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Interplay of Phenology and Reproduction in Ring-Tailed Lemurs: Implications for Ring-Tailed Lemur Conservation

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Key Words

Lemurs · Ring-tailed lemur · Diet · Phenology · Reproduction · Food availability · Female dominance · Conservation

Abstract

Data are presented on ring-tailed lemur feeding ecology and resource use at the Beza Mahafaly Special Reserve in southwestern Madagascar. The phenological availability of food resources was sampled monthly from 199 trees and 31 species. Results indicate that *Lemur catta* feeding ecology is finely tuned to the seasonal nature of specific food resources. Key species provide important food items during critical periods of the reproductive cycle. During a drought year, mortality for mothers and infants increased dramatically, providing indirect evidence that this species is highly dependent on the phenological reliability of food resources. These results indicate that in such highly seasonal habitats, the loss of any key species could have enormous impact on ring-tailed lemur demography and survival.

Introduction

It is obvious that any successful lemur conservation program will require the establishment and maintenance of adequate natural habitats. The question then becomes: what *types* of habitat are essential for normal lemur population growth? For most lemur species, little is known about the minimum ecological requirements needed for a habitat to sustain lemur populations. The ring-tailed lemur, *Lemur catta*, is the only remaining semi-terrestrial lemur species. Its range is limited, as it is found only in southern Madagascar. This species cannot inhabit savanna or open woodland [1], nor can it survive year round in subdesert vegetation without forest [2]. It is instead dependent on riparian, gallery forests and dense euphorbia bush that are being reduced in size due to fires, overgrazing, and tree-felling for charcoal [3]. Recent research on the demography of ring-tailed lemurs indicates that this species is highly sensitive to habitat quality and change. For example, denser populations and smaller

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home ranges are characteristic of groups inhabiting gallery forest, as opposed to transitional dry forest [4]. Due to the extreme seasonality of its habitat, ring-tailed lemurs appear to be highly dependent on specific food resources [5]. The focus of this paper is to address ecological concerns for *Lemur catta,* a lemur that is often considered a common species. I hope to demonstrate that even for this species there are specific ecological requirements that are essential to maintain an healthy existence in the wild.

Materials and Methods

The work presented here is based on a 12-month study of the feeding ecology of two ring-tailed lemur groups at the Beza Mahafaly Special Reserve. This reserve is located in southwestern Madagascar, and is part of one of the largest remaining continuous tracts of classic dry gallery forest. The area contains a deciduous and semi-deciduous riverine forest that becomes more xerophytic as one moves from the east to the west. It is dominated by *Tamarindus indica* (commonly known as 'kily') in the eastern portion of the reserve, which becomes codominant with *Salvadora augustifolia* and *Euphorbia tirucalli* as one moves to the west. Grazing by sheep and cattle is prohibited, and a rich understory of herbs and lianas is present within the reserve. The habitat is very seasonal, with a hot/wet and a cool/dry season. Based on daily records of precipitation taken on-site, total annual precipitation was 522 mm, with 505 mm falling during the austral summer (November–April).

The phenology of 119 trees and 31 species was monitored monthly. Within each troop's home range, all trees located along 6 separate 100 m trails were monitored. These 6 trails were distributed randomly within each troop's home range. Each phenological sample was made the day just prior to the start of the monthly observations for the troops. Samples included ring-tailed lemur food trees as well as trees not included in their diet during the 12-month study. Phenological availability was estimated for flowers, fruits, leaf buds, young leaves, and mature leaves for each tree by a scoring system. Tree scores could be from 0 to 4, with 4 denoting 100% coverage. Thus, a tree in full fruit would have a score of 4, a score of 3 if approximately 3/4 of the tree's crown had fruit, a score of 2 if 1/2 of the crown was covered, a score of 1 if only 1/4 was covered and a score of 0 if none was present. Because *T. indica* has asynchronous peaks in production they have been depicted in the figures as *T. indica* 1 and *T indica* 2. Similarily, both peaks of *Enterospermum pruinosum* have also been graphed.

Along with living in a seasonal environment, ring-tailed lemurs at the reserve exhibit a highly seasonal reproductive cycle. Females are in estrus once a year for about a 24 h period [6, 7], infants are weaned around 4–5 months of age [7, 8], and females produce infants on a yearly basis [7]. In addition, ring-tailed lemurs show considerable reproductive synchrony in the wild [6, 7]. For example, during this research all study females mated within the same 20-day period. We thus have female primates facing very similar reproductive costs in a highly seasonal environment.

Results

Vegetation availability changes dramatically between the dry and wet season at the reserve. With the coming of the rains there is a general 'greening' of the forest. Figure 1 shows the seasonality of this environment during the study period (1987–1988). Most rainfall in non-drought years occurs roughly between October and April. This seasonal rainfall pattern has a dramatic effect on the availability of various plant parts in the reserve. Availability of fruit and young leaves is highly correlated with rainfall – with higher availability during periods of relatively greater rainfall (correlation coefficient of rainfall with leaves: 0.92, $p < 0.001$; correlation coefficient of rainfall with fruit: 0.70, $p < 0.01$). Flowers show a different pattern, with peak availability occurring just before the onset of the rainy period (early October).

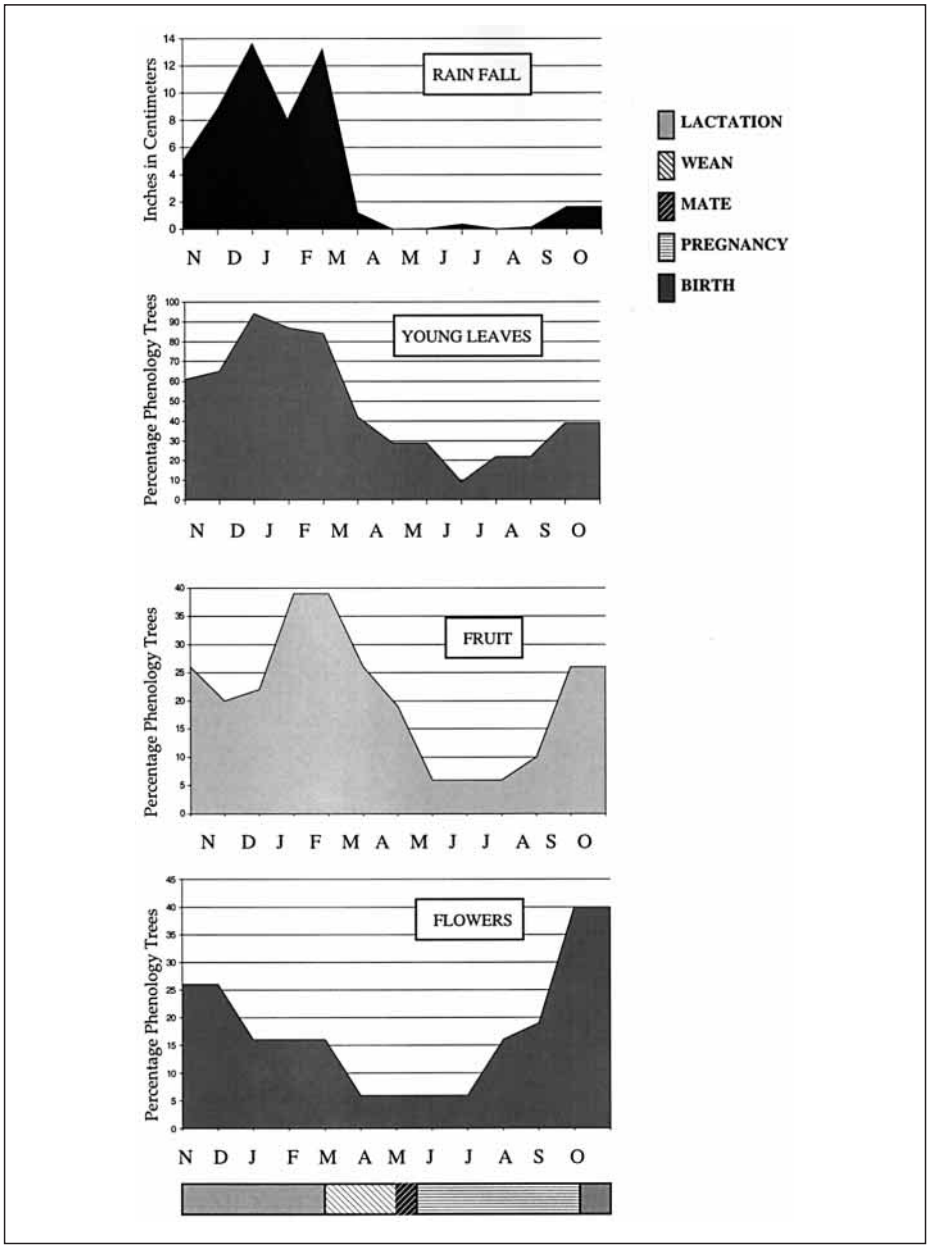
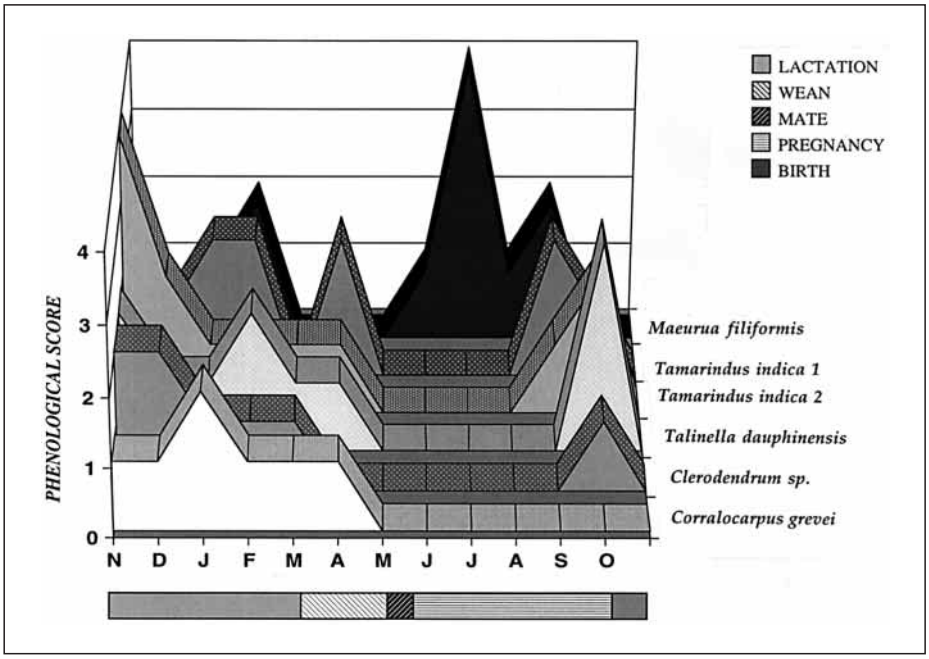


Fig. 1. Rainfall and phenology at Beza Mahafaly Special Reserve: 1987–1988.



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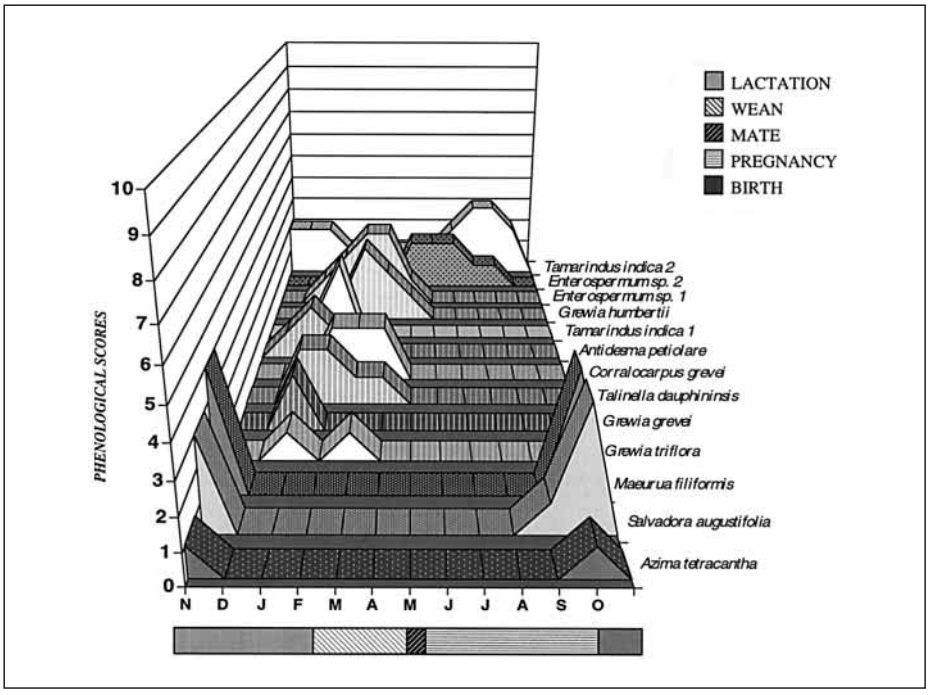

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Fig. 2. Availability of ring-tailed lemur foods: young leaves.
Fig. 3. Availability of ring-tailed lemur foods: fruits.

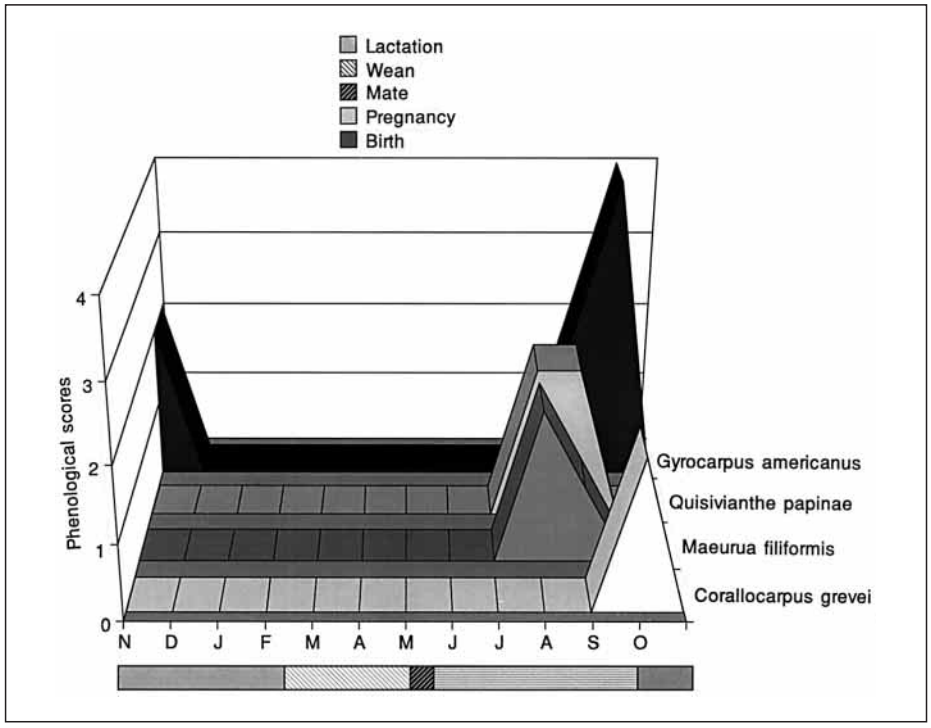

Fig. 4. Availability of ring-tailed lemur foods: flowers.

When focusing just on those species used as food resources by ring-tailed lemurs, there are a number of patterns regarding seasonal availability. In figure 2 the availability of young leaves is represented. A flush of young leaves coincides with the birth season and early lactation period, with more species producing young leaves during this period. There are also several peaks of young leaf availability that coincide with the weaning period. During the dry season when females are pregnant, small, isolated patches of herbs such as *Hildebrandtia* sp. and a single tree species, *Maeurua filiformis,* provide the only sources of young leaves. It was during this period that I observed the lemurs eating dry, desiccated leaves.

As can be seen in figure 3, there are two basic peaks of fruit availability, one during the birth, early lactation period (October–November) and one during the late lactation/weaning period (March–April). As with young leaves, for most of the dry season fruit availability is drastically reduced, being limited to two species, *Tamarindus indica* and *Enterospermum pruinosum.*

Flower availability is depicted in figure 4. Some of the plant species used by ring-tailed lemurs at Beza provide a large mast of flowers during key periods. Flower availability peaks during the late pregnancy-birth season. Two of these species, *Quisivianthe papinae* and *Maeurua filiformis* provide flowers during the period when few leaves or fruits are available.

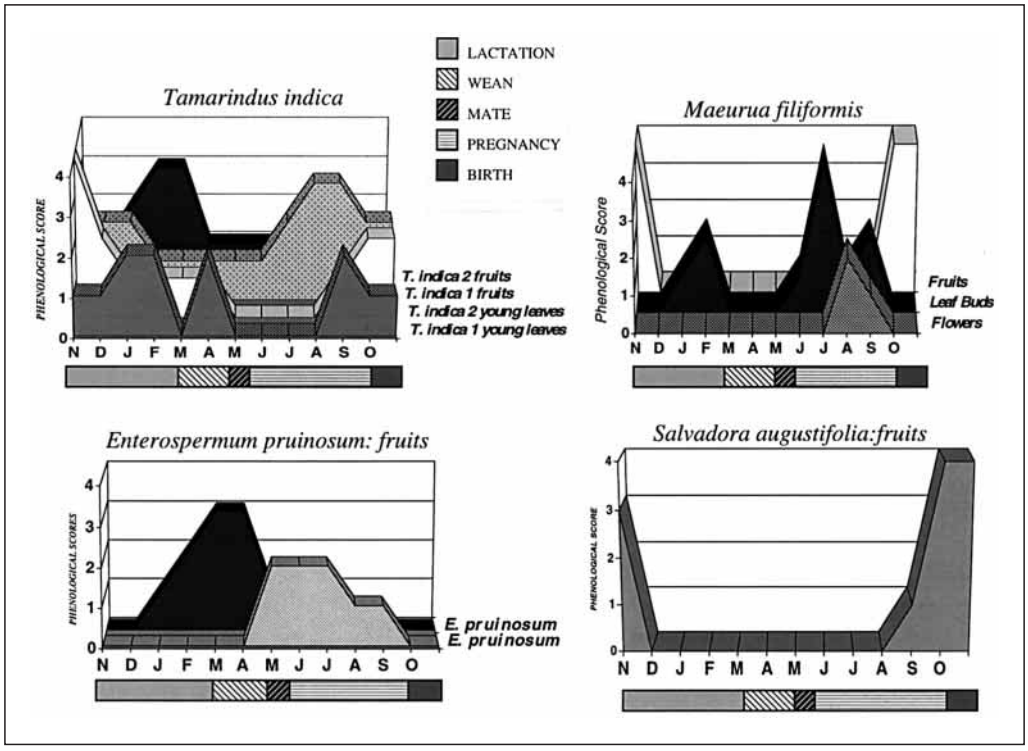

Fig. 5. Ring-tailed lemur foods: keystone species.

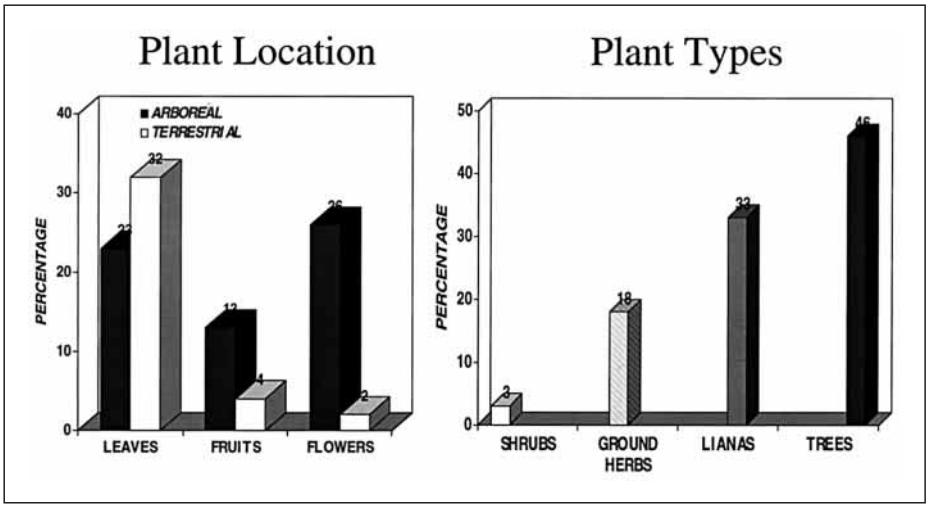

Fig. 6. Ring-tailed lemur foods: plant types and location.

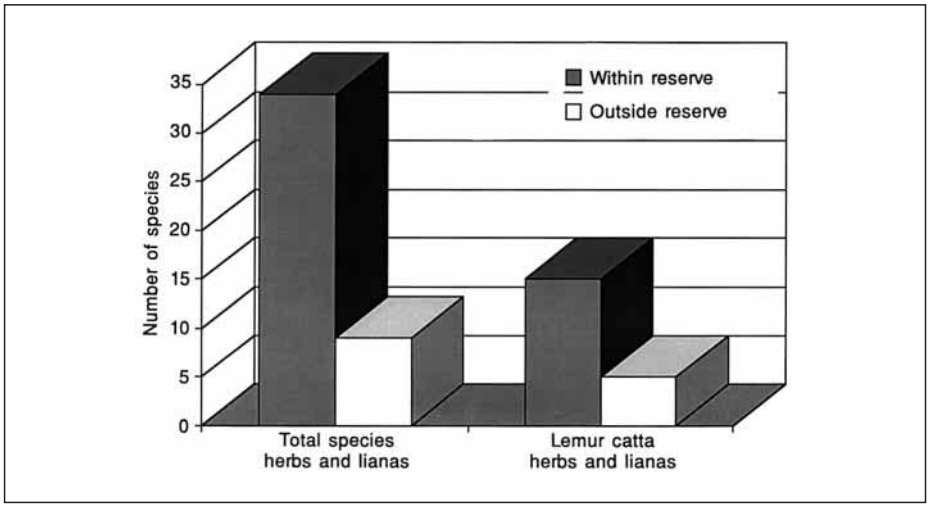

Fig. 7. Total number of species of herbs and lianas in seedling plots within protected and unprotected forest at Beza Mahafaly Reserve and number eaten by *Lemur catta*. Data from Sussman and Rakotozaty [9].

Figure 5 illustrates the phenology of resources that can be considered keystone species for the lemurs at this reserve. They either provide a variety of plant parts as foods throughout the year, especially in seasons during which little else is available (e.g. *T. indica*), or they produce large amounts of food during a short but critical period (e.g. *Salvadora augustifolia*).

T. indica has been previously noted as an important food source for *L. catta*, but this is demonstrated graphically in figure 5. This species produces fruit and young leaves asynchronously, which means that it is a potential food resource for *L. catta* year-round. Likewise, *E. pruinosum* also produces fruits asynchronously, providing fruits at different, critical periods. Although not an asynchronous producer, *Maeurua filiformis* provides a food resource throughout the year as all parts are used by ring-tailed lemurs as foods.

The species, *S. augustifolia*, occurs in only one area within the reserve – it produces a large amount of fruit, but it is available for only a short time. All troops within this reserve migrate to this area to exploit these resources – many of them moving far from their normal home ranges. In addition, troops from outside the reserve travel to this area to exploit this seasonal resource.

Ring-tailed lemurs at Beza Mahafaly are highly dependent on the leaves of herbaceous species, and low-level lianas located on small shrubs [5]. Figure 6 indicates that most leaf feeding occurs at ground level. In addition, of the types of food resources exploited by ring-tailed lemurs, 54% are located near or at ground level (ground herbs, shrubs or lianas found on bushes).

Recently, a study by Sussman and Rakotozafy [9] looked at plant diversity and structure by comparing areas within Beza Mahafaly Reserve with areas outside the protected forest where grazing by cows and goats occur. Figure 7 compares the total

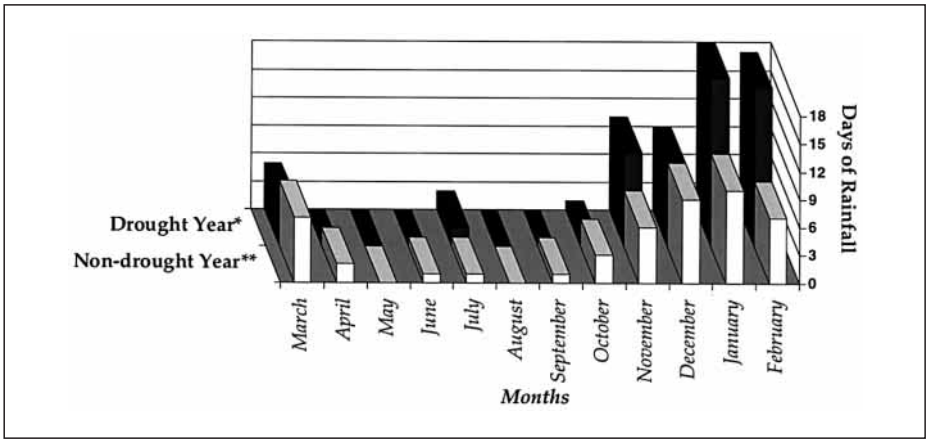

Fig. 8. Number of rainfall days at Beza Mahafaly Reserve during drought and non-drought years. * From Gould [10] for March 1992 to March 1993. ** From Sauther [5] for November 1987 to November 1988.

number of species of herbs and lianas in seedling plots located within and outside the reserve. There are fewer of these species in the unprotected portions. Outside the reserve there are also fewer herbs and lianas which are specifically eaten by ring-tailed lemurs (fig. 7).

Is there any evidence that alterations in food availability might adversely affect ring-tailed lemur ecology? There is indirect evidence of the close tie between ring-tailed lemurs and their seasonal resource base. In 1991 there was an El Nino drought that included southern Madagascar and which continued on into 1992. Figure 8 shows the comparison of rainfall data collected by Gould [10] during her study of the ring-tailed lemurs at Beza from March 1992 to March 1993, and my rainfall data from November 1987 to November 1988 [5], which was not a drought year. This revealed two important differences in rainfall patterns during the drought and non-drought years. First, during my study there were only 2 months during which no measurable rain fell. However, during the drought year, there was no rainfall for a total of 5 months. Second, the patterns of rainfall also differed. In the drought year, the rains began 1 month later than in the non-drought year. Furthermore, the rains ended 1 month earlier than in the non-drought year. The result was a shorter rainy season (by 2 months) during the drought year. Although not measured directly during Gould's study, the change in rainfall pattern had an observable effect on phenology, with an extended dry season which followed the earlier drought year of 1991. Drought could also affect the availability of water. During a normal year the rainy season provides free-standing water for ring-tailed lemurs at the reserve. The lemurs drink directly from the nearby Sakamena River, which flows only during the rainy season, from rain-water which is trapped in the shells of land snails, and tree hollows. In the dry season, water is provided by dew which is licked from tree leaves early in the morning, and from trapped water in tree hollows. During the drought year the Sakamena River began flowing much later.

What effect did this have on the ring-tailed lemurs? During her 1992–1993 field study, Gould noted that females suffered drastic mortality, with a total of 10 mothers with infants disappearing during the birth and lactation seasons [Gould, pers. commun.]. At least two of these are confirmed deaths. During my study, in a non-drought year, only 2 females disappeared, with one of these a confirmed death.

Discussion

These results indicate that the feeding ecology of *L. catta* is finely tuned to the seasonal nature of specific food resources. Reproduction in this species is patterned to coincide with important, seasonally available subsets of resources. As females move through different reproductive states, they depend on phenologically distinct species. Lactation is the most costly reproductive period for placental mammals in general [11, 12], as well as primates in particular [13]. In ring-tailed lemurs at Beza, early lactation coincides with an initial peak in fruit availability. Late lactation and weaning occur during a second peak in fruit availability, and the entire lactation/weaning period corresponds with greater availability of young leaves. Pregnancy in ring-tailed lemurs coincides with relatively lower food availability. During this period *L. catta* at Beza must focus on a few critical species, including small pockets of ground herbs, leaves from one tree species, *Maeurua filiformis*, the fruits of *T. indica* and *E. pruinosum* and an initial burst of the flowers of *Quisivianthe papinae* and *Maeurua filiformis.* Finally, the birth season corresponds to a second short burst of flowers from *Gyrocarpus americanus* and *Corallocarpus grevei*, as well as the fruits of *Salvadora augustifolia.*

Terborgh [14] has pointed out that in primate species inhabiting seasonal areas, foraging patterns may alter during periods of low food availability. Individuals may concentrate on a few essential resources that are fewer in number, phenologically predictable, and which are referred to as keystone species. At Beza Mahafaly Reserve several plant resources appear to function as keystone species, especially those producing during the dry season. They either provide resources throughout the year, such as *T. indica*, or produce large amounts of food during short but critical periods, such as *S. augustifolia.* For the reasons cited above, these resources can be viewed as critical from a reproductive perspective.

Such a close mesh between reproduction and plant phenology in ring-tailed lemurs indicates that ecological conditions can have profound effects on physiological processes, which, in turn, may also affect social organization. Ring-tailed lemurs are under considerable reproductive stress, not simply because they live in an highly seasonal environment. Lemurs, including *L. catta*, characteristically produce infants which exhibit an accelerated rate of growth that creates high demands on the mother during lactation [15, 16]. One likely consequence of this rapid growth is a particularly high proportion of energy being obtained from protein in lemur milk, which averages 19% and which is among the highest for primates [17]. High rate of infant growth lends support to the view that many of the Malagasy lemurs are under higher stress during reproduction [18, 19]. Along this line, it has also been suggested that female social dominance exhibited by some lemurs is tied to these exceedingly high costs of reproduction, which require that females have priority of access to all food sources [18, 19]. However, not all lemur species exhibit true female dominance [20]. For

example, Sussman [21] found no indication of a dominance hierarchy, and low levels of aggression in red-fronted lemurs, *Lemur fulvus rufus*, a species similar in body size and proportions to *L. catta* [22]. Similarly, Pereira et al. [23] found no evidence of female dominance in any context for semicaptive or wild red-fronted lemurs. Among the lemurs, true female dominance involving both feeding and nonfeeding contexts [24] has only been clearly demonstrated in captive and wild populations of *Lemur catta* [5, 24, 25], although it is also said to exist in *Indri indri* [26], *Propithecus verreauxi* [27], *Phaner furcifer* [28], *Microcebus murinus* [29, 30], *Varecia variegata variegata* [31], and *Daubentonia madagascariensis* [32]. I suggest that while many of the Malagasy lemurs appear to have high reproductive costs, female dominance functions as a female feeding strategy in those species which are additionally stressed, e.g. by extreme seasonality of resources-*L. catta* [5]; *Propithecus verreauxi verreauxi* [33]; by extended infant dependency-*Indri indri* [26]; by multiple births-*Varecia variegata* [34].

It is tempting to suggest that seasonal reproduction in lemurs is tied, ultimately, to seasonal availability of food resources for lactation and for weaning infants [35]. In actuality, this would not be pleading a special case for the lemurs of Madagascar, as resource seasonality has been implicated in seasonal reproductive patterns in anthropoid primates as well [36–38]. What is problematic is the lack of information on the interplay of phenology and reproduction in other lemur species [39]. Some support does come from several ecological studies. In a study of the feeding strategies of five nocturnal prosimian species living in the Marasalaza forest of western Madagascar, Hladik et al. [40] noted seasonal variations in flower, fruit and leaf production similar to that observed at Beza Mahafaly. Flower production peaked in October and November, and fruits were abundant during the weaning period for young lemurs. Births occurred in *Cheirogaleus medius* in January, when food availability was relatively high. Similarly, the golden-crowned sifaka, *Propithecus tattersalli* and Milne-Edward's sifaka *P. diadema edwardsi*, both appear to pattern their seasonal reproduction so that late lactation and weaning coincide with high immature leaf availability [41]. What of lemur species inhabiting environments with less predictable phenological patterns? In some rain forests, for example, specific fruit species may be unpredictable in the short term as they may produce fruit every other year [42, 43]. In these contexts, primate species exhibit behavioral adaptations that may help alleviate seasonal reproductive stresses, e.g. alterations in ranging patterns to include areas of greater food abundance [42, 44].

Finally, as the effect of drought on this population indirectly indicates, reproductive females are very sensitive to changes in their environment. Recall that ring-tailed lemur females are pregnant during the season of reduced food availability. Thus, a pregnant female most likely enters lactation with little or no nutrient reserves. Furthermore, lactating *L. catta* females exhibit obvious signs of stress. During lactation they visibly lose weight, which is a common pattern among lactating mammals [45], and in this study they had clearly duller coats relative to males. Such weight decline has also been observed in captivity, and is associated with late lactation and infants' growth acceleration [16]. During a normal year, females have only a 2-month period (from March to April) after weaning their infants in which to replenish nutrient reserves depleted during lactation [39]. They then go directly into pregnancy, which occurs during the dry season. However, during 1992–1993, rainfall was reduced during those critical months – in fact there was no rain at all during April. In addition, the

advent of the rainy season was delayed, requiring mothers to begin nursing without the new flush of leaves and fruits which normally accompanies the arrival of the rainy season. For many females, this appears to have been too much of a reproductive burden, resulting in a high maternal mortality rate. In other words, changes in rainfall pattern appear to affect resource (including potentially, water) availability leading to higher mortality rates. In such highly seasonal habitats, the loss of ground plants or any keystone species could thus have an enormous impact on ring-tailed lemur demography and survival. Ring-tailed lemur dependence on key seasonal resources also provides evidence that the conservation of this species may in fact be directly tied to the continuing presence of the relatively lusher riverine forests in an otherwise dry environment.

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References

1 Sussman RW, Richard A: Lemur conservation in Madagascar: The status of lemurs in the south. Primate Conserv 1986;7:85–92.
2 Budnitz N: Feeding behavior of *Lemur catta* in different habitats; PhD thesis, Duke University, 1976.
3 Harcourt C, Thornback J: Lemurs of Madagascar and the Comoros. The IUCN Red Data Book. Gland, Switzerland and Cambridge, UK, IUCN, 1990.
4 Sussman RW: Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. Am J Phys Anthrop 1991;84:43–58.
5 Sauther ML: Effect of Reproductive State, Social Rank and Group Size on Resource use among Free-Ranging Ringtailed Lemurs *(Lemur catta)* of Madagascar; PhD thesis, Washington University, 1992.
6 Jolly A: Lemur Behavior. Chicago, University Press, 1966.
7 Sauther ML: Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. Am J Phys Anthrop 1991;84:463–477.
8 Gould L: The social development of free-ranging infant *Lemur catta* at Berenty Reserve, Madagascar. Int J Primatol 1990;11:297–318.
9 Sussman RW, Rakotozafy A: Plant diversity and structural analysis of a tropical dry forest in southwestern Madagascar. Biotropica 1994;26:241–254.
10 Gould L: Patterns of Affiliative Behavior in Adult Male Ringtailed Lemurs *(Lemur catta)* at the Beza-Mahafaly Reserve, Madagascar; PhD thesis, Washington University, 1994.
11 Robbins CT: Wildlife Feeding and Nutrition. London, Academic Press, 1983.
12 Clutton-Brock TH, Albon SD, Guiness FE: Fitness costs of gestation and lactation in wild mammals. Nature 1989;337:360–363.
13 Sauther ML, Nash LT: The effect of reproductive state and body size on food consumption in captive *Galago senegalensis braccatus.* Am J Phys Anthrop 1986;73:81–88.
14 Terborgh J: Community aspects of frugivory in tropical forests; in Estrada A, Fleming TH (eds): Frugivores and Seed Dispersal. Dordrecht, Dr. W. Junk, 1986, pp 371–384.
15 Benirschke K, Miller CJ: Weights and neonatal growth of ringtailed lemurs *(Lemur catta)* and ruffed lemurs *(Lemur variegatus).* J Zool Anim Med 1981;12:107–110.
16 Pereira ME: Seasonal adjustment of growth rate and adult body weight in ringtailed lemurs; in Kappeler PM, Ganzhorn JU (eds): Lemur Social Systems and Their Ecological Basis. New York, Plenum Press, 1993, pp 205–221.
17 Buss DH, Cooper RW, Wallen K: Composition of lemur milk. Folia Primatol 1976;26:301–305.
18 Jolly A: The puzzle of female feeding priority; in Small MF (ed): Female Primates: Studies by Women Primatologists. New York, Liss, 1984, pp 197–215.
19 Young AL, Richard AF, Aiello LC: Female dominance and maternal investment in strepsirhine primates. Am Nat 1990;135:473–488.

20 Sauther ML: Resource competition in wild populations of ringtailed lemurs *(Lemur catta):* Implications for female dominance; in Kappeler PM, Ganzhorn JU (eds): Lemur Social Systems and Their Ecological Basis. New York, Plenum Press, 1993, pp 135–152.
21 Sussman RW: An Ecological Study of Two Madagascan Primates: *Lemur fulvus rufus* (Audebert) and *Lemur catta* (Linnaeus); unpubl PhD thesis, Duke University, 1972.
22 Tattersall I: The Primates of Madagascar. New York, Columbia University Press, 1982.
23 Pereira ME, Kaufman R, Kappeler PM, Overdorff D: Female dominance does not characterize all of the Lemuridae. Folia Primatol 1990;55:96–103.
24 Taylor, L: Kinship, Dominance, and Social Organization in a Semi Free-ranging Group of Ringtailed Lemurs *(Lemur catta);* PhD thesis, Washington University, 1986.
25 Kappeler PM: Female dominance in *Lemur catta:* More than just female feeding priority? Folia Primatol 1990;55:92–95.
26 Pollock J: Female dominance in *Indri indri.* Folia Primatol 1979;31:143–164.
27 Richard AF, Heimbuch R: An analysis of the social behavior of three groups of *Propithecus verreauxi;* in Tattersall I, Sussman RW (eds): Lemur Biology. New York, Plenum Press, 1975, pp 313–333.
28 Charles-Dominique P, Petter JJ: Ecology and social life of *Phaner furcifer;* in Charles-Dominique CP, Cooper HM, Hladik A, Pages E, Pariente GF, Petter-Rousseaux A, Petter JJ, Schilling A (eds): Nocturnal Malagasy Primates: Ecology, Physiology and Behavior. New York, Academic Press, 1980, pp 75–96.
29 Perret M: Influence du groupement social sur la reproduction de la femelle de *Microcebus murinus.* Z Tierpsychol 1982;60:47–65.
30 Pages-Feuillade E: Modalités de l'occupation de l'espace et relations interindividuelles chez un prosimien nocturne malgache *(Microcebus murinus).* Folia Primatol 1988;50:204–220.
31 Kaufman R: Female dominance in semifree-ranging black and white ruffed lemurs, *Varecia variegata variegata.* Folia Primatol 1991;57:39–41.
32 Rendall D: Does female social precedence characterize captive aye-ayes *(Daubentonia madagascariensis)*? Folia Primatol 1993;14:125–130.
33 Richard AF: The feeding behaviour of *Propithecus verreauxi;* in Clutton-Brock TH (ed): Primate Ecology. New York, Academic Press, 1977, pp 71–96.
34 Mittermeier R, Tattersall I, Konstant WR, Meyers DM, Mast RB: Lemurs of Madagascar. Washington, Conservation International, 1994.
35 Petter-Rousseaux A: Cycles génitaux saisonniers des lémuriens malgaches; in Canivenc R (ed): Cycles Génitaux Saisonniers des Mammifères Sauvages. Paris, Masson, 1968, pp 11–22.
36 Chism J, Rowell T, Olson D: Life history pattern of female patas monkeys; in Small, MF (ed): Female Primates: Studies by Women Primatologists. New York, Liss, 1984, pp 175–190.
37 Butynski TM: Guenon birth seasons and correlates with rainfall and food; in Gautier-Hion A, Bourliere F, Gautier H, Kingdon J (eds): A Primate Radiation: Evolutionary Biology of the African Guenons. New York, Cambridge University Press, 1988, pp 284–322.
38 Boinski S: Birth synchrony in squirrel monkeys *(Saimiri oerstedi):* A strategy to reduce neonatal predation. Behav Ecol Sociobiol 1987;21:393–400.
39 Sauther ML: Seasonal resources and their implication for ring-tailed lemur conservation (abstract). Folia Primatol 1998;69(suppl 1): 414.
40 Hladik CM, Charles-Dominique P, Petter JJ: Feeding strategies of five nocturnal prosimians in the dry forest of the west coast of Madagascar; in Charles-Dominique P, Cooper HM, Hladik A, Hladik CM, Pages E, Pariente GF, Petter-Rousseaux A, Schilling A (eds): Nocturnal Malagasy Primates: Ecology, Physiology, and Behavior. New York, Academic Press,1980, pp 41–73.
41 Meyers DM, Wright PC: Resource tracking: Food availability and *Propithecus* seasonal reproduction; in Kappeler PM, Ganzhorn JU (eds): Lemur Social Systems and their Ecological Basis. New York, Plenum Press, 1993, pp 179–192.
42 Overdorff DJ: Similarities, differences, and seasonal patterns in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana National Park, Madagascar. Int J Primat 1993;14:721–753.
43 Hill DA, Agetsuma M: Supra-annual variation in the influence of *Myrica rubra* fruit on the behavior of a troop of Japanese macaques. Am J Primatol 1995;35:241–250.
44 Caldecott JO: An ecological and behavioural study of the pig-tailed macaque; Contrib Primatol. Basel, Karger, 1986, vol 21, pp 1–259.
45 Sadleir RMFS: The Ecology of Reproduction in Wild and Domestic Mammals. London, Methuen, 1969.