Chapter 3
Beza Mahafaly Special Reserve: Long-Term Research on Lemurs in Southwestern Madagascar

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Abstract The Beza Mahafaly Project in southwestern Madagascar was founded in 1975. It was established as a collaborative effort among the University of Madagascar (now University of Antananarivo), Washington University, Yale University, and the local communities for long-term training and research, biodiversity

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conservation, and socioeconomic development. Beza Mahafaly consists of two noncontiguous forest parcels separated by 10 km that became a protected area (Réserve Spéciale) in 1986: an 80-ha gallery forest and a 520-ha xerophytic spiny forest. The region has a diversity of habitats and a very diverse and highly endemic flora and fauna, including four species of lemurs found in or near the reserve. The ringtailed lemur (*Lemur catta*) and Verreaux's sifaka (*Propithecus verreauxi*) have been the subject of our long-term research. In this chapter we highlight some of the results of this research. Our multidisciplinary studies illustrate the feasibility of collecting long-term data on careers of individual animals and of obtaining large samples on numerous animals, across numerous social groups, in relatively isolated breeding populations. Thus, we can provide insights into many of the demographic, socioecological, anthropogenic, and epidemiological factors that shape the local ringtailed lemur and sifaka population. Here we summarize how ringtailed lemur demographic structure is affected by climatic perturbations (drought); how aspects of general health (parasite loads and dental health) are directly related to habitat, dietary, and anthropogenic factors; how tight birth seasonality in sifaka can elicit stress responses in males associated with increased male aggression, group takeovers, and infanticide risk; how life history schedules are related to evolutionary responses to extreme climatic fluctuations; and how directional selection among sifaka males leads to longer, stronger legs, but not to increase in male body mass relative to females.

3.1 The Beza Mahafaly Reserve

3.1.1 History of the Reserve

In the mid-1970s, R.W. Sussman received a phone call from Edward Steele of the Defenders of Wildlife (DOW) asking: "What can we do to save Madagascar's wildlife?" Steele (1975) had recently returned from Madagascar and had fallen in love with the country. Sussman, along with Alison Richard, then at Yale University, and Guy Ramanantsoa, then the Head of the Forestry Department of the School of Agronomy at the University of Madagascar (Ecole Supérieure des Sciences Agronomiques, ESSA/Forêts), had been discussing establishing a unique type of reserve in Madagascar. They envisaged a protected area for long-term research on biodiversity and conservation, but also to be used as a training and research center and springboard for socioeconomic development for local villagers.

Sussman explained this vision to Steele, who set up a meeting of DOW board members with Richard and Sussman. The board was impressed with the proposal. However, DOW worked mainly on litigation within the United States. Therefore, Richard Pough, a board member also on the Board of Directors of World Wildlife Fund, volunteered to present our ideas to WWF, which agreed to fund the project. In 1975, Ramanantsoa, with his collaborator the late Pothin Rakotomanga, set out to survey southwestern Madagascar, looking for a relatively accessible, undisturbed area with a representative faunal and floristic diversity. Another criterion was that local villagers agree to the project. He met the President of the Firaisana (Commune) of Beavoha, who proposed Anala Sakamena (forest bordering the Sakamena river) as this site. The site was named "Beza Mahafaly" in recognition of the commune President, who came from the village Beza Mahafaly, 8 km from the Reserve.

Local villagers were conscious of the vital importance of preserving this habitat and were enthusiastic about the project. In July 1978, the advisory committee of the local community agreed to grant two noncontiguous parcels of forest to the School of Agronomy. Thus, ESSA/Forêts began collaborative work with local communities, Yale and Washington Universities, as well as other national and international partners, to establish the Beza Mahafaly Reserve. Between 1978 and 1985, with funding mainly from WWF, reserve boundaries were demarcated, basic facilities were constructed, local guards were recruited and trained, and a field ecology school was developed for students from ESSA/Forêts.

On June 4, 1986, Beza Mahafaly was inaugurated as a Réserve Spéciale (Beza Mahafaly Special Reserve; BMSR) by government decree No. 86–168. Biodiversity research, especially on lemurs, had already begun and has continued to this day. Integration of conservation and development in villages surrounding the reserve, an integral component of the plan since the project's conception, continued, with increasing support from WWF and the U.S. Agency for International Development (USAID). In a coordinated effort with the local people, including their input and requests for assistance, community projects were begun to improve the production and marketing of crops (irrigation projects and road construction), education (construction of a local school), and health (water well construction). Students and faculty from ESSA/Forêts with local residents played an important role in the development of these activities, in partnership with Yale and Washington University.

In 1989, WWF took over management of the reserve, and in November 1995, ESSA/Forêts became the principal administrator. Research, training, and education programs as well as local development projects have continued to flourish. The site has hosted a multidisciplinary field course for fifth-year ESSA/Forêts students since 1986 (Ratsirarson 2003). Since 1994, additional support has been received from a large number of sources (see Acknowledgments).

In 2005, the management of the Reserve was transferred to Madagascar National Parks (MNP), like all protected areas in Madagascar. The School of Agronomy became the principal partner in research and training. ESSA's activities address the Reserve's management and development plan needs, and research specifically follows the annual work plan agreed by both parties (ESSA and MNP). The main objectives of the reserve continue to be long-term biodiversity monitoring and research on community ecology and conservation biology, long-term research on the lemur populations, education at the local, national, and international level and integrated research in the social and natural sciences with the goal of improving the lives of local communities while conserving the biodiversity in surrounding habitats. The main specific goals of our long-term lemur research are to provide a better understanding of behavioral ecology, demography, population genetics, reproductive biology, health status, and mating and life history strategies. Success at achieving these goals depends on, and results from, the connection between research and local development.

3.1.2 Physical Description of the Reserve

The reserve is located in southern Madagascar, 35 km to the northeast of the town of Betioky-Sud at 23°41′60″S and 44°32′20″E. Southern Madagascar is characterized by a long dry season and short wet season. During a non-drought, non-cyclone year, annual rainfall is about 700 mm, of which 600 mm falls during the austral summer between November and March. The Sakamena River is dry during the long dry season. Annual daily maximum temperatures average 25°C. Averages for wet season are high ambient temperatures (32°C), and daily maxima reach 46°C. Temperatures during the coolest months (July–August) usually range between 20°C and 30°C during the day, but can fall to 2°C at night (Sussman and Rakotozafy 1994; Ratsirarson 2003).

The reserve consists of two noncontiguous parcels separated by 10 km (Fig. 3.1). Parcel 1 is characterized by a gallery forest dominated by *Tamarindus indica*. It covers 80 ha of fenced and protected forest located on the banks of the Sakamena River, and is relatively flat with a slightly elevated plateau starting at the banks of the river (Fig. 3.2). The gallery forest is divided by marked transects whose paths intersect to form squares of 100 × 100 m. This parcel has been enclosed by barbed wire fence since 1979. Before this it was exposed to cattle and goats and used by the local people for various resources, as is the surrounding forest currently. Parcel 1 is surrounded by similar but unprotected and somewhat degraded gallery forest on the north and south. To the east is the Sakamena River and to the west is contiguous dry forest. The parcel is bounded on the south by the dirt road that runs from Betioky to the reserve and on to the small village of Analafaly 2 km east. The campsite and reception center is just south of the road. The infrastructure includes two wooden houses, a museum, an office building, a large open gazebo for courses and meetings, camping space, as well as solar energy and a water well.

Parcel 2 is a 520-ha area of xerophytic forest dominated by species adapted for the long dry season (Ratsirarson 2003, 2008). This parcel is often referred to as spiny forest. Between the two noncontiguous parcels, the vegetation transitional between the gallery and the xerophytic habitats is more degraded than the reserve, because it is used for grazing and for the collection of various forest products for food, medicines, building, etc.

3.1.3 Flora of Beza Mahafaly

The forest represented in Parcel 1 is western Malagasy dry deciduous forest (White 1983). It has an average of 369 trees of $\geq$2.5 cm DBH/1,000 m^2 (Sussman and

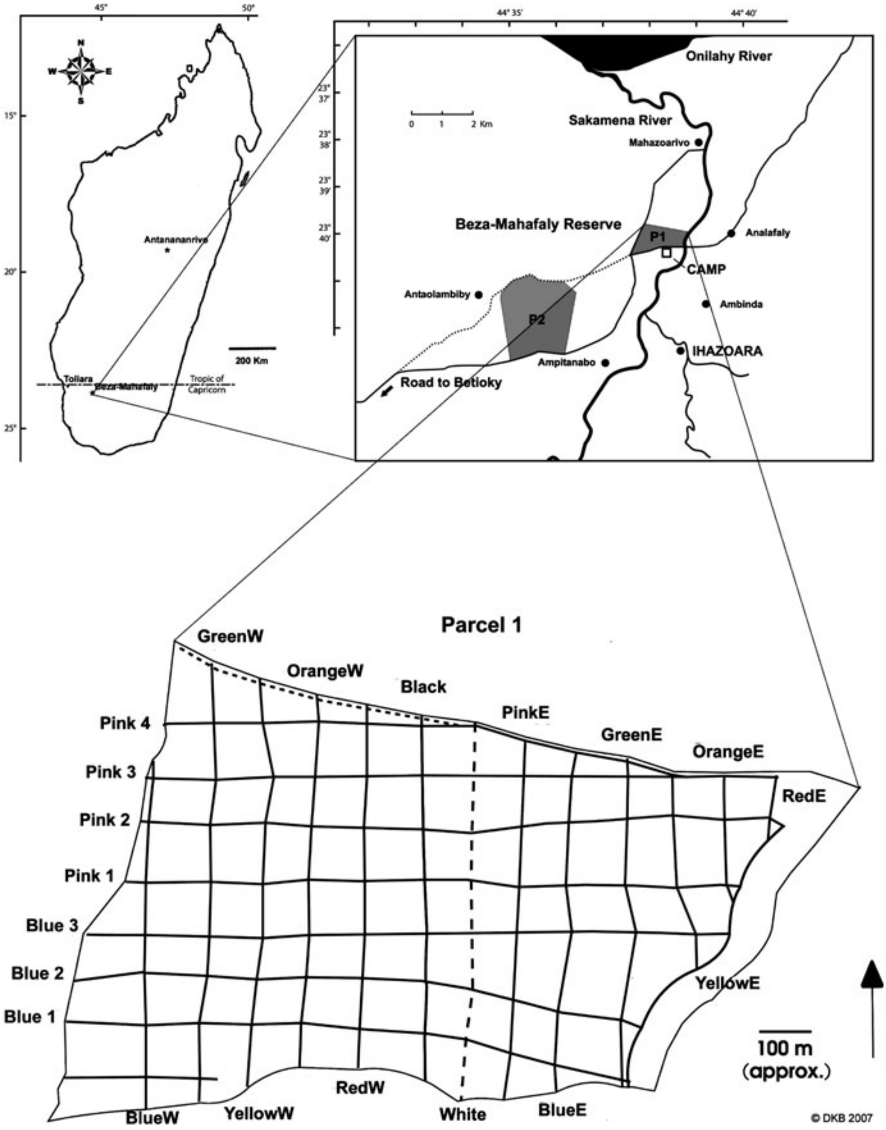

Fig. 3.1 Map of the Beza Mahafaly Special Reserve showing both parcels and marked path system in Parcel # 1 (provided by D. Brockman)

Rakotozafy 1994), which is typical of dry forests in Africa and the Neotropics (Gentry 1993). A soil moisture gradient exists, with soils becoming dryer farther from the river. Overall tree density does not decline with distance from the river, but the density of larger trees does; a uniformly closed upper canopy occurs on wet soil, but this grades into denser bush on dryer soil, where distinctions between the

Fig. 3.2 Aerial photograph of Parcel # 1 to the right of the dry Sakamena River. Photo taken from Northeast of the reserve

canopy strata are obscured and forest gradually passes into thicket. Tree height and diameter decrease progressively with increasing distance from the river (Ratsirarson 2003). On wet soils, the upper strata form a closed canopy, mostly uniform in height (15–20 m). Members of the upper stratum are species whose trunks generally exceed 25 cm DBH and may attain 50 cm or more, especially on wet soils. However, the average height of trees in Parcel 1 is 6.33 m, with an average diameter of 7.93 cm (Ratsirarson et al. 2001). *T. indica* is the dominant tree species. Other common canopy species are *Acacia rovumae*, *Euphorbia tirucalli*, and *Salvadora augustifolia*. In general, those species found in both microhabitats are not distributed equally between them. Five of the most common species are found mainly on wet soils and eight mainly on dry. Parcel 2 contains desert-like vegetation dominated by *Alluaudia procera*, *Cedrelopsis grevei*, *Commiphora* spp., and *Euphorbia* spp. (Ratsirarson 2003, 2008). Average height of trees is 4.5 m, with an average diameter of 6.5 cm (Ratsirarson et al. 2001). This forest has been the subject of fewer studies than the gallery forest.

Twelve permanent transects, each 1,000 m × 10 m, have been set inside and outside the two parcels to continuously monitor the density and distribution of plant species. All trees of $\geq$3 cm diameters were identified, tagged and their diameter as well as height measured. Overall, the flora of BMSR contains approximately 120 species and 49 families (Ratsirarson 2003). However, half the families are represented by a sole species. Euphorbiaceae and Mimosaceae are the most species-rich. A local reference herbarium and the Beza Mahafaly Osteological Collection are currently housed at the onsite Museum.

3.1.4 Fauna of Beza Mahafaly

There are four species of lemur at BMSR, two of them diurnal (Verreaux's sifaka, *Propithecus verreauxi*, and ringtailed lemurs, *Lemur catta*), and two nocturnal species (the white-footed sportive lemur, *Lepilemur leucopus*, and the grey-and-red mouse lemur, *Microcebus griseorufus*). We initially thought there were more species of *Microcebus*. However, recent genetic analysis revealed only one species with three color morphs (Heckman et al. 2006).

Three introduced carnivores (the domestic dog, *Canis lupus familiaris*, the small Indian civet, *Viverricula indica*, and the invasive wildcat, *Felis silvestris*) occur in the reserve (Brockman et al. 2008). The wildcat is semi-arboreal and distinguished from domestic cats by its large, pronounced ear lobes (Ratsirarson et al. 2001), brown and gray tabby pattern, larger size, and substantial sexual dimorphism (Brockman et al. 2008). Ratsirarson et al. (2001) saw an adult *Felis* carrying an infant ringtailed lemur in its mouth. The one endemic carnivore, the fossa, *Cryptoprocta ferox*, had not been directly observed in the reserve since 1993 (Brockman et al. 2008), but a camera trap image of a fossa moving through the reserve in 2008 and other recent observations confirm that it still exists in the area (Sauther et al. unpublished data). For a list of other mammalian species found in the Reserve, see Ratsirarson et al. (2001), Ratsirarson (2003), and Sussman and Ratsirarson (2006).

One hundred and two species of birds representing 43 families have been observed at Beza Mahafaly. Over half of the families are represented by only one species (Ratsirarson et al. 2001). The Reserve is home to at least 15 species of snakes, 17 species of lizards, one species of tortoise and fresh water turtle, and one species of crocodile; there are three species of amphibians. There also is a notable diversity of insects (Ratsirarson 2003).

3.1.5 Collection and Management of Long-Term Data

The long-term research focuses especially on the socioecology, population demography, life history, reproductive biology, mating behavior, socioendocrinology, feeding and nutritional ecology, population genetics, and health status of the diurnal lemurs (Fig. 3.3a, b). It also includes work on the conservation biology of other elements of the fauna and of the flora, monitoring of plant phenology, and research on the socioeconomics of the human population in relation to economic stability, development, and conservation. We maintain the education and training component of the reserve locally, regionally, and internationally. Each component of the project requires different strategies for data collection and management.

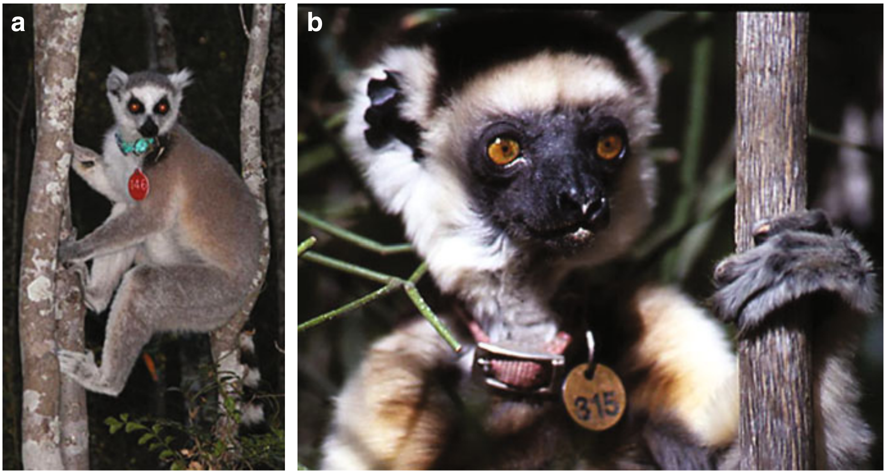

Fig. 3.3 (**a**) Collared ringtailed lemur (*Lemur catta*; photo © M. Sauther); (**b**) collared Verreauxi's sifaka (*Propithecus verreauxi*; photo © D. Brockman)

3.1.6 Future Plans for the Reserve

Beza Mahafaly Reserve was included among the sites of implementation of President Ravalomanana's "Durban vision" declared in 2003, where he set the goal of extending Madagascar's protected areas from 1.7 to 6 million ha, which is 10% of the national territory. BMSR's surface area was to increase from 500 to 4,600 ha. The two Parcels would be united into one protected zone, which would ensure better conservation of the region. Zones for controlled human utilization have been established around the protected zone in response to the needs of neighboring communities. Use of resources for commercial purposes is prohibited. However, strictly controlled harvesting of ligneous and non-ligneous products (honey, medicinal plants, wood for building, pastureland) is allowed. The right to utilize paths and trails located outside the protected zone is granted to inhabitants and livestock.

3.2 Socioecology of the Diurnal Lemurs

Two vital aspects of long-term data collection and management of socioecological information are: (1) Permanent identification of individual animals and regular censusing of these populations to document life history parameters and facilitate recensusing. Most adult ringtailed lemurs, all adult sifaka, and ~90% of all sifaka at least 1 year old are tranquilized and given color-coded collars or other marks that allow individual recognition and facilitate repeated censuses. Collection of these baseline data allows accumulation of data on known individuals and groups on topics including diet and nutrition, general and dental health status, and stress responses to demographic perturbations both inside and outside the reserve (Sussman and Ratsirarson 2006). (2) Obtaining baseline data on the flora within and surrounding the reserve. Using vegetation analysis and satellite images from BMSR as a baseline, we have estimated characteristics of vegetation cover and ringtailed lemur population density throughout this species' entire geographical range (Sussman et al. 2003, 2006). The relationship of population structure to habitat thus can be measured, as can changes over time under various conditions.

In the following, we provide some specific strategies for data collection and management in relationship to ringtailed lemur and sifaka socioecology. For more detailed information on phenological monitoring and vegetation analysis, see Sussman and Rakotozafy (1994) and Ratsirarson (2003, 2008). We also have collected data on the socioeconomy of the human population surrounding the Reserve (see Ratsirarson et al. 2001), but will not discuss these.

3.2.1 Collection and Management of Long-Term Data for Individual Identification and Population Censuses of Ringtailed Lemurs

Between June 1987 and February 1988, nine groups of *L. catta* were censused, 85 of the 88 adults in the groups were given collars for individual identification, and monitoring of the groups was initiated (Sussman 1991). This included all groups that ranged mainly in the 80-ha fenced portion of Parcel 1 and one group adjacent to it. In November, the groups were recensused and 155 individuals were identified, including infants and juveniles. Collaring of three of the groups was renewed between 2001 and 2004 (Gould et al. 2003, 2005). As of 2008, 218 individuals in nine groups had been collared; this represented virtually all of the approximately 225 individuals in the study area, which in 2003 was expanded to include 9 km^2 of fragmented forest south and west of the reserve (Cuozzo and Sauther 2006; Sauther et al. 2006). Beginning in May 2003, captured animals also received a subcutaneous microchip (PIT tag). The size and composition of these groups is monitored monthly, with new individuals captured and collared yearly (Sauther et al. 2006). Census data and data on individual identification have been computerized since 2003. Mean group size is 11.5 individuals, with a range of 3–21. Home ranges of 8–9 groups have a mean area of 25 ha and overlap extensively.

While animals are tranquilized, researchers collect systematic data on body mass, reproductive state, general physical condition, internal body temperature, ectoparasites, and dental condition. Body measurements, hair samples, and dental casts also are collected. Beginning in 2003, blood samples have been collected for white blood cell counts and measurement of packed cell volumes. Hair and blood samples also allow disease screening, isotope studies, and extraction of DNA for analyses of kinship and genealogical reconstruction. Data are recorded into the project's database on Excel. Initially, age grades were established through a combination of body weights, canine eruption patterns, general tooth wear, nipple length for females, and presence or absence of testes in males (Sauther et al. 2002). Since 2003, actual ages are known for most animals.

3.2.2 Collection and Management of Sifaka Long-Term Data

The ecology, life history, social behavior, reproductive biology, and population genetics of the sifaka population at BMSR have been studied continuously by Richard and colleagues since 1984, focusing on populations residing in, and adjacent to, Parcel 1. From 1984 to 2009, 718 individuals residing in 50–55 social groups have been captured, measured, and marked. The sifaka study population currently comprises ~280 marked and habituated individuals residing in 38 core social groups. Mean group size is 5–6 individuals, with a range of 2–16. The 38 social groups have 4–6 ha, overlapping home ranges within the boundaries of Parcel 1 (Richard et al. 1991, 2002; Lawler et al. 2009).

Individuals are immobilized using Telazol delivered from a Telinject blowgun dart (Richard et al. 2002). During the subsequent ~90-min processing period, individuals are marked and data similar to those on ringtailed lemurs are collected (see above). Data are recorded on individual capture sheets. At the end of the annual capture season, data sheets are copied and sent to Marion Schwartz, BMSR Sifaka Database Manager, who enters the capture, census, and morphological data into the sifaka database. During processing, each individual is given an identification collar and individuals are also ear-notched using a binary system that duplicates the tag number. Captures of unmarked juveniles born the previous year and of new immigrants typically occur during the austral July–August birth season, but birth season captures do not include likely pregnant females and those with dependent young. Initially, individuals were assigned to 1 of 5 age classes based on tooth wear, with the age classes calibrated from recaptures of individuals of known age (Richard et al. 1991). Today, the exact ages of most animals are known because they were born into the population.

Censuses were carried out annually between 1984 and 1991 and have been done at monthly intervals since, yielding an unparalleled computerized dataset. Also, life history data (age at first reproduction, fertility, longevity, etc.) derived from the Sifaka Database have been incorporated into the Primate Life History Database starting in 2007 (PLHD, Strier et al. 2010; http://demo.plhdb.org) to facilitate comparative analyses of species-specific mortality and fertility schedules in seven primate taxa and to test specific hypotheses about life history evolution (e.g. Morris et al. 2011).

3.3 Research Highlights

3.3.1 Ringtailed Lemurs

3.3.1.1 Demography and Life Histories

Long-term census data allowed us to determine who survived during a 2-year drought in 1991–1992, which deaths could be directly attributed to the drought, and how the population recovered (Gould et al. 1999, 2003). During this period, approximately half of the adult females died and 80% of the infants died in the second year of the drought. The population declined considerably up to 1994, 2 years after the drought ended. However, by 1997 it was recovering well. Annual reproduction, early sexual maturity, high birth rates, and dietary adaptability likely contributed to the population recovery.

Tracking which males disperse into which groups every year from the beginning of the project has contributed greatly to the analysis of patterns of male affiliative behavior (Sussman 1992; Gould 1997a,b) and has allowed us to assess migration status and to understand the strategies that males of different ages use to disperse successfully between groups (Gould 2006). Furthermore, the hormonal correlates of mating and post-mating behavior in adult males were investigated (Gould et al. 2005; Gould and Ziegler 2007). By knowing relative ages and which groups the older males had resided in over the previous years, Gould has determined how male tenure and the number of males in a group affect physiological stress levels, and how rank, tenure, and age affect testosterone levels and rates of aggression.

For example, results obtained from mating and post-mating seasons were compared to test Wingfield et al.'s (1990) "challenge hypothesis,", which predicts a strong positive relationship between male testosterone levels and investment in male–male competition for access to receptive females during the breeding season. Fecal testosterone (fT) levels and rates of intermale aggression were significantly higher during mating season compared to the post-mating period. Mean fT levels and aggression rates were higher in the first half of the mating season compared with the second half. The number of males in a group affected rates of intermale agonism, but not mean fT levels. The highest-ranking males exhibited higher mean fT levels than did lower-ranking males, and young males exhibited lower fT levels than prime-aged and old males. In the post-mating period, mean male fT levels did not differ between groups, nor were there rank or age effects. Thus, although male testosterone levels rose in relation to mating and heightened male–male aggression, fT levels fell to baseline breeding levels shortly after the early mating period, and to baseline non-breeding levels immediately after mating season had ended, offsetting the high cost of maintaining both high testosterone and high levels of male–male aggression in the early breeding period.

3.3.1.2 Effects of Habitat Fragmentation on Ringtailed Lemur Biology and Ecology

In 2003, Sauther and Cuozzo established the Beza Mahafaly Lemur Biology Project. This synergistic research program involves collaborative ties with zoos, toxicologists, virologists, and veterinarians and uses a broad perspective and a wide range of interdisciplinary approaches to study the effects of environmental change (both natural and human-induced) on lemur biology.

Health and disease ecology. Long-term monitoring of health parameters among ringtailed lemurs has allowed us to establish baseline health data and then to perform yearly assessments of how the lemurs are affected by ongoing environmental change and human disturbance. For example, Rainwater (2009) examined lemur blood for signs of environmental toxins and documented exposure of ringtailed lemurs at BMSR to multiple organochlorine pesticides and metals. The large number of captures has also allowed us to document a range of morphological variants within a natural population, including female virilization, microtia, and dental variants such as supernumerary teeth, maxillary incisor agenesis, and severe malocclusion. Such data are important for understanding natural variation in wild populations and provide a critical first step for assessing whether habitat change is creating abnormal patterns (Sauther and Cuozzo 2008).

Data on ringtailed lemurs show that habitat disturbance can have important effects on health in wild primates. For example, more degraded habitats are linked to lower body weights, reduced body fat, a higher incidence of tooth damage, and smaller body size (Sauther et al. 2006). Female dominance and residence patterns add complexity because males and females experience different pressures that result in differences in health and trauma (Sauther et al. 2006). For example, as males migrate from their natal groups, they often enter groups in which they lack established social relationships. The result can be reduced allogrooming, which can lead to serious health issues, including a higher incidence of parasite infestation, skin lesions, and hair loss (Sauther et al. 2006).

Long-term parasitological monitoring of the diurnal lemur species (Loudon et al. 2006; Loudon 2009) is revealing how socioecological variation interacts with anthropogenic change to affect the types and prevalence of parasites in each, and indicates that local domestic animals such as dogs and cattle may be transmitting parasites. Sifaka and ringtailed lemurs live in both intact and altered habitats, but ringtailed lemurs exhibit more nematodes and protistan parasites. Differences in each primate's parasite profile appear to be linked to host behavior and the ecological distribution of parasites. Ringtailed lemurs spend much more time on the ground than the sifaka and terrestrial substrate use provides greater opportunities for soil-transmitted parasites to acquire hosts. Ringtailed lemurs using the anthropogenically disturbed forests surrounding the reserve also harbor novel parasites that they may be acquiring via coprophagy or via physical contact.

Dental ecology. One of the most important health findings resulting from long-term research on ringtailed lemurs at BMSR is that severe tooth wear and loss is common. Sauther et al. (2002) initiated a systematic study of this phenomenon, which had been noted upon the initial examination of ringtailed lemurs in 1987/1988. Since then, they have documented exceptionally high frequencies of severe wear and antemortem tooth loss (greater than 20% of the population), largely due to processing the mechanically challenging fruit of the tamarind tree (*Tamarindus indica*), the dominant food and the essential fallback resource of ringtailed lemurs (Sauther and Cuozzo 2009). Severe tooth wear and tooth loss is more common in areas of degraded habitat, and, in some cases, is linked to exploitation of introduced foods (Sauther and Cuozzo 2009).

The ringtailed lemurs respond to decreases in food processing ability due to tooth loss and dental wear by changing their activity patterns and feeding behavior. For example, individuals who have lost teeth spend more time feeding and foraging throughout the day than individuals who are not dentally impaired, and in particular they forage more during early afternoon when other lemurs are resting. They also spend more time licking tamarind fruit to soften it before ingestion (Cuozzo and Sauther 2004, 2006; Millette et al. 2009).

Isotope ecology. Assessing stable isotope values has proven fruitful for understanding the ecology and habitat of living and fossil primates (e.g, Sponheimer et al. 2009). More specifically, stable isotopes have often been used to reconstruct the ecology of Madagascar's now-extinct "giant" lemurs (e.g., Crowley et al. 2011). Until recently, isotopic analyses of extinct lemur ecology have not been based on data from living lemur populations. Our comparative data from the BMSR ringtailed lemur population as well as from other sites are now providing points of comparison for interpreting the ecology of Madagascar's extinct lemurs. For example, Loudon et al. (2007) found that C_{13} and N_{13} signatures of ringtailed lemurs with poor dental health differ from other members of the population, possibly reflecting dietary changes resulting from severe wear and tooth loss, and that the C_{13} and N_{13} signatures of immigrant males differ from those in their original troops and resemble more closely those in their new groups, which exploit different resources. Also, comparisons between the ringtailed lemurs at two sites (Beza Mahafaly and Tsimanampesotse) reveal habitat-related differences in isotopic signatures. These data also have implications for the conservation biology of extant lemur species and as a tool for understanding changing environments in Madagascar.

3.3.2 Verreaux's Sifaka

3.3.2.1 Sifaka Behavioral Endocrinology

Brockman and colleagues have used a combination of endocrine data (derived from analysis of fecal steroids) and behavioral data to examine the impact of physical and social environments on reproduction and mating, social strategies, male life history, and demography in Verreaux's sifaka (Brockman 1994, 1999; Brockman and Whitten 1996; Brockman et al. 1998, 2001, 2009).

Brockman found that females have flexible mating strategies and that both sexes exercise mate choice, with the opportunity to do so enhanced by estrous synchrony within groups. She also documented intense androgen-mediated mating competition in both sexes; coercive mating tactics by males; and situation-dependent receptivity in which anovulatory females mate with immigrant males regardless of season (Brockman 1994, 1999; Brockman and Whitten 1996; Brockman et al. 1998).

Beginning in 1998, Brockman et al. (2001) used longitudinal data from individually marked sifaka to document age-specific patterns of male dispersal. They showed that males exhibit marked hormonal responses to socially disruptive events during the birth season, including substantially elevated fT concentrations in alpha males residing in unstable groups, in males making aggressive attempts to immigrate into neighboring groups, and in resident males evicting subordinates.

Previous studies examining fecal glucocorticoid (*fGC*) interactions with behavior in male sifaka at BMSR showed that high fGC levels are not a predictable cost of high rank during the birth season, and that elevated fGC concentrations coincide with specific behavioral traits and social contexts, including social instability (Brockman et al. 2001) and the aggressive eviction of subordinates by resident alpha males (Brockman et al. 1998). Using data on 124 males in 55 groups collected over several seasons, Brockman et al. (2009) found that fGC levels in males were unrelated to age, residence, group stability, or rank, but were substantially higher in males residing in groups containing infants than in those without infants. Also, annual variation in male fGC levels paralleled annual changes in infant birth rates (Brockman et al. 2009). These findings support the proposition that anticipation of relatively predictable future events, such as the birth of infants, can elicit GC responses. The entire birth season is probably a stressor, especially when births coincide with uncontrollable events such as increased intergroup male transfers and infanticides (ibid.). Of the five groups targeted for aggressive male transfers during this study, four suffered takeovers and three of those groups contained one or more infants which disappeared the following day or were mortally wounded by immigrant males. This research is the first to show that in seasonal plural breeding species, elevated fGC in males reflects specific events related to reproduction rather than states or social context during the birth season. These data provide new insights into the role of endocrine mechanisms in mediating male strategies to cope with natural sources of stress in wild lemur populations.

3.3.2.2 Sifaka Life History, Demography, and Population Genetics

Life history and demography. The combination of life history, demographic, phenotypic, and genetic datasets on the sifaka population provides powerful means to test major hypotheses in life history theory, to determine patterns of selection and adaptation, and to measure fitness. For example, Richard et al. (2000) documented how body mass influences female fertility by repeatedly capturing individual females and measuring changes in body mass over time, then combining this information with rainfall and other ecological data and data on reproduction. Male and female sifaka show seasonal fluctuations in body mass, which also is lower during drought years. When the primary productivity of the forest is low, body mass is particularly low. Females who were heavier during the previous mating season were significantly more likely than lighter females to give birth in the following birth season. Richard et al. (2000) showed specifically that (1) females lose more mass than males on a seasonal basis, (2) fertility is linked to body mass, and (3) gestation and lactation are uncorrelated with periods of high body mass. These findings suggest that sifaka females follow a strategy akin to "capital breeding," in which animals store energy for reproduction rather than immediately converting it into reproduction – that is, by decoupling energy acquisition and reproduction by storing energy to be used at a later, more adaptively advantageous time period (but see Brockman and van Schaik (2005) for a reassessment of this view).

Richard et al. (2002) also documented age-specific patterns of fertility, mortality, and dispersal. They showed that female sifaka reproduce later and live longer, in relation to body size, than females of any other primate species. The life history strategy associated with delayed reproduction and extended longevity is known as bet-hedging, where animals are selected to slow down the pace of reproduction and growth to mitigate the negative effects of stochastic fluctuations in the environment that influence animal livelihoods. Because climate determines food availability, Richard et al. (2002) argued that particular rainfall patterns in Madagascar were the main drivers of the life history schedules of Malagasy fauna, which (especially those of mammals) are characterized by extreme "fastness" or "slowness" as evolutionary responses to climatic fluctuations.

Subsequently, Dewar and Richard (2007) provided additional evidence that patterns of rainfall on Madagascar show uniquely high intra- and inter-annual variability compared to locales outside of Madagascar. The influence of rainfall on sifaka demography was modeled explicitly by Lawler et al. (2009). They showed that demographic parameters such as survival, reproductive value, and expected life span were depressed when annual rainfall was below 300 mm. Furthermore, a decrease in mean annual rainfall or an increase in the variance in annual rainfall resulted in negative population growth rates. These studies concur in finding that climate plays a key role in shaping both life history and demographic traits in the sifaka population.

Population genetics. Lawler et al. (2003) genotyped 444 sifaka to assess population structure and patterns of reproduction. The genetic structure of the population mimicked the dispersal and sex-ratio pattern first observed by Richard et al. (1991, 1993). Specifically, within social groups, both average and pair-wise genetic relatedness was higher for females than for males. This makes sense given that female sifaka are mostly philopatric, whereas males disperse from their natal groups on reaching sexual maturity (Richard et al. 1993; see also Kappeler and Fichtel 2011). This results in genetically distinct matrilines across social groups and creates a population more strongly structured through female lineages than male lineages. Similarly, offspring are more genetically distinct than adults across the population, because those in any given group can share the same father but have different mothers. Thus, offspring cohorts are united through paternal alleles within social groups, but across the population each cohort of offspring is genetically different.

However, as Richard et al. (1991, 2002) have documented, most of the infants that survive to 1 year are male (60–70% in most years studied). When males reach sexual maturity they disperse, somewhat randomly, into adjacent groups. At the genetic level, this randomizes the genetic structure of the offspring cohort and results in adults within social groups retaining less genetic structure than offspring. These results also show that the sex ratio, in addition to genetic relatedness, is an important factor with respect to the evolution of social behavior. For example, Richard et al. (2002) argued that the behavioral effects of a male-biased sex ratio include intense competition between females, heightened importance of female mate choice, and female social dominance.

Genetic data coupled with phenotypic and demographic data can elucidate reproductive strategies. Lawler et al. (2005) analyzed paternity and combined phenotypic data with information on reproductive success to measure the strength of intrasexual selection on male traits relevant to male–male competition during the mating season. They found that directional selection targets leg length and size, while stabilizing selection targets body mass. That is, males with longer, stronger legs, and an intermediate body size were more successful at reproduction. These results suggest that traits related to chasing are more important to male fitness than traits related directly to fighting involving physical contact (e.g., overall body size, canine size) and provide one possible explanation for the sexual monomorphism in body mass among male and female sifaka (Fig. 3.4). During male mating competition, there is no intrasexual directional selection acting to increase male body mass relative to that of females (see Lawler 2009).

Lawler (2007) also examined male reproductive success from a population-wide perspective. Specifically, he decomposed variation in male fitness (i.e., total reproductive output) into three components: reproductive lifespan, fertility (i.e. the per-year reproductive output), and infant survival. These components were estimated for males reproducing in their resident groups and those who reproduced outside of their resident groups. The results reveal that fertility makes the greatest contribution to variance in male fitness, followed by reproductive lifespan, and offspring survival. Factors that enhance opportunities for extra-group mating include female choice, a high density of social groups with overlapping home ranges, and a restricted mating season (Lawler 2007). Thus, long-term genetic studies provide a powerful complement to behavioral-ecological studies, since they can reveal the fitness consequences of particular behaviors that occur during an animal's lifetime.

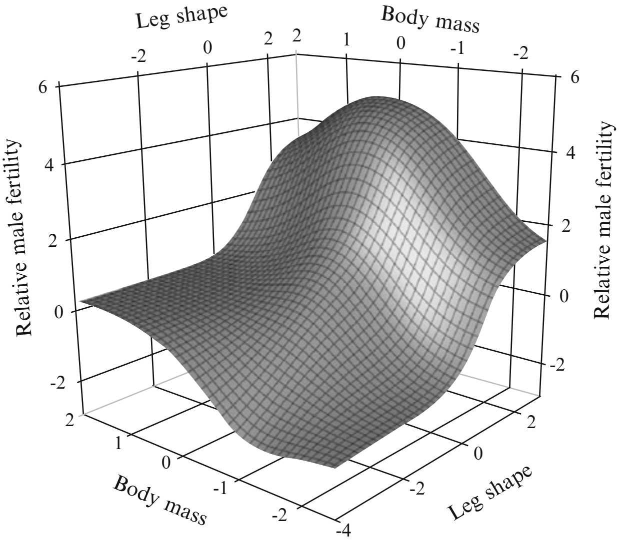

Fig. 3.4 Fitness surface showing relationship between male fertility and body mass and leg shape: Lawler et al. (2005) found that directional selection acts on leg length and thigh circumference, whereas stabilizing selection acts on body mass

3.4 Conclusions

Compared to other mammals, primates are characterized by delayed maturation, slow rates of growth, complex social behavior, and long lifespans. Because of these characteristics, many field studies of wild primates have traditionally focused on documenting behavioral interactions among one or a few individuals throughout their lives. This approach emphasizes the collection of longitudinal data on the careers of individuals rather than the collection of data on numerous individuals that comprise a population. The multidisciplinary studies of ringtailed lemurs and sifaka discussed above show that it is possible to obtain long-term data on careers of individual animals along with extensive data on many animals in multiple social groups and even on entire populations. These data have been, and continue to be, analyzed from various perspectives, thus providing important new insights into the demographic, socioecological, anthropogenic, and epidemiological factors that shape an evolving population.

The following are a few specific examples of research highlighting the benefits of long-term research at Beza Mahafaly:

1. Knowledge of the demographic structure of the ringtailed lemur population in the reserve over the long-term allowed us to determine the effects of a severe drought on the population and the factors that enabled the population to recover.

2. Research on hormone levels in ringtailed lemur males has revealed that male–male aggression and testosterone levels rise at the beginning of mating season. However, these levels fall to non-breeding baseline levels immediately after the early mating season, thus offsetting the high cost of stress related to high testosterone and high levels of aggression. Furthermore, fT levels are not affected by the number of males in a group, nor are there rank or age effects.
3. The parasite loads, types of parasites, and dental health of the ringtailed lemur and sifaka populations, both inside and out of the reserve, are affected directly by habitat structure, dietary differences, and amount and type of interaction with humans.
4. Female sifaka reproduce later and live longer, in relation to body size, than any other primate species, thus displaying a life history strategy in which the pace of reproduction and growth is slowed down to mitigate the negative effects of extreme fluctuations typical of southern Madagascar.
5. Male sifaka exhibit hormonal responses to socially disruptive events during the birth season, including marked fCG elevations in the presence of newborns associated with increased group takeovers and infanticide risk.
6. The combination of long-term genetic, phenotypic, and demographic studies allowed measurement of the strength of sexual selection in a wild primate. Specifically, sifaka males with longer, stronger legs were more successful at reproduction than were males with larger body mass, thus suggesting that traits related to chasing and locomotion were more important to male fitness than those related directly to fighting (e.g., body mass).

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[http://www.umass.edu/anthmorphometricslab/BezaMahafalyOsteoCollection.htm]. Finally, we thank Peter Kappeler, David Watts, and an anonymous reviewer for their excellent comments on this paper.

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