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MAMMALIAN SPECIES 42(854):58–74

Lemur catta (Primates: Lemuridae)

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Abstract: *Lemur catta* Linnaeus, 1758, is a lemurid commonly called the ring-tailed lemur. A strikingly colored, long-tailed lemur, it is the only species in the genus *Lemur*. It occurs in the southern half of Madagascar, where it inhabits a variety of forested habitats. It is listed as Vulnerable by the International Union for Conservation of Nature and Natural Resources. DOI: 10.1644/854.1.

Key words: island, Madagascar, lemurid, primate, ring-tailed lemur

Synonymies completed 10 September 2008

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Lemur Linnaeus, 1758

Lemur Linnaeus, 1758:29. Type species *Lemur catta* Linnaeus, 1758, by subsequent designation (Thomas 1911).

Prosimia Brisson, 1762:156. Type species *Lemur catta* Linnaeus, 1758, by subsequent designation (Elliot 1913). Unavailable name (International Commission on Zoological Nomenclature 1998, Opinion 1894; see "Nomenclatural Notes").

Procebus Storr, 1780:32. Type species *Lemur catta* Linnaeus, 1758, by original designation.

Catta Link, 1806:7. Type species *Catta mococo* Link, 1806 (= *Lemur catta* Linnaeus, 1758), by tautonymy.

Maki Muirhead, 1819:405. Type species *Maki mococo* Desmarest (= *Lemur catta* Linnaeus, 1758), by subsequent designation (Schwarz 1931; see "Nomenclatural Notes").

Mococo Trouessart, 1878:163. Type species *Prosimia catta* Lesson (= *Lemur catta* Linnaeus, 1758), by monotypy.

Odorlemur Bolwig, 1960. Type species *Odorlemur* (*Lemur*) *catta* (= *Lemur catta* Linnaeus, 1758), by original designation.

CONTEXT AND CONTENT. Order Primates, suborder Strepsirrhini, infraorder Lemuriformes, superfamily Lemuroidea, family Lemuridae. *Lemur* is monotypic.

Lemur catta Linnaeus, 1758
Ring-tailed Lemur

Lemur catta Linnaeus, 1758:30. Type locality "Madagascar."

Maki mococo Muirhead, 1819:405. Type locality unknown (see "Nomenclatural Notes").

CONTEXT AND CONTENT. Context as for genus. *Lemur catta* is monotypic (Groves 2001), but Goodman and Langrand (1996) described geographic variation that suggested further taxonomic study was warranted.

NOMENCLATURAL NOTES. Linnaeus (1758) included 3 species in his description of *Lemur*. Because Thomas (1911) fixed the type as *L. catta*, the subsequent separation of the other species into what is now called *Eulemur* Simons and Rumpler, 1988, left *Lemur* monotypic (Groves and Eaglen 1988). *Prosimia* Brisson, 1762, was declared unavailable by the International Commission on Zoological Nomenclature (1998).

The earliest mention in the literature of what is clearly *L. catta* is a brief description by Samuel Purchas (1625), who compared them to monkeys in size, but with a long tail like a fox, ringed with black and white. *Lemur* is from the Latin

Fig. 1.—An adult *Lemur catta* in the Berenty Nature Reserve, Madagascar. Photograph by Don E. Wilson.

lemurs, which means ghosts or specters, a reference to the animal's nocturnal habits and stealthy movements. The specific epithet *catta* refers to the animal's catlike form. The name *Maki mococo* is attributable to Muirhead (1819) even though he cites authorship of the name from Desmarest (1817) because Desmarest's name was simply a vernacular term.

DIAGNOSIS

Lemur catta is a medium-sized lemur with a distinctive black-and-white ringed tail (Fig. 1). There are perianal glands and males have a naked, black scrotum. Females have 2 pairs of mammae, only 1 of which is functional. There is a cutaneous brachial gland that is quite large and distinct in males, less so in females. Both males and females have an antebrachial or carpal gland on the palmar surface of the wrist although in females this is nonfunctional. In addition, males have a horny spur on the forearm, which overlays the antebrachial gland (Tattersall 1982). All lemurs have some pigmentation of the ocular fundus, obscuring the tapetum lucidum to varying degrees. In *L. catta*, this pigmentation is quite spotty, leaving most of the tapetum lucidum brightly visible (Groves 2001). In addition, there is a rudimentary foveal depression (Pariente 1970). The sole of the hind foot is naked to the heel, whereas in other species of lemurs, the heel is covered with hair.

GENERAL CHARACTERS

"*Lemur catta* looks rather like a Paris-styled raccoon" (Jolly 1967:3). The slightly built body and narrow muzzle give this handsome animal a somewhat foxlike appearance (Fig. 1). The hind limbs are much longer than the forelimbs, and this is the most terrestrial of the lemurs. The forelimbs are furnished with long, slender, padded, somewhat dexterous fingers bearing nails. The hind limbs have a keratinous toilet-claw on the 2nd digit, used for grooming. An additional grooming aid is the toothcomb, formed by procumbent lower incisors and canines (Fig. 2).

The body of *L. catta* is covered with dense, gray to gray-brown pelage, slightly darker around head and neck, with the exception of the ventral side and face. The underside, throat, and face are lightly haired with a paler, off-white color that allows darker skin to show beneath. The eyes are accentuated by conspicuous black, triangular rings around them, contrasting sharply with the white interocular area (Garbutt 1999; Jolly 1966; Mittermeier et al. 2006; Tattersall 1982). The ears are large and well furred, but without tufts. There is no obvious body color difference between males and females but variation may exist between individuals in the facial region (Jolly 1966). Dorsally, they are warm rosy brown grading into pale gray or grayish brown on the rump, sometimes accompanied by a brown pygal patch, and a somewhat darker gray toward the crown and neck. The half-meter–long, nonprehensile tail is sharply ringed with 12 or 13 white rings alternating with 13 or 14 black ones, and is longer than the head and body. The tip of the tail is black. Dark black skin is visible on the nose, hands, feet, genitals, eyelids, and lips, but the fur of the throat, ears, cheeks, and forehead are white (Jolly 1966; Montagna and Yun 1962). The smooth but leathery texture of the hands and feet allow for terrestrial movement (Shaw 1879).

Fig. 2.—Dorsal, ventral, and lateral views of the skull and lateral view of the lower mandible of *Lemur catta* (adult male, United States National Museum no. 589559), collector and locality unknown.

Field measurements (mm) of 9 individuals with range (mean) were: length of head and body, 385–455 (423); length of tail, 560–624 (595); length of hind foot, 102–113 (108); length of ear, 40–48 (44). Range (mean) of length of cranium for 27 specimens, 78–88 (84) mm (Tattersall 1982). Body mass (mean) of 11 individuals ranged from 3.0 to 3.5 (2.8) kg (Tattersall 1982).

DISTRIBUTION

Lemur catta is found in the wild only in Madagascar (Fig. 3; also see map in Goodman et al. [2006]). Lying off the southeastern coast of Africa and separated from the continent by the Mozambique Channel, Madagascar is in the Indian Ocean and is the 4th largest island in the world (Swindler 2002). *L. catta* occurs only in the southern and southwestern portion of the island, reaching its northern limit near the town of Belo sur Mer on the western coast and Ambalavao in the central east (Goodman et al. 2006). The southeastern limit is the town of Tolagnaro on the southern coast (Jolly 2003; Mittermeier et al. 2006). *L. catta* was introduced to the United States on St. Catherine's Island, Georgia, in an attempt to establish a free-ranging, breeding population that could be studied and perhaps serve as a source for restocking parks in Madagascar (Iaderosa and Lessnau 1995).

FOSSIL RECORD

Fossil lemurs have been found in Europe, America, and Asia, but there are only subfossils known from Madagascar (Burney et al. 2008; Godfrey and Jungers 2002; Godfrey et al. 1998). There are deposits of subfossil bones that contain several extinct species of lemurs, including some very large ones (Mittermeier et al. 2006). Radiocarbon dates extend back only about 2,600 years for most of this material (Burney et al. 2004).

FORM AND FUNCTION

Form.—The fur of *Lemur catta* is so dense that it is difficult to clip with electric clippers without clogging them. The skin is hairy and glabrous, and dark gray or black in color. The skin underlying the white rings in the tail is actually black. The entire epidermis is heavily pigmented, but this is most evident in the regions lacking hair, such as the lips, eyelids, palms, soles, and scrotum (Montagna and Yun 1962).

The peculiar vulpine aspect of the head of *L. catta* is not so much due to an elongation of the muzzle as to the retention of a moist, glandular rhinarium and the upper jaw supporting it projecting beyond the level of the chin. The naked rhinarium continues down in front as a strip of grooved, naked skin that cleaves the upper lip. The upper lip adheres to the premaxillae, making it incapable of protruding. This is related to their habit of lapping water, a primitive character compared to more derived Primates, which use suction aided by protrusible lips to drink (Pocock 1918).

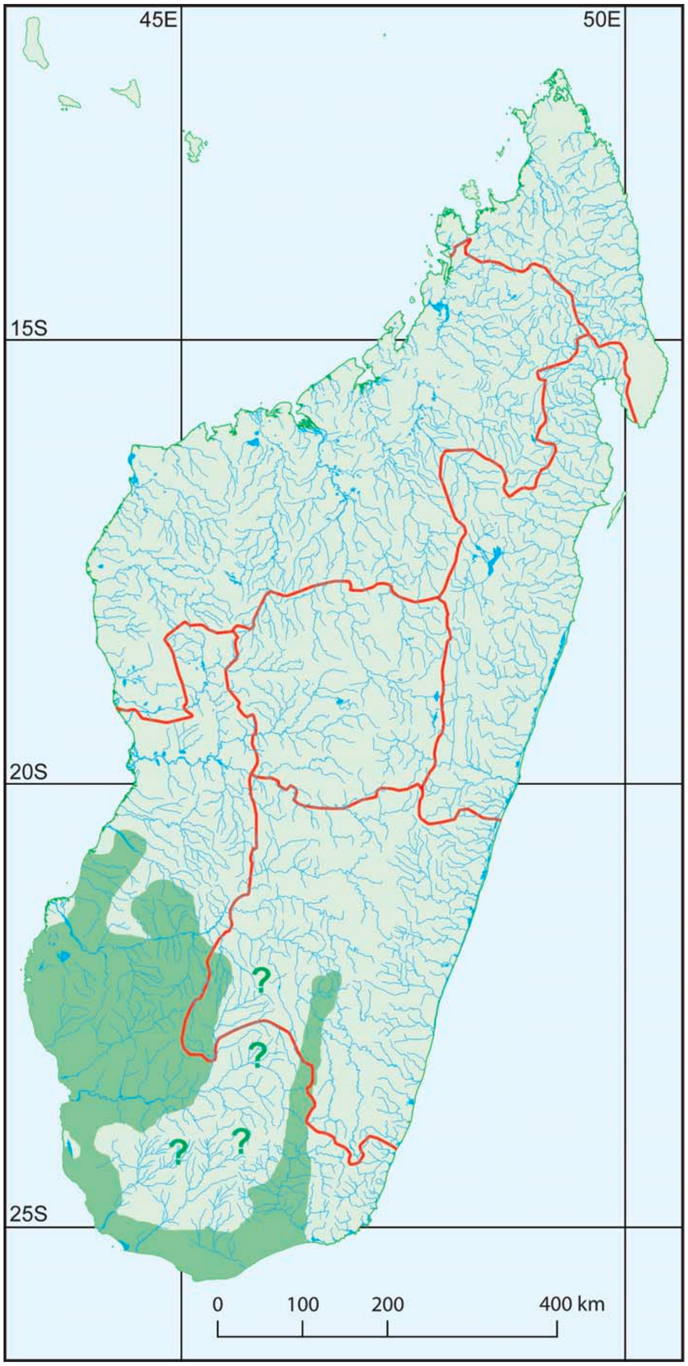

Fig. 3.—Distribution of *Lemur catta.*

The ears of *L. catta* are relatively larger than those of some other lemurs. The anterior edge of the upper one-half of the pinna forms a ridge that overlaps the shelflike supratragus, descends below it, and disappears into the capsule of the pinna above and within the small, lobate tragus. The antitragus is much larger than the tragus, and the deep notch between them is at the level of the external auditory meatus. The supertragus forms the upper boundary of the capsule of the pinna, and is rather high, about halfway between the notch and the upper edge of the pinna (Pocock 1918). Facial vibrissae are well developed, including mystacial, superciliary, and genal tufts. There is also a small patch of carpal vibrissae, located just above the wrist area on the underside of the forearm (Pocock 1918).

There is a brachial gland located on the underside of the upper arm in the shoulder region. A small elliptical mound about the size of an almond covered with short hair bears a crescent-shaped naked area in the center, which forms the orifice of the gland (Montagna and Yun 1962). The gland secretes a brownish, sticky substance that is strong-smelling. This gland is barely developed in females (Pocock 1918).

The forearms contain an antebrachial gland, covered by a small spur that forms part of a comblike organ. It lies about 25 cm above the wrist joint, and is about 1 cm long. It is oval, soft, compressible, and marked with fine lines like those that form fingerprints. Black in color, and continuous with the palm through a thin, hairless strip, it is raised above the rest of the integument by about 2 mm. Present in both sexes, in males it develops a hard spur as the animals age. It seems to be developed from the secretions of the underlying gland, which may have up to 1,000 tiny ducts connecting through the skin (Sutton 1887).

The fingers are long and slender, and relatively free of webbing. The thumb is the shortest, and well separated from the remainder. Although it can be extended at right angles from the palm, it is not truly opposable, as the ball of the thumb at its base is stationary. Of the remaining digits, the 4th is the longest by a small margin over the 3rd, and the 5th is slightly longer than the 2nd. The hand is ectaxonic (the axis passes through the 4th digit) as in all strepsirrhines, not mesaxonic (the axis passes through the 3rd digit) as in monkeys and apes. The palms on the forelimbs are long, smooth, and leathery (Shaw 1879).

In general, the semidigitigrade foot is more specialized than the hand. The big toe on the hind limb is smaller than that of more-arboreal lemurs, and is opposable. The 2nd digit is short, with a small terminal pad and a long, semierect claw (Pocock 1918).

The anus is located just below the joint of the tail, which closes over it when lowered. The perineal and circumanal areas are covered with hair. The scrotum is naked, black, glabrous, and covered with tiny, horny spines. The 2 sacs are separated by a deep, longitudinal furrow. The penis is subcylindrical and bears small spines. In addition there are 2 pairs of larger spines on each side. The terminal urethral orifice is located just below the tip of the baculum. The baculum is a short, slender rod, larger proximally and bearing a bilobed distal expansion. Compared to the size of the animal, the baculum is relatively small. The scrotum, penis, and prepuce frequently have a viscid, foul-smelling coating (Montagna and Yun 1962).

In females, the clitoris is thick, elongated, and protrudes from the labia of the vulva. The thick labia originate slightly above the orifice, and surround it, disappearing into the naked integument posteriorly from which the clitoris arises. The urinary orifice is a bit closer to the clitoris than to the vaginal orifice. This allows the urinary channel to run from the opening down to the tip of the clitoris, forming a drip tip. There are 4 nipples, with the anterior pair almost in the axillae (Montagna and Yun 1962).

The dental formula for *L. catta* is i 2/2, c 1/1, p 3/3, m 3/3, total 36. The sequence of eruption of these teeth is: m 1/1, i 2/2, i 3/3, C1, m 2/2, c1, m 3/3, p 4/4, p 3/3, p 2/2. The upper incisors are small and the central ones are widely spaced, but closer to the lateral ones. All are compressed buccolingually (Swindler 1976).

The lower incisors are long, narrow, spatulate, and protrude almost straight forward. The lower canines are incisiform and in line with the incisors such that these 6 teeth form a comblike structure that is used to groom the fur (Pocock 1918). This "dental comb" is widespread in lemurs, and also may be used to scoop resins and gums from trees in some species (Swindler 1976). The lower canines are slightly larger than the incisors, and flared laterally, with a narrow, longitudinal groove on the occlusal surface (Swindler 2002).

The upper canines are large and sexually dimorphic, with the males having slightly larger ones than the females. The upper canines are long and recurved, with a broad base. These are used by both sexes in slashing attack, males primarily during the mating season and females in intra- and intertroop aggression. There is a small diastema between the canine and P2 (Swindler 2002).

The smallest premolar is P2. It is compressed buccolingually, and is more caniniform than the other premolars. There is a small lingular cingulum at the base of the paracone. P3 has a paracone with a median lingual ridge and a narrow buccal cingulum. P4 is molariform in size, structure, and function. It also bears a lingual cingulum (Swindler 2002).

Of the lower premolars, p2 is compressed buccolingually and is essentially caniniform, with the sharp tip projecting well above the occlusal plane. It occludes with the upper canine, taking the place of the incisiform lower canine. There is a diastema between p2 and p3, which is essentially a unicuspid, much smaller than p2 but with mesial and distal borders terminating in small stylids and a lingual cingulum. p4 is much more molariform, expanded to include both protoconid and metaconid, with an obvious talonid between the hypoconid and entoconid (Swindler 2002).

The tribosphenic upper molars each bear a distinct paracone, protocone, and metacone. Cristae from these cusps form a trigon basin that occludes with the talonid of the lower molars. M1 and M2 have prominent lingual cingulae, but lack a protostyle, in contrast to most other lemurs (Swindler 2002).

The lower molars are compressed buccolingually and bear prominent trigonid and talonid basins. The trigonid is higher than the talonid, but lacks a paraconid. The talonid basin is clearly outlined by ridges around the margin (Swindler 2002). There is intriguing evidence of temporal change in tooth size in *L. catta* in response to rapid ecological change, such as drought (Cuozzo and Sauther 2006).

There is a sublingual organ beneath the tongue that is used to clean the comblike set of lower incisor teeth. It covers a considerable portion of the lower side of the tongue and consists of a thin, flat, fibrous plate, somewhat leaflike in form with free lateral margins and a free apex. The apex is serrated and the underside is strengthened by 3 longitudinal ridges. The tongue is connected to the sublingual organ via the frenum, which arises from a notch in the posterior border of the sublingua. Under the sublingua, the floor of the mouth has a pair of small, soft flaps, the frenal lamellae, which arise from the bottom of the frenum and continue back as a free narrow edge toward the base of the tongue (Pocock 1918).

Function.—Grooming the fur is a never-ending process in *Lemur catta*, and its spatulate fingertips with short nails are of little use in this regard. Only a single digit in *L. catta* is functional for grooming, the 2nd on the hind foot, which is short with a small terminal pad and a long, semierect claw. Rather than groom with its fingers, *L. catta* uses the comblike lower incisors to groom itself and others, and then uses the sublingual organ to clean the lower incisors (Pocock 1918).

There is little evidence to suggest that the tooth-comb also is used in feeding to crop vegetable matter much like ungulates and insectivores do (Avis 1961). Others have argued that it is used to scrape sap and gums from tree bark (Gingerich 1975; Martin 1972). Small fruits are sometimes grasped between the tooth-comb and the upper incisors to pull them from the stem, and leaves are removed from stems in the same fashion (Sauther et al. 2002).

Ten female *L. catta* from 2 social groups were observed during a 5-month period including both wet and dry seasons in southwestern Madagascar (Cavigelli 1999). Behavioral measures were used to estimate predation threat, food accessibility, and individual dominance status, to determine whether these variables predict fecal cortisol levels. Fecal cortisol levels were high during late gestation, and also during the dry season. High-intensity antipredator behavior and feeding effort were elevated during the dry season. Fecal cortisol measures were positively correlated with dominance indices. These results suggested that fecal cortisol measures could be used to determine seasonal and individual differences in adrenal activity. Such measures could provide a means to quantify physiological stress in free-ranging lemurs (Pride 2006).

ONTOGENY AND REPRODUCTION

Ontogeny.—The sex ratio is equal at birth (Koyama et al. 2001), with neonates approximately 10 cm in length and colored similar to adults (Jolly 1966). Neonates weigh between 50 and 70 g but individuals under 55 g are considered premature (Benirscke and Miller 1981). Infants are physically active within days of birth; they may begin climbing branches within 2 weeks and may begin eating solid foods before 2 months of age (Jolly 1966). Infant mortality may be as high as 50% in a given population (Gould et al. 2003) but this often relates to the age of the mother, environmental conditions, and developmental state (Benirscke and Miller 1981; Gould et al. 2003; Koyama et al. 2001; Parga and Lessnau 2005). Neonatal mortality within the 1st month accounts for about one-third of all infant deaths (Koyama et al. 2001).

Infant *Lemur catta* develop rapidly, both physically and socially, during the first 4 months of their lives. The neonatal stage, when infants stay in constant contact with their mothers, lasts for about 2–3 weeks. Then infants begin exploring their environment at an increasing rate, spending less time on or with the mother, and the frequency of maternal grooming decreases as well. Exploration peaks at 7–8 weeks, and levels off to 5% of their total time by week 16 (Gould 1990).

Dominance relationships become established early on, with birth peers settling on hierarchies through rough-and-tumble play by the age of 4–5 months. Relationships with peers and other group members remain stable from weaning through puberty. Adults and adolescents of both sexes dominate all juveniles and infants, and juveniles dominate infants. Puberty occurs at about 16 months, and female dominance comes into play at the same time (Pereira 1993).

In the wild, subadults reach adult size by 1.5 years of age but do not reach sexual maturity until 2.5 years of age (Jolly 1966). In captive populations, sexual maturity and successful mating is more commonly observed at 3 years of age (Koyama et al. 2001; Sauther 1991; Sussman 1991). Annual birthrates are low for 2-year-old females (11%), higher for 3-year-olds (50%), and highest for those aged 4 years or more (75–80%), and more than 90% have a 1-year interval between births (Koyama et al. 2001). Multiple births are rare, with 3 sets of twins and 1 set of triplets recorded from 204 births documented in the wild (Koyama et al. 2001). Female *L. catta* rarely live past 16 years of age and the oldest known wild female was between 18 and 20 years old. Male life span is less well known, because of the social system, but there are records of males living to at least 15 years of age in the wild (Gould et al. 2003). In captivity, maximum life span recorded was 27 years (Jolly 2003).

Reproduction.—Assuming that a female *Lemur catta* does not become pregnant, she will experience 2 consecutive cycles each year during a breeding season lasting $<$ 3 months (Evans and Goy 1968); however, females are more likely to conceive during the 1st estrus (Sauther 1991). According to Evans and Goy (1968:189), average cycle length ($n = 17$) is 39.3 days and the average "vaginal oestrus" cycle ($n = 18$) is 4.7 days. The breeding season is regulated by photoperiod (Jolly 1967) and reduction in day length is believed to activate estrus (Van Horn 1975). The breeding season of a captive population subjected to constant 14L:10D cycles shifted 6 months later than Madagascar populations (Van Horn 1975).

Lemur catta is a strict seasonal breeder (Jolly 1966) with the onset of estrus and consequent annual birthing season both varying relative to geographic location. In Madagascar, the 1st estrus occurs in April and the 2nd estrus occurs in May or early June. Mating often was observed in the first 2 weeks of April (Jolly 1966). The gestation period ranges from about 130 to 144 days (Evans and Goy 1968; Sauther 1991; Van Horn and Eaton 1979) and the precocious young are born singly or in pairs in August through November (Budnitz and Dainis 1975), just before the beginning of the austral summer, with a peak in September (Koyama et al. 2001). In wild populations, births were observed to begin in late August and nursing continued as late as March (Jolly 1966). Gestation occurred in the dry season and lactation in the wet season (Gould et al. 2003; Sauther 1991; Sauther et al. 1999). Female genitalia change in physical appearance during the brief breeding season; genitalia enlarge from 1.5 cm to 3.0 cm in length and change in color from black to bright pink (Jolly 1966). Changes in the genital area are most pronounced in a troop's alpha female and least pronounced in nulliparous females (Sauther 1991). Nulliparous females may also exhibit a 1- to 2-month delayed estrous period compared to their more experienced female counterparts (Koyama 1988). Within 2 days of mating, the genitalia reduce in size and return to normal color (Sauther 1991).

Some male lemurs may show a change in testicular size that also coincides with breeding season (Evans and Goy 1968). Males also have been observed to lose weight and their vibrant pelage after the mating season ended, similar to physical changes observed in lactating females (Sauther 1991). Female receptivity may be restricted to as little as 4 h (Koyama 1988) or as long as 24 h (Jolly 1967). The gestation period is estimated to be about 4.5 months (Jolly 1966) and this duration was repeatedly observed across various research sites.

As with changes exhibited during the breeding season, the vulva changes size and coloration about 10 days before labor occurs (Sauther 1991). In a population of free-ranging *L. catta* at the Beza Mahafaly Special Reserve, all females ($n = 4$) had solitary, arboreal births with troop members still in close range (Sauther 1991). Delivery is not likely to occur in the daytime but it does occasionally happen (Koyama et al. 2001). Parturition lasts 60–90 min, and the mother eats the placenta after delivery. An extensive look at 204 births occurring at the Berenty Reserve revealed that about 95% of infants were singleton births. Multiple births, although they do occur, are rare in both wild and captive populations (Benirschke and Miller 1981; Hill 1953; Koyama et al. 2001). A rather high infant mortality appears to be related to predation, disease, accidents (falling), and maternal indifference (Jolly 1972).

ECOLOGY

Population characteristics.—Lemurs are the only prosimians that are diurnal, and that share many ecological characteristics with monkeys and apes, even though they have evolved in isolation from other Primates for 60 million years (Sussman 1992). *Lemur catta* occupies an ecological niche on Madagascar somewhat like that of baboons and macaques on the mainland, although perhaps more comparable to vervets in their continued dependence on forest cover for food and sleep. Population densities range from about 1–6 per hectare at the Berenty Reserve, where many long-term studies have been done (Jolly et al. 2002, 2006a). Additional long-term studies have been done at Bez Mahafaly Special Reserve in southwestern Madagascar (Sussman and Ratsirarson 2006). Troop density in a given area is much greater in gallery forest than elsewhere. A larger area of poorer, sparser vegetation is required to support a troop in more arid regions. Jolly et al. (2006b) suggested that multigenerational territories are a bet-hedging strategy that allows bridging of poor years for the greater advantage of good years.

Troop size is highly variable, but fission tends to occur at about 15–25 individuals, or 6–10 adult females. Social changes, including troop fission, female evictions, and range takeover are more common in large troops (Ichino and Koyama 2006). There seems to be no correlation between sex ratio, troop fissions, birthrates, or survival. Birthrate is negatively correlated with troop size, such that in troops with only 2 females, the birthrate is 80–100%, but in troops with 8–10 females, the birthrate falls to 50%. Survival seems to be more closely related to habitat quality than to troop size (Jolly et al. 2002). However, fecal cortisol levels suggested that females are more stressed at both high and low troop sizes, a finding that argues for the maintenance of intermediate-sized troops (Pride 2005).

Mortality rates are strongly affected by climatic cycles (Jolly et al. 2006c). A 2-year drought in southwestern Madagascar resulted in a 27% decrease in the adult population. Although normal mortality rates for adult females are in the range of 3%, mortality rate was 10 times greater in the 2-year drought period. Similarly, infant mortality rates, which normally range from 20% to 50%, jumped to 80% during the drought (Gould et al. 1999).

Space use.—*Lemur catta* should not be considered strictly territorial, individuals have overlapping home ranges that vary with season and habitat (Sauther and Sussman

1993). However, it does have strong territorial defense (Jolly et al. 2006b). The troop home ranges are strongly affected by vegetation type, individual species of preferred feeding trees, and the proximity to water (Koyama et al. 2006). Home ranges of troops in favorable forest areas along rivers may be only one-half to one-third as large as those occupying marginal or unfavorable areas. Tamarind trees (*Tamarindus indica*), a favorite for both food and shade, are good predictors of density, with higher density of *L. catta* occurring in areas with higher density of tamarind trees (Jolly et al. 2006c). Nevertheless, territorial boundaries can remain relatively stable for periods of up to 25 years (Mertl-Millhollen 2000).

In areas where the trees are at lower densities, the troops are less numerous and more widely spaced (Howarth et al. 1986). Less than 50% of the area occupied by a troop was utilized by that troop exclusively (Jolly 1972). The remainder was "time-shared" with other troops. Similarly, night dormitories (1 or more large adjoining trees that could shelter the whole troop), siesta spots (liana tangles in dense shade used for several hours at midday), and major feeding trees (fruit trees and tamarinds) were all visited by more than 1 troop (Jolly 1972). Studies of semi–free-ranging groups of *L. catta* in captivity suggested that they are adapted to variable habitat conditions where it is advantageous to react quickly to changes in abiotic factors (Ganzhorn 1985).

Diet.—*Lemur catta* feeds primarily on fruit, but extensively on leaves as well, and it has favorite species of feeding trees (Sussman 1977). Tamarind leaves and seed pods are heavily utilized by *L. catta*, one of the more important food sources in their diet (Blumenfeld-Jones et al. 2006). At least 109 species of plants have been found in the diet of *L. catta* at Berenty (Simmen et al. 2006b). *L. catta* has high taste sensitivity to secondary metabolites, which should minimize consumption of potentially noxious substances (Simmen et al. 2006a). At a high-mountain site on the Andringitra Massif, the diet differs from the lowland sites, and also differs seasonally (Goodman et al. 2006).

Because females are dominant over males in feeding interactions, females likely have the option to choose a higher quality diet, and their feeding strategy may vary seasonally. Males cope easily by simply focusing their foraging strategy on maximizing food consumption on familiar foods (Rasamimanana 1999). Most folivorous primates supplement their diet by consuming soil, and *L. catta* is no exception. The hypothesis is that they supplement their sodium intake by doing this, because there is some evidence of their preferentially selecting soils rich in sodium (Ganzhorn 1987).

Lemur catta drinks water daily, using springs and streams in its home range (Rand 1935). The succulent leaves of small bushes and vines such as *Xerosicyos perrieri* are an important source of moisture for some troops in times of drought, and for others in drier and less favorable habitats, may be the major source of water throughout the year, along with dew. *L. catta* can live in spiny forest without free water, gaining water from endemic succulents or from introduced *Opuntia*. Troops in the gallery forest were observed to descend to the river in tangles of roots and lianas to drink, or to the water tanks of buildings in the vicinity of the troop's home range (Jolly 1972).

In some human-altered habitats, introduced plant species can have a detrimental effect on *L. catta* (Sauther et al. 2006). *Leucaena*, a Central American legume that has been widely planted worldwide for fuelwood and forage, can be poisonous to lemurs (Crawford et al. 2006; Jolly et al. 2006c). On the other hand, *L. catta* feeds on other introduced species, especially during the dry season (Soma 2006). Introduced brown lemurs (*Eulemur fulvus*) may compete with *L. catta* for food resources during the birth season at Berenty Reserve (Pinkus et al. 2006).

Interspecific interactions.—One potential predator of *Lemur catta* is the Madagascar harrier hawk (*Polyboroides radiatus*). When one is seen overhead by *L. catta*, brown lemur, or Verreaux's sifaka (*Propithecus verreauxi*), individuals of all 3 species give loud alarm calls in unison and dash into the nearest cover (Sussman 1975). A similar reaction is shown in response to the Madagascar buzzard (*Buteo brachypterus*), another large predator that frequently perches in trees near lemurs (Sauther 1989). This rarely happens in response to other common large birds such as the barn owl (*Tyto alba*) or black kite (*Milvus migrans*), or to the megachiropteran fruit bat, Malagasy flying fox (*Pteropus rufus*), often seen flying over trees in the evening. Similar responses to avian predators are seen in semi–free-ranging, captive colonies of *L. catta* (Macedonia 1993a).

Goodman et al. (1993) summarized the few instances of predation that had been documented for *L. catta*. Predators include several euplerid carnivores, other lemurs, raptors, owls, crocodiles, and snakes (Goodman 2003). The most likely mammalian predators are the fosa (*Cryptoprocta ferox*), spotted fanaloka (*Fossa fossana*), and perhaps the ring-tailed vontsira (*Galidia elegans*). In the northernmost reaches of the range of *L. catta*, in the eastern woodlands, a widely distributed snake (*Acrantophis madagascariensis*) may be a potential predator, because it has been found to prey on both young and adult gray bamboo lemurs (*Hapalemur griseus*—Petter and Peyrieras 1975).

HUSBANDRY

Lemur catta takes to captivity readily and captive animals are known to make a contented sound reminiscent of the purring of cats, as do wild ones when relaxed and in contact with others. Captive individuals adapt to various diets, including cooked rice and bananas, and may become fond of sweets. However, this deprives them of their normal high-fiber and high-tannin diet, raising risks of hemosiderosis (iron overload). In the wild *L. catta* drinks water daily, using springs and streams in its home range. Captive individuals also readily drink water. Captives, like wild animals, like to sun themselves by sitting on their haunches and spreading their limbs, exposing the ventral surface to the sun. They sleep with their nose tucked between the hind legs, and the tail curled up over the back. Captives showed little fear of snakes, but the shadow of passing large birds sent them to shelter (Rand 1935).

A 7-year study of captive animals released on St. Catherine's Island, Georgia, showed that the animals slowly developed behavior similar to that seen in the wild. The animals initially lost their obesity and increased their agility, as they explored the area for novel plants. They adapted slowly over the succeeding 1–3 years, but eventually resembled a wild troop in behavior and long-distance vocalizations. Troop characteristics such as female dominance and male emigration eventually developed (Keith-Lucas et al. 1999).

BEHAVIOR

Grouping behavior.*—Lemur catta* was originally thought to resemble both baboons and macaques in many aspects of its ecology and social behavior (Sussman 1977). These animals live in large groups that include resident females and multiple males, as well as offspring of various ages. Unlike other primates, but like most other lemurs, *L. catta* females are dominant over males, and frequently agonistic toward them (Jolly 1966; Kappeler 1990a; Pereira 2006). Females and infants take the 1st opportunity to feed or drink. Males are last, and if a resource such as a watering hole is used up, many of the peripheral, subsidiary males may have to do without. This may be critical in unfavorable or marginal areas, as a means of selection or maintenance of troop size. Troops with an average of from 10 to 20 individuals are common, with an equal sex ratio and young of all ages. There is evidence of some advantage to larger group size in resource defense (Pride 2006).

Territories are relatively stable, with remarkably little change over a 20-year period in which one troop was regularly surveyed at Berenty Reserve (Mertl-Millhollen 2000). Troop fission seems to be driven primarily by female–female competition. Affiliative interactions between females lead to formation of subgroups, and eventually the dominant subgroup ousts the other (Nakamichi et al. 1997).

It was suggested that female dominance in *L. catta* may have evolved in response to high reproductive costs exacerbated by seasonality of food resources (Hrdy 1981; Jolly 1984; Young et al. 1990). That seasonality, combined with patchy food resources, has led to highly synchronized reproduction. This allows all females to lactate and wean their young during periods of relative food abundance, but it also exacerbates food competition among females. Females compete with other troop females, and they are also the major protector of resources from other troops (Jolly et al. 2006c). Males forage further from optimal resources, but reproductive constraints on females preclude that option. Instead, females compete directly for high-quality, seasonal resources (Mertl-Milhollen et al. 2006). They reduce competition from males by practicing female dominance, such that males are actively excluded from prime resources. Males compete directly and indirectly with females, especially in times of seasonal shortages. All females are affected, but lower ranking females compete both with males and with higher ranking females. Female dominance may be especially important for these lower ranking females and their infants (Sauther 1993). However, this "female need" hypothesis has been challenged by the finding that lemur infants in fact grow slowly in comparison to those of higher primates, and that the milk is no richer than that of higher primates (Tilden 2008; Tilden and Oftedal 1997). Apparently, energetic strategy does not explain female dominance (Rasamimanana et al. 2006).

Group activities encompass the entire day's routine, from foraging to defense of territory to locomotion or even sleeping. The basic social structure involves resident groups of females with males that migrate between groups. The nucleus of a troop seems to consist of about 3 or 4 adult females and their offspring, with 1 dominant female that serves as a focal point for the others (Sauther and Sussman 1993). Females rarely leave the group into which they are born. Males, on the other hand, occupy a more peripheral position, both literally and figuratively. They often can be seen on the outskirts of a troop in a sort of "Drone's Club" (Jolly 1966:89) of mostly subadult males. A single, nonnatal, central male can be identified in most troops (Sauther and Sussman 1993). At different times of the year, usually following the breeding season, there may be considerable exchange of males between one troop and another (Budnitz and Dainis 1975).

The amount of movement of males between groups is mitigated by resource availability, such that more movement occurs in the September–November migration season. A male's initial such movement is from his natal troop, and depends on his age, tenure, and current social context, but often occurs between 3 and 5 years of age. He then remains in his new group for a few years while reaching full growth and mature status. Thereafter, movement between groups occurs every 3–5 years. This rate of transfer decreases with old age. Males may migrate individually, or in groups of 2 or 3, perhaps in response to uneven sex ratios in both their old and new groups. The long-term effect is to minimize inbreeding and maximize gene flow (Sussman 1992). Such movement also aids in dispersal of individuals into new habitats and diffuses competition in either densely populated or unfavorable areas where food resources may be at a premium (Gould 2006).

One result of male emigration and female residency is close kinship through matrilineal relationships. Closely related animals spend more time grooming each other and remain in close proximity more so than distantly related animals or nonkin. Perhaps most important is the fact that no copulations occur within matrilines, resulting in outbreeding maintenance through female choice (Taylor and Sussman 1985).

Lemur catta exhibits a fairly high degree of intraspecific aggression compared to other lemurs. This may be between members of the same troop or a rival troop, as is the case in territorial disputes. Most of these encounters are fairly nonviolent, instantaneous spats between females over tamarind pods or a favored tree branch (Sussman et al. 2003). Yawning is sometimes an accompaniment to stressful encounters (Roeder et al. 1994). Male–male interactions are somewhat more intense, especially during the breeding season, involving chasing, cuffing, and occasionally even biting (which is seldom employed either outside breeding season or in territorial encounters between troops). Interestingly, individuals show no reconciliatory behavior after conflicts, an unusual situation for an animal with a pronounced dominance hierarchy and kinship structure (Kappeler 1993).

There are also short-term individual male–female affiliations that result in some pairs spending more time together (Gould 1996a). If males lack opportunity to affiliate with females, there also are male–male affiliations that are usually short in duration. In addition to social benefits, such affiliations may increase mutual grooming to rid ectoparasites, and afford some protection from inclement weather by joint huddling. Migrating males enjoy increased predator detection and protection when affiliated, and may be better able to join a new troop in the face of attack from resident males (Gould 1997b).

Some encounters are highly ritualized, such as "stink fights" between males (Jolly 1966), which also reach a maximum frequency during the breeding season. Tail marking, using secretions of the sebaceous glands of the shoulder patches and the antebrachial complex, is an essential characteristic of the stink fight. The tail is pulled down and rubbed between the arms and draped back over a shoulder to maximize contact with the sebaceous secretions. Then it is raised almost vertically, fluffed, held aloft for a moment and brought down over the animal's back in a series of rapid tail flicks, or in slow, spasmodic quivers. It is quickly reloaded with sebaceous secretions, after which the whole procedure is repeated. All this occurs while the 2 males face each other from a few meters apart, each looking much like a mirror image of the other (Budnitz and Dainis 1975; Evans and Goy 1968; Jolly 1966, 1972).

This strongly ritualized behavior argues for the importance of olfaction and perhaps explains the necessity of an elongated muzzle even at the expense of stereoscopic vision. Perhaps analogous to the use of pheromones in insects, the purpose here is to repel rather than attract. However, when addressed to a female, the function is to inform the female of the male's existence and prowess. Additionally, visual cues in the form of the highly visible, boldly striped tail, are important. The effectiveness of the display and its ultimate purpose, displacing a rival and establishing a dominance hierarchy, would be less if either the olfactory or visual elements were missing. The ritual has broad implications in lemur biology for the maintenance of intratroop hierarchies, as well as maintenance of territorial boundaries between troops (Jolly 1966).

Rank in the dominance hierarchy is determined partially by age, such that 3-year-old females tend to have the lowest ranks among adult females. Mothers are dominant over daughters, and older siblings over younger ones (Nakamichi and Koyama 1997). Alpha females retain that status for 1–5 years or even more. Similarly, 3-year-old males occupy the lowest ranks among adult males in their natal troop. They begin to emigrate to nonnatal troops at about 4 years of age, and ascend in rank in their new troops from about 4 to 6 years of age. Alpha males retain that status for just over 2 years, on average, and there is some tendency for larger males to outrank smaller ones (Koyama et al. 2005). Regardless of rank, adult males constantly try to drive solitary males away from the troop (Nakamichi and Koyama 1997). In both sexes, low-ranking individuals greet and groom dominants more frequently than the reverse (Nakamichi and Koyama 1997).

Territorial battles are generally dominated by females, although behavior varies from one encounter to the next (Jolly et al. 1993). Some individual females are more likely to participate in these agonistic interactions than others, regardless of rank in the dominance hierarchy (Nakamichi and Koyama 1997). There is no standardized behavior, as in male stink fights, but rather facing off between 2 opposing troops. Individuals face each other, with lunges and cuffs across territorial boundaries, sometimes with the raucous "war-cry" of mixed meows and alarm barks. They may run the whole gamut of vocalizations, as there seems to be no set established behavior. Females are the prime aggressors, but males of 1 troop actively stink fight with their counterparts in the other troop. Juveniles may take part in such encounters or stay off to one side, as do many subordinate males. Occasionally juveniles from the 2 different troops will play with each other during the course of such squabbles. Males may remain behind after the females depart, sniffing the area enthusiastically for up to an hour before rejoining the troop (Budnitz and Dainis 1975; Evans and Goy 1968; Jolly 1966, 1972).

Reproductive behavior.—There is widespread synchrony of estrus among females, in that all females of a troop reach estrus within 2 weeks. However, females space out such that no 2 females are in estrus on the same day, or are separated at least by morning or afternoon (Pereira 1991). Estrous females remain receptive for varying amounts of time, ranging from 0 to 44 h, with an average of 22 h (Van Horn and Eaton 1979). Jolly (1966, 1967) suggested that females remain receptive for only 1 day, and Evans and Goy (1968) estimated a receptive period of about 10 h in captive animals. Two females were documented to have receptive periods of only 4 h (Koyama 1988), a much commoner duration in the wild than the prolonged estrus of captivity. A single female may copulate with multiple males as many as 33 times during that 4-h period. Only adult males aged 3 years or more have been observed to mate (Sauther 1991). Mating may occur during the daytime, or at night in the sleeping trees (Jolly 1966; Koyama 1988; Petter 1965). *Lemur catta* exhibits female mate choice, with females preferentially mating with unrelated troop males, or males from other troops, to the exclusion of related males (Sauther 1991).

In a semifree-ranging colony, introduced unrelated males enjoyed sexual proceptivity and even copulation solicitation from resident females. The same females repelled their sons, matrilineal brothers, and other resident males from copulation attempts. The immigrant males successfully sired the offspring of each proceptive female, suggesting that female choice trumps male dominance to determine reproductive success. The same study offered evidence of attempted infanticide by males who had not fathered the targeted infants, and successful guarding by the females to counter this. The predicted model of the mating system of *L. catta* from this study stems from female avoidance of incest that has led to natal male dispersal from resident troops (Pereira and Weiss 1991).

When males transfer into other troops, they may practice infanticide on existing infants to both increase their chances in the females' next reproductive cycles, and terminate current fathers' reproductive eligibility in a group. Such attacks by immigrant males on an infant were recorded in the wild at Berenty Reserve in Madagascar. After the lone resident male and a lactating female disappeared from a troop, the female's orphaned infant was killed by immigrant males. The primary attacker subsequently mated with troop females in the next mating season (Ichino 2005). A similar attack by a nontroop male was recorded during an intertroop encounter, and resulted in the death of the infant, which was not an orphan, but had become dislodged during the encounter (Hood 1994). However, this is rarely recorded behavior.

Interestingly, the strict dominance hierarchy among males seems to break down when it comes to access to receptive females. The dominant male does not always get the maximum number of copulations (Jolly 1967; Koyama 1988), although in many instances he does mate 1st and guards the estrous female (Sauther 1991). Furthermore, Sauther (1991) suggested that the earlier accounts of subdominant males copulating frequently were cases of misidentified dominant males. Females develop a copulatory plug made from hardened ejaculate in the vaginal canal within minutes of copulation, but it may not be visible until 1–2 days after mating (Sauther 1991). This would argue that postcopulatory guarding by dominant males would help to impede sperm from subsequent copulations with other males. There is also evidence of copulatory plug displacement by subsequent copulations (Parga 2003).

Labor can be divided into 4 stages. Stage 1 begins with contractions, includes rupture of the amniotic sac, and ends with the appearance of the neonate's head. Stage 2 continues until the fetus is expelled from the uterus. Stage 3 is from delivery to expulsion of the placenta. Stage 4 is the time taken to eat the placenta (Sauther 1991). Parturition in primates is usually at night or in the very early morning, but *L. catta* frequently gives birth during the daytime (Takahata et al. 2001). Another interesting difference is that postpartum mothers who lose their infants have been observed kidnapping other infants and adopting them (Koyama et al. 2001).

Alloparenting, or infant care by troop members other than the mother, is common in *L. catta*. Alloparenting ranges from play through carrying of infants, through mutual grooming to allonursing. Group members of all sexes and age classes participate in some form of alloparenting. Even adult males occasionally groom and play with infants, regardless of the rank of the infant or adult. Such behavior may afford the adult males better central placement within the troop, affording better predator protection as well as opportunities for affiliation with females (Gould 1997a). Infants develop social skills and gain protection from alloparents. Mothers gain free time to forage and rest in peace. Adult females and prereproductive individuals aid kin through alloparenting, and adult males may gain access to females through alloparenting of young (Gould 1992).

An interesting case of alloparenting in captive, semifree-ranging *L. catta* was documented by Pereira and Izard (1989). An adult female known to have not been pregnant, began to lactate spontaneously when an unrelated female had twins. Both females carried the infants, usually 1 at a time, and both were found to be lactating when the infants were 2 months old. A 3rd troopmate, who showed no interest in carrying the infants, was not lactating, although she did aid in attacking males who approached the infants (Pereira and Izard 1989). There is also a documented instance of adoption of an orphaned 7-week-old by a subadult male and an adult female. Other natal troop members also aided in care of the orphan (Gould 2000).

Mothers carry their infants more or less continually, especially during the earliest stages of growth. Dead or dying infants unable to cling to the mother are eventually abandoned as the troop moves on, but only after repeated visits that involve sniffing, licking, and touching. Mothers also emitted distinctive vocalizations toward the infants both before and after moving away (Nakamichi et al. 1996).

Communication.—*Lemur catta* has a broad range of vocalizations consisting of at least 22 distinct adult calls and an additional 6 distinct infant calls, both including variations within specific call types (Macedonia 1993b). Macedonia (1993b), who completed the 1st extensive overview of *L. catta* vocalizations since Jolly's 1966 field report, generalized adult call types into 3 categories ("affiliative," "agnostic," and "alarm" vocalizations) and infant call types into 2 categories ("affiliative" and "distress" vocalizations). Among the 8 adult affiliative vocalizations, the "moan" and "wail" variants are inferred to promote group cohesion during varying levels of arousal (Macedonia 1993b).

The moan and wail (also known as "meow") are often produced before group troop movements (Jolly 1966). Vocalization of the meow call depends on the proximity of other individuals in the troop; when others are not nearby, the call is produced more rapidly and at a higher frequency, likely aiding in localization of the caller (Oda 1996). Studies focusing on cohesion calls also support that these calls provide unique identifying information about the individual producing the call but this may also be influenced by other factors. Acoustic analysis in a semicaptive population was able to correctly identify a caller with 75.3% accuracy (Macedonia 1986), whereas another similar study could only correctly identify callers with 25.5% accuracy (Oda 2002). Individuality communicated through a contact call may stem from its usefulness for a given population and environment; a troop living in a small cramped territory may rely less on acoustic recognition of troop members (Macedonia 1986; Oda 2002).

The "howl," "hmm," "huh," and "chirp" are inferred to play a role in group positioning, relocation, and movement (Macedonia 1993b). The "howl," a primarily male call, has mostly been observed before long periods of inactivity (i.e., evening rest and afternoon "siesta") and during the breeding season as a self-advertising call (Jolly 1966). Lastly, the "purr" is the only identified adult vocalization suspected to convey friendly mood (Macedonia 1993b). Adult agonistic vocalizations, "yip," "cackle," "squeal," "twitter," "plosive bark," and "chutter," each are expressed as unique displays of dominance or submission and vary in frequency of use by age, rank, and sex of individuals (Macedonia 1993b). Alarm calls are capable of providing general alert signals ("gulp") as well as specific information about location and type of predator ("rasp" and "shriek" variants—Macedonia 1993b). At varying levels of arousal, alert calls can call attention to the vocalizer ("click," "closed-mouth click series," and "open-mouth click series") and also provoke targeted mobbing behavior by the group ("yap"—Macedonia 1993b).

Although results are not definitive, research suggests that *L. catta* utilizes referential signaling (specific calls for different threats) and does not base vocalizations on response urgency (Macedonia 1990; Pereira and Macedonia 1991). *L. catta* can demonstrate consistent behavioral and vocal response to aerial versus terrestrial predators despite manipulated degrees of endangerment (Pereira and Macedonia 1991). For example, rasps and shrieks are produced exclusively in response to aerial threats and may be provoked by specific artificial visual stimuli (Macedonia and Polak 1990). *L. catta* also responds consistently to playbacks of prerecorded alarm calls by conspecifics (Macedonia 1990). Supporting previous assumptions, the subjects were more likely to look up, move bipedally, and take refuge in the trees upon hearing an "anticarnivore" alarm call and were more likely to climb lower in trees in response to an "antiraptor" alarm call (Macedonia 1990). *L. catta* additionally demonstrates discrimination of the calls produced by the actual predators. *L. catta* may identify hawk species from other nondangerous avian species by a "long frequency downslope," and maturity, experience, and other acoustic features may influence an individual's appropriate response (Macedonia and Yount 1991:180).

Infant affiliative calls ("infant contact call" and "trill" variants) mainly express desired contact with a mother or other conspecifics while distress vocalizations express mild ("whit" variant 1) to extreme ("whit" variant 2 and "yelp") discomfort (Macedonia 1993b). As with adult calls, infant calls may contain identifying information about the vocalizer. In a recent study by Nunn (2000) involving 5 mother–infant pairs, mothers were able to recognize the distress call of their own infant with 58% accuracy.

There is still more to be learned about the communicative functions of *L. catta* vocalizations. Although the contextual evidence for a certain call may be limited, it is believed that each call maintains some useful purpose (Macedonia 1993b). As individuals transition into adulthood, it is rare that they will continue to emit infant vocalizations but they retain the physical ability to produce and understand such calls (Macedonia 1993b).

Olfaction is important to *L. catta*, as is evidenced by the long rostrum with well-developed ethmoturbinals. Both males and females are known to genital mark (Dugmore et al. 1984). As described by Jolly (1966), the animal assumes a handstand-like posture and rubs its genitals on a thin, vertical substrate. It makes a mark about 2 cm in length and repeats the application of its scent 2 or 3 times. The females use the surface of their vulva and the males use a scrotal gland, and neither uses their anal region for genital marking. However, males tend to genital mark less frequently than do females (Evans and Goy 1968).

Other scent-marking behaviors are sex specific to males because of their exclusive possession of antebrachial and brachial glands. Adult males additionally exhibit other scent-marking behaviors. In agonistic encounters, males have been observed to "tail mark" before demonstrating "tail waving" (Jolly 1966). During tail marking, the animal uses its own tail as the substrate for antebrachial marking and later uses that tail in an elaborate intimidating, aggressive display that may escalate into a stink fight (Jolly 1966).

Field observations indicate that the broad use of smell by *L. catta* can involve finding and evaluating food sources (Jolly 1966) or friendly social interaction (Evans and Goy 1968). However, the various applications of scent marking are much more extensive, and the behavioral complexities and potential communicative properties of scent are the aspects most currently studied about scent marking in *L. catta* (Oda 1999).

Generally, individual *L. catta* will only use plants and their own bodies as substrates for scent and will only scent mark with brachial glands, antebrachial glands, or genital glands (Jolly 1966). They do not scent mark each other (Schilling 1974) and are never observed scent marking with urine or feces (Jolly 1966). Unsuccessful marking by males, as when branches are too thin or flimsy, may often result in a redirected behavior involving the rapid rubbing together of the spurs on the forearm, causing a characteristic clicking sound (Evans and Goy 1968). This behavior is more common in captive than wild animals, possibly due to inappropriate marking material.

The appearance of scent investigation and scent-marking behaviors appears to be closely linked with specific phases of development. At 3 weeks of age, an infant *L. catta* can begin to sniff environmental substrates and other nearby lemurs; sniffing nonlemur substrates plays a more significant role because it can represent up to 90% of sniffing behavior during juvenile and adolescent development. At about 12 months, males begin marking with their brachial and antebrachial glands. By 13 months, males begin displaying tail-anointing behavior and, between their 16th and 18th month, the almost sexually mature lemurs begin to genital mark and countermark (Palagi et al. 2002).

Scent communication may have a significant relationship with the reproductive cycle of females. Intraspecific agonistic encounters, male stink fights, scent marking, and chasing between males all reach their peak during the breeding season, at the close of the rainy season, generally in April–July, although the exact time varies with climatic conditions and precipitation (Budnitz and Dainis 1975). Both sexes show a high frequency for body sniffing during the breeding season and males exhibit an increase in genital sniffing (Palagi et al. 2003, 2004). Males also scent mark more during the breeding season and migration periods, indicating a link to reproductive competition with other males and intratroop conflict when males enter a troop (Gould and Overdorff 2002). There is an accompanying increase in howling, especially in males, calling between members of the opposite sex within a troop, as well as challenge calls between males of neighboring troops. Overall, the scent marks likely represent honest signals about an individual's reproductive state (Kappeler 1990b, 1998). An individual of either sex encountering the scent mark of a conspecific will sniff enthusiastically and often produce a flehman response (Evans and Goy 1968).

Scent marking may communicate information about home ranges. *L. catta* is more responsive when it recognizes an unfamiliar scent of a lemur outside of its troop; individuals are more likely to investigate the smell and countermark it (Ramsay and Giller 1996). Males have the capability to recognize the scent mark of an individual male and can respond more vigorously to unfamiliar scents, although they also can habituate to "position specific" scent markings (Mertl 1976, 1977). Current research indicates that most scent marking does not occur at territorial borders but instead within the overlapping regions of neighboring troop home ranges (Mertl-Millhollen 1988). Although it represents a fraction of a home range, troop members may spend the majority of their time in these confrontation zones and also may explain why more scent marks are found in this region (Mertl-Millhollen 1988).

Miscellaneous behavior.—*Lemur catta* is diurnal and crepuscular, easily seen moving about and feeding on the ground during the day, but also frequently heard calling in the early evening hours. At such times, the animals are usually already settled into communal group resting areas in trees. They are gregarious, foraging in small bands of 4–15 individuals containing both sexes and all ages. Although in many areas they spend more than half of their time on the ground, they are at home in the trees, moving along branches and leaping from tree to tree as necessary.

The large troop size provides extra eyes and ears for vigilance behavior. There are no sex or age differences in vigilance behavior, although the dominant female exhibits significantly more vigilance behavior than any other member of her troop (Gould 1996b). Their escape behavior is more likely to be bounding away on the ground rather than taking to the trees (Rand 1935).

Aggressive displays are mostly intraspecific and rarely violent, usually being instantaneous spats between females or stink fights between males (Jolly 1966), or highly ritualized, nonviolent encounters between members of different troops, involving much chasing but little physical contact. Interspecific aggression was seldom reported (Sussman 1975). *L. catta* quickly becomes accustomed to people, and goes about its business, little disturbed by the presence of humans. In fact, it also may be somewhat curious and approach intruding humans, as long as one remains still and quiet. They are somewhat noisy, even when foraging, where several members of the band may make a locomoter click series, calls that may function to help with group cohesion. Alarm calls consist of lower-pitched grunts and higher-pitched wac-wac-wac barks.

GENETICS

The karyotype consists of 56 chromosomes including 4 metacentrics, 4 submetacentrics, 46 acrocentrics, a metacentric X, and an acrocentric Y (Rumpler 1975). Yoder et al.

(2000) used mitochondrial genes to suggest that genetic patterns observed among the Andringitra and lowland mitochondrial haplotypes were consistent with those expected for a single species. The development of microsatellite markers for *Lemur catta* should prove useful for future studies (Pastorini et al. 2005).

CONSERVATION

Lemur catta is listed as Near Threatened on the *International Union for Conservation of Nature and Natural Resources Red List of Threatened Species* (International Union for Conservation of Nature and Natural Resources 2008), and the population is listed as decreasing. Total population estimates are unknown but several estimates of population densities for local areas exist, ranging from 5 to 30 individuals/km^2 (Mittermeier et al. 1992; Sussman et al. 2006). This is a widely studied species commonly found in zoos and, according to a 1990 estimate, nearly 1,000 individuals were in captivity (Harcourt and Thornback 1990). Because they are widely seen in captivity, and in some of the most visited reserves in Madagascar, the public may have a false impression of their abundance (Mittermeier et al. 2006).

The biggest threat facing this species is loss of habitat; controlled fires and overgrazing are decreasing the amount of bush and forests available (Sussman and Richard 1986). There is also evidence of hunting pressure (Jolly et al. 2006c). The natural habitat for this species is limited to the southern one-half of Madagascar (Goodman et al. 2006; Richard and Sussman 1987). These animals live mostly in dry forest and bush areas but also may be found in dry, mountainous terrain, and especially in gallery forests along rivers (Jolly et al. 2006c). Unlike other extant lemur species, they spend much of their time on the ground (Budnitz 1978). There is evidence that annual reproductive cycles in this species are tightly tied to seasonality of rainfall and subsequent availability of food resources (Sauther 1998). *L. catta* is protected by national and international law, but it is still difficult to guard this species from illegal hunting practices (Harcourt and Thornback 1990). These animals are hunted for food in some areas, and are also captured and kept as pets (Mittermeier et al. 2006).

LITERATURE CITED

Avis, V. 1961. The significance of the angle of the mandible: an experimental and comparative study. American Journal of Physical Anthropology 19:55–61.

Benirschke, K., and C. J. Miller. 1981. Weights and neonatal growth of ring-tailed lemurs (*Lemur catta*) and ruffed lemurs (*Lemur variegatus*). Journal of Zoo Animal Medicine 12:107–111.

Blumenfeld-Jones, K., et al. 2006. Tamarind recruitment and long-term stability in the gallery forest at Berenty, Madagascar. Pp. 69–85 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Bolwig, N. 1960. A comparative study of the behavior of various lemurs. Mémoirs of the Institute of Science of Madagascar, Séries A 14:205–217.

Brisson, M. J. 1762. Le regnum animale in classes IX distributum, sive synopsis methodica sistens generalem animalium distributionem in classes IX, & duarum primarum classium, quadrupedum scilicet & cetaceorum, particularem dibvisionem in ordines, sectiones, genera & species. T. Haak, Paris, France.

Budnitz, N. 1978. Feeding behavior *of Lemur catta* in different habitats. Pp. 85–108 in Perspectives in ethology (K. Bateson and P. Klopfer, eds.), Vol. 3. Plenum Press, New York.

Budnitz, N., and K. Dainis. 1975. *Lemur catta*: ecology and behavior. Pp. 219–235 in Lemur biology (I. Tattersall and R. W. Sussman, eds.). Plenum Press, New York.

Burney, D. A., et al. 2004. A chronology for late prehistoric Madagascar. Journal of Human Evolution 47:25–63.

Burney, D. A., et al. 2008. New findings at Andrahomana Cave, southeastern Madagascar. Journal of Cave and Karst Studies 70: 13–24.

Cavigelli, S. A. 1999. Behavioural patterns associated with faecal cortisol levels in free-ranging female ring-tailed lemurs, *Lemur catta*. Animal Behaviour 57:935–944.

Crawford, G. C., et al. 2006. Bald lemur syndrome and the miracle tree: Alopecia associated with *Leucaena leucocephala* at Berenty Reserve, Madagascar. Pp. 332–342 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Cuozzo, F. P., and M. L. Sauther. 2006. Temporal change in tooth size among ringtailed lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve, Madagascar: effects of an environmental fluctuation. Pp. 343–366 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Desmarest, A. G. 1817. Nouveau dictionnaire d'histoire naturelle, appliquée aux arts, à l'agriculture, à l'économie rurale et domestique, à la médecine, etc. Par une société de naturalistes et d'agriculteurs. Nouv. éd. Deterville, Paris, France.

Dugmore, S. J., K. Bailey, and C. S. Evans. 1984. Discrimination by male ring-tailed lemurs (*Lemur catta*) between the scent marks of male and those of female conspecifics. International Journal of Primatology 5:235–245.

Elliot, D. G. 1913. A review of the Primates. Monograph, American Museum of Natural History 1:1–317.

Evans, C. S., and R. W. Goy. 1968. Social behaviour and reproductive cycles in captive ring-tailed lemurs (*Lemur catta*). Journal of Zoology (London) 156:181–197.

Ganzhorn, J. U. 1985. Habitat separation of semifree-ranging *Lemur catta* and *Lemur fulvus*. Folia Primatologica 45:76–88.

Ganzhorn, J. U. 1987. Soil consumption of two groups of semi-free ranging lemurs (*Lemur catta* and *Lemur fulvus*). Ethology 74: 146–154.

Garbutt, N. 1999. Mammals of Madagascar. Pica Press, Sussex, United Kingdom.

Gingerich, P. D. 1975. Dentition of *Adapis parisiensis* and the evolution of the lemuriform toothcomb. Pp. 65–80 in Lemur biology (I. Tattersall and R. W. Sussman, eds.). Plenum Press, New York.

Godfrey, L. R., and W. L. Jungers. 2002. Quaternary fossil lemurs. Pp. 97–121 in The primate fossil record (W. Hartwig, ed.). Cambridge University Press, Cambridge, United Kingdom.

Godfrey, L. R., W. L. Jungers, E. L. Simons, P. S. Chatrath, and B. Rakotosamimanana. 1998. Past and present distributions of lemurs in Madagascar. Pp. 19–53 in New directions in lemur studies (B. Rakotosamimanana, H. Rasamimanana, J. U. Ganzhorn, and S. M. Goodman, eds.). Kluwer, New York.

Goodman, S. M. 2003. Predation on lemurs. Pp. 1221–1225 in The natural history of Madagascar (S. M. Goodman and J. P. Benstead, eds.). University of Chicago Press, Chicago, Illinois.

Goodman, S. M., and O. Langrand. 1996. A high mountain population of the ring-tailed lemur *Lemur catta* on the Andringitra Massif, Madagascar. Oryx 30:259–268.

Goodman, S. M., S. O'connor, and O. Langrand. 1993. A review of predation on lemurs: implications for the evolution of social behavior in small, nocturnal primates. Pp. 51–66 in Lemur social systems and their ecological basis (P. M. Kappeler and J. U. Ganzhorn, eds.). Plenum Press, New York.

Goodman, S. M., S. V. Rakotoarisoa, and L. Wilmé. 2006. The distribution and biogrography of the ringtailed lemur (*Lemur catta*) in Madagascar. Pp. 3–15 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Gould, L. 1990. The social development of free-ranging infant *Lemur catta* at Berenty Reserve, Madagascar. International Journal of Primatology 11:297–318.

Gould, L. 1992. Alloparental care in free-ranging *Lemur catta* at Berenty Reserve, Madagascar. Folia Primatologica 58:72–83.

Gould, L. 1996a. Male–female affiliative relationships in naturally occurring ringtailed lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. American Journal of Primatology 39:63–78.

Gould, L. 1996b. Vigilance behavior during the birth and lactation season in naturally occurring ring-tailed lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. International Journal of Primatology 17:331–347.

Gould, L. 1997a. Affiliative relationships between adult male and immature group members in naturally occurring ringtailed lemurs (*Lemur catta*). American Journal of Physical Anthropology 103: 163–171.

Gould, L. 1997b. Intermale affiliative behavior in ringtailed lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. Primates 38:15–30.

Gould, L. 2000. Adoption of a wild orphaned ringtailed lemur infant by natal group members: adaptive explanations. Primates 41: 413–419.

Gould, L. 2006. Male sociality and integration during the dispersal process in *Lemur catta*: a case study. Pp. 296–310 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Gould, L., and D. J. Overdorff. 2002. Adult male scent-marking in *Lemur catta* and *Eulemur fulvus rufus*. International Journal of Primatology 23:575–586.

Gould, L., R. W. Sussman, and M. L. Sauther. 1999. Natural disasters and primate populations: the effects of a two-year drought on a naturally occurring population of ring-tailed lemurs (*Lemur catta*) in southwestern Madagascar. International Journal of Primatology 20:69–84.

Gould, L., R. W. Sussman, and M. L. Sauther. 2003. Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: a 15-year perspective. American Journal of Physical Anthropology 120: 182–194.

Groves, C. 2001. Primate taxonomy. Smithsonian Institution Press, Washington, D.C.

Groves, C. P., and R. H. Eaglen. 1988. Systematics of the Lemuridae (Primates, Strepsirhini). Journal of Human Evolution 17:513–538.

Harcourt, C., and J. Thornback. 1990. Lemurs of Madagascar and the Comoros: the IUCN red data book. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.

Hill, W. C. O. 1953. Primates: comparative anatomy and taxonomy. I. Strepsirrhini. The University Press, Edinburgh, United Kingdom.

Hood, L. C. 1994. Infanticide among ringtailed lemurs (*Lemur catta*) at Berenty Reserve, Madagascar. American Journal of Primatology 33:65–69.

Howarth, C. J., J. M. Wilson, A. P. Adamson, M. E. Wilson, and M. J. Boase. 1986. Population ecology of the ring-tailed lemur, *Lemur catta*, and the white sifaka, *Propithecus verreauxi verreauxi*, at Berenty, Madagascar, 1981. Folia Primatologica 47:39–48.

Hrdy, S. 1981. The woman that never evolved. Harvard University Press, Cambridge Massachusetts.

Iaderosa, J. F., and R. G. Lessnau. 1995. Opening the door: primate reintroductions and the St. Catherine's Island free-ranging primate programs. American Zoo and Aquarium Association Annual Conference Proceedings 1995:256–261.

Ichino, S. 2005. Attacks on a wild infant ring-tailed lemur (*Lemur catta*) by immigrant males at Berenty, Madagascar: interpreting infanticide by males. American Journal of Primatology 67: 267–272.

Ichino, S., and N. Koyama. 2006. Social changes in a wild population of ringtailed lemurs (*Lemur catta*) at Berenty, Madagascar. Pp. 233–244 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

International Commission on Zoological Nomenclature. 1998. Opinion 1894. Regnum Animals …, Ed. 2 (M.J. Brisson, 1762): rejected for nomenclatural purposes, with the conservation of the mammalian generic names Philander (Marsupialia), Pteropus (Chiroptera), Glis, Cuniculus and Hydrochoerus (Rodentia), Meles, Lutra and Hyaena (Carnivora), Tapirus (Perissodactyla), Tragulus and Giraffa (Artiodactyla). Bulletin of Zoological Nomenclature 55(1):64–71.

International Union for Conservation of Nature and Natural Resources. 2008. The IUCN Red list of threatened species. www.iucnredlist.org, accessed 6 January 2010.

Jolly, A. 1966. Lemur behavior: a Madagascar field study. University of Chicago Press, Chicago, Illinois.

Jolly, A. 1967. Breeding synchrony in wild *Lemur catta*. Pp. 3–14 in Social communication among primates (S. A. Altman, ed.). University of Chicago Press, Chicago, Illinois.

Jolly, A. 1972. Troop continuity and troop spacing in *Propithecus verreauxii* and *Lemur catta* at Berenty (Madagascar). Folia Primatologica 17:335–362.

Jolly, A. 1984. The puzzle of female feeding priority. Pp. 197–215 in Female primates: studies by women primatologists (M. Small, ed.). Alan R. Liss, New York.

Jolly, A. 2003. Mammals: *Lemur catta*, ring-tailed lemur, *Maky*. Pp. 1329–1331 in The natural history of Madagascar (S. M. Goodman and J. P. Benstead, eds.). University of Chicago Press, Chicago, Illinois.

Jolly, A., et al. 2002. Demography of *Lemur catta* at Berenty Reserve, Madagascar: effects of troop size, habitat and rainfall. International Journal of Primatology 23:327–353.

Jolly, A., N. Koyama, H. Rasamimanana, H. Crowley, and G. Williams. 2006a. Berenty Reserve: a research site in southern Madagascar. Pp. 32–42 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Jolly, A., H. R. Rasamimanana, M. Braun, T. Dubovick, C. Mills, and G. Williams. 2006b. Territory as bet-hedging: *Lemur catta* in a rich forest and an erratic climate. Pp. 187–207 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Jolly, A., et al. 1993. Territoriality in *Lemur catta* groups during the birth season at Berenty, Madagascar. Pp. 85–109 in Lemur social systems and their ecological basis (P. M. Kappeler and J. U. Ganzhorn, eds.). Plenum Press, New York.

Jolly, A., R. W. Sussman, N. Koyama, and H. Rasamimanana (eds). 2006c. Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York.

Kappeler, P. M. 1990a. Female dominance in *Lemur catta*: more than just female feeding priority? Folia Primatologica 55:92–95.

Kappeler, P. M. 1990b. Social status and scent marking behavior in *Lemur catta*. Animal Behaviour 40:774–778.

Kappeler, P. M. 1993. Reconciliation and post conflict behavior in ringtailed lemurs, *Lemur catta*, and redfronted lemurs, *Eulemur fulvus*. Animal Behaviour 45:901–915.

Kappeler, P. M. 1998. To whom it may concern: the transmission and function of chemical signals in *Lemur catta*. Behavioral Ecology and Sociobiology 42:774–778.

Kieth-Lucas, T., F. J. White, L. Keith-Lucas, and L. G. Vick. 1999. Changes in behavior in free-ranging *Lemur catta* following release in a natural habitat. American Journal of Primatology 47:15–28.

Koyama, N. 1988. Mating behavior of ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. Primates 29:163–175.

Koyama, N., S. Ichino, M. Nakamichi, and Y. Takahata. 2005. Long-term changes in dominance ranks among ring-tailed lemurs at Berenty Reserve, Madagascar. Primates 46:225–234.

Koyama, N., M. Nakamichi, R. Oda, N. Miyamoto, and Y. Takahata. 2001. A ten-year summary of reproductive parameters for ring-tailed lemurs at Berenty, Madagascar. Primates 42:1–14.

Koyama, N., T. Soma, S. Ichino, and Y. Takahata. 2006. Home ranges of ringtailed lemur troops and the density of large trees at Berenty Reserve, Madagascar. Pp. 86–101 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Link, H. F. 1806. Beschreibung der Naturalien Sammlung der Universität zu Rostock, Adlers Erben, Rostock, Germany, 1:7–8.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. 10th ed. Vol. 1. Laurentii Salvii, Stockholm, Sweden.

MacEdonia, J. M. 1986. Individuality in a contact call of the ringtailed lemur (*Lemur catta*). American Journal of Primatology 11: 163–179.

MacEdonia, J. M. 1990. What is communicated in the antipredator calls of lemurs: evidence from playback experiments with ring-tailed and ruffed lemurs. Ethology 86:177–190.

MacEdonia, J. M. 1993a. Adaptation and phylogenetic constraints in the antipredator behavior of ringtailed and ruffed lemurs. Pp. 67–84 in Lemur social systems and their ecological basis (P. M. Kappeler and J. U. Ganzhorn, eds.). Plenum Press, New York.

MacEdonia, J. M. 1993b. The vocal repertoire of the ringtailed lemur (*Lemur catta*). Folia Primatologica 61:186–217.

MacEdonia, J. M., and J. F. Polak. 1990. Visual assessment of avian threat in semi-captive ringtailed lemurs (*Lemur catta*). Behaviour 111:291–304.

MacEdonia, J. M., and P. L. Yount. 1991. Auditory assessment of avian predator threat in semi-captive ringtailed lemurs (*Lemur catta*). Primates 32:169–182.

Martin, R. D. 1972. Adaptive variation of behavior of Malagasy lemurs. Philosophical Transactions of the Royal Society of London, B. Biological Sciences 26:295–352.

Mertl, A. S. 1976. Olfactory and visual cues in social interactions of *Lemur catta*. Folia Primatologica 26:151–161.

Mertl, A. S. 1977. Habituation to territorial scent marks in the field by *Lemur catta*. Behavioral Biology 21:500–507.

Mertl-Millhollen, A. S. 1988. Olfactory demarcation of territorial but not home range boundaries by *Lemur catta*. Folia Primatologica 50:175–187.

Mertl-Millhollen, A. S. 2000. Tradition in *Lemur catta* behavior at Berenty Reserve, Madagascar. International Journal of Primatology 21:287–297.

Mertl-Millhollen, A. S., et al. 2006. The influence of tamarind tree quality and quantity on *Lemur catta* behavior. Pp. 102–118 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Mittermeier, R. A., W. R. Konstant, M. E. Nicoll, and O. Langrand. 1992. Lemurs of Madagascar: an action plan for their conservation 1993–1999. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.

Mittermeier, R. A., I. Tattersall, W. R. Konstant, D. M. Meyers, and R. B. Mast. 2006. Lemurs of Madagascar. 2nd ed. Conservation International, Washington, D.C.

Montagna, W., and J. S. Yun. 1962. The skin of primates. X. The skin of the ring-tailed lemur (Lemur catta). American Journal of Physical Anthropology 20:95–118.

Muirhead, L. 1819. Mazology. Pp. 393–486 in The Edinburgh encyclopaedia (D. Brewster, ed.), 4th ed. [pls. 353–358.] William Blackwood, Edinburgh, United Kingdom.

Nakamichi, M., and N. Koyama. 1997. Social relationships among ring-tailed lemurs (*Lemur catta*) in two free-ranging troops at Berenty Reserve, Madagascar. International Journal of Primatology 18:73–93.

Nakamichi, M., N. Koyama, and A. Jolly. 1996. Maternal responses to dead and dying infants in wild troops of ring-tailed lemurs at the Berenty Reserve, Madagascar. International Journal of Primatology 17:505–523.

Nakamichi, M., M. L. O. Rakatotiana, and N. Koyama. 1997. Effects of spatial proximity and alliances on dominance relations among female ring-tailed (*Lemur catta*) at Berenty Reserve, Madagascar. Primates 38:331–340.

Nunn, C. L. 2000. Maternal recognition of infant calls in ring-tailed lemurs. Folia Primatologica 71:142–146.

Oda, R. 1996. Effects of contextual and social variables on contact call production in free-ranging ringtailed lemurs (*Lemur catta*). International Journal of Primatology 17:191–205.

Oda, R. 1999. Scent marking and contact call production in ring-tailed lemurs (*Lemur catta*). Folia Primatologica 70:121–124.

Oda, R. 2002. Individual distinctiveness of the contact calls of ring-tailed lemurs. Folia Primatologica 73:132–136.

Palagi, E., A. Greogorace, and S. M. Borgognini Tarli. 2002. Development of olfactory behavior in captive ring-tailed lemurs (*Lemur catta*). International Journal of Primatology 23:587–599.

Palagi, E., S. Telara, and S. M. Borgognini Tarli. 2003. Sniffing behavior in *Lemur catta*: seasonality, sex, and rank. International Journal of Primatology 24:335–350.

Palagi, E., S. Telara, and S. M. Borgogini Tarli. 2004. Reproductive strategies in *Lemur catta*: balance among sending, receiving, and countermarking scent signals. International Journal of Primatology 25:1019–1031.

Parga, J. A. 2003. Copulatory plug displacement evidences sperm competition in *Lemur catta*. International Journal of Primatology 24:889–899.

Parga, J. A., and R. G. Lessnau. 2005. Female age-specific reproductive rates, birth seasonality, and infant mortality of ring-tailed lemurs on St. Catherines Island: 17-year reproductive history of free-ranging colony. Zoo Biology 24:295–309.

Pariente, G. 1970. Rétinographies compares des lémuriens malgaches. Comptes Rendus de l'Académie des Sciences (Paris) 270: 1404–1407.

Pastorini, J., P. Fernando, M. R. J. Forstner, and D. J. Melnicks. 2005. Characterization of new microsatellite loci for the ring-tailed lemur (*Lemur catta*). Molecular Ecology Notes 5:149–151.

Pereira, M. E. 1991. Asynchrony within estrus synchrony among ringtailed lemurs (Primates, Lemuridae.) Psychology and Behavior 49:47–52.

Pereira, M. E. 1993. Agonistic interaction, dominance relation, and ontogenetic trajectories in ringtailed lemurs. Pp. 285–305 in Juvenile primates: life history, development and behavior (M. E. Pereira and L. A. Fairbanks, eds.). Oxford University Press, New York.

Pereira, M. E. 2006. Obsession with agonistic power. Pp. 245–270 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Pereira, M., and M. K. Izard. 1989. Lactation and care for unrelated infants in forest-living ringtailed lemurs. American Journal of Primatology 18:101–108.

Pereira, M. E., and J. M. Macedonia. 1991. Ringtailed lemur anti-predator calls denote predator class, not response urgency. Animal Behaviour 41:543–544.

Pereira, M. E., and M. L. Weiss. 1991. Female mate choice, male migration and the threat of infanticide in ringtailed lemurs. Behavioral Ecology and Sociobiology 28:141–152.

Petter, J.-J. 1965. The lemurs of Madagascar. Pp. 292–319 in Primate behavior (I. DeVore, ed.). Holt, Rinehart, and Winston, Inc., New York.

Petter, J.-J., and A. Peyrieras. 1975. Behavior and ecology of *Hapalemur griseus*. Pp. 281–287 in Lemur biology (I. Tattersall and R. W. Sussman, eds.). Plenum Press, New York.

Pinkus, S., J. N. M. Smith, and A. Jolly. 2006. Feeding competition between introduced *Eulemur fulvus* and native *Lemur catta* during the birth season at Berenty Reserve, southern Madagascar. Pp. 119–140 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Pocock, R. I. 1918. On the external characters of the lemurs and of *Tarsius*. Proceedings of the Zoological Society of London 1918: 19–53.

Pride, R. E. 2005. Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). Behavioral Ecology 16:550–560.

Pride, R. E. 2006. Resource defense in *Lemur catta*: the importance of group size. Pp. 208–232 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Purchas, S. 1625. Hakluytus posthumus or Purchas his pilgrims. 5 vols. Henry Fetherston, London, United Kingdom.

Ramsay, N. F., and P. S. Giller. 1996. Scent-marking in ring-tailed lemurs: responses to the introduction of "foreign" scent in the home range. Primates 37:13–23.

Rand, A. L. 1935. On the habits of some Madagascar mammals. Journal of Mammalogy 16:89–104.

Rasamimanana, H. 1999. Influence of social organization patterns on food intake of *Lemur catta* in the Berenty Reserve. Pp. 173–188 in New directions in lemur studies (B. Rakotosamimanana, H. Rasamimanana, J. U. Ganzhorn, and S. M. Goodman, eds.). Kluwer Academic/Plenum Publishers, New York.

Rasamimanana, H., V. N. Andrianome, H. Rambeloarivony, and P. Pasquet. 2006. Male and female ringtailed lemurs' energetic strategy does not explain female dominance. Pp. 271–296 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Richard, A. F., and R. W. Sussman. 1987. Framework for primate conservation in Madagascar. Pp. 329–341 in Primate conservation in the tropical forest (C. W. March and R. Mittermeier, eds.). Alan R. Liss, Inc., New York.

Roeder, J. J., I. Fornasieri, and J. R. Anderson. 1994. Yawning in ringtailed lemurs (*Lemur catta*). Pp. 77–319 in Current primatology. Vol. 2: social development, learning, and behavior (J. J. Roeder, B. Theirry, J. R. Anderson, and N. Herrenschmidt, eds.). Université Louis Pasteur, Strasbourg, France.

Rumpler, Y. 1975. The significance of chromosomal studies in the systemics of the Malagasy lemurs. Pp. 25–40 in Lemur biology (I. Tattersall and R. W. Sussman, eds.). Plenum Press, New York.

Sauther, M. 1989. Antipredator behavior in troops of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. International Journal of Primatology 10:595–606.

Sauther, M. L. 1991. Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. American Journal of Physical Anthropology 84:463–477.

Sauther, M. L. 1993. Resource competition in wild populations of ringtailed lemurs (*Lemur catta*): implications for female dominance. Pp. 135–152 in Lemur social systems and their ecological basis (P. M. Kappeler and J. U. Ganzhorn, eds.). Plenum Press, New York.

Sauther, M. 1998. Interplay of phenology and reproduction in ring-tailed lemurs: implications for ring-tailed lemur conservation. Folia Primatologica, supplement 69:309–320.

Sauther, M. L., K. D. Fish, F. P. Cuozzo, D. S. Miller, M. Hunter-Ishikawa, and H. Culbertson. 2006. Patterns of health, disease, and behavior among wild ringtailed lemurs, *Lemur catta*: effects of habitat and sex. Pp. 296–310 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Sauther, M. L., and R. E. Sussman. 1993. A new interpretation of the social organization and mating system of ringtailed lemur (*Lemur catta*). Pp. 111–121 in Lemur social systems and their ecological basis (P. M. Kappeler and J. U. Ganzhorn, eds.). Plenum Press, New York.

Sauther, M. L., R. W. Sussman, and F. Cuozzo. 2002. Dental and general health in a population of wild ring-tailed lemurs: a life history approach. American Journal of Physical Anthropology 117:122–132.

Sauther, M. L., R. W. Sussman, and L. Gould. 1999. The socioecology of the ringtailed lemur: thirty-five years of research. Evolutionary Anthropology 8:120–132.

Schilling, A. 1974. A study of marking behaviour in *Lemur catta*. Pp. 347–362 in Prosimian biology (R. D. Martin, G. A. Doyle, and A. C. Walker, eds.). Duckworth, London, United Kingdom.

Schwarz, E. 1931. A revision of the genera and species of Madagascar Lemuridae. Proceedings of the Zoological Society of London 1931:399–410.

Shaw, G. A. 1879. A few notes upon four species of lemurs, specimens of which were brought alive to England in 1878. Proceedings of the Zoological Society of London 1879:132–136.

Simmen, B., S. Peronny, M. Jeanson, A. Hladik, and A. Marez. 2006a. Diet quality and taste perception of plant secondary metabolites by *Lemur catta*. Pp. 160–184 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Simmen, B., et al. 2006b. Plant species fed on by *Lemur catta* in gallery forests of the southern domain of Madagascar. Pp. 55–68 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Simons, E. L., and Y. Rumpler. 1988. *Eulemur*: new generic name for species of *Lemur* other than *Lemur catta*. Comptes Rendus de l'Acadèmie des Sciences (Paris), Série 3 307:547–551.

Soma, T. 2006. Tradition and novelty: *Lemur catta* feeding strategy on introduced tree species at Berenty Reserve. Pp. 141–159 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Storr, G. C. C. 1780. Prodromus methodi mammalium. Inaugeralem disputationem propositus praeside G. C. C. Storr. Respondente F. Wolffer Litteris Reissimis, Tubingae, Germany.

Sussman, R. W. 1975. A preliminary study of the behavior and ecology of *Lemur fulvus rufus* Audebert 1800. Pp. 237–258 in Lemur biology (I. Tattersall and R. W. Sussman, eds.). Plenum Press, New York.

Sussman, R. W. 1977. Feeding behaviour of *Lemur catta* and *Lemur fulvus*. Pp. 3–36 in Primate ecology (T. H. Clutton-Brock, ed.). Academic Press, New York.

Sussman, R. W. 1991. Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. American Journal of Physical Anthropology 84:43–58.

Sussman, R. W. 1992. Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). International Journal of Primatology 13:395–412.

Sussman, R. W., O. Andrianasolondraibe, T. Soma, and I. Ichina. 2003. Social behavior and aggression among ringtailed lemurs. Folia Primatologica 74:168–172.

Sussman, R. W., and J. Ratsirarson. 2006. Beza Mahafaly Special Reserve: a research site in southwestern Madagascar. Pp. 43–52 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Sussman, R. W., and A. Richard. 1986. Lemur conservation in Madagascar: the status of lemurs in the south. Primate Conservation 7:85–92.

Sussman, R. W., S. Sweeney, G. M. Green, I. Porton, O. L. Andrianasolondraibe, and J. Ratsirarson. 2006. A preliminary estimate of *Lemur catta* population density using satellite imagery. Pp. 16–31 in Ringtailed lemur biology: *Lemur catta* in Madagascar (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.

Sutton, B. 1887. On the arm-glands of the lemurs. Proceedings of the Zoological Society of London 1887:369–372.

Swindler, D. R. 1976. Dentition of living primates. Academic Press, London, United Kingdom.

Swindler, D. R. 2002. Primate dentition: an introduction to the teeth of non-human primates. Cambridge University Press, Cambridge, United Kingdom.

Takahata, Y., N. Koyama, N. Miyamoto, and M. Okamoto. 2001. Daytime deliveries observed for the ring-tailed lemurs of the Berenty Reserve, Madagascar. Primates 42:267–271.

Tattersall, I. 1982. The primates of Madagascar. Columbia University Press, New York.

Taylor, L., and R. W. Sussman. 1985. A preliminary study of kinship and social organization in a semi–free-ranging group of *Lemur catta*. International Journal of Primatology 6:601–614.

Thomas, O. 1911. The mammals of the tenth edition of Linnaeus; an attempt to fix the types of the genera and the exact bases and localities of the species. Proceedings of the Zoological Society of London 1911:120–158.

Tilden, C. 2008. Low fetal energy deposition rates in lemurs: another energy conservation strategy. Pp. 311–318 in Elwyn Simons: a search for origins (J. Fleagle and C. C. Gilbert, eds.). Springer, New York.

Tilden, C., and O. T. Oftedal. 1997. Milk composition reflects pattern of maternal care in prosimian primates. American Journal of Primatology 41:195–212.

Trouessart, E.-L. 1878. Catalogue de mammifères vivants et fossiles. Revue et Magasin de Zoologie 3:163.

Van Horn, R. N. 1975. Primate breeding season: photoperiodic regulation in captive *Lemur catta*. Folia Primatologica 24:203–220.

Van Horn, R. N., and G. Eaton. 1979. Reproductive physiology and behavior in prosimians. Pp. 111–153 in The study of prosimian behavior (G. A. Doyle and R. D. Martin, eds.). Academic Press, New York.

Yoder, A. D., J. A. Irwin, S. M. Goodman, and S. V. Rakotoarisoa. 2000. Genetic tests of the taxonomic status of the ring-tailed lemur (*Lemur catta*) from the high mountain zone of the Andringitra Massif, Madagascar. Journal of Zoology (London) 252:1–9.

Young, A. L., A. F. Richard, and L. C. Aiello. 1990. Female dominance and maternal investment in strepsirhine primates. American Naturalist 135:473–488.

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