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Variations in behavioural patterns between *Lemur catta* groups living in different forest types: implications for conservation

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ABSTRACT: Implementing effective primate conservation strategies requires knowledge of species' ecological and behavioural parameters. The protection of all habitat types required for preserving viable dispersion and gene flow between disparate populations necessitates a thorough understanding of the behavioural flexibility of a species. Ring-tailed lemurs *Lemur catta* inhabit a plethora of habitats throughout southern Madagascar but, hitherto, research has been restricted primarily to riverine gallery forests. The present study presents comparative data on the activity budgets and foraging behaviour of 2 *L. catta* groups living in different habitats at Berenty Reserve, Madagascar. Data were collected for 2 mo on groups living in a xerophytic spiny forest and a riverine gallery forest. The spiny forest group spent significantly more time in inactive behaviours compared with the gallery forest group. This strategy of apparent energy minimization allows *L. catta* to thermoregulate despite decreased water availability and high ambient temperatures. The spiny forest group spent significantly more time feeding on small fruits of succulent trees, which we associate with the group's significantly higher rate of feeding agonism compared with the gallery forest group. These results demonstrate the high behavioural and ecological flexibility of *L. catta*, suggesting that xerophytic spiny forests might be a vital habitat type for *L. catta* conservation efforts. Future research should advance knowledge of the resources needed to sustain *L. catta* populations in other xerophytic spiny forests.

KEY WORDS: *Lemur catta* · Spiny forest · Gallery forest · Activity budget · Behavioural flexibility

INTRODUCTION

The island of Madagascar, a hotspot of biodiversity (Myers et al. 2000), has experienced anthropogenic modification for nearly 2 millennia, but habitat destruction has recently accelerated in intensity (Green & Sussman 1990, Casse et al. 2004). Northern and eastern rainforests have received vital research and conservation attention, but much of the endemic spiny forest of southern Madagascar is poorly understood, and thus should be a focus of future research efforts (Bodin et al. 2006). This arid eco-region, estimated to have been 5 million hectares large in 2003 (Wells 2003), is highly impacted by continual anthropogenic change, including slash and burn agriculture, charcoal production and livestock maintenance (Scott et al. 2006). Spiny forests contain a high diversity of lemurs, including members of the taxonomic families Cheirogaleidae, Lepilemuridae, Lemuridae and Indridae (Sussman 2002). Thus, the spiny forest ecoregion is a conservation focal point, and its preservation is essential to sustaining lemur diversity throughout the region.

A key species in the maintenance of spiny forests is the ring-tailed lemur *Lemur catta* (Bodin et al. 2006, Scott et al. 2006). *L. catta* are highly adaptable and

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currently range in numerous habitat types throughout southern Madagascar, including gallery forest, xerophytic forest, brush and scrub, spiny, dry deciduous forest, sub-alpine ericoid bush and rocky outcrop forest surrounded by anthropogenic savannah (Sussman et al. 2003, Goodman et al. 2006, Gould 2006). Although *L. catta* occur in these varied habitats, the majority of *L. catta* behavioural and population ecology field studies have been conducted in riverine gallery forests (e.g. Jolly 1966, Sussman 1974, 1977, 1991, 1992, Gould 1990, 1992, 1996a,b, 1997a,b, Sauther 1993, 1994, 1998, Nakamichi & Koyama 1997, Gould et al. 1999, 2003, Koyama et al. 2001, Jolly et al. 2002, but see Gould et al. 2009). Little research has focused on populations in other habitats, although non-gallery forest research is beginning to occur at a few sites, including sub-alpine ericoid bush (Goodman & Langrand 1996, Goodman & Rasolonandrasana 2001), spiny forest (Gould et al. 2009, 2011, E. Kelley unpubl. data, M. LaFleur unpubl. data) and rocky outcrop forests surrounded by anthropogenic crop production (Gould et al. 2010, A. Cameron & L. Gould unpubl. data).

Goodman et al. (2006) suggest that *Lemur catta* may have evolved in arid habitats rather than gallery forests throughout southern Madagascar and, although they are found in smaller populations in these areas than in riverine gallery forests (Goodman & Langrand 1996, Sussman et al. 2003, Jolly et al. 2006), several physical and behavioural traits support this claim. *L. catta* is characterized by the ability to live in areas without groundwater and with few water-based food items (Goodman et al. 2006). Furthermore, *L. catta* has the ability to decrease basal metabolic rate when food resource availability is low (Pereira et al. 1999). *L. catta* is more terrestrial than other lemur taxa, spending an average of 30% of its time on the ground (Sussman 1977). Moreover, *L. catta* populations can rebound from periods of decreased habitat productivity, natural disasters and extended periods of drought, as their relatively precocial life history pattern allows juveniles to reach reproductive age quickly, compared with many Haplorhine primates (Gould et al. 1999, 2003, Gould 2006, Goodman et al. 2006), and females normally give birth once per year (Jolly 1966, 1984, Sauther 1991). Thus, *L. catta* have been characterized as a ‘weed’ species because of their abilities to live in harsh environments with extremes of heat and frost, exploit a variety of high and low quality food items, and survive periods of intense water scarcity (Gould et al. 1999, 2003, Goodman et al. 2006, Gould 2006).

Lemur catta is currently categorized as Near Threatened on the IUCN Red List, because one quarter of its population has disappeared over the past 25 yr owing to substantial habitat loss (IUCN 2009). The future of this species and the endemic spiny forests are intricately tied together. Because individuals and groups disperse across dry riverbeds and open habitats (Goodman et al. 2006), *L. catta* serve as primary seed dispersers between different patches of spiny forest habitats, a function that can maintain seemingly fragmented pockets of forest (Ganzhorn et al. 1999, Bodin et al. 2006). Although traditional taboos on vast forest destruction may help to maintain, even unintentionally, *L. catta* populations at a sustainable level (Bodin et al. 2006), small spiny forest patches are highly vulnerable to anthropogenic pressures, decreasing the ability of *L. catta* to occupy such forests. Intensive agricultural practices, specifically tavy slash and burn forest clearance, have reduced viable habitats for *L. catta* throughout their range (Fenn & Rebara 2003, Kelley et al. 2007). Sustained spiny forest habitat destruction limits *L. catta* gene flow because of the lack of small forest patches through which to disperse (Bodin et al. 2006). Thus, an improved effort to ensure the viability of *L. catta* populations must identify spiny forest fragments that can be effectively protected and monitored.

Long-term conservation strategies require knowledge of the resource use and behaviour of a species within its geographic range. The lack of comparable data on *Lemur catta* in highly diverse habitats makes current knowledge of this species' behavioural ecology incomplete (Gould 2006). Furthermore, proposed models of *L. catta* evolution may be better understood with a more complete account of behavioural trends in habitats in which its evolutionary history has occurred (Gould 2006). The present study provides initial data on behavioural strategies of *L. catta* in spiny forest habitats and aims to engender future studies that will enhance the ability to sustain and connect genetically diverse populations of this species of lemur.

In this study, we contrast activity budgets, feeding behaviour and feeding competition of *Lemur catta* living in spiny forest habitats with those living in gallery forest habitats in Berenty Reserve, southern Madagascar. This comparative study provides a better understanding of simultaneous behavioural variation and reports behavioural strategies of *L. catta* in xerophytic spiny forests. We report differing behavioural strategies used in ecological settings that vary in ambient temperature, water availability, canopy cover and food type during the annual birth and early lactation season (September to November). This period coincides with the height of the dry season in southern Madagascar (Jolly 1984, Sauther 1994, 1998), which is characterized by very high ambient temperatures and a decrease in available drinking water (Fenn 2003). Because resource abundance is low during this period compared with the rainy season (Jolly 1984, Rasamimanana & Rafidinarivo 1993, Sauther 1998, Sauther et al. 1999), strict reproductive seasonality in this primate means that lactating females are in need of, and competing for, scarce resources (Sauther 1993, Sauther et al. 1999).

MATERIALS AND METHODS

Research site: Berenty Reserve, Madagascar

Berenty Private Reserve, southern Madagascar, is a 240 km^2 ecotourism site located on the banks of the Mandare River: 25° 0.5′ S, 46° 18.5′ E (Jolly 1966, Jolly et al. 2006) (Fig. 1), owned and managed by the de Heaulme family (Jolly et al. 2006). The reserve receives 400 to 520 mm of rainfall between November and February, comprising 70% of the annual rainfall (Pride 2003). During our study, maximum daily mid-day temperatures in the open spiny forest reached 40 to 45°C, whereas temperatures were greater than 5°C cooler at the same time in the closed canopy gallery forest.

Data were collected between 4 September and 4 November 2006, corresponding to the end of the dry season in southern Madagascar and the late gestation and early to mid lactation seasons of *Lemur catta*. Data were collected on *L. catta* groups in 2 different ecological zones: the closed canopy Ankoba gallery forest and the xerophytic spiny forest parcel, 3 km from one another (Fig. 1). At Berenty, the gallery forest is a secondary forest, which contains both native and introduced plant species. Along with native *Tamarindus indica* trees, this habitat contains introduced *Pithecellobium dulce*, *Azadirachta indica* and *Leucaena leucocephala* (Soma 2006). The forest borders the Mandare River, which provides ample groundwater for large fruit trees. The river also provides drinking water for *L. catta* groups, even in the middle of the dry season when small puddles remain in the large riverbed. One of the reserve's main water wells is located in the middle of the forest along with small water troughs, which provide easily accessible drinking water for *L. catta* groups.

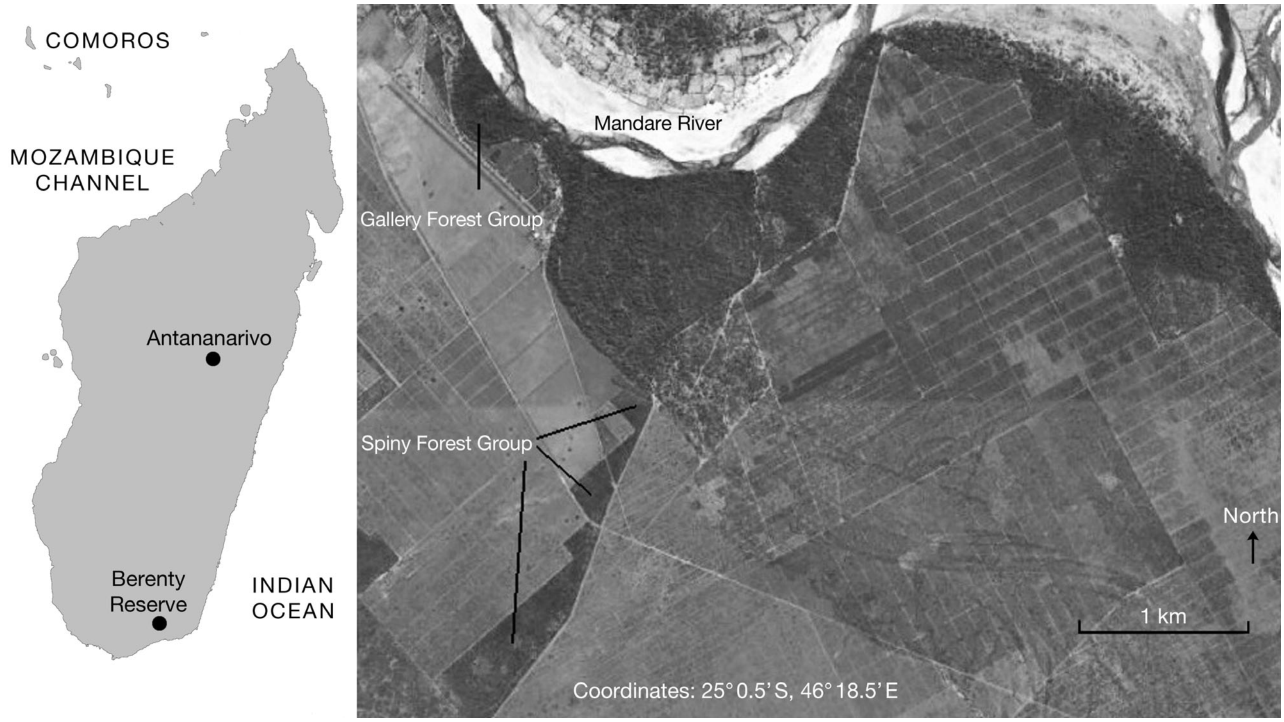

Fig. 1. Location of the study site in Madagascar (left) and within Berenty Reserve (right), with Mandare River forming the northern boundary of the reserve. The spatial proximity between the habitats of the 2 study groups (gallery forest and spiny forest) is shown; the remainder of the park is anthropogenic sisal plantation

The entry point to the spiny forest at Berenty Reserve is marked by a nearly 7 m vertical hill above a scrub forest habitat, which was most likely the outer edge of the Mandare River in the past, and thus represents the end of the supply of groundwater that supports large fruiting trees (Jolly et al. 2006). No extensive studies of spiny forest ecology at Berenty Reserve currently exist, but all plant species found in the spiny forest are endemic to this specific forest type, which has evolved to survive in areas with low-nutrient soils, high temperatures during the summers and low amounts of rainfall (Grubb 2003, Fenn 2003). This forest type is dominated by the plant family Didiereaceae, especially the genus *Alluaudia*, which is characterized by tall yet slender trees with thorny trunks and branches, and *Euphorbia candelabra*, characterized by low-lying succulent vines (Fenn 2003, Grubb 2003). *Gyrocarpus americanus*, *Agave sisalana* and *Opuntia vulgaris* are also found in the Berenty spiny forest parcel (Charrier et al. 2007). All trees have small and exposed canopies and are significantly shorter than trees in the gallery forest at Berenty. Compared with the gallery forests, all spiny forest plants are highly exposed to solar rays, resulting in a lack of a true canopy and very little shade (Gautier & Goodman 2003). Beginning in late October 2006, the spiny forest group periodically moved into the surrounding sisal plantations to feed on the flower buds, flowers and pith of *Agave sisalana*. These plants produce no canopy or shade and are characterized by tall exposed stalks with flowers at the tip.

Data collection methods

Data were collected using 15-min continuous time focal animal sampling methods (Altmann 1974). All behaviours of the focal animal were recorded and the exact start and stop time of each behaviour was noted. Ad libitum sampling was used to collect unusual occurrences, such as predation attempts on *Lemur catta* and inter-group conflicts between *L. catta* groups. Time, to the second, was recorded at the beginning of each behaviour. A total of 942 15 min focal animal data sessions were collected (mean no. of sessions: spiny = 54, gallery = 84), totalling 235 h of data collection (Table 1). Data were collected 6 d per week for the entire study period. Groups were observed on alternating days to ensure that hours of data collected were similar between groups and that changes in flora in either habitat were accounted for. Within study groups, the day was separated into 5 periods (morning, 7:00–10:00 h; late morning, 10:00–12:00 h; early afternoon, 12:00–14:00 h; mid-afternoon, 14:00-16:00 h; late afternoon, after 16:00 h). These time periods were used to establish daily patterns of activity within and between groups and are referred to numerically as time periods 1 to 5 in the 'Results' section.

Table 1. Number of hours and sessions of data collected in each habitat on individual focal *Lemur catta*. Abbreviations present names of study individuals. F: female; M: male

Individual	Sex	Hours	Sessions
Spiny forest			
LOL	F	14.08	56
LUC	F	13.43	53
LIN	F	14.03	56
DRA	M	12	48
DAN	M	14.16	56
DNT	M	14.26	57
Mean		13.66	54.33
Gallery forest			
KRS	F	18.9	76
MAJ	F	22.4	90
HLN	F	21.8	87
FNA	F	22.1	88
GAS	M	21.2	85
JAC	M	20.7	83
SEB	M	19.9	80
Mean		21.02	84.14

Behaviours scored in time allocation data were: feeding, foraging, locomotion, sitting, resting, social behaviour and vigilance. Resting and sitting were categorized as inactive behaviours, whereas all other behaviours were categorized as active behaviours. Nearest neighbour distance was scored as near (<2 m), medium (2 to 5 m) and far (>5 m).

The total rate of agonism was calculated by dividing the total number of agonistic behaviours by the total number of hours recorded. The rate of agonism in behavioural contexts was calculated by dividing the total number of agonism events during the behaviour by the total duration of the behaviour.

Sample sizes for each group were too small to meet the assumptions of parametric statistical tests, so comparisons of behaviours between groups were assessed using non-parametric statistical tests. The Mann-Whitney *U*-test was used to compare data between groups. Friedman's ANOVA was used to test for variations in activity between different time periods throughout the day within the spiny forest group. Results were deemed significant at $p < 0.05$.

RESULTS

Time allocation

Individuals living in the gallery forest group (n = 7) spent a significantly greater proportion of time feeding and foraging than those in the spiny forest group (n = 6) (Table 2). Resting occurred significantly more often in the spiny forest group than in the gallery forest group, as did sitting while awake. Lemurs in the gallery forest group engaged in significantly more social behaviour compared with the spiny forest group (Table 2). There were no significant differences in the proportion of time spent in locomotion. Cumulatively, the gallery forest group spent a greater proportion of time engaged in active behaviours compared with the gallery forest group.

To identify patterns of behaviour throughout the day, the percentage of time spent in active behaviours was analyzed within 5 separate time categories. Individuals in the gallery forest group spent significantly more time in active behaviours in the early morning, late morning, and mid-afternoon compared with individuals in the spiny forest group, whereas the groups spent similar proportions of time in active behaviours in the early and late afternoon (Table 3). There were significant differences in the proportion of active behaviours between all time categories (Friedman test: $p < 0.001$, n = 6) among the spiny forest group only. Post hoc tests were conducted to determine which time categories were significantly different from each other. Based on an alpha value of 0.001, pairwise ranked sums were used to compare the proportion of active behaviour between time categories. There were no significant differences in the percentage of active behaviour between time periods 2, 3 and 4 or between time periods 1 and 5 ($p = 0.001$). However, *Lemur catta* in the spiny forest were significantly more active in the early morning and later afternoon than during the middle of the day ($p = 0.01$, Bonferoni adjustment; Table 2). This analysis shows that the spiny forest group limited active behaviours except during the earliest and latest periods of the day.

Table 2. *Lemur catta*. Median (interquartile range) percentage of time allocated by lemurs to behaviours between spiny forest and gallery forest groups

Behaviour	Spiny	Gallery	*U*	p
Foraging/feeding	14.9 (5)	30 (4.4)	0	<0.005
Locomotion	7.6 (1.4)	7.1 (2.3)	17	0.63
Resting	52.3 (3.7)	34.3 (5.4)	0	<0.005
Sitting	20.5 (4.6)	14.8 (1.3)	0	<0.005
Socialising	2.6 (2.9)	8.8 (4.25)	3	<0.01
Active	26.4 (7.7)	49.1 (3.3)	0	<0.005
Inactive	73.6 (7.6)	50.9 (3.3)	0	<0.005

Table 3. *Lemur catta*. Median (interquartile range) percentage of time spent by lemurs in active behaviours between spiny forest and gallery forest groups in different time periods

Time period (h)	Spiny	Gallery	*U*	p
7:00–10:00	48 (15.3)	80 (13)	3	<0.005
10:00–12:00	15 (8.3)	37 (6.5)	3	<0.005
12:00–14:00	8 (9.3)	12 (6)	31.5	0.14
14:00–16:00	23 (8.8)	47 (13)	3	<0.005
After 16:00	68 (18.5)	73 (4.5)	27	0.45

Feeding and foraging behaviour

The spiny forest group consumed 14 plant species during the study period. Two of these, *Agave sisalana* (sisal) and *Opuntia vulgaris* (Mexican prickly pear), are not native to Madagascar's spiny forest ecosystem and are found in some semi-desert habitats outside Madagascar (Felger 2000). The gallery forest group consumed a total of 11 species, the majority of which (6 out of 11) are not endemic to Madagascar. Both study groups were observed consuming fruit and leaves of *Tamarindus indica* and leaves of *Opuntia vulgaris*. *T. indica* are located throughout the gallery and scrub forests at Berenty but not in the spiny forest; the spiny forest group occasionally moved into the scrub forest area to feed on *T. indica.*

Individuals in both groups consumed a variety of plant parts, including mature and immature fruits and leaves, stems, leaf buds, flowers and leaves of succulent plants. Soil was consumed occasionally. The 2 groups differed significantly in their consumption of both fruits and flowers. The spiny forest group spent significantly more time eating fruit (57.1%) compared with the gallery forest group (26.2%) ($U = 0$, $p < 0.005$), whereas the gallery forest group spent significantly more time consuming leaves ($U = 0$, $p < 0.005$; Fig. 2). The 2 groups showed significant differences in spacing while feeding on the 2 most common food items: fruit and leaves. While feeding on fruit, the spiny forest group spent a significantly greater proportion of time within 2 m of their nearest neighbour ($U = 4$, $p < 0.05$) and a significantly smaller proportion of their feeding time more than 5 m from

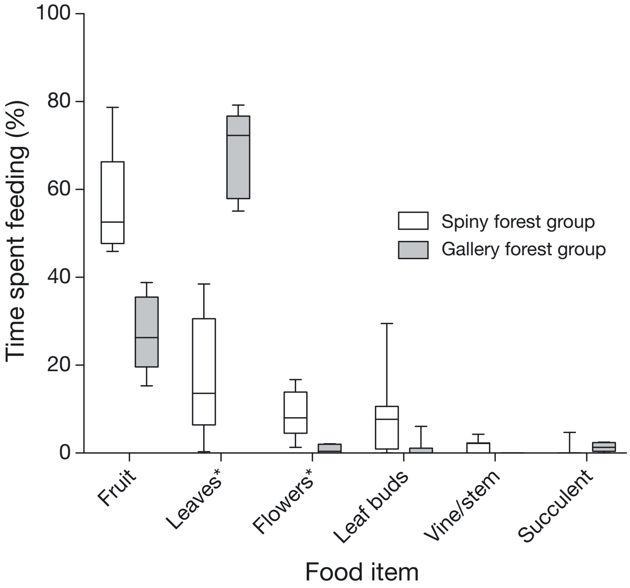

Fig. 2. *Lemur catta*. Proportion of time spent feeding on different plant parts. Asterisks indicate significant differences between spiny forest and gallery forest groups at $p < 0.05$

a nearest neighbour compared with the gallery forest group ($U = 3$, $p < 0.05$; Fig. 3). The 2 groups also differed in spacing patterns while feeding on leaves. Individuals in the spiny forest group spent a significantly smaller proportion of their time in close proximity to a nearest neighbour ($U = 7$, $p < 0.05$) and a significantly greater proportion of their time far from a nearest neighbour compared with the gallery forest group ($U = 6$, $p < 0.05$; Fig. 3).

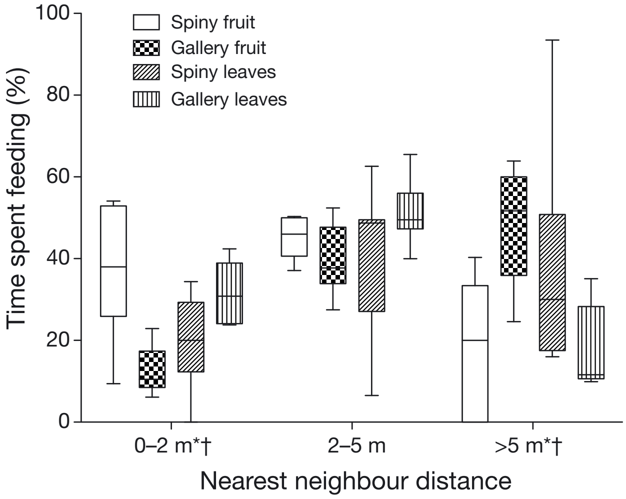

Fig. 3. *Lemur catta*. Proportion of time spent feeding on fruit and leaves at locations with different nearest neighbour distances. Asterisks and daggers indicate significant differences between spiny forest and gallery forest groups for fruit and leaves, respectively, at $p < 0.05$

The rate of total agonism was used as a baseline for comparison of feeding and social agonism. There were no significant differences in the rate of total agonism or social agonism between groups, but individuals in the spiny forest group engaged in a significantly higher rate of agonistic events per feeding hour compared with individuals in the gallery forest group ($U = 4.5$, $p < 0.05$; Fig. 4). Because of small sample sizes, the rate of feeding agonism in the spiny forest group was much greater than any other agonism rate in either group.

DISCUSSION

Primates are renowned for their ability successfully to modify behavioural strategies to cope with environmental heterogeneity (Hill et al. 2003, Brockman & van Schaik 2005, Jones 2005). Thus, the investigation of activity patterns is central to the study of varying behavioural strategies in space and time. To sustain thermoregulation, physiological maintenance and reproductive capabilities, individuals are likely to modify activity patterns to increase energy intake and decrease energy expenditure (Whiten et al. 1987, Barton et al. 1992, Dunbar 1992, Menon & Poirier 1996). Species seek to balance energy expenditure and intake during seasonal periods of resource scarcity (Overdorff et al. 1997, Remis 1997, Hemingway & Bynum 2005) by using energy maximization or minimization strategies (Strier 1992). Studies of behavioural patterns of primates provide unique insights into adaptive strategies when environmental conditions challenge physiological processes. Fur-

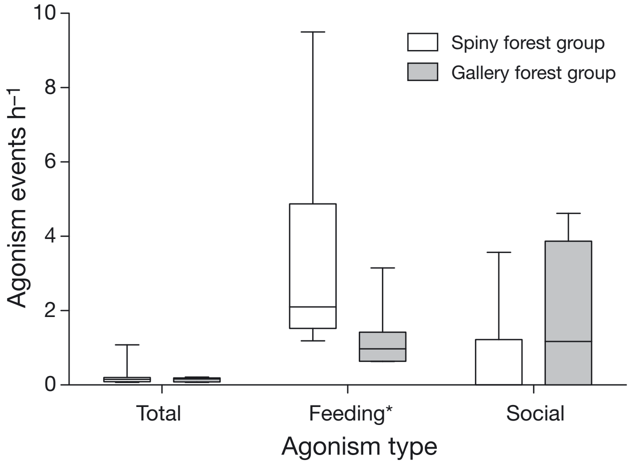

Fig. 4. *Lemur catta*. Rate of agonistic behaviour by lemurs. Asterisks indicate significant differences between spiny forest and gallery forest groups at $p < 0.05$

thermore, studies of resource use and social responses to locally available resources are essential to proper conservation action plans.

Although sample sizes are necessarily limited for this Near Threatened and declining species, our study suggests that *Lemur catta* adjust behavioural strategies between habitat types during the hot dry season. The modification of activity patterns is probably associated with ambient temperature and water availability, which we propose are limiting factors in the proportion of time spent in active behaviours by *L. catta* living in the spiny forest. *L. catta* occupying spiny forest habitats spent significantly more time consuming fruits, a highly spatially clumped and contested resource among *L. catta* (Sauther 1993). These factors produced a much higher rate of feeding agonism within the spiny forest group, raising intriguing questions about resource availability and quality, and their interconnected effects on *L. catta* feeding agonism in non-gallery forest habitats.

This study, limited to one season, indicates that *L. catta* groups can survive, reproduce and lactate in this harsh environment; however, more data are needed to understand better the behavioural and ecological parameters of *L. catta* in spiny forests throughout southwestern Madagascar (Gould 2006). Below, we discuss potential causes for modifications in behavioural patterns between *L. catta* groups in different habitats and provide questions that future studies of *L. catta* occupying spiny forest habitats should address.

Time allocation

The data from our study show that individuals living in the spiny forest habitat significantly reduced their time spent in active behaviours, including feeding, during the dry season. The data support the contention that *Lemur catta* are energy minimizers (Rasamimanana et al. 2006) and that increased levels of resting are associated with less time spent feeding (Sussman 1977). Both study groups tended towards bimodal activity patterns, with early morning and late afternoon active periods broken up by a long period of mid-day resting. Significant differences in intergroup activity patterns were primarily related to the spiny forest group's extended periods of rest during the intense heat of mid-day. This group compensated for deficiencies in mid-day foraging effort by using abbreviated yet intensive feeding periods during the early and later periods of the day.

Energy conservation strategies, which enable primates to maintain physiological processes when resource availability is low (Iwamoto & Dunbar 1983, Barton et al. 1992, Dasilva 1992, Wright 1999, Di Fiore & Rodman 2001) are widespread in primates (lemurs: Richard 1978, Wright 1999, Norscia et al. 2006; atelines: Milton 1980, Estrada et al. 1999, Di Fiore & Rodman 2001; colobines: Dasilva 1992, Zhou et al. 2007). *Lemur catta* in the spiny forest may be able to use an energy-minimizing strategy by taking advantage of their inherently low basal metabolic rate (BMR). *L. catta* deviates further from the Kleiber regression line of primate BMR to body size than any other primate sampled, including other small-bodied strepsirrhines (Snodgrass et al. 2007). A low BMR slows the rate of oxidation, which in turn lowers the amount of energy processed by the body. All *L. catta* use energy-minimizing behavioural strategies because of this inherent physiological characteristic (Rasamimanana et al. 2006), but differences in resource availability between habitats likely leads to variant behavioural patterns. The spiny forest group likely maximizes energy retention by increasing time spent resting, particularly during times of high ambient temperatures and in spaces with little shade. Gould et al. (2011) found that *L. catta* select foods with relatively high levels of protein, calories and water, allowing them to compensate for time lost feeding.

Water availability is most likely a limiting factor in the allotment of active behaviour. Pre-existing reports of water content show that floral families in the spiny forests, predominantly Didiereaceae, Hernandiaceae and Euphorbiaceae, have evolved to withstand long periods of drought and high amounts of solar radiation (Fenn 2003) and, therefore, maintain lower levels of water per part than floral species in gallery forests (Grubb 2003). Water content in leaves of *Tamarindus indica*, the only food species shared by both groups, is positively correlated with proximity to the Mandare River (Mertl-Millhollen et al. 2006). Thus, leaves and presumably fruits from the spiny forest likely provide significantly less water needed for energy production, although the lemurs did benefit by consuming plants such as *Opuntia* cacti. Furthermore, the 5 plants most commonly consumed by the lemurs in the spiny forest contained significant amounts of water compared with less frequently consumed plant species (Gould et al. 2011). Moreover, individuals in the gallery forest had access to drinking water from small pools in the Mandare River and cement troughs in the Ankoba gallery parcel. Thus, although groups in the spiny forest can maintain sufficient hydration by consuming plant parts (Goodman & Langrand 1996, Gould et al. 2011), they may lose more water than the gallery forest group because of lack of access to actual standing water, increased ambient temperatures in the spiny forest, and greater solar exposure due to lack of forest canopy. Reduced water intake by spiny forest dwelling *Lemur catta* (compared with gallery forest dwelling conspecifics) particularly in the hot season, could have indirect effects on female reproduction, but reduced activity may be a compensatory strategy. Our study occurred during the birth and lactation period, when female *L. catta* must produce a large quantity of dilute milk to aid in survival of rapidly growing infants that suckle on demand (Power et al. 2006). A relationship between milk composition and infant thermoregulation in primates has been suggested (Tilden & Oftedal 1997) and maternal production of dilute milk can be a reproductive survival strategy, particularly when infants must cope with high temperatures, such as in the spiny forest (Gould et al. 2011). Therefore, although no sex differences in resting time were found, lactating females could still benefit from engaging in such energy-minimizing behaviours (Rasamimanana et al. 2006) in a spiny forest habitat, because reduced activity would result in less water loss.

High ambient temperatures have been considered to have a significant influence on primate activity cycles (*Macaca nemestrina*, Bernstein 1972; *Papio cynocephalus cynocephalus*, Stelzner 1988, Pochron 2000; *Papio cynocephalus ursinus*, Hill 2006) because evaporative water loss in primates increases when ambient temperature rises over 30°C and rises sharply when temperatures exceed 40°C (Elizondo 1977). Stelzner (1988) has suggested that ambient temperature is a primary constraint to behaviour, as primate physiological abilities to reduce thermal stress are limited. Our study was conducted during some of the hottest months in southern Madagascar, with daily maximum temperatures in the Berenty spiny forest and surrounding matrix at times reaching over 40°C; in December and January, temperatures would rise even further in the entire region (Jolly et al. 2006). The spiny forest group, therefore, most likely increased time spent resting in the little shade that exists in this habitat to avoid intense solar radiation and to decrease evaporative water loss. Energy-intensive behaviours, especially locomotion and foraging, took place at a fast pace and were most pronounced when temperatures were at their lowest.

Foraging strategy

Lemur catta quickly modify their feeding strategies as resources become available in gallery forest habitats (Sauther 1994, 1998, Soma 2006). The present study shows that *L. catta* alter foraging strategies between habitat types based on the available flora species within their home ranges. Furthermore, both groups fit into the dietary niche of flexible folivore/frugivore previously ascribed to *L. catta* (Jolly 1966, Sussman 1977, Sauther 1994, Sauther et al. 1999, Soma 2006, Gould 2006). However, the difference in selection between plant reproductive parts and leaves between groups was striking. *L. catta* in the spiny forest focused their foraging effort on locating small fruits, especially from *Gyrocarpus americanus* and *Tarenna* sp. and consuming leaves of succulent species such as *Alluaudia procera*, *Aloe vahome* and *Opuntia vulgaris* (Gould et al. 2011). Furthermore, towards the conclusion of the study, the spiny forest group spent much of its foraging time consuming flowers of *Agave sisalana* in fields outside of the spiny forest parcel. In contrast, *L. catta* in the gallery forest spent much of their foraging time consuming leaves, especially from *Leucaena lercoephalla, Pithecellobium dulce* and *Azadirachta indicus*, and consumed fruits from *P. dulce* and *Tamarindus indica* as they became available. A comparison of nutrient intake between populations living in the 2 diverse habitats would be useful to understand whether activity-minimization strategies are associated with significantly lower levels of energy and nutrient intake.

Distinctly different patterns of social spacing while foraging between the 2 groups are most likely associated with significant differences in *Lemur catta* foraging agonism. Contest competition is more likely to occur when primate groups feed on plant reproductive parts, which are often spatially clumped, compared with leaves, which tend to be ubiquitous throughout habitats (Wrangham 1980, van Schaik 1989). We suggest that because fruit is clumped in small tree crowns in the spiny forest, *L. catta* in that habitat engaged in higher levels of feeding competition while searching for these preferred food items. During the study period, *L. catta* in the gallery forest increased inter-individual spacing while consuming fruit because of increased spatial distances between fruit items in large *Pithecellobium dulce* and *Tamarindus indica* trees, and decreased individual spacing while consuming leaves, which are more plentiful and spatially clumped. Further research on *L. catta* feeding behaviour in spiny forest habitats can further identify patterns in relation to food type, seasonal effects on feeding competition, competition over specific plant part species, and the possible effect of feeding competition on differently ranked individuals.

CONCLUSIONS

We suggest that because *Lemur catta* successfully negotiate the ecological challenges of the spiny forest in Berenty Reserve, other populations of this species could consistently occupy spiny forest habitats if enough of the important food resources were available. Unfortunately, very little is known about the seasonal and annual patterns of resource use, distribution and activity of *L. catta* populations living in other spiny forests (although at the time of writing, one year-long study was underway in a different spiny forest region of southern Madagascar; M. LaFleur unpubl. data). Although population density is relatively low in non-gallery forest habitats (Sussman et al. 2003), these spiny forest groups are essential in preserving a diverse population gene pool and retaining the possibility of conserving the species outside of a small number of gallery forests near rivers. Goodman et al. (2006) have noted that ring-tailed lemurs may disperse through low-resource corridors; thus maintaining primary or secondary forest throughout southern Madagascar may be vital to this species' future. Moreover, as seed dispersers, *L. catta* are vital for the survival of both gallery forests (Blumenfeld-Jones et al. 2006) and spiny forests (Bodin et al. 2006). The endemic spiny forests are vanishing at a rapid pace because of anthropogenic deforestation, and the remaining small fragments of this endemic forest type should be viewed as essential to maintaining a genetically variable primate species (Bodin et al. 2006). Thus, in the evaluation of habitats to be designated as protected for *L. catta*, all habitat types that contain the species, especially xerophytic spiny forest, should be considered.

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Appendix. Table A1. Plant species eaten by spiny forest and gallery forest groups of *Lemur catta*. A number of individuals also selected soil off the ground as a supplementary part of their diet

Taxonomic family	Species	Food type
Spiny forest		
Agave[a]	*Agave sisalana*	Succulent leaves
Burserceae	*Commiphora* sp.	Leaf buds
Boraginaceae	*Cordia caffra*	Leaves
Cactaceae[a,b]	*Opuntia* sp.	Succulent leaves
Caesalpiniodae[b]	*Tamarindus indica*	Fruit, leaves, leaf buds
Capparaceae	*Maeura folfimus*	Leaves
Didiereaceae	*Alluadia procera*	Flowers, leaves, fruit
Euphorbia	*Euphorbia* sp.	Stems
Hernandiaceae	*Gyrocarpus americanus*	Flowers, leaves, fruit
Liliaceae	*Aloe* sp.	Succulent leaves
Mimosoideae	*Acacia* sp.	Leaves
Ribiacae	*Tarenna* sp.	Fruit
Salvadoraceae	*Azima tetracantha*	Leaves, flowers
Salvadoraceae	*Salvadora augustifolia*	Fruit, leaf buds
		Soil
Gallery forest		
Cactaceae[a,b]	*Opuntia* sp.	Succulent leaves
Caesalpiniodeae[b]	*Tamarindus indica*	Leaves, leaf buds, fruit
Capparaceae[a]	*Cordia* sp.	Leaves and fruit
Capparaceae	*Craveta excelsa*	Flowers
Capparidaceae	*Cadaba virgata*	Leaves
Convolvulaceae[a]	*Iporea robbers*	Flowers
Mimosoideae	*Acacia rovumae*	Leaves
Mimosoideae[a]	*Leucaena lercoephalla*	Leaves
Mimosoideae[a]	*Pithecellobium dulce*	Fruit, flowers
Meleaceae[a]	*Azadirachta indica*	Leaves
		Soil

[a] non-native species to Madagascar (i.e. introduced and non-endemic); [b] species consumed by both groups

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