refuges [Hamilton, 1982]. For a diurnal primate, therefore, nocturnal (or cathemeral) predators represent a significant threat even when the animals are on a refuge. It is thus highly likely that a baboon foraging away from a refuge during the nocturnal period would experience an even greater risk. For baboons and probably most primates, therefore, the costs of predation outside of their normal activity phase are likely to be prohibitively high and prevent activity from extending into a different phase under all but the most extreme ecological conditions.

What does this mean for cathemerality? If predation is the principal constraint preventing cathemerality in most primate species, then a logical corollary is that the unique predatory environment of Madagascar must in some way permit the behavioural flexibility exhibited by the cathemeral lemurs. It has certainly been suggested that for owl monkeys, the presence of the nocturnal great horned owl, coupled with

the absence of large diurnal raptors in the Paraguayan Chaco, may be the ecological conditions favouring diurnal activity and thus cathemerality in this *Aotus* population [Wright, 1989, 1994]. While greater knowledge of owl monkey predator communities is undoubtedly required before differential predation risk can be used to account for *Aotus* cathemerality in certain populations [Fernandez-Duque et al., 2001], the results are certainly consistent with predation being a key constraint on the evolution of cathemerality. Furthermore, certain authors have proposed that the switch to a cathemeral or diurnal lifestyle in the lemurs of Madagascar has been possible due only to the recent extinction of several large, mostly diurnal raptors [Goodman, 1994; van Schaik and Kappeler, 1996; Kappeler and Erkert, 2003; but see Csermely, 1996], and that cathemerality may thus represent a transitional stage.

Colquhoun [2006] has argued that lemur cathemerality may be a specific response to the threat of predation by fossa, with the predator-prey relationship developing via one of two routes. Firstly, fossa may have become cathemeral to track the activity of their cathemeral lemurid prey, such that a stable system of cathemeral predator and prey now exists. In such a scenario, predation is unlikely to be the driving force for lemur cathemerality. Alternatively, fossa may have become cathemeral in response to prey seasonality, with lemurs responding to the fossa activity patterns by adopting cathemeral activity as a means of temporal crypticity. In light of the discussion here, this latter argument has merit, although such a system could probably develop only under specific conditions. For example, any transition from a nocturnal lifestyle to one involving significant activity in the diurnal phase is unlikely to proceed with a full guild of diurnal predators [cf. van Schaik and Kappeler, 1996; Kappeler and Erkert, 2003]. As such, it is probably only consistent with cathemerality as a recent transition. Nevertheless, under certain conditions it seems likely that fossa predation could be the primary selective force favouring an ancestral evolution of cathemerality. Kappeler and Erkert [2003] have argued, on the basis of available data, that cathemeral activity in extant lemurs evolved from nocturnal or crepuscular ancestors. This latter ancestral state seems particularly relevant to the importance of predation in the evolution of cathemerality and may account for how the unique predator guild of Madagascar permits such a flexible strategy.

Curtis and Rasmussen [2002] review the three major modes of cathemerality in lemurs, with each mode differing in terms of the seasonality and frequency of use of the diurnal and nocturnal periods. A consistent feature of all of the cathemeral activity patterns, however, is the activity peaks around dawn and dusk. While bimodal activity patterns are observed for many diurnal and nocturnal species [Aschoff, 1966], activity is nevertheless confined to either the light or dark phase. What is unusual in cathemeral species, however, is that the activity peaks are often centred on sunrise and sunset and thus extend into both phases. These crepuscular peaks in activity could result from an adaptive response to fossa predation that could ultimately explain the evolution of cathemeral activity patterns.

Although cathemeral, recent evidence suggests that the fossa exhibits a peak in activity during the middle of the nocturnal phase [Hawkins, 1998]. As a consequence, risk of predation is also likely to peak at this time for nocturnal species. For a nocturnal lemur exhibiting a bimodal pattern of activity, a temporal shift in activity towards the crepuscular periods may thus represent an adaptive response to the risk of predation. Through shifting activity away from the peak in fossa activity, a crepuscular species may affect a degree of temporal avoidance of this predator, with-

out completely exposing themselves to the risks presented by diurnal predators. Furthermore, since fossa often attack lemurs in their sleeping trees [Wright et al., 1997], this temporal shift may further reduce risks if animals are most easily located as they are retiring to, or waking from, these rest periods. It is certainly true that cathemeral lemurs (*E. fulvus*) are underrepresented in the diet of fossa in relation to their availability at Kirindy, with most nocturnal genera (*Microcebus*, *Lepilemur*, *Phaner* and *Mirza*) as well as the diurnal sifaka (*Propithecus verreauxi*) overrepresented in relation to their abundance [Hawkins, 1998]. This suggests that an ancestral shift from a nocturnal bimodal activity pattern to a crepuscular bimodal pattern with peaks centred on sunrise and sunset may have been an adaptive response to temporal variation in the risk of predation posed by the fossa.

Since the transition from a nocturnal to a low-light crepuscular species is unlikely to require the same degree of morphological adaptations as a complete transition to the diurnal phase, this could account for the unusual and intermediate characteristics of the visual system of cathemeral lemurs [Heesy and Ross, 2001]. Nevertheless, while potentially reducing the risk of fossa predation, the crepuscular period provides insufficient time for the primates of the body size of *Eulemur* and *Hapalemur* to conduct all of their essential (foraging) activities. Thus cathemerality, through the extension of activity into the diurnal and/or nocturnal phase, is essential. These troughs [Aschoff, 1966] or 'tails of activity' outside the crepuscular period are determined on the basis of the prevailing ecological constraints. The costs and benefits of each phase in relation to factors such as nocturnal illumination, thermoregulation, differential food availability and the risk of predation by raptors will determine whether the additional activity extends into the diurnal or nocturnal period. Such costs and benefits would be expected to vary over the annual cycle giving rise to seasonal shifts in activity period. Nevertheless, if the specific hunting strategy of the fossa is central to the evolution of cathemerality in lemurs, crepuscular peaks in activity should remain consistent throughout the year.

In summary, baboons will exploit extended activity periods to respond strategically to factors such as temperature, food availability and the risk of predation. For most primates though, the costs of predation appear to prevent the expansion of activity outside the phase for which their visual system has adapted. In Madagascar, however, the unique predator community, dominated by the cathemeral fossa, may have created a niche for the temporal avoidance of this predator through cathemeral activity, based on a crepuscular template. This suggests that cathemerality is an ancestral state for *Eulemur* and *Hapalemur*, arising through a crepuscular ancestor. Nevertheless, a recent transition to a more diurnal lifestyle is also consistent with this framework if the reduction in diurnal raptor predation risk changes the cost-benefit ratio for greater 'tails of activity' into the diurnal phase. It is clear, however, that there is still much to be explained. Future research needs to determine whether the crepuscular peaks in activity do indeed represent a temporal response to fossa predation or are simply the characteristic bimodal activity patterns observed in many species. Furthermore, the behavioural ecology of the fossa is still relatively poorly understood and thus further studies of its activity patterns, diet and hunting strategy are required to elucidate fully the importance of this predatory species.

## Acknowledgments

I thank Debbie Curtis, Guiseppe Donati and Michele Rasmussen for the invitation to participate in the cathemerality symposium at IPS and to contribute this paper. Attendance at the IPS Conference in Turin was assisted by a Royal Society Conference Grant. I am grateful to Louise Barrett, Peter Henzi and Cape Nature Conservation for permission to work at De Hoop Nature Reserve, and to Tony Weingrill for assistance in the field. I thank Debbie Curtis and two anonymous referees for their constructive comments on an earlier draft of this paper.

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