The Socioecology of the Ringtailed Lemur: Thirty-Five Years of Research

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Linnaeus'[1] original scientific description of *Lemur catta*, the ringtailed lemur, was based on a living animal brought to England in 1749.[1] Although there were many brief descriptions of wild ringtailed lemurs,[2–5] it was not until Jolly[6] wrote her now classic book, *Lemur Behavior,* that we had our first detailed description of the natural history of these beautiful animals (Fig. 1). Since then, long-term field studies, mainly from two study sites in Madagascar, Berenty and Beza Mahafaly (Fig. 2), as well as studies on forest-living groups in captivity at the Duke University Primate Center in Durham, North Carolina, have greatly expanded our knowledge of the ecology and behavior of this species (Table 1, Box 1). Thirty-five years of research on this species at these various sites indicates that *Lemur catta* is proving to be every bit as complex in its behavior as are many anthropoid primates. This very complexity has been reflected in the current controversies and questions concerning the ecology and behavior of this species.

SOCIAL ORGANIZATION

Like many cercopithecine monkeys, *Lemur catta* lives in multi-male female resident groups that usually contain 10 to 20 animals.[6–8,10] Sex ratios are approximately 1:1[7,8,10,11] and sexual dimorphism is slight.[12] Females usually remain in their natal group, (but see below) whereas males migrate.[13–16]

Groups are centered around a core of adult females and their offspring.[6] As in Old World monkeys, ringtailed lemur groups characteristically contain more than one matriline, with some matrilines being dominant over others.[17–19] More friendly social interactions occur between close relatives and more serious aggressive encounters take place between less closely related individuals.[18,20,21] However, unlike cercopithecine monkeys, ringtail lemurs rarely form third-party alliances during agonistic encounters.[20,21] Furthermore, reconciliation after conflict, which is common among anthropoid primates, has not been noted in this species, indicating that this is not a necessary prerequisite for permanent social group life in primates.[22]

In free-ranging populations, if a group becomes too large fission may occur, with one matriline evicting another.[8,14,17,18,23] Dividing along matrilineal lines is also common among female-bonded cercopithecine monkeys.[24–26] One important mechanism for facilitating such fission among ringtailed lemurs is episodic targeting aggression.[27] When groups reach a critical size, females repeatedly attack and chase individuals of another matriline, sometimes resulting in the eviction of the latter.[27,28] Although there are no documented cases of individual female transfer, there have been rare cases of mother and adult daughter pairs joining other groups.[8,15] At Beza Mahafaly, such a pair entered an extant group that contained only four adult females and became the two top-ranking females. This is not always the case, however. In another case, the attempt of a mother-daughter pair to join a group was repulsed. They eventually joined a different, smaller group that contained only two resident females.[15]

In all groups studied at Beza Mahafaly, the top-ranking male has been of prime adult age.[8] Peripheral males are not a cohesive subgroup, but include lower-ranking males and males attempting to immigrate into the group. Male migration is regular, with young males first migrating from their natal

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Figure 1. Ringtailed lemurs live in large social groups in the dry and very seasonal forests of southern Madgascar.
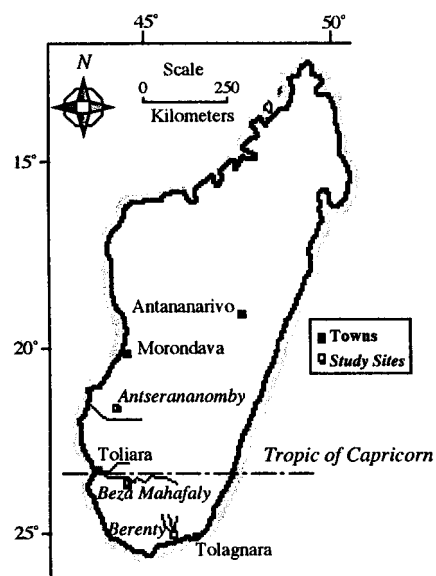

Figure 2. Formal field studies of *Lemur catta* began in the 1960s at various sites in Madagascar. Information from long-term studies at Berenty and Beza Mahafaly are expanding our knowledge of the socioecology of this species.

group when they are between 3 and 5 years of age.[14] On average, mature males migrate every three-and-a-half years, with approximately 30% migrating each year.[14] Males form partnerships while transferring, although these partnerships do not necessarily continue once group membership is attained.[13,14,29,30] At Berenty, the majority of male migrations occur at the end of the dry season and overlap, in part, with the birth season.[13] In all cases of male transfer, the males initially hold low-ranking and peripheral positions upon entering a new group and are challenged by other group members of both sexes for many months.[8,19,29,30]

A single top-ranking female appears to be the focal point for the rest of the group. She often initiates the direction of group progressions, although other individuals, including low-ranking adult males, may lead the actual travel.[6,19] This female is also responsible for the greatest number of aggressive encounters overall, with the majority of these involving access to food.[31] Females show strong, differentiated relationships within matrilines, as measured by grooming and proximity.[18–20] Mothers are always dominant over daughters.[19,32,33] While female dominance relationships in ringtailed lemurs can be linear, transitive, and stable over long periods,[19] these rela-tionships are not invariably linear and can change quite abruptly.[20,29,33]

There is also a developmental component in the establishment of dominance relationships: Adolescent and young adult females may rank above some adult females.[20,32] Perhaps because alliances are rare and mothers

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seldom support their daughters agonistically, female offspring do not invariably inherit their mother's rank.[20,32] This is different from the relatively stable linear dominance hierarchies found among group-living baboons and macaques. Among these species, ranks are actively maintained by female agonistic intervention and daughters acquire ranks just below those of their mothers through affiliative interactions and alliances among female relatives.[34] It thus appears that although female ringtailed lemurs have dominance relationships, they do not maintain dominance hierarchies in the manner of multi-male groups of cercopithecine primates.[32]

Unlike the males of many group-living anthropoid primates, male ringtailed lemurs appear to lack a consistent linear hierarchy and rank reversals occur.[16,18,22,29] This may relate to a lack of the stable alliances and coalitions between migrating males that are found in some macaque and baboon species, but have yet to be observed in ringtailed lemurs.[32] In most studies, a single, dominant male could be clearly identified and, at Beza Mahafaly, three males were able to maintain their dominance for six years, a pattern more similar to that of male rhesus macaques than that of male baboons.[8,35] Male ringtailed lemurs also develop preferred partnerships with one another, although these usually do not persist through an entire year.[29,30] (However, see Nakamichi and Koyama.[20])

Intergroup encounters are common at both field research sites.[6,13,19,36–39]

TABLE 1. Main Study Sites of the Ringtailed Lemur, *Lemur catta* (Studies of at Least One Year)

Sites and Dates	Main Researchers
Berenty, 1963–present	A. Jolly, N. Budnitz, K. (Dainis) Jones, A.S. Mertl-Mill-hollen, S. O'Conner, N. Koyama, M. Nakamichi
Beza Mahafaly, 1987–present	R.W. Sussman, M.L. Sauther, L. Gould
Antserananomby, 1969–71	R.W. Sussman
Duke University Primate Center, 1986–present	L. Taylor, M. Pereira, P. Kappeler, J. Macedonia, J. Ganzhorn

These primarily involve females, and can escalate into serious physical confrontations resulting in injury.[19,28,38] Many of these encounters involve access to food[19] or appear to be designed to keep others away from core areas of the home range.[19,38–40] The peaks in frequency of such encounters happen when females are especially motivated to defend resources to provide food for infants during weaning or for themselves in preparation for the dry season, as well as during the costly periods of birth and early lactation.[13,19,41]

FEEDING ECOLOGY

Ringtailed lemurs can best be characterized as opportunistic omnivores with a wide dietary regime that includes fruits, leaves, leaf stems, flowers, flower stems, spiders, spider webs, caterpillars, cicadas, insect cocoons, birds, and even dirt.[19] At Beza Mahafaly, daily consumption of soil from termite mounds has been observed (Fig. 3).[19] This has also been seen at the Duke University Primate Center.[42] Generally, *L. catta* spend 30% to 60% of their time feeding on fruit, 30% to 51% on leaves and herbs, 5% to 12% on flowers, and less than 3% on insects.[6,19,37,43] They display limited dexterity in the handling of food items as compared to anthropoid primates,[19] although they do exhibit handedness.[44] Food items are not manually manipulated, but rather are simply grasped and held.

Ringtailed lemurs are highly synchronous in their activities, with all individuals feeding at the same time when there is ample food. If a resource is limited—for example, if there is only a single drinking site—individuals may queue up for access to that resource. Infants often smell or taste food in their mothers' mouths, and individual adults commonly smell each others' mouths, perhaps to monitor available food sources.[19] In response to the seasonal nature of foods, *L. catta* are able to switch their dietary focus quickly as new foods become available and often make long excursions out of their normal home range to monitor seasonal food sources.[8,43,45] In addition, they can exploit water

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sources such as tree hollows that are unavailable to most other mammals. Drinking from tree hollows is a difficult procedure because these hollows tend to be on the vertical face of a tree, and often only one branch is available to sit on (Fig. 4). A ringtailed lemur inserts a hand into the hole and reaches down, immersing the hand in the collected water, then withdraws the hand and licks the water from it. In captivity, some ringtailed lemurs have even been observed immersing their tails in water and then drinking water from the wet tail.[46] Depending on the study site, ringtailed lemurs spend 18% to 30% of their time feeding on the ground.[10,19] Reproductive state affects feeding behavior. At Beza Mahafaly, lactating females focus more on low-cost, predictable, high-protein plant resources such as young leaves, whereas during pregnancy they switch to flowers and seek out rare fruits.[43]

REPRODUCTIVE ECOLOGY

Ringtailed lemurs exhibit the basic prosimian reproductive physiology. They have a highly constrained breeding period that lasts approximately 6 to 24 hours per year.[6,47,48] Among free-ranging and captive *L. catta*, all females within a group experience estrus within 1 to 3 weeks of each other; all females living within the same forest enter estrus during similar periods.[47,49] However, unlike nocturnal prosimians, they do not show periodic closure of the vagina.[50] Long-term census data at Beza Mahafaly indicate that 80% to 85% of females give birth annually.[8]

Infants are weaned when they are about four to five months of age. Infant mortality during the first year is between 30 and 51%, depending on the year and locality,[8,10,13-14,51] although during drought years infant mortality can be as high as 80%.[15] As in many mammals, the survival of infant ringtailed lemurs at Beza Mahafaly is related to the age of the mothers, with the infants of young-prime and prime-aged females having higher survival rates than those of older females.[8] Female ringtailed lemurs also show a well-developed maternal affectional system paralleling that seen among anthropoid primates.[6,8,30,31,47,49,51–53] For example, female ringtailed lemurs will go to great lengths to care for sick or injured infants, even attempting to carry infants in their arms while walking bipedally.[51] In addition, male ringtailed lemurs show an interest in infants, behave in an affiliative manner toward them, and occasionally engage in alloparental care.[29]

As in other placental mammals,[54,55] lactation is the most costly reproductive period for prosiman primates.[56,57] Ringtailed lemurs, along with other *Eulemur* sp., appear to produce dilute milk more like that of anthropoid primates and unlike those of lorises and bushbabies, which contain high con-

Box 1. Ringtailed Lemur Study Sites

The Berenty Nature Reserve (**A**) is a private, independent forest reserve set aside by the de Heaulme family in the 1940s, located in the extreme south of Madagascar. It consists of 100 ha of riverine gallery forest, as well as 140 ha of open-canopy scrub and dry spiny desert forest. Bordered on the north by the Mandraré river, it is almost completely surrounded by sisal plantations. Currently, the forest contains approximately 400 ringtailed lemurs, which have been studied and counted at intervals since 1963[7].

The Beza Mahafaly Special Reserve (**B**) located in southwestern Madagascar, was established in 1978 and decreed a Special Government Reserve in 1986. This reserve is the field site for a cooperative interuniversity project developed to promote conservation, education, research, and development in southern Madagascar. It consists of two parcels, one of 500 ha containing desert-like didierea forest and the other of approximately 80 ha of riverine gallery forest bordered on the east by the Sakamena River. Reserve boundaries are within a much larger tract of continuous forest. Studies of ringtailed lemur socioecology have been carried out since 1987. At least nine troops of ringtailed lemurs live within the riverine gallery forest; their total population was 124 individuals in 1987-1988.[8]

The Duke University Primate Center (**C**) was originally conceived by J. Buettner-Janusch while he was at the Department of Anthropology at Yale University. In 1966, Dr. Buettner-Janusch moved his prosimian colony of 80 bushbadies, plus a small number of captive lemurs obtained from Parc Tsimbazaza in Madagascar, to Durham. In 1971, the current facility was opened in the Duke Forest. At that time the colony consisted of approximately 180 prosimians, including 14 ringtailed lemurs. In October 1981, a group of 15 ringtailed lemurs was moved into a 1.2-square-acre outdoor natural enclosure. Today the Primate Center's total enclosures include more than 30 contiguous hectares of forest.[9]

A. The Berenty Nature Reserve in southern Madagascar.

B. The forest at Beza Mahafalay Special Reserve in southwestern Madagascar.

C. Forests of the southeastern United States at the Duke University Primate Center.

Figure 3. Ringtailed lemurs are opportunistic omnivores, their diet even includes daily consumption of the soil from termite nests.

Figure 4. *Lemur catta* are able to exploit sources of water not readily available to other animals. Here a female inserts her hand into a tree hollow filled with water, then pulls it out and licks the water from her wet hand.

centrations of fat, protein, and energy.[57] This may reflect differences in patterns of maternal care. Nocturnal lorises and bushbabies leave their infants unattended for long periods while they forage, which means that infants must be sustained during long intervals between nursing.[57] Ringtailed lemurs, like most other diurnal lemurs (with the exception of *Varecia* sp.) and anthropoid primates carry their infants with them, and suckle them on demand.

Long-term studies at Beza Mahafaly have revealed that reproduction in *L. catta* is tuned to the seasonal nature of specific food resources (Fig. 5).[58] Because females all mate during the same short period, they move as a group through different reproductive states during which they depend on phenologically distinct plant species.[58] For ringtailed lemurs at Beza Mahafaly, early lactation coincides with an initial peak in fruit availability, although this timing is more variable at Berenty.[59] Late lactation and weaning occur during a second peak in fruit availability, and the entire lactation and

weaning period corresponds with greater availability of young leaves. Pregnancy in ringtailed lemurs coincides with relatively low food availability. During this period, *L. catta* at Beza Mahafaly must focus on a few keystone fruit species. The birth season corresponds to a short burst of flowers. Given the seasonality of their environment, female ringtailed lemurs are thus on a tight schedule in that they must not only nurse their infants but also wean them during the wet season (Fig. 6). An extensive and unique longitudinal study of growth and body weights among ringtailed lemurs living within forest enclosures at the Duke University Primate Center indicates that several ringtailed lemur life-history traits reflect this stress of resource seasonality.[60] For example, infants grew quickly during the first seven months of life, and then showed dramatic reduction in growth rates in the eighth month despite being provisioned. Remarkably, this fits extremely well with the phenological and reproductive data from Beza Mahafaly. Here, the birth peak occurs in October,

the beginning of the wet season, with its concomitant increase in resource availability, while eight months later there is a dramatic drop in food resources. Thus, infant ringtailed lemur's pattern of growth allows maximum velocity when mothers, and later their weaning infants, have access to more resources but, even in captivity, slows when, under natural conditions in Madagascar, resource availability drops precipitously.

During estrus, females characteristically mate with more than one male, including group males, transferring males, and males from adjacent groups.[6,14,29,47] Despite the basic mammalian pattern of seasonal estrus, female mate choice does occur. During behavioral estrus, females reject repeated mating attempts by sons and closely related males,[17,47] an observation that is supported by genetic evidence.[61] Similar behavior has been noted for many free-ranging anthropoid species.[62,63] Female mate choice also affects mating order, insuring that most females mate with more than one male, and that some of these mates are either from another group or are transferring males.[14,47,64] Partner preferences have also been observed among captive *L. catta* females.[18,48]
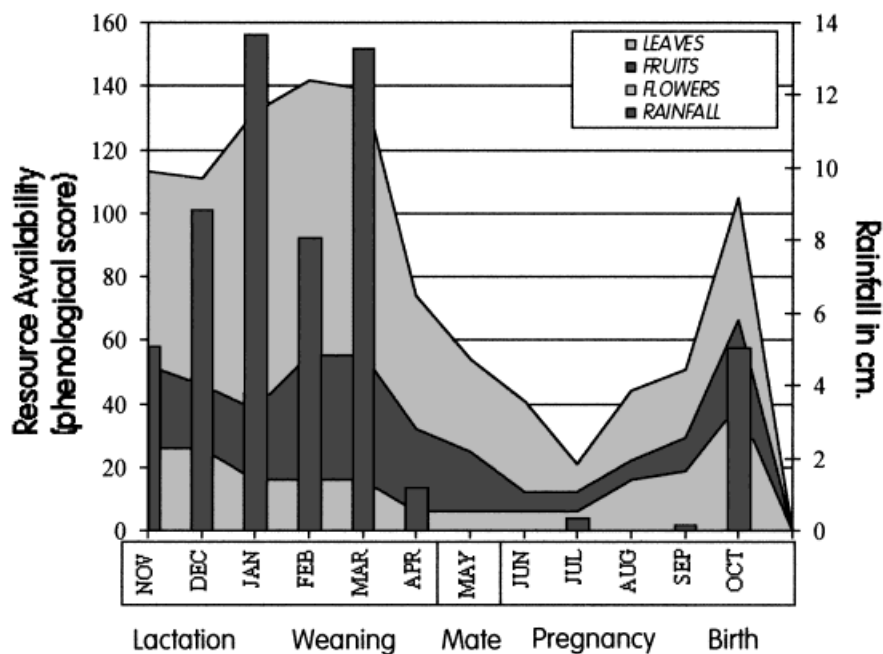
Figure 5. The relationships of rainfall and resource availability to reproductive state in ringtailed lemurs at Beza Mahafaly, Madagascar, 1987–1988.[58] Given the seasonality of resource availability in ringtailed lemur habitats in southern Madagascar, mothers are on a tight schedule in that they must nurse and wean their infants when resources are abundant.

Figure 6. Due to the highly seasonal nature of resources, female dominance in this species may function to reduce feeding competition during stressful reproductive periods such as lactation and weaning.

In extensive studies of collared ringtailed lemurs at Beza Mahafaly, we found that high-ranking males often exhibited sexual consortships that were reminiscent of those among group-living cercopithecine primates.[34] Such consortships were maintained solely by the male, who basically shadowed the female's movements.[47] During the mating season, the month of May, these males approached, sat near, and even rested or slept in contact with females during the midday rests.[47] High-ranking males also curtailed close contact between females nearing estrus and other males by "stink fights" and aggressive displacements[6,47] and were therefore nearest when receptivity occurred. This behavior was exhibited only toward females who had not yet mated, and began one or two days before the female became receptive.[47] Although factors such as female choice, length of male tenure, and inbreeding avoidance create some variability, there is a tendency for top-ranking males to be receptive females' first mating partners at both Beza Mahafaly and Berenty.[47,64] Mating order may affect male reproductive success in this species. First, there is evidence that mating with ejaculation may lead to a loss of receptivity.[48,52]

Second, paternity data from captive groups suggest a first-mate advantage in this species,[61] although this has yet to be tested in the wild.

There is increasing evidence that sperm competition is a viable reproductive strategy for male ringtailed lemurs.[47,65] Male *L. catta* have the larg-

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est relative testes of all strepsirhines.[65,66] Also, as noted earlier, in most cases receptive females are approached by and mate with more than one male. Males continuously harrass most mating couples so that a male will mount, then quickly dismount to chase away approaching males. Dur-

ing this time a male can mount as many as 25 times before ejaculation.[47] Postejaculatory guarding is commonly observed.[47–48] At Beza Mahafaly, the top-ranked males guarded the longest, and group males guarded longer than nongroup males.[47] Postejaculatory guarding may increase the male's chances for paternity. Because copulatory plugs are common to this species, and form within minutes in the vaginal canal,[52] the longer after ejaculation a male can guard a female, the greater the possibility that a plug may form and block or at least impede subsequent sperm. The possibility that further copulations might interfere with plug formation may also explain why males at Beza Mahafaly ceased to mount females after a single ejaculation, even though they continued to guard the female for up to 62 minutes.[47] A comparative study of penile morphology and testicular volume in nonhuman primates has shown that these reproductive organs are more specialized in species with multimale mating systems.[67] *L. catta* possess penile spines and a complex distal penis

Figure 7. Ringtailed lemurs combine the basic prosimian emphasis on olfaction with visual signals more common to anthropoid primates. Here a male marks a tree with both scent and a visual mark.
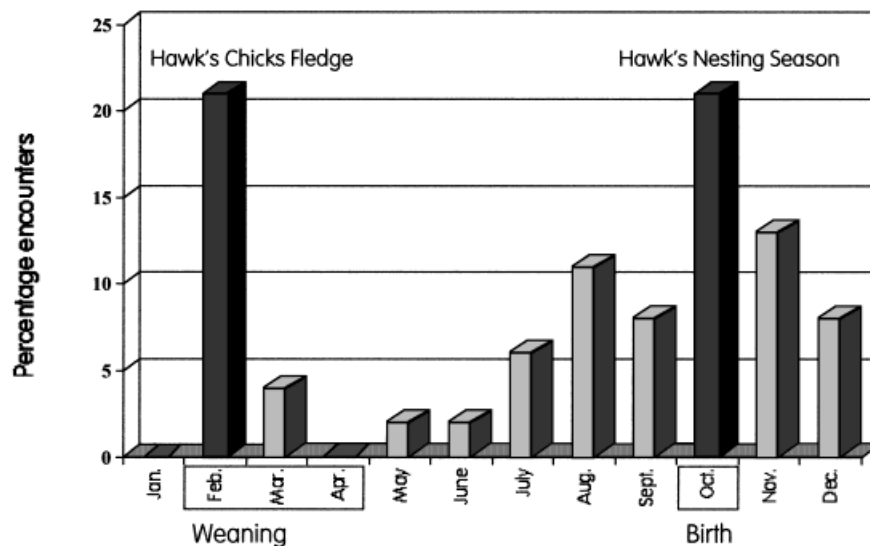

Figure 8. The percentage of encounters between *Lemur catta* and the Madagascar harrier hawk at Beza Mahafaly, Madagascar, 1987–1988. Encounters peak during the period when the raptors have increased food requirements (nesting and fledging periods). These are times when infant ringtailed lemurs are especially vulnerable to predation.[47]

morphology, including an enlarged glans penis. Because male *L. catta* mating involves repeated brief intromissions with thrusting prior to ejaculation,[47,52,64] such morphology could facilitate displacement or break-up of previously formed copulatory plugs, but little is known about this in primates.[66,67]

COMMUNICATION

Ringtailed lemurs show a combination of olfactory, visual, and vocal modes of communication. Although they exhibit the basic prosimian pattern in that they use olfactory communication to a greater degree than do most anthropoid primates, they also have adaptations to a diurnal and group-living existence. Both males and females have genital scent glands. In addition, males have wrist glands associated with a hard, sharp, horny spur and a well-developed brachial gland just above the clavicle.[52,68] Ringtailed lemurs also have trichromatic color vision, although it is not as sensitive as that in catarrhine primates.[69,70] An example of this combination of visual and olfactory communication can be seen in male marking behavior. Males use both wrist and brachial glands to mark their tails, which they then wave at another male during "stink fights."[6]

In addition, they use the spur to scratch the surface of trees which, in tandem with the wrist glands, leaves both an olfactory and a visual mark (Fig. 7).[6,68] Investigations of the role of scent-marking behavior indicates that these

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lemurs may use olfaction in spatial, sexual, and social contexts.[71–74]

Relatively speaking, the vocalizations of ringtailed lemurs are similar to those of Old World monkeys in both structural diversity and repertoire size, although comprising more discrete calls without so much intergrada-

tion.[75–77] Ringtailed lemurs have numerous contact calls as well as a male loud call that can be heard one kilometer away and somewhat resembles the song of *Indri.*[6] Of particular interest is the documentation of alarm calls in this species. *L. catta* are semi-terrestrial and are therefore exposed to many of terrestrial as well as arboreal predators.[6,37,78] Antipredator defense in this species involves vigilance and mobbing behaviors as well as alarm calls, once potential predators are sighted.[6,78] Recent field and captive work indicates that representational signaling is present in ringtailed lemur alarm calls,[79,80] but may be absent from the alarm calls of some other lemur species.[79] *L. catta,* like many anthropoid primates,[81,82] have differentiated alarm calls in response to different potential predators, with avian predators evoking a separate repertoire of vocalizations and behaviors than do mammalian and reptilian predators.[33,36,78,79]

Such alarm calls may function, in part, to protect infants. At Beza Mahafaly, predation on infant ringtailed lemurs by the Madagascar harrier hawk has been observed.[83] Furthermore, bones of adult and juvenile ringtailed lemurs have been found below roosting sites of this raptor.[84] Encounters with avian predators, including vocalizations and mobbing, peak during the birth season and when infants are

being weaned. These peaks in encounters coincide with previously observed periods of greater food requirements for the harrier hawk and the Madagascar buzzard, for example, during their nesting and fledging periods (Fig. 8).[78] Both of these are times when *L. catta* infants are especially vulnerable to predation.

FEMALE DOMINANCE

While female dominance was once thought to characterize all the Malagasy primates, recent field and captive studies have revealed that this is not the case.[85–87] The ringtailed lemur is, in fact, one of only a few group-living lemur species documented as exhibiting true female dominance, including both feeding priority and social dominance in nonfeeding contexts.[12,18,19,85–87] Female dominance in this species appears to have both a developmental and a neurophysiological component. From a developmental perspective, it is important to note there are no apparent sex differences with regard to rough-and-tumble play among ringtailed lemurs.[53] In this respect, they differ from most male-dominant group-living anthropoids, among which young males show higher levels of such play.[88] Infant ringtailed lemurs exhibit dominance-related behaviors as early as four months of age. In the one study of infant behavior in the wild, female infants initiated nearly all fights with other infants.[53]

Adult males do not inherently avoid females and, in fact, subadult females who have not yet bred can be nonaggressively displaced by adult males in all contexts, albeit most often over food.[31] At Beza Mahafaly, this was observed to change during the females' first mating season, when these same females began aggressively cuffing and biting males that attempted to mate with them outside their estrus period. Males reacted to such rebuffs by retreating without physical counter-aggression and by submissive vocalizations. What is especially significant is that after this change in the relationship between young females and adult males, males could no longer directly supplant these females, and the normal dominant female behavioral pattern ensued: These females began actively displacing males in feeding and

social contexts.[31] At the Duke University Primate Center, adult males began spontaneously (not as a response to female aggression) showing submissive signals to maturing females, and they did this before the mating season.[89] Thus, along with a developmental component, males appear predisposed to retreat or exhibit other submissive behaviors either spontaneously or in direct response to female aggression.[19,31,89]

Why and how female dominance evolved among some Malagasy lemurs have been long standing questions.[21,90,91] The main hypothesis argues that female dominance is a necessary behavior for successful female reproduction because lemurs have unusually high energetic costs associated with reproduction.[90,91] However, several recent studies have not supported this view. An analysis of strepsirhine

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life-history variation comparing lemurs with lorises, which do not exhibit female dominance, found that while lemurs do have greater prenatal maternal investment rates than lorises do, this was not a consequence of constraints on basal metabolic rates.[92] In this analysis, lemurs and lorises showed no significant differences in postnatal litter growth rates, one measure of maternal investment during reproduction. Moreover, a study that compared lemurs (*Eulemur* sp.) and lorises (*Otolemur* sp.) with regard to energy transfer during gestation and lactation found that for these particular species, the lemurs actually had the lower prenatal and postnatal maternal investment.[93] These results indicate that we cannot make a special case for the Malagasy lemurs with regard to energetic costs of reproduction as measured in these studies. However, there

are other factors that may increase reproductive costs, but which have yet to be documented for lemurs as well as most other primates. These include, but are not limited to, larger body size in diurnal forms, infant carrying, greater potential feeding competition in large social groups, seasonal resource availability, and reproductive seasonality.[58,62,90] Of these, the last two factors appear to be especially important to understanding female dominance among ringtailed lemurs.[31,58,90]

As noted, at Beza Mahafaly strict breeding seasonality is tied to the availability of resources. Females lactate during the period of food abundance, gestate during the period of relatively low food availability, and give birth during peaks of important food resources such as flowers.[58] Given the close reproductive synchrony in this species,[6,37,47,49] reproducing females will experience identical reproductive events and undergo similar reproductive stresses, leading to high levels of interindividual resource competition. This can be mediated somewhat by behaviors that reduce energy costs.[43,58] Under such conditions, extra feeding competition from group males would be a distinct disadvantage not only to females, but also to their infants, unless adult females had feeding priority. At Beza Mahafaly, males provide constant direct and indirect feeding competition for females throughout the year. This feeding competition is especially acute during the physiologically stressful periods of late lactation and weaning, during which female-male feeding agonism peaks.[31] There is no indication that males are simply deferring to females in naturally occurring groups,[85,94] at least with regard to feeding priority, as most feeding agonism between males and females involves a female aggressively displacing the male.

True female dominance in this species may function, at least in part, as a reproductive strategy to minimize male feeding competition within a highly seasonal environment. In this regard, ringtailed lemurs are similar to polygamous but sexually dimorphic anthropoids such as the vervet and patas monkey among which smaller females cannot easily displace males individually, but instead use female-

female coalitions to affect male behavior.[95–98] Female vervets commonly form aggressive coalitions against males in both feeding and nonfeeding contexts.[98] Patas monkey females can attack males both in coalitions and sometimes singly.[96,97] Both of these species also live in highly seasonal habitats and exhibit seasonal reproduction. Put in this context, female dominance in ringtailed lemurs ceases to be a peculiarly lemur trait that requires some special explanation. It becomes, rather, a behavioral response of group-living female primates of a nondimorphic species to mitigate feeding competition within a consistently seasonally-stressed environment. The role of female dominance as "behavioral compensation"[99] to minimize reproductive costs remains a viable and important approach. The robustness of reproductive and environmental factors, both singly and in tandem, in explaining the variety of lemur life-history patterns,[62] as well as social systems, is a promising arena of research that has been addressed in only a few other lemur species.[100–102]

CURRENT CONTROVERSIES

In addition to what we now know of ringtailed lemur socioecology, there continues to be vigorous debate concerning other aspects of their behavior. Two especially lively controversies revolve around territoriality and infant-killing in this species. There has been some controversy about how to define the spatial relationships of ringtailed lemurs. For example, based on earlier reports from Berenty, *L. catta* has been referred to as the only primate species with multimale groups that is territorial.[103] However, because groups at Berenty have highly overlapping ranges, ringtailed lemurs have since been deemed a "dubious case" for territoriality, one "best considered [to be] intermediates like the Nairobi baboons."[6,7,104] Currently, however, ringtailed lemurs at Berenty are viewed as being territorial or quasi-territorial; that is, they become territorial at particular population densities.[38,40] Part of this confusion is related to the lack of a reliable operational definition of territoriality, which often makes the meaning of this concept quite different in different contexts. If territorial-

ity is "the active defense of individual or group home range boundaries by actual or ritualized agonistic encounters, thereby maintaining essentially exclusive use of the home range,"[105] then ringtailed lemurs are not territorial.[40,106]

At Berenty there is considerable overlap of home ranges, and at Beza Mahafaly there is, in some cases, almost total home range overlap, so that many troops may time-share sites for feeding, sleeping, or resting.[39] Furthermore, home ranges can change seasonally.[8,38,58,40] Nevertheless, there are core areas that are more intensely used by *L. catta* groups at both Berenty and

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Beza Mahafaly. As noted, intergroup encounters are common and may function, in part, to keep other groups out of these core areas. Data from both sites indicate that such intergroup encounters of ringtailed lemurs might best be seen as spatial defense,[40] with population density and resource richness playing key roles in explaining some of the variability seen.[19,40] At Berenty, troops using more marginal scrub areas have home range sizes, range use, and intertroop behavior that are similar to those of troops living in more marginal habitats at Beza Mahafaly. The differing behavior

of Berenty troops in richer zones was noted as long ago as 1975,[16] and underscores *L. catta's* adaptability.

Another area of contention concerns the role of infant-killing. Ringtailed lemurs suffer high annual infant-mortality rates, which can be exacerbated by drought.[15,58] The killing of infants, albeit rare, has been observed. However, the pattern varies between Berenty and Beza Mahafaly. At Berenty two cases of killing, one by an immigrant male and one by a resident female, have been observed, in addition to seven cases of infant-wounding by unknown causes.[28,107] One eyewitness account of infant wounding by an immigrant male also has been seen at this site.[107] At Beza Mahafaly, no case has been observed in which a male killed or wounded an infant, despite three year-long intensive studies and another concentrated study during the birth and lactation season.[8,19,29] In fact, not a single episode of male aggression toward any infant has been observed at this reserve.[19,30,108–110] There has, however, been one eyewitness account of a female wounding another female's infant. In this case, the infant belonged to a female who was attempting to join the group. The infant was attacked and bitten on the head by a resident female. The infant survived, but lost one eye.

It has been recently suggested that infanticide may be an adaptive aspect of the mating system of male ringtailed lemurs.[61] In groups of ringtailed lemurs living in forest enclosures at the Duke University Primate Center, immigrant males have never been observed killing infants. However, they have been seen attacking or preparing to attack infants on four separate occasions, and females have been reported to attack and chase males repeatedly if they attempt to immigrate during the lactation period. It has been argued that such female aggression is a response to preventing infanticide by males, which, in turn, is suggested to be an established male strategy that has developed in tandem with patterns of female mate choice in this species. If a female loses her infant one year, it is suggested that her next infant has a better chance at survival. If infants die, for whatever reason, it is argued that their mothers will not

choose to mate again with the same males, but rather will choose the immigrant males. This is called the "incompetent father" hypothesis.[61]

This hypothesis is problematic on several levels. First, despite thousands of hours of observation on identified, habituated individuals, the phenomena of increased agonism by females toward males during the lactation period has not been observed in other studies of free-ranging or semi-free-ranging populations.[18,30,53,106,108] Second, as noted earlier, most females give birth annually, and between 30 to 51% of these infants perish each year.[8] If male infanticide is a viable male strategy, presumably a high proportion of these deaths should be the result of male infanticide. Yet only one case of male infanticide by *L. catta* has been seen at Berenty, and, as previously noted, neither male aggression toward infants nor infanticide has been observed at Beza Mahafaly. Males in three focal groups at Beza Mahafaly have been observed engaged in alloparental care of infants and, in some cases, the male alloparent did not mate with the mother of the infant.[108] Third, current data indicate that losing an infant one year does not enhance the chances of survival of the next year's infant.[15] Finally, because females regularly mate with males both from within and outside of the group, it is difficult to conceive of either the female or the male recognizing the father of any particular infant, a prerequisite for the incompetant father hypothesis.[61] The advantages of infanticide as a male reproductive strategy in *L. catta* thus remain problematic.

What is clear from the data is that socially[28] and perhaps even ecologically mediated wounding and killing of infants does occur among ringtailed lemurs. During intergroup fights, infants fall off, are abandoned, and even attacked by individuals of their own and other groups.[28,42,107] The two clearly documented observations of infant-killing are cases in point. The male infanticide at Berenty was observed during a time of great social upheaval, a group fission.[111] In this case, an infant of one subgroup was dropped during a confrontation with the other subgroup. After the infant's subgroup retreated, the infant was investigated by the other subgroup's fe-

males, who then abandoned it. The male of that subgroup then bit and killed the infant. In this case, the death resulted from separation during intergroup fighting.[28] The second case involved a dominant female attacking a subordinate female and her infant. The infant died from its wounds.[107] Attacks by higher ranking females against lower ranking mothers have also been observed at Beza Mahafaly and in semi-free-ranging contexts.[18,27,42] What is not clear in these cases is whether the infant or the mother is the target. Nevertheless, increases in such targeting aggression have been linked to birth seasons in semi-free-ranging groups and thus may be a form of reproductive competition.[27]

Reproductive competition also could

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occur through less direct ways. For example, one study reported that six of the seven deaths in four study groups at Berenty were not associated with either killing or wounding, but these infants were the offspring of middle- or low-ranking mothers.[51] This pattern also is seen at Beza Mahafaly.[47] Rank affects access to resources as well as levels of feeding competition. At Beza Mahafaly, low-ranking females face such competition from both males and high-ranking females.[31] It remains to be demonstrated that this directly and adversely affects the ability of low-ranking females to nurse and care for their infants. Ecologically mediated infanticide and infant wounding may also occur. Intergroup encounters and agonism between fe-

males of different groups peak during the birth season when access to resources is especially critical.[13,19,42] Infants can be wounded or killed during aggressive encounters between females of different groups.[19] The controversy is thus not whether killing and wounding of infants occurs in this species, but whether such acts are a by-product of social aggression, intergroup encounters, resource competition, or a form of reproductive competition for males or females or, perhaps, both. On a wider scope, the high infant mortality rate has yet to be explained, although determining the interplay among stochastic events such as predation, parasites, illness, and falls, socially induced fatalities, female reproductive stress, and precocial infant development would clearly be critical.

WHERE NEXT?

Clearly, one can no longer make the case that female dominance is systematic for the Lemuridae.[87] Furthermore, female dominance and even female feeding priority have different implications depending on social organization (for example, group-living, pair bonds, or solitary but social). Direct feeding competition, and hence advantages of female feeding priority, will presumably be more intense in larger groups. Thus, it makes little sense to treat female dominance among lemurs as either a ubiquitous or unitary trait. In addition, even if there is some identifiable stressor common to all lemurs, (such as more seasonal rainfall or extreme temperature), there is no inherent reason to expect all lemurs to respond in the same manner. Studies of ringtailed lemurs indicate that female dominance may indeed be one way to minimize the effects of resource seasonality on successful reproduction, but there are additional and even alternative strategies for other lemur species that are just beginning to be documented.[102,112]

Based on earlier reports by Shaw,[2] Elliot[113] stated that ringtailed lemurs "dwell among the rocks . . . and are not arboreal" (p. 60). Rand[3] reported that "the animals spend as much time on the ground as in the trees. In the trees . . . they are not as agile or as active as

others of this group. On the ground they are quite at home. . . ." (p. 96). Napier and Walker[114] concluded that *L. catta* is intermediate, both evolutionarily and behaviorally, between a vertical clinger and leaper and an arboreal quadruped. Others have said that the ringtailed lemur is mainly arboreal and restricted to forests.[6] This may seem to be an old and not very interesting question because it is now obvious from quantitative studies that the ringtailed lemur spends a great deal of time both on the ground and in trees.[6,10,19] However, these observations exemplify an important characteristic of *L. catta*—their behavioral flexibility. This is an edge species and, like many other edge or weed species, it has an amazing ability to rebound from environmental perturbations.[15] Furthermore, as an edge species, the ringtailed lemur is adapted to many habitats that do not provide continuous arboreal pathways. Thus it is found in dense brush, on the edges of savannah, in the low limestone forests of the southwest, on the edges of the desert-like didierea forest,[115] and even on rocks. Recently, a potential new subspecies was located living in the rocks and low bush on the Andringitra Massif above the tree line at an elevation of more than 2,510 meters.[116] The ringtailed lemur is the only extant lemur that can take advantage of these transitional and even marginal regions, partly because of its behavioral flexibility and in part because it does so much of its traveling on the ground.

In this edge adaptation, the ringtailed lemur is in many ways an ecological equivalent of vervet monkeys and many macaque species. The behavioral and life-history data that continue to accumulate from Berenty, Beza Mahafaly, and the Duke University Primate Center are allowing researchers to expand their understanding of such flexibility. In just these three sites, we see considerable variability in terms of agonistic relationships among females, ranging behavior, and male transfer behavior. One potentially fruitful approach is to view such variability as "reaction norms,"[117] or the range of phenotypes expressed by a single genotype in response to varying environmental conditions.[118] Along this line, a detailed comparison of the ecological constraints (or lack thereof) and the

life-history characteristics of lemurs at these three sites could give fresh insight to the nature of this primate's physiological and behavioral flexibility.

Yet even with such flexibility, there is increasing demographic evidence that this species is highly sensitive to habitat quality and change. For example, denser populations and smaller home ranges are characteristic of groups inhabiting gallery forest as opposed to transitional dry forest.[8,119] Due to the extreme seasonality of their habitat, ringtailed lemurs appear to be highly dependent on specific keystone resources. Key species provide important food items during critical periods of the reproductive cycle.[58] During drought years, mortality for mothers and infants increases dramatically,

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. . . in the highly seasonal habitats characteristic for this species, the loss of key resources can be expected to have an enormous impact on ringtailed lemur demography and survival.

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providing indirect evidence that this species is highly dependent on the phenological reliability of food resources.[58] Thus, in the highly seasonal habitats characteristic for this species, the loss of key resources can be expected to have an enormous impact on ringtailed lemur demography and survival.

Although much has been written about the degradation of the eastern rainforests of Madagascar, it appears that the dry forests of the southwest may be disappearing at an even faster rate than the forests of the east.[120] For example, from preliminary analyses, we believe that only around 4,510 ha of gallery forest still exists in southern Madagascar. This is the habitat in which ringtail lemur populations are most dense. Often considered among the most common of the lemurs, we

believe that a detailed survey of the distribution and abundance of *L. catta* may reveal that this intriguing lemur and its habitat are in far greater danger than is generally believed.

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