

Chapter 2

Berenty Reserve, Madagascar: A Long Time in a Small Space

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Abstract Berenty Reserve is a privately owned reserve established in 1936. At 200 ha, it holds the largest remaining gallery forest on the Mandrare River. Scientists of many nationalities have studied there: research follows their diverse interests rather than being coordinated overall. One finding which emerged from long-term monitoring concerns the importance of both within- and between-troop competition for female *Lemur catta* and their inheritance of territory in the female line, at least in this islanded population. This may play a role in the maintenance of female dominance over males. Another aspect of long-term study is the changes brought by introduced species, including *Leucaena leucocephala*, a favored, but toxic, forage tree. The growth of leucaena stands paralleled population growth of the *L. catta* troops with access to these stands, although highly affected females lost fur and had low infant survival; eradication produced a local population crash. Introduced *Eulemur rufus x collaris* have grown from about 16 individuals in 1975–1980 to almost 600 in 2009. They are taking over the central gallery forest. *L. catta* troops maintain their original sleeping areas in the gallery forest but increasingly forage on the periphery, recreating the niche separation described for *Lemur* and *Eulemur* in natural sympatry. Overall, Berenty Reserve is drying out, with closed-canopy gallery forest giving way to more open scrub. Research on Berenty's lemurs is thus the study of evolved adaptations confronted with a changing environment.

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2.1 Introduction

Berenty Estate was founded in 1936 by the de Heaulme family in consultation with local Tandroy clans. It lies beside the Mandrare River in southern Madagascar at about S 25°00'E 46°18'. The estate comprises 6,000 ha: sisal fields, pasture, a tourist complex, and 1,000 ha of forest established as nature reserves long before conservation became fashionable, just because the forest was too beautiful to cut down. The largest reserve parcel, often just called Berenty Reserve, is 200 ha. It is continuous with about 400 further hectares of gallery and spiny forest. Berenty Reserve and the 100 ha Bealoka Reserve, which is also on Berenty Estate, are the two largest of only four remaining blocks of gallery forest on the Mandrare river below the steep tributaries of the headwaters. This is one of the most threatened forest types of Madagascar.

Lemur research at Berenty began with my arrival in 1963. Since then the de Heaulmes have welcomed scientists of all nationalities. There have been long gaps between studies, and many different projects and teams. Research follows individual interests and possibilities rather than being coordinated overall. This article focuses on two aspects of long-term interest: *Lemur catta* social behavior and the influence of introduced species on *L. catta* behavior and ecology. It also provides a bibliography to follow up other aspects of research at Berenty.

Much of what is ecologically interesting about Berenty relates to the fact that it is so small. This forest fragment serves as a scale model of large wilderness reserves. Of the various threats to a small reserve, much of the early theoretical literature focused on inbreeding depression, or on variation in reproductive success either stochastically or due to fluctuating weather, or else on edge effects (Soulé and Wilcox 1980; Frankel and Soulé 1981). At Berenty it has been the accidental or deliberate introduction of exotic species that has most profoundly changed the ecology of this limited space. Especially important have been brown lemurs, *Eulemur rufus x collaris*, and the nutritious but toxic tree *Leucaena leucocephala*. Lemur research at Berenty thus involves the study both of long-evolved species norms of behavior, and of how these adapt in the face of environmental challenges new to these species' history.

The wider importance of Berenty will be scarcely considered here. Berenty Estate is a kaleidoscope of human cultures. Local Tandroy people, traditional warrior-pastoralists, are now agriculturalists who submit to rules on forest use in return for employment that buffers them against the region's recurrent famines. Tourists (*Homo sapiens garbagedispersiensis*) provide income which ensures the reserve's support and survival. Most of the tourist personnel are multilingual Tanosy people from neighboring Fort Dauphin. The scientists themselves function like a clan or tribe: distinct from but dependent on the others. Berenty is the most televised spot in Madagascar. Nearly every foreign film features its parading ringtails and dancing Verreaux's sifaka. This may in fact be its most important contribution, as a show window for Madagascar. In 1992–1994, Helen Crowley became the first manager of the forest reserves, funded by the Wildlife Trust and by

the de Heulmes. Subsequent managers were Hajarimanitra Rambeloarivony and Sahoby Marin Raharison. The forest is now managed by Claire de Heulme Foulon and her husband Didier Foulon (Jolly 2004, 2010).

2.2 Habitat Zones and Fauna

For a general description of Berenty Reserve see Jolly et al. (2006a Fig. 2.1). There is also a fundamental study by Sheila O'Connor and Mark Pigeon comparing Berenty and the 100 ha Bealoka Reserve. Bealoka was still grazed by goats and zebu until 1985, which gave it a much more open understory. Its one ringtail troop used the whole of the 100 ha forest, moving round from season to season with no identifiable core area – most unlike the defended, stable territories of Berenty. O'Connor went on to a career with WWF rather than publishing research, but her thesis remains a baseline for many Berenty ecological studies (O'Connor 1987).

The natural habitat zones of Berenty grade from rich alluvial Gallery forest through transitional Scrub to Spiny forest (Figs. 2.2 and 2.3). The Front zone has many introduced trees which supplement natural lemur diet (Fig. 2.4). These four zones form the 100-ha study area are called Malaza. The Ankoba zone is 70-year-old secondary forest, combining natural and introduced trees for the highest lemur population densities. There is a fivefold difference in ringtailed lemur density from about 500/km² in Front and Ankoba to about 100/km² in the Spiny zone (Jolly 1966a; Budnitz and Dainis 1975; Budnitz 1978; Mertl-Millhollen et al. 1979; Blumenfeld-Jones et al. 2006; Jolly et al. 2006a; Razafindramanana et al. 2008).

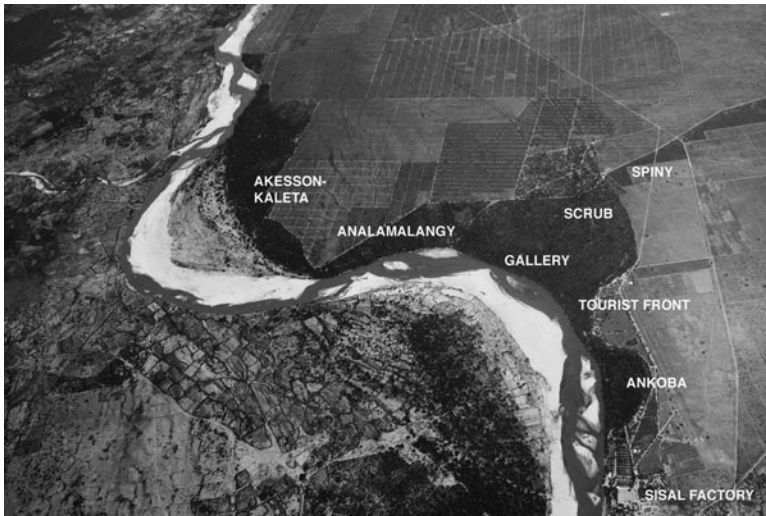


Fig. 2.1 Air photo of Berenty Reserve from the north, with habitat zones. Courtesy Barry Ferguson and the Libanona Ecoly Centre. From Jolly et al. (2006a)



Fig. 2.2 Gallery forest. Giant tamarind trees traditionally provide half the ringtails' feeding time, as well as highways and sleeping sites, though they are now largely occupied by brown lemurs. Photo © Cyril Ruoso



Fig. 2.3 Spiny forest. Verreaux's sifaka and ringtails can live without free water, gaining their food from leaves and stems. Photo © Cyril Ruoso

Southern Madagascar's climate alternates hot wet summers, with temperatures at or above 40°C at mid-day, and cold dry winters, when temperatures fall below 10°C at night. Rainfall varies erratically from 300 to 900 cm if calculated in years beginning Oct 1, which group all of the summer wet season together (Fig. 2.5). Even this masks some of the variation, as in 1991–1992, when two-thirds of the season's rain fell during a 3-day storm in January. El Niño years usually mean drought for the south of Madagascar as for southern Africa, but some El Niño years are exceptionally wet. In 1997 a violent windstorm damaged many canopy trees. Lemurs and other species are adapted to survive recurrent catastrophic years



Fig. 2.4 Front zone. Berenty’s non-human primates are used to ignoring tourists. Photo © A. Jolly

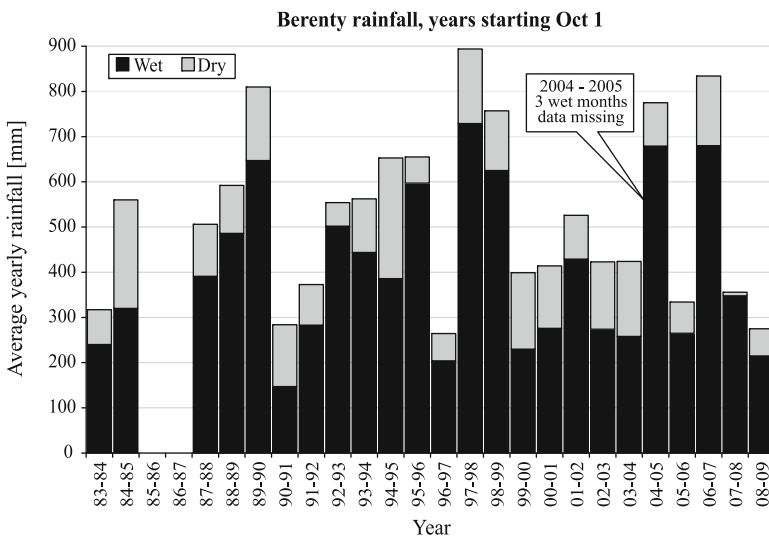


Fig. 2.5 Yearly rainfall at Berenty, which can vary threefold between years. Years begin Oct. 1, which keeps the rainy season as one block (data thanks to K. Blumenfeld-Jones, S. O’Connor, C. and A. Rakotomalala)

(Gould et al. 1999; Wright 1999; Rasamimanana et al. 2000; Richard et al. 2002; Jolly et al. 2006b).

Ringtailed lemurs (*L. catta*) numbered about 450 animals in the Malaza-Ankoba zones in 2009. The ecology of the different zones varies dramatically, with almost no overlap between plant species eaten by any lemurs in the Gallery and Spiny zones. Ringtailed lemurs rely more on leaves in the natural habitats than in the Front and Ankoba zones, since a higher proportion of fruit is available in the modified zones. Niche separation between ringtails and Verreaux’s sifaka (*Propithecus verreauxi*) is clear, with the sifaka eating more leaves and flowers, and better able

to detoxify secondary compounds, though the ringtails also have high tannin tolerance. Ringtails eat little prey: seasonal locusts, acacia army caterpillars, and the occasional chameleon. (Niche separation between ringtails and brown lemurs will be considered below, with the influence of introduced species; Rasamimanana and Rafidinarivo 1993; Pitts 1995; Oda 1996b; Rasamimanana 1999; Simmen et al. 1999, 2003a, b, 2005, 2006a, b, 2010; Rasamimanana et al. 2000, 2006; Rasamimanana and Anjaranantenaina 2008).

Berenty's five other lemur species each have populations of several hundred animals. Most research on Verreaux's sifaka has been done by Alison Richard and her colleagues at Beza Mahafaly (Sussman et al. 2011) further enlarged by the Kappeler team at Kirindy (Kappeler and Fichtel 2011). Sifaka research at Berenty has recently been revived by Norscia, Palagi, Simmen, Rasamimanana, and Fichtel with their colleagues and students. A strong male bias appeared in the 2006 Norscia–Palagi census: 62% of 206 animals counted were male. As Richard originally suggested, the varying sifaka sex ratios seen at Berenty may reflect greater stress on sifaka females during hard years. However, different methods so far give very different total numbers, from 206 in Malaza and Ankoba to Rasamimanana's census of 230 in Malaza alone (Richard 1978; Oda 1998; Charrier et al. 2007; Fichtel 2008; Norscia and Palagi 2008; Palagi et al. 2008; Norscia et al. 2009; Fichtel and Kappeler 2011; Rasamimanana personal communication).

Lepilemurs (*Lepilemur leucopus*) and mouse lemurs (*Microcebus murinus*, *Microcebus griseorufus*) have not been fully censused. It remains a puzzle how small-bodied lepilemurs survive the cold nights of winter on a diet of mature leaves (Charles-Dominique and Hladik 1971; Russell 1977). Grey mouse lemurs eat fruit and insects. Grey-and-red mouse lemurs (only recently identified as a separate species: Rasoloarison et al. 2000) are largely gummivorous during the dry season food shortages, with a complex pattern of sleeping associations (Génin 2001, 2007, 2008, 2010, in press; Génin et al. 2010). Hybrid brown lemurs (*Eulemur rufus* x *E. collaris*) were introduced in 1975, and will be discussed under the changing influence of exotic species (Sect. 2.4).

Berenty holds southern Madagascar's largest colony of the Madagascar giant fruit bat (*Pteropus rufus*). This colony seems to be diminishing from several thousand in 2000 to 927 in a census of 2006 to only 100 in a 2009 census. However, there are wide seasonal variations in numbers (Long 2002; Razafindramanana personal communication). Other mammals include Commerson's leaf-nosed bat *Hipposideros commersoni*, the rufus trident bat *Triaenops rufus*, *Miniopterus majori*, *Miniopterus manavi*, and the Malagasy mouse-eared bat *Myotis goudoti* (Fish 2010), as well as the spiny tenrec *Setifer setosus*, the large tenrec *Tenrec ecaudatus*, and the shrew-like tenrec *Microgale* spp., and the Madagascar tree-rat *Eliurus myoxinus*. There is an all-too flourishing population of *Rattus rattus*, the scourge of Malagasy small mammals (Crowley 1995; Goodman 1995). The forest is too small to hold *Cryptoprocta ferox*, the fossa, and there are no reports of the feral species of wildcat, but domestic dogs and cats, and possibly the Indian civet (*Viverricula indica*) take their place as potential lemur predators.

Fifty-two species of resident birds have been recorded out of a total of 99 species seen, of which 41% are endemic to Madagascar (Goodman et al. 1997). The genetics of the two male color morphs of the Madagascar paradise flycatcher (*Terpsiphone mutata*) have been studied in the Bealoka parcel of gallery forest (Mulder et al. 2002). Crested coua (*Coua cristata*) calls, especially alarm calls, are remarkably similar to ringtail vocalizations (McGeorge 1978a, b). Lemur predators include the harrier hawk (*Polyboroides radiatus*), the Madagascar buzzard (*Buteo madagascariensis*), and the black kite (*Milvus migrans*) (Crowley 1995; Karpanty and Goodman 1999).

Parasitism and disease are a neglected part of the ringtail story, with few published veterinary studies. The most obvious parasites are red ticks which cluster round the eyes of debilitated animals (Takahata et al. 1998; Koyama et al. 2008).

Two constants at Berenty shape much of ringtailed lemur ranging behavior: the prevalence of tamarind trees, and the year-round availability of water. *Tamarindus indica* are the dominant tree of the gallery forest. About 50% of gallery forest ringtailed lemur feeding time is on tamarind fruit pulp or leaves through all seasons. Population density largely mirrors the availability of tamarind trees, and in seasons where there is a dearth in the usual range, troops may make long excursions to fruiting trees (Rasamimanana and Rafidinarivo 1993; Mertl-Millhollen et al. 2003, 2004, 2006; Blumenfeld-Jones et al. 2006; Koyama et al. 2006; Soma 2006). This means that there are fixed points of great importance to ranging patterns, and these major food sources persist over many generations of lemurs. This is less true in the spiny forest, where not only is there less food overall, but the important food trees are smaller and more numerous in a given home range.

The Mandrare River dries up only in September–October of the worst drought years (historically about once every 10 years), and even then a few stagnant puddles remain near the bank. Gallery forest ringtails prefer to descend to the river in places where there are overhanging trees and shrubs that provide cover from aerial predators: again fixed points of great value. In the Scrub and Spiny zones water is obtained from the leaves of succulent plants. These may be in limited stands of the vine *Xerocysios* or introduced *Opuntia*, also points of value which may be worth defending, which influence daily ranging and inter-troop competition (Budnitz 1978).

2.3 Ringtailed Lemur Social Behavior

My early work focused on behavior of ringtailed lemurs, especially their near-absolute female dominance, their highly compressed mating season, and the fact that their social complexity seemed to far outweigh their interest in manipulating objects (Jolly 1966a, b, 1967). The long-term studies which followed have hugely enriched our knowledge, but not actually solved my initial questions.

2.3.1 *Communication*

Ringtailed lemur troops are multi-male and multi-female, ranging in size from 3 to 34 non-infants. They are highly social, with a wide range of vocal, visual, tactile, and scent communication. Vocal signals include the adult male howl or song, contact calls ranging from a soft mew to a loud meow (often given in chorus) locomotor and alarm calls (Oda 1996a). Like vervet monkeys, they use different calls toward different predators: clicks and mobbing toward snakes, yap chorus toward ground predators, and screams toward hawks, often followed by movement upward or downward as appropriate. Scent marking still has subtleties that we do not appreciate, but is done along with stereotyped posturing. A handstand during genital marking by either sex puts the mark at the height of other lemurs' noses. Male spur marking is done with side-to-side jerking of the upper body; male stink-fighting with anointing and waving the tail (Jolly 1966a; Mertl-Millhollen 2007). Urine-marking with raised tail and a "bottom-drag" along a substrate, differs from normal urination (Palagi et al. 2005a; Palagi and Norscia 2009). The scents and vocalizations are individually identifiable (Mertl 1977; Palagi and Dapporto 2006) but also are responded to between troops and even, in the case of alarm calls, between ringtails and sifaka (Oda 1996a, 1998, 1999, 2001; Oda and Masataka 1996). Mertl-Millhollen and Palagi independently conclude that females are more attentive to female marks (especially as inter-troop territorial communication), and males to both males and females (especially for mating opportunities). Mertl-Millhollen first identified the scent-marked ring of territorial boundary well within home range boundaries for both ringtails and Verreaux's sifaka in the gallery forest. The ring of intensive marking is a "battle zone" where troops confront others of their own species. (Mertl 1977; Mertl-Millhollen 1979, 1986, 1988, 2000a, b, 2004, 2006; Mertl-Millhollen et al. 1979). Visual attention, like olfactory attention, is largely directed within members of each sex, except during the brief mating season (Lane and Bard 2007, 2008).

2.3.2 *Female Affiliation and Aggression*

The core of each troop is a female matriline. Subgroups (cliques) reflect kinship, mainly mothers with adult daughters. Time spent in affiliative cuddling and grooming greatly outweighs time spent in aggressive behavior but aggression plays a large part in troop life (Nakamichi and Koyama 1997, 2000; Nakamichi et al. 1997; Sussman et al. 2003; Sussman and Garber 2004). Female dominance rank is highly contested and reversals may be violent (Koyama et al. 2001, 2005). The alpha female has a special role in vigilance and defense toward other troops. If she does not defend personally, her henchwomen, usually a daughter, takes a lead role (Gould 1996). An alpha female may have a relaxed style of dominance with little friction within the troop, but some are actively "spiteful," chasing

subordinates and males from feeding sites even if the dominant does not feed there herself (Dubovick 1998). One may suppose that this behavior eventually pays off for the dominant in reproductive success, by imposing greater costs on her within-troop rivals. In the short term, it clearly costs the alpha energy in the chase and in lost feeding time for herself. If the observer knows enough of the troop history, the differences in alphas' style may sometimes be attributed to outside causes: for instance, if the alpha herself is an immigrant who has fought her way in from another troop, or if there is challenge from a rising sister or cousin, or if the pressure from successful adjacent troops is compressing troop range and thus exacerbating within-troop rivalries.

Larger troops, on average, have lower reproductive success, though optimal group size is smaller in the sparser areas of the reserve, and there are complex tradeoffs between group size and seasonality (Jolly et al. 2002; Pride 2003, 2005b; Pride et al. 2006). In the highest-density area of the reserve, the highest number of surviving infants was found among mid-ranked females in middle-sized and large groups with 4–9 adult females. Smaller groups with only 2–3 adult females had fewer surviving infants (Koyama et al. 2001, 2002, 2005). The somewhat lower success among the highest ranked females in large groups seems like an anomaly, but the variation in aggressivity and cortisol levels between different females, and the pressures of high-density territoriality, may need analysis on an individual by individual basis (Cavigelli et al. 2003; Pride 2003, 2005a, b).

Long-term, when a troop grows too large or when a grandmother dies or is deposed, the troop splits. A group fission involves active targeting by the dominant clique of a subordinate clique, their most distant cousins. Subordinates, once forced out, can fight to establish new territory by subdividing the original home range, or taking neighbor troops' ranges. The evicted group may remain nomadic through others' home ranges for up to 2 years before claiming discrete home range of its own with active defense of a part of this range as a territory. In 23 observed cases, the subordinate daughter troop remained in ranges adjacent to the dominants which had driven them out (Koechlin 1972; Koyama 1991; Hood and Jolly 1995; Koyama et al. 2002; Takahata et al. 2005; Ichino 2006; Ichino and Koyama 2006; Jolly et al. 2006b).

The alpha female often gives a soft call which alerts the troop that it is time to move, and nearly always leads the troop in progressions of over 30 m. A few anecdotal reports of alpha females leading troops on excursions well outside their normal range raise the suggestion whether the memory of old female lemurs is also a resource for their troops (Dolins and Jolly 2007; Miles and Rambeloarivony 2008).

Elsewhere, I argued that within-troop competition between female ringtails evolved within the constraints of a territorial system where it may be easier to evict your cousins than to expand a home range into areas used by neighbors. Frequency of encounters between troops varies with population density: Front troops may meet five or more times per day, in the Gallery forest only once per day, and in the Scrub in the 1990s only twice a week – though these figures have changed with recent population shifts. However, when troops do meet, they are

equally likely to be aggressive whether at high or low densities – and much depends on the individual troop histories which neighbors are treated as the worst threats (Jolly et al. 1993, 2006b; Takahata et al. 2006). Pride showed that even in a case where owners were gaining less food per individual than raiders, the owners continued to actively defend their territory, suggesting that long-term ownership might be worth short-term loss (Pride et al. 2006). Scent marking not only indicates the territory boundaries, but serves as a long-term tradition to maintain those boundaries (Mertl-Millhollen 2000b, 2006).

One of the earliest Berenty studies was conducted by Peter Klopfer. He observed that my 1963 study troop was still in the same area in 1969, with many of the same territorial boundaries (Klopfer and Jolly 1970). Mertl-Millhollen brought order to all studies up to 1975, again noting that troops remained in the same ranges (Mertl-Millhollen et al. 1979). We now know that the ranges of subdivided troops at Berenty remain adjacent to each other, such that female descendents of the first known troops still occupy the same parts of the forest after 40 years (Jolly and Pride 1999; Jolly et al. 2006b).

2.3.3 Males, Infants, and Juveniles

Male transfer between ringtail troops during the birth season was first recorded at Berenty (Jones 1983). It has been much more extensively studied in the tagged population at Beza Mahafaly, as has male behavior (Sussman et al. 2011). Males thus choose new troops 6 months prior to actual mating. Females are only receptive for a few hours of 1 day, though the few that do not conceive may cycle again a month later. Within a troop, all females reach oestrus in a 2-week period, though there is “asynchrony within synchrony,” such that no two are receptive on the same day. The troop’s dominant male sometime, but far from always, has mating priority. Males, including extra-troop individuals, may vie in violent “jump-fights,” which often lead to canine slashes to head or body. Oddly, the female retains absolute mate choice: if she does not like the current winner of a jump-fight she remains in the open, inviting other challengers – and she may mate with several males in succession. In short, behaviorally it seems that males gain little advantage from their year-round dominance contests, their jump-fights, and from their attempts to mate-guard (including copulatory plugs which can be removed by the next male). Actual male reproductive success at Berenty is now under active investigation (Ichino personal communication).

Infants are born in September–October, with most births within about 3 weeks. Births are generally at night or during siesta hours (Okamoto 1998; Takahata et al. 2001). Infants are precocial for lemurs, transferring to the mother’s back at about 2 weeks, and are weaned in about February–March at the peak of the wet season (Gould 1990). Infants grow rapidly during in the wet season, and cease to grow in the following dry season, even under constant conditions in captivity (Pereira 1993b). Wild females normally give birth for the first time at age 3 or 4, though

in captivity they give birth at 2 years. Twins are rare in the wild, common in the better-nourished conditions of captivity. Males have little to do with raising infants, but a mother's close kin may carry her infant or even let it suckle (Gould 1992; Koyama 1992; Koyama et al. 2006). Infanticide happens, though very rarely. In the few cases seen, some perpetrators were extra-troop or immigrant males, but others were females suppressing the reproduction of a subordinate (Hood 1994; Jolly et al. 2000; Ichino 2005). A quarter to a half of infants die in the first year, many during very early lactation when the mother is losing body condition at the end of the dry season (Jolly et al. 2002; Koyama et al. 2002). The mother stays with her fallen infant, or starts to follow the troop and returns as long as it can cry, but she eventually leaves it to rejoin the troop. Lemurs, unlike monkeys, do not have hands that can support a dead infant, though the mother may return to the corpse or site some hours later. The high mortality rate does not reflect maternal indifference (Nakamichi et al. 1996). What it does reflect is the extreme variability of yearly climate, such that infants die but the vast majority of females survive (Jolly et al. 2002, 2006b).

One major difference between ringtailed lemurs and anthropoid primates is in rough-and-tumble play. In most primates including humans, males have more physical contact play than females. In ringtails the sexes spend equal time in rough contact play. Juveniles of both sexes also have occasional serious wrestling bouts which lead to dominance decisions (Gould 1990; Pereira 1993a).

2.3.4 Female Dominance over Males

This is not the place for a full review of theories and studies relating to the evolution and maintenance of lemur female dominance over males. That will largely concern the differences between lemur species' intensity or expression of female dominance, first pointed out by Pereira and Kappeler (Pereira et al. 1990; Pereira and Kappeler 1997). Three lines of study at Berenty contribute to this still unsolved question.

First, it is clear that ringtailed lemur females can be highly aggressive, both within and between troops, as well as toward males. Pereira argues (and I agree) that this involves motivation to gain power per se (Pereira 2006). The adaptive advantages of such motivation are a different question. Lewis argues for "leverage" or "power" as an evolutionary correlate of female dominance (Lewis 2002). In species which are ecologically constrained to have slight or no sexual dimorphism, and where the male-female ratio is equal (or even irrelevant), females may be able to exert their leverage of mate choice over males, achieving behavioral dominance. Lewis' evolutionary reasoning may or may not apply to all the lemur species which show female dominance. The motivational aspect similarly does not apply to all species – in particular, female Verreaux's sifaka, which Lewis studied, have full female dominance but show very rare aggression within a troop, unlike the power-hungry ringtails.

A different line of argument suggested that lemur females as a whole have exceptional need for food, either physiologically or because of the highly erratic Malagasy climate (Jolly 1984; Dewar and Wallis 1999; Wright 1999; Richard et al. 2000, 2002; Dewar and Richard 2007). However, time and locomotion assessment of male and female Berenty ringtails showed that the two sexes actually consume similar amounts of protein and calories, though males' diet is more fibrous, and that the two sexes also expend similar amounts of energy (Rasamimanana and Rafidinarivo 1993; Rasamimanana 1999; Rasamimanana et al. 2006). A double-labeled water study of oxygen consumption during March (after lactation and before the mating season) also showed similar energy budgets between males and females of both ringtailed and brown lemurs (Simmen et al. 2010). It may be that seasonal changes and erratic year-to-year climate still impose extra costs on the females, since they fatten up very markedly during the rainy season in preparation for gestation during the dry season (Simmen et al. 2010), but this is also true of the males in preparation for energy expenditure during mating. Seasonality of breeding in relation to seasonality of food supply will be a part of the story, as first suggested by Hrdy, but female need is not a simple explanation for female dominance (Hrdy 1981; Pride 2005a).

The third argument is so far in need of much more evidence. Jolly et al. (2006b) suggested that inheritance of material property in the female line can increase the variance in female reproductive fitness over that of males. Males start over again in each generation with variance reflecting only their genes, their luck, and their bodily prowess. Female ringtails at Berenty inherit territory which must be defended in each generation, but which is hard to reclaim once lost. This territorial stability may be an artifact of Berenty's high density, though the aggression shown between troops at all densities, and the rough-and-tumble play of young females suggests that female competitive behavior is an evolutionary norm for ringtails. However, proving the importance of maternal inheritance of property needs mathematical rigor and actual data on males' reproductive variance as well as females', as well as further data on troop range, territoriality, and territorial inheritance in other species and at sites outside Berenty. Interestingly, E.O. Wilson now argues that the evolutionary origins of social insect society should be traced to defense of a nest or nest site, a rare and heritable resource. In Hymenoptera, with maternal inheritance, this arguably involves an extraordinary form of female dominance, while in Isoptera both the resident reproductives and the worker cast are male and female (Hölldobler and Wilson 2009; Nowak et al. 2010)

2.3.5 Complexity of Social Relations

The other interest of the very early studies was the comparison between lemur social relations and those of anthropoids. I believed that the simple composition of multi-male, multi-female troops would favor social intelligence (Jolly 1966b). I did point out that tripartite reactions in which one animal would threaten another while

ensuring support from a third had not been seen in the lemurs (Kummer 1967). Since then, it seems that ringtailed lemur interactions are much more black and white than in many anthropoids – either affiliative or aggressive between any two animals, with minimal ambiguity, and no reconciliation after quarrels (Kappeler 1993). Reconciliation has recently been asserted for sifaka, ringtails and brown lemurs, using different measurements (Palagi et al. 2001, 2005b, 2008). More obvious in the field is the careful geometry of a troop, where distance between animals is a very good measure of affiliation or aggression, and arguably involves awareness of multiple individuals, not just dyads (Nakamichi et al. 1997). Complexity of social relations would be worth revisiting by someone very familiar with behavior of both monkeys and prosimians.

2.4 The Changing Ecology of Introduced Species

2.4.1 Nurse Trees and Food Trees

The concentration of fruit trees with different phenologies from the highly seasonal native forest is one of the main reasons for high lemur density in the Front zone (Rasamimanana and Rafidinarivo 1993). Introduced tree species from which lemurs obtain food and those that serve as forest nurse trees represent benign interventions, though they are far from natural. *Pithecellobium dulce*, the “monkeypod” or “ape’s earring” tree is a nurse tree, has promoted the regeneration of the Ankoba zone with its high density of all lemur species. Prickly pear, *Opuntia*, is found at the periphery, and is now spreading along the river bank. Too much would be disastrous, but it serves as an important water source for lemurs in both the Front and Scrub zones.

2.4.2 *Cissus quadrangularis*

Cissus, the “veldt grape” or “Devil’s backbone,” is a euphorb imported to Madagascar from India or Africa either as an ornamental, or for its curative qualities on broken bones and other ailments. In Berenty it is a smothering vine that blankets whole trees or sections of forest. Management campaigns have cleared sections of forest by hand, but it re-grows from tiny dropped fragments, so this is an endless process. There is nothing good to be said about *Cissus* in a forest reserve.

2.4.3 *Leucaena leucocephala*

Stands of leucaena were planted in or just before 1990, in the bottleneck between Ankoba and Malaza and also at the northern tip of Ankoba. They were an

experiment, to see if they could provide extra fodder for cattle and ostriches. The rise in ringtail population in the Front zone tracked the growth of this fast-growing tree. Demography was studied by the Koyama team during this period of rapid population expansion. Unfortunately, leucaena contains mimosine, a non-protein amino acid that blocks cell division. Some troops became so dependent on leucaena that they ate it for 40–50% of their feeding time during dry season months. This produced “Bald Lemur Syndrome,” or rather, naked lemur syndrome in which the loss of fur from body and tail mimicked chemotherapy (Fig. 2.6). Adults mostly recovered full pelage when the diet changed with the onset of rains. Embryos seemed to be buffered against the leucaena effect. The birth rate of highly affected females was not lower, but survival of infants with no fur to cling to, and of juveniles weaned onto the toxic tree fell markedly by the end of the leucaena period in 2006–2007. Nearly all of these trees have now been removed. However, the loss of a major foodstuff has also increased adult mortality in the Japanese study troops, which are concentrated at the bottleneck (Jolly 1980, 2009a, b; Crawford et al. 2006, 2008; Soma 2006, in press; Soma et al. 2008; Berg et al. 2009; Ichino et al. in press).

2.4.4 *Brown Lemurs*

By far the largest influence on ringtails has been the introduction of brown lemurs. About eight orphaned pet *E. rufus* from the Menabe in western Madagascar, escaped to the forest during a 1975 cyclone. About eight more *E. collaris* from the Fort Dauphin region were deliberately released in the years up to 1985. These two species have different chromosome numbers, and should not be able to breed, but no one told the lemurs. They are direct and dominant competitors with the



Fig. 2.6 Bald lemur. Photo © Wiebke Berg

ringtails for habitat and food, although their social structure is quite different, as is their cathemeral activity. The hybrid population of Malaza and Ankoba numbered 596 in 2009, compared to 462 ringtails (Figs. 2.6 and 2.7). The brown population grew exponentially from their introduction until a peak of 653 in 2007 (Fig. 2.7). At that point, scientists persuaded the management to stop providing water in artificial basins in the forest. This might have finally limited the brown lemur population in space, if not in numbers, since they do not spend much time in the sunny scrub zone. Ringtailed lemur troops have largely abandoned the rich gallery forest to the brown lemurs. Although they maintain a foothold, and sleep in their old ranges, much of the daytime foraging is now concentrated on the reserve's periphery. However, their numbers have not fallen (Pinkus et al. 2006; Tanaka 2007; Razafindramanana et al. 2008; Donati et al. 2009; Norscia and Palagi 2011; Palagi and Norscia 2011; Rasamimanana et al. in press).

It is still not clear whether brown and ringtailed lemurs will continue to co-exist stably. They have re-created the classic ecological niche separation described by Sussman (1974), with browns in the central shade, feeding on the gallery forest trees once favored by ringtails, and ringtails in the peripheral sun with a diet increasingly based on plants of scrub and spiny forest. There is no clear sign that the two species are over-browsing their habitat. However, one needs perhaps another 5 years to be sure of this conclusion (Fig. 2.8).

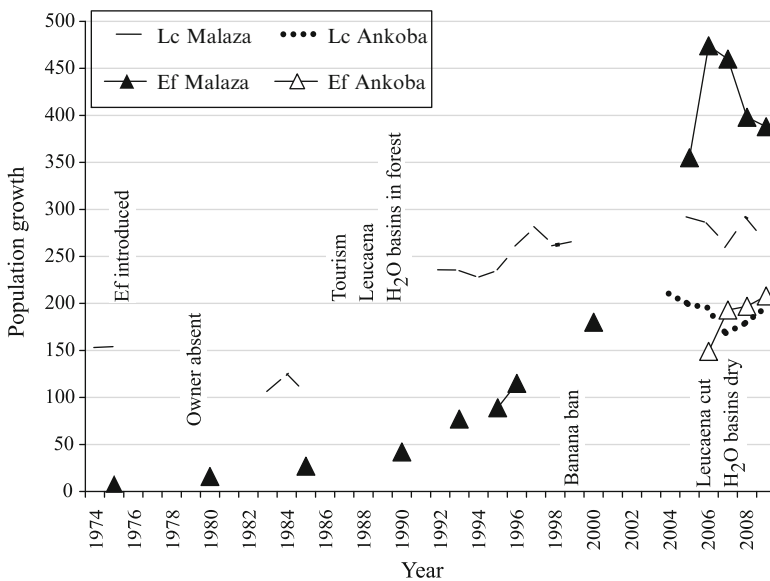


Fig. 2.7 Population growth of ringtailed and brown lemurs (Razafindramanana, Pinkus, O'Connor, Dainis, Jolly)



Fig. 2.8 Hybrid brown lemurs at Berenty. The male has the crest and eyebrows of *Eulemur rufus*, the full beard of *E. collaris*. The female has the grey head of *E. collaris* and the frontal stripe of *E. rufus*. Photo © Cyril Ruoso

2.5 The Future

Berenty is drying out. The loss of tamarind trees and closed canopy forest is clear over the decades (Blumenfeld-Jones et al. 2006; Ichino 2007). It is not clear why. One reason may be natural succession within the gallery forest. If the reserve were not so bounded there might be re-growth in other places. Another likely cause is the lowering of the water table. The Mandrare River suffers from deforestation in the headwaters, and loss of grass cover lower down; flood crests which used to pass in days now pass in hours.

Add to this the effects of climate change. Berenty has suffered repeated droughts in this decade. El Niño years commonly bring drought, and they seem to be growing commoner. All global climate models predict a greater intensity of cyclones. These can sometimes bring needed rain to the south, but a mis-timed cyclone ruins the years' crops. Madagascar lies on the intertropical convergence, in the latitudes most vulnerable to climate change. All types of native forest are much better buffered against extremes than are the annual crops, but progressive drying out could eventually destroy the forest.

Berenty Estate is also vulnerable to social change and unrest. Its reserve system has survived for 70 years. This is due to the care of the de Heaulme family, and to the fact that local people have had salaries that allied their interests with the estate. Any reserve's survival depends on the good will and enthusiasm of particular people, and on an enabling economy. When the reserve is as small as Berenty, the people are few, and outside income comes only from sisal and tourism.

Subsistence farming is at the mercy of the weather. The weather itself is at the mercy of southern deforestation and the northern greed for carbon (Koyama 2009).

Berenty has provided much, though certainly not all of our understanding of the behavior of ringtailed and other southern lemurs – especially the interplay of within- and between-troop aggression in a female-dominant species. It has served as a base for ecological research, but an ecologist at Berenty cannot simply produce a picture of the “environment of ecological adaptation” – it takes all the running a scientist can do to keep up with the changes brought by introduced species and climate fluctuations in such a small space.

The very things that make Berenty interesting, though – lemur social interactions in a region of maximum population density, and the constantly changing ecological background – also make it vulnerable. Its survival is by no means guaranteed, in the face of physical or social changes to come.

References

- Berg W, Jolly A, Rambeloarivony H, Andrianome VN, Rasamimanana HR (2009) A scoring system for coat and tail condition in ringtailed lemurs, *Lemur catta*. *Am J Primatol* 71:183–190
- Blumenfeld-Jones KC, Randriamboavonjy TM, Williams GW, Mertl-Millhollen AS, Pinkus S, Rasamimanana HR (2006) Tamarind recruitment and long-term stability in the gallery forest at Berenty, Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana HR (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 69–85
- Budnitz N (1978) Feeding behavior of *Lemur catta* in different habitats. In: Bateson PPG, Klopfer PH (eds) Perspectives in ethology, vol 3. Plenum, New York, pp 85–108
- Budnitz N, Dainis K (1975) *Lemur catta*: ecology and behavior. In: Tattersall I, Sussman RW (eds) Lemur biology. Plenum, New York, pp 219–235
- Cavigelli SA, Dubovick TH, Levash WA, Jolly A, Pitts A (2003) Female dominance status and fecal corticoids in a cooperative breeder with low reproductive skew: ring-tailed lemurs (*Lemur catta*). *Horm Behav* 43:166–179
- Charles-Dominique P, Hladik CM (1971) Le lépilemur du sud de Madagascar: écologie, alimentation et vie sociale. *Rev Écol* 25:3–66
- Charrier A, Hladik A, Simmen B (2007) Stratégie alimentaire et dominance des femelles propithèque de Verreaux (*Propithecus v. verreauxi*) dans la forêt à Didiereacea du sud de Madagascar. *Rev Écol* 62:257–263
- Crawford GC, Andriafaneva L-E, Blumenfeld-Jones KC, Calaba G, Clarke L, Gray L, Ichino S, Jolly A, Koyama N, Mertl-Millhollen AS, Ostpak S, Pride RE, Rasamimanana HR, Simmen B, Soma T, Tarnaud L, Tew A, Williams GW (2006) Bald lemur syndrome and the miracle tree: alopecia associated with *Leucaena leucocephala* at Berenty Reserve, Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana HR (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 332–342
- Crawford GC, Ostapak SE, Davidson A, Baker T, Puschner B, Affolter L, Stalis I, Rasamimanana HR, Jolly A (2008) Bald lemur syndrome: the systematic effects of *Leucaena leucocephala* on *Lemur catta* at Berenty Reserve, Madagascar. *Primate Eye* 96 (special issue):187
- Crowley HM (1995) Berenty reserve management plan. Wildlife Preservation Trust International, Philadelphia
- Dewar RE, Richard AF (2007) Evolution in the hypervariable environment of Madagascar. *Proc Natl Acad Sci USA* 104:13723–13727

- Dewar RE, Wallis JR (1999) Geographical patterning of interannual rainfall variability in the tropics and near tropics: an L-moments approach. *J Climate* 12:3457–3466
- Dolins F, Jolly A (2007) Ranging behavior and social decision-making in two species of lemurs (*Lemur catta* & *Propithecus verreauxi verreauxi*) at Berenty Reserve, Madagascar. EG-Meeting: Social organization and cognitive tools: general patterns in vertebrates? Konrad Lorenz Forschungsstelle, Grünau
- Donati G, Baldi N, Morelli V, Ganzhorn JU, Borgognini-Tarli SM (2009) Proximate and ultimate determinants of cathemeral activity in brown lemurs. *Anim Behav* 77:317–325
- Dubovick TH (1998) A historical, social and ecological analysis of three tourist ranging troops of Lemur catta, Berenty Reserve, Madagascar. BA thesis, University of Princeton/NJ
- Fichtel C (2008) Ontogeny of conspecific and heterospecific alarm call recognition in wild Verreaux's sifakas (*Propithecus verreauxi verreauxi*). *Am J Primatol* 70:127–135
- Fichtel C, Kappeler PM (2011) Variation in the meaning of alarm calls in Coquerel's and Verreaux's sifakas (*Propithecus coquereli*, *P. verreauxi*). *Int J Primatol* 32:346–361
- Fish KD (2010) Niche separation between mouse lemurs (*Microcebus murinus*) and clutter-foraging bats at Berenty Private Reserve, Madagascar. PhD thesis, University of Colorado, Boulder/CO
- Frankel OH, Soulé ME (1981) Conservation and evolution. Cambridge University Press, Cambridge
- Génin F (2001) Gummivory in mouse lemurs during the dry season in Madagascar. *Folia Primatol* 72:119–120
- Génin F (2007) Energy-dependent plasticity of grey mouse lemur social systems: lessons from field and captive studies. *Rev Écol* 62:245–256
- Génin F (2008) Life in unpredictable environments: first investigation of the natural history of *Microcebus griseorufus*. *Int J Primatol* 29:303–321
- Génin F (2010) Who sleeps with whom? Sleeping associations and socio-territoriality in *Microcebus griseorufus*. *J Mammal* 91:942–951
- Génin F (in press) Living in unpredictable environments: energy management and socio-spatial organization of *Microcebus griseorufus* in the southern spiny forest of Madagascar. In: Masters JC, Gamba M, Génin F (eds) Leaping ahead: advances in prosimian biology. Springer, New York
- Génin F, Masters JC, Ganzhorn JU (2010) Gummivory in cheirogaleids: primitive retention or adaptation to hypervariable environments? In: Burrows AM, Nash LT (eds) The evolution of exudativory in primates. Springer, New York
- Goodman SM (1995) *Rattus* on Madagascar and the dilemma of protecting the endemic rodent fauna. *Conserv Biol* 9:450–453
- Goodman SM, Pidgeon M, Hawkins AFA, Schulenberg TS (1997) The birds of southern Madagascar. *Fieldiana Zool* 187:1–132
- Gould L (1990) The social development of free-ranging infant *Lemur catta* at Berenty Reserve, Madagascar. *Int J Primatol* 11:297–318
- Gould L (1992) Alloparental care in free-ranging *Lemur catta* at Berenty Reserve, Madagascar. *Folia Primatol* 58:72–83
- Gould L (1996) Vigilance behavior during the birth and lactation season in naturally occurring ring-tailed lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. *Int J Primatol* 17:331–347
- Gould L, Sussman RW, Sauther ML (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. *Int J Primatol* 20:69–84
- Hölldobler B, Wilson EO (2009) The superorganism: the beauty, elegance, and strangeness of insect societies. Norton and Company, New York
- Hood LC (1994) Infanticide among ringtailed lemurs (*Lemur catta*) at Berenty Reserve, Madagascar. *Am J Primatol* 33:65–69

- Hood LC, Jolly A (1995) Troop fission in female *Lemur catta* at Berenty Reserve, Madagascar. *Int J Primatol* 16:997–1015
- Hrdy SB (1981) The woman that never evolved. Harvard University Press, Cambridge, MA
- Ichino S (2005) Attacks on a wild infant ring-tailed lemur (*Lemur catta*) by immigrant males at Berenty, Madagascar: interpreting infanticide by males. *Am J Primatol* 67:267–272
- Ichino S (2006) Troop fission in wild ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. *Am J Primatol* 68:97–102
- Ichino S (2007) The status and problems of lemur conservation in the Berenty Reserve, southern Madagascar [Japanese with English abstract]. *Asian Afr Area Stud* 6:197–214
- Ichino S, Koyama N (2006) Social changes in a wild population of ringtailed lemurs (*Lemur catta*) at Berenty, Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana HR (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 233–244
- Ichino S, Soma T, Koyama N (in press) The alopecia syndrome of ring-tailed lemurs (*Lemur catta*) at Berenty Reserve, Madagascar: a preliminary report on impact on female reproductive parameters. In: Masters JC, Gamba M, Génin F (eds) Leaping ahead: advances in prosimian biology. Springer, New York
- Jolly A (1966a) Lemur behavior: a Madagascar field study. University of Chicago Press, Chicago
- Jolly A (1966b) Lemur social behavior and primate intelligence. *Science* 153:501–506
- Jolly A (1967) Breeding synchrony in wild *Lemur catta*. In: Altmann SA (ed) Social communication among primates. University of Chicago Press, Chicago, pp 3–14
- Jolly A (1980) A world like our own: man and nature in Madagascar. Yale University Press, New Haven
- Jolly A (1984) The puzzle of female feeding priority. In: Small MF (ed) Female primates: studies by women primatologists. Liss, New York, pp 197–215
- Jolly A (2004) Lords and lemurs: Mad scientists, kings with spears, and the survival of diversity in Madagascar. Houghton Mifflin, Boston
- Jolly A (2009a) Coat condition of ringtailed lemurs, *Lemur catta*, at Berenty Reserve, Madagascar: I. Differences by age, sex, density and tourism 1996–2006. *Am J Primatol* 71:191–198
- Jolly A (2009b) Coat condition of ringtailed lemurs, *Lemur catta*, at Berenty Reserve, Madagascar: II. Coat and tail alopecia associated with *Leucaena leucocephala*, 2001–2006. *Am J Primatol* 71:199–205
- Jolly A (2010) The narrator's stance: story-telling and science at Berenty Reserve. In: MacClancy J, Fuentes A (eds) Centralizing fieldwork: critical perspectives from primatology, biological and social anthropology. Berghan Books, New York, pp 223–241
- Jolly A, Pride RE (1999) Troop histories and range inertia of *Lemur catta* at Berenty, Madagascar: a 33-year perspective. *Int J Primatol* 20:359–373
- Jolly A, Rasamimanana HR, Kinnaird MF, O'Brien TG, Crowley HM, Harcourt CS, Gardner S, Davidson JM (1993) Territoriality in *Lemur catta* groups during the birth season at Berenty, Madagascar. In: Kappeler PM, Ganzhorn JU (eds) Lemur social systems and their ecological basis. Plenum, New York, pp 85–109
- Jolly A, Caless S, Cavigelli S, Gould L, Pereira ME, Pitts A, Pride RE, Rabenandrasana HD, Walker JD, Zafison T (2000) Infant killing, wounding and predation in *Eulemur* and *Lemur*. *Int J Primatol* 21:21–40
- Jolly A, Dobson A, Rasamimanana HR, Walker J, O'Connor S, Solberg M, Perel V (2002) Demography of *Lemur catta* at Berenty Reserve, Madagascar: effects of troop size, habitat and rainfall. *Int J Primatol* 23:327–353
- Jolly A, Koyama N, Rasamimanana HR, Crowley H, Williams GW (2006a) Berenty Reserve: a research site in southern Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana HR (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 32–42
- Jolly A, Rasamimanana HR, Braun MA, Dubovick TH, Mills CN, Williams GW (2006b) Territory as bet-hedging: *Lemur catta* in a rich forest and an erratic climate. In: Jolly A, Sussman RW, Koyama N, Rasamimanana HR (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 187–207

- Jones KC (1983) Inter-troop transfer of *Lemur catta* males at Berenty, Madagascar. *Folia Primatol* 40:145–160
- Kappeler PM (1993) Reconciliation and post-conflict behaviour in ringtailed lemurs, *Lemur catta* and redfronted lemurs, *Eulemur fulvus rufus*. *Anim Behav* 45:901–915
- Kappeler PM, Fichtel C (2011) A 15-year perspective on the social organization and life history of Sifaka in Kirindy Forest. In: Kappeler PM (ed) Long-term field studies of primates. Springer, Heidelberg
- Karpanty SM, Goodman SM (1999) Diet of the Madagascar harrier-hawk, *Polyboroides radiatus*, in southeastern Madagascar. *J Raptor Res* 4:313–316
- Klopfer PH, Jolly A (1970) The stability of territorial boundaries in a lemur troop. *Folia Primatol* 12:199–208
- Koechlin J (1972) Flora and vegetation of Madagascar. In: Battistini R, Richard-Vindard G (eds) Biogeography and ecology of Madagascar. Dr. W. Junk B.V Publishers, The Hague, pp 145–190
- Koyama N (1991) Troop division and inter-troop relationships of ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. In: Ehara A, Kimura T, Takenaka O, Iwamoto M (eds) Primatology today. Elsevier, Amsterdam, pp 173–176
- Koyama N (1992) Multiple births and care-taking behavior of ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. In: Yamagishi S (ed) Social structure of Madagascar higher vertebrates in relation to their adaptive radiation. Osaka City University, Osaka, pp 5–9
- Koyama N (2009) Madagascar tou-Nishiindoyou chiikikennyuu nyuumon (The Island of Madagascar: an introduction to area studies in the Western Indian Ocean Region) [in Japanese]. Tokaidaigaku Press, Kanagawa
- Koyama N, Nakamichi M, Oda R, Miyamoto N, Ichino S, Takahata Y (2001) A ten-year summary of reproductive parameters for ring-tailed lemurs at Berenty, Madagascar. *Primates* 42:1–14
- Koyama N, Nakamichi M, Ichino S, Takahata Y (2002) Population and social dynamics changes in ring-tailed lemur troops at Berenty, Madagascar between 1989–1999. *Primates* 43:291–314
- Koyama N, Ichino S, Nakamichi M, Takahata Y (2005) Long-term changes in dominance ranks among ring-tailed lemurs at Berenty Reserve, Madagascar. *Primates* 46:225–234
- Koyama N, Soma T, Ichino S, Takahata Y (2006) Home ranges of ringtailed lemur troops and the density of large trees at Berenty Reserve, Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana HR (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 86–101
- Koyama N, Aimi M, Kawamoto Y, Hirai H, Go Y, Ichino S, Takahata Y (2008) Body mass of wild ring-tailed lemurs in Berenty Reserve, Madagascar, with reference to tick infestation: a preliminary analysis. *Primates* 49:9–15
- Kummer H (1967) Tripartite relations in hamadryas baboons. In: Altmann SA (ed) Social communication among primates. University of Chicago Press, Chicago, pp 63–71
- Lane L, Bard KA (2007) Seasonal influences on visual social monitoring in free ranging *Lemur catta* at Berenty Reserve, Madagascar. *Am J Primatol* 69(suppl 1):32
- Lane L, Bard KA (2008) Assessing dyadic social attention in *Lemur catta*. *Primate Eye* 96:107
- Lewis RJ (2002) Beyond dominance: the importance of leverage. *Quart Rev Biol* 77:149–164
- Long E (2002) The feeding ecology of *Pteropus rufus* in a remnant gallery forest surrounded by sisal plantations in south-east Madagascar. PhD thesis, University of Aberdeen
- McGeorge LW (1978a) Circumvention of noise in the communication channel by the structure and timing of the calls of forest animals. PhD thesis, Duke University, Durham, NC
- McGeorge LW (1978b) Influences on the structure of vocalizations of three Malagasy lemurs. In: Chivers DJ, Joysey KA (eds) Recent advances in primatology. Academic, London, pp 103–109
- Mertl AS (1977) Habituation to territorial scent marks in the field by *Lemur catta*. *Behav Biol* 21:500–507
- Mertl-Millhollen AS (1979) Olfactory demarcation of territorial boundaries by a primate – *Propithecus verreauxi*. *Folia Primatol* 32:35–42

- Mertl-Millhollen AS (1986) Territorial scent-marking by two sympatric lemur species. In: Duvall D, Muller-Schwarze D, Silverstein RM (eds) Chemical signals in vertebrates, vol 4, Ecology, evolution and comparative biology. Plenum, New York, pp 647–652
- Mertl-Millhollen AS (1988) Olfactory demarcation of territorial but not home range boundaries by *Lemur catta*. *Folia Primatol* 50:175–187
- Mertl-Millhollen AS (2000a) Components of scent marking behavior by male ringtailed lemurs (*Lemur catta*) at Berenty Reserve, Madagascar. *Am J Primatol* 51(suppl):74
- Mertl-Millhollen AS (2000b) Ringtailed lemur (*Lemur catta*) over-marking as an example of resource defense. *Am J Primatol* 51(suppl):73–74
- Mertl-Millhollen AS (2004) Primate scent marking as resource defence. *Folia Primatol* 75(suppl 1):49–50
- Mertl-Millhollen AS (2006) Scent marking as resource defense by female *Lemur catta*. *Am J Primatol* 68:605–621
- Mertl-Millhollen AS (2007) Lateral bias to the leading limb in an olfactory social signal by male ring-tailed lemurs. *Am J Primatol* 69:635–640
- Mertl-Millhollen AS, Gustafson HL, Budnitz N, Dainis K, Jolly A (1979) Population and territory stability of the *Lemur catta* at Berenty, Madagascar. *Folia Primatol* 31:106–122
- Mertl-Millhollen AS, Moret ES, Felantsoa D, Rasamimanana HR, Blumenfeld-Jones KC, Jolly A (2003) Ring-tailed lemur home ranges correlate with food abundance and nutritional content at a time of environmental stress. *Int J Primatol* 24:969–985
- Mertl-Millhollen AS, Rambeloarivony H, Miles W, Rasamimanana HR (2004) Tamarind leaf quality and *Lemur catta* population density and behavior. *Folia Primatol* 75(suppl 1):157–158
- Mertl-Millhollen AS, Rambeloarivony H, Miles W, Kaiser VA, Gray L, Dorn LT, Williams GW, Rasamimanana HR (2006) The influence of tamarind tree quality and quantity on *Lemur catta* behavior. In: Jolly A, Sussman RW, Koyama N, Rasamimanana HR (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 102–118
- Miles W, Rambeloarivony H (2008) Initiation and leading of travel in *Lemur catta*. *Lemur News* 13:22–24
- Mulder RA, Ramiarison R, Emahalala RE (2002) Ontogeny of male plumage dichromatism in Madagascar paradise flycatchers. *J Avian Biol* 33:342–348
- Nakamichi M, Koyama N (1997) Social relationships among ring-tailed lemurs (*Lemur catta*) in two free-ranging troops at Berenty Reserve, Madagascar. *Int J Primatol* 18:73–93
- Nakamichi M, Koyama N (2000) Intra-troop affiliative relationships of females with newborn infants in wild ring-tailed lemurs (*Lemur catta*). *Am J Primatol* 50:187–203
- Nakamichi M, Koyama N, Jolly A (1996) Maternal responses to dead and dying infants in wild troops of ring-tailed lemurs at the Berenty Reserve, Madagascar. *Int J Primatol* 17:505–523
- Nakamichi M, Rakototiana MLO, Koyama N (1997) Effects of spatial proximity and alliances on dominance relations among female ring-tailed lemurs (*Lemur catta*) at Berenty Reserve, Madagascar. *Primates* 38:331–340
- Norscia I, Palagi E (2008) Berenty 2006: census of *Propithecus verreauxi* and possible evidence of population stress. *Int J Primatol* 29:1099–1115
- Norscia I, Palagi E (2011) Do wild brown lemurs reconcile? Not always. *J Ethol* 29:181–185
- Norscia I, Antonacci D, Palagi E (2009) Mating first, mating more: biological market fluctuation in a wild prosimian. *PLoS One* 4:e4679. doi:10.1371/journal.pone.0004679
- Nowak MA, Tarnita CE, Wilson EO (2010) The evolution of eusociality. *Nature* 466:1057–1062
- O'Connor SM (1987) The effect of human impact on vegetation and the consequences to primates in two riverine forests, southern Madagascar. PhD thesis, Cambridge University
- Oda R (1996a) Effects of contextual and social variables on contact call production in free-ranging ringtailed lemurs (*Lemur catta*). *Int J Primatol* 17:191–205
- Oda R (1996b) Predation on a chameleon by a ring-tailed lemur (*Lemur catta*) in the Berenty Reserve, Madagascar. *Folia Primatol* 67:40–43
- Oda R (1998) The responses of Verreaux's sifakas to anti-predator alarm calls given by sympatric ring-tailed lemurs. *Folia Primatol* 69:357–360

- Oda R (1999) Scent marking and contact call production in ring-tailed lemurs (*Lemur catta*). *Folia Primatol* 70:121–124
- Oda R (2001) Lemur vocal communication and the origin of human language. In: Matsuzawa T (ed) Primate origins of human cognition and behavior. Springer, Tokyo, pp 115–134
- Oda R, Masataka N (1996) Interspecific responses of ringtailed lemurs to playback of antipredator alarm calls given by Verreaux's sifakas. *Ethology* 102:441–453
- Okamoto M (1998) The birth of wild ring-tailed lemurs at Berenty Reserve, Madagascar [Japanese with English Abstract]. *Primate Res* 14:25–34
- Palagi E, Dapporto L (2006) Beyond odor discrimination: demonstrating individual recognition by scent in *Lemur catta*. *Chem Senses* 31:437–443
- Palagi E, Norscia I (2009) Multimodal signaling in wild *Lemur catta*: economic design and territorial function of urine marking. *Am J Phys Anthropol* 139:182–192
- Palagi E, Norscia I (2011) Scratching around stress: hierarchy and reconciliation make the difference in wild brown lemurs (*Eulemur fulvus*). *Stress* 14:93–97
- Palagi E, Bastianelli E, Borgognini Tarli SM (2001) Social relationships, target aggressions and post-conflict behaviour in ringtailed lemurs (*Lemur catta*). *Folia Primatol* 72:129
- Palagi E, Dapporto L, Borgognini Tarli SM (2005a) The neglected scent: on the marking function of urine in *Lemur catta*. *Behav Ecol Sociobiol* 58:437–445
- Palagi E, Paoli T, Borgognini Tarli SM (2005b) Aggression and reconciliation in two captive groups of *Lemur catta*. *Int J Primatol* 26:279–294
- Palagi E, Antonacci D, Norscia I (2008) Peacemaking on treetops: first evidence of reconciliation from a wild prosimian (*Propithecus verreauxi*). *Anim Behav* 76:737–747
- Pereira ME (1993a) Agonistic interaction, dominance relations, and ontogenetic trajectories in ringtailed lemurs. In: Pereira ME, Fairbanks LA (eds) Juvenile primates: life history, development, and behavior. Oxford University Press, New York, pp 285–305
- Pereira ME (1993b) Seasonal adjustment of growth rate and adult body weight in ringtailed lemurs. In: Kappeler PM, Ganzhorn JU (eds) Lemur social systems and their ecological basis. Plenum, New York, pp 205–221
- Pereira ME (2006) Obsession with agonistic power. In: Jolly A, Sussman RW, Koyama N, Rasamimanana HR (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 245–270
- Pereira ME, Kappeler PM (1997) Divergent systems of agonistic behaviour in lemurid primates. *Behaviour* 134:225–274
- Pereira ME, Kaufman R, Kappeler PM, Overdorff DJ (1990) Female dominance does not characterize all of the Lemuridae. *Folia Primatol* 55:96–103
- Pinkus S, Smith JNM, Jolly A (2006) Feeding competition between introduced *Eulemur fulvus* and native *Lemur catta* during the birth season at Berenty Reserve, southern Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana HR (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 119–140
- Pitts A (1995) Predation by *Eulemur fulvus rufus* on an infant *Lemur catta* at Berenty, Madagascar. *Folia Primatol* 65:169–171
- Pride RE (2003) The socio-endocrinology of group size in *Lemur catta*. PhD thesis, Princeton University, NJ
- Pride RE (2005a) High faecal glucocorticoid levels predict mortality in ring-tailed lemurs (*Lemur catta*). *Biol Lett* 1:60–63
- Pride RE (2005b) Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). *Behav Ecol* 16:550–560
- Pride RE, Felantsoa D, Randriamboavonjy TM, Randriambelona R (2006) Resource defence in *Lemur catta*: the importance of group size. In: Jolly A, Sussman RW, Koyama N, Rasamimanana HR (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 208–232
- Rasamimanana HR (1999) Influence of social organization patterns on food intake of *Lemur catta* in the Berenty Reserve. In: Rakotosamimanana B, Rasamimanana HR, Ganzhorn JU,

- Goodman SM (eds) New directions in lemur studies. Kluwer Academic Press, Plenum Publishers, New York, pp 173–188
- Rasamimanana HR, Anjarantenaina S (2008) Influence of hierarchy on the social behaviour of female ring-tailed lemurs at Berenty Reserve, south Madagascar. *Primate Eye* 96 (special issue):91
- Rasamimanana HR, Rafidinarivo E (1993) Feeding behavior of *Lemur catta* females in relation to their physiological state. In: Kappeler PM, Ganzhorn JU (eds) Lemur social systems and their ecological basis. Plenum, New York, pp 123–133
- Rasamimanana HR, Ratovonirina JA, Pride E (2000) Storm damage at Berenty Reserve. *Lemur News* 5:7–8
- Rasamimanana HR, Andrianome VN, Rambeloarivony H, Pasquet P (2006) Male and female ringtailed lemurs' energetic strategy does not explain female dominance. In: Jolly A, Sussman RW, Koyama N, Rasamimanana HR (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 271–295
- Rasamimanana HR, Razafindramanana J, Mertil-Millhollen A, Blumenfeld-Jones KC, Raharison SM, Tsaramanana RD, Razolliharisoa V, Tarnaud L (in press) Berenty Reserve: interactions between the diurnal lemur species and their gallery forest. In: Masters JC, Gamba M, Génin F (eds) Leaping ahead: advances in prosimian biology. Springer, New York
- Rasoloarison RM, Goodman SM, Ganzhorn JU (2000) Taxonomic revision of mouse lemurs (*Microcebus*) in the western portions of Madagascar. *Int J Primatol* 21:963–1019
- Razafindramanana J, Jolly A, Rasamimanana HR (2008) Population dynamics and distribution of brown and ringtailed lemurs at Berenty Reserve, southeastern Madagascar. *Primate Eye* 96 (special issue):166
- Richard AF (1978) Behavioral variation: case study of a Malagasy lemur. Bucknell University Press, Lewisburg, PA
- Richard AF, Dewar RE, Schwartz M, Ratsirarson J (2000) Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. *J Hum Evol* 39:381–391
- Richard AF, Dewar RE, Schwartz M, Ratsirarson J (2002) Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). *J Zool Lond* 256:421–436
- Russell RJ (1977) The behavior, ecology, and environmental physiology of a nocturnal primate, *Lepilemur mustelinus* (Strepsirhini, Lemuriformes, Lepilemuridae). PhD thesis, Duke University, Durham, NC
- Simmen B, Hladik A, Ramasiarisoa PL, Iaconelli S, Hladik CM (1999) Taste discrimination in lemurs and other primates, and the relationships to distribution of plant allelochemicals in different habitats of Madagascar. In: Rakotosamimanana B, Rasamimanana HR, Ganzhorn JU, Goodman SM (eds) New directions in lemur studies. Kluwer Academic Press, Plenum Publishers, New York, pp 201–219
- Simmen B, Hladik A, Hladik CM, Ramasiarisoa PL (2003a) Occurrence of alkaloids and phenolics in Malagasy forests and responses by primates. In: Goodman SM, Benstead JM (eds) The natural history of Madagascar. University of Chicago Press, Chicago, pp 268–271
- Simmen B, Hladik A, Ramasiarisoa PL (2003b) Food intake and dietary overlap in native *Lemur catta* and *Propithecus verreauxi* and introduced *Eulemur fulvus* at Berenty, southern Madagascar. *Int J Primatol* 24:949–968
- Simmen B, Tarnaud L, Bayart F, Hladik A, Thiberge A-L, Jaspard S, Jeanson M, Marez A (2005) Richesse en métabolites secondaires des forêts de Mayotte et de Madagascar et incidence sur la consommation de feuillage chez deux espèces de lémurs (*Eulemur* spp.). *Rev Écol* 60:297–324
- Simmen B, Peronny S, Jeanson M, Hladik A, Marez A (2006a) Diet quality and taste perception of plant secondary metabolites by *Lemur catta*. In: Jolly A, Sussman RW, Koyama N, Rasamimanana HR (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 160–183
- Simmen B, Sautther ML, Soma T, Rasamimanana HR, Sussman RW, Jolly A, Tarnaud L, Hladik A (2006b) Plant species fed on by *Lemur catta* in gallery forests of the southern domain of

- Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana HR (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 55–68
- Simmen B, Bayart F, Rasamimanana HR, Zahariev A, Blanc S, Pasquet P (2010) Total energy expenditure and body composition in two free-living sympatric lemurs. PLoS One 5:e9860. doi:[10.1371/journal.pone.0009860](https://doi.org/10.1371/journal.pone.0009860)
- Soma T (2006) Tradition and novelty: *Lemur catta* feeding strategy on introduced tree species at Berenty Reserve. In: Jolly A, Sussman RW, Koyama N, Rasamimanana HR (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 141–159
- Soma T (in press) The cause of alopecia? The difference of feeding ecology of two ring-tailed lemurs in relation to introduced plant species. In: Masters JC, Gamba M, Génin F (eds) Leaping ahead: advances in prosimian biology. Springer, New York
- Soma T, Ichino S, Koyama N, Jolly A (2008) The influence of toxic *Leucaena leucocephala* on the demography of ring-tailed lemurs, *Lemur catta*, at Berenty Reserve, Madagascar. Primate Eye 96 (special issue):195–196
- Soulé ME, Wilcox BA (1980) Conservation biology: an evolutionary-ecological perspective. Sinauer, Sunderland, MA
- Sussman RW (1974) Ecological distinctions in sympatric species of *Lemur*. In: Martin RD, Doyle GA, Walker AC (eds) Prosimian biology. Duckworth, London, pp 75–108
- Sussman RW, Garber PA (2004) Rethinking sociality: cooperation and aggression among primates. In: Sussman RW, Chapman AR (eds) The origins and nature of sociality. Aldine de Gruyter, New York, pp 161–190
- Sussman RW, Andrianasolondraibe O, Soma T, Ichino S (2003) Social behavior and aggression among ringtailed lemurs. Folia Primatol 74:168–172
- Sussman RW, Richard AF, Ratsirarson J, Sauther ML, Brockman DK, Gould L, Lawler R, Cuozzo FP, Mahafaly B (2011) Special reserve: long-term research on lemurs in Southwestern Madagascar. In: Kappeler PM (ed) Long-term field studies of primates. Springer, Heidelberg
- Takahata Y, Kawamoto Y, Hirai H, Miyamoto N, Koyama N, Kitaoka S, Suzuki H (1998) Ticks found among the wild ringtailed lemurs at Berenty Reserve, Madagascar. Afr Stud Monogr 19:217–222
- Takahata Y, Koyama N, Miyamoto N, Okamoto M (2001) Daytime deliveries observed for the ring-tailed lemurs of the Berenty Reserve, Madagascar. Primates 42:267–271
- Takahata Y, Koyama N, Ichino S, Miyamoto N (2005) Inter- and within-troop competition of female ring-tailed lemurs: a preliminary report. Afr Stud Monogr 26:1–14
- Takahata Y, Koyama N, Ichino S, Miyamoto N, Nakamichi M (2006) Influence of group size on reproductive success of female ring-tailed lemurs: distinguishing between IGFC and PFC hypotheses. Primates 47:383–387
- Tanaka M (2007) Habitat use and social structure of a brown lemur hybrid population in the Berenty Reserve, Madagascar. Am J Primatol 69:1189–1194
- Wright PC (1999) Lemur traits and Madagascar ecology: coping with an island environment. Yearbk Phys Anthropol 42:31–72