Chapter 4. Diurnal lemurs at Bezà Mahafaly: Resilience and risk

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Abstract

The Bezà Mahafaly Special Reserve in southwest Madagascar was established in 1986 in partnership with the local community, to protect forest and wildlife and serve as a center for training and research. The Bezà Mahafaly Monitoring Program began in 1995, with Monitoring Team members recruited from villages around the reserve. The team gathered data on climate and biodiversity, and on the demography, socio-economy, and views of the local community. The findings of the Monitoring Program and contributing research indicate four interacting sets of environmental pressures on endemic mammal populations: destruction and disturbance of the forest, climate fluctuations and directional change, hunting and collecting, and incursions by introduced or invasive species. This paper provides a qualitative description and assessment of these pressures, with a particular focus on the two diurnal lemur populations, *Lemur catta* and *Propithecus verreauxi*. Perturbations during the Holocene, documented at nearby Antaolambiby, demonstrate that these populations have been highly resilient during environmental change in the past. Today, population size in well-protected forest in the reserve remains about the same as 10-15 years ago. However, field observations and a range of demographic, morphological, and biological analyses indicate that *L. catta* and *P. verreauxi* will be at increasing risk of local or regional extinction without sustained conservation measures. Climate change may pose the greatest long-term risk, but the immediate pressures are clearer, and represent the greatest short- to medium-term risk to the survival of mammals at Bezà Mahafaly.

Key words: Ecological monitoring, lemurs, climate change, invasive species

Résumé détaillé

La Réserve Spéciale Bezà Mahafaly, localisée dans le Sud-ouest de Madagascar a été créée en 1986, dans le cadre d'un vaste effort national visant à arrêter la destruction du patrimoine naturel unique de l'île et développer le partenariat avec la communauté locale. Le Programme de suivi à Bezà Mahafaly a commencé en 1995, avec des membres de l'équipe de suivi recrutés dans les villages autour de la réserve. Différentes catégories de données complémentaires, comprenant le climat, la biodiversité, la démographie, les conditions socio-économiques locales, ainsi que les perceptions des communautés locales sur la conservation de la biodiversité locale ont été collectées. Les résultats du programme de suivi et des activités de recherche indiquent que quatre séries de facteurs environnementaux interagissent sur la dynamique des populations de mammifères endémiques pour les menaces et les pressions qu'ils occasionnent : la destruction et la perturbation de la forêt, la chasse et la collecte, les incursions par des espèces invasives, la variabilité climatique et le changement climatique à long terme.

La présente étude donne une description qualitative de l'évaluation des pressions des mammifères, avec un accent particulier sur les deux espèces de lémuriens diurnes, *Propithecus verreauxi* (*sifaka*) et *Lemur catta* (*maki*). Les perturbations au cours de l'Holocène, illustrées par des données issues des environs du site archéologique d'Antaolambiby, démontrent que ces deux espèces

Richard, A., Ratsirarson, J., Jaonarisoa, E., Mahereza, S., Youssouf Jacky, I. A., Sauther, M. & Fiorentino, I. 2016. Diurnal lemurs at Bezà Mahafaly: Resilience and risk, eds. J. Ranaivonasy, J. Ratsirarson & A. F. Richard. *Malagasy Nature*, 10: 37-49.

ont été très résilientes dans des conditions extrêmes de changement de l'environnement. Aujourd'hui, la taille de la population dans les forêts protégées à l'intérieur de la réserve n'a pas varié depuis 10 à 15 ans. Ceci se reflète par des taux de natalité et de survie très stables des jeunes *sifaka*, bien qu'étroitement liés à la disponibilité des ressources vitales, donc de la variabilité climatique.

Cependant, les observations sur le terrain et les analyses démographiques, morphologiques et écologiques indiquent que *L. catta* et *P. verreauxi* sont soumis à une augmentation croissante du risque d'extinction locale ou régionale. La déforestation reste la plus importante pression sur la survie des mammifères de Bezà Mahafaly. Toutefois, l'on ne peut négliger l'importance des impacts environnementaux du contact avec l'homme, qui se manifestent par l'augmentation de l'exposition aux parasites et pathologies, l'augmentation de la compétition pour la nourriture face aux espèces commensales à l'homme et la perturbation des habitats naturels par ces dernières. L'extension de la réserve de 600 ha à 4200 ha, officialisée en 2015, donne des perspectives encourageantes pour sauvegarder ou restaurer la connectivité des habitats de la population des mammifères à l'intérieur de la réserve. Le changement climatique constitue le risque majeur à long terme, mais à court et à moyen terme, les impacts directs et indirects de la population humaine croissante dans la région sont la plus grande menace sur la survie des mammifères à Bezà Mahafaly.

Mots clés : Suivi écologique, lémuriens, changement climatique, espèces envahissantes

Introduction

Madagascar is widely known for its rich biodiversity and intriguingly idiosyncratic patterns of endemism, and as a result, it is a magnet for ecologists and evolutionary biologists (Myers *et al*., 2000; Thalmann, 2006; Vences *et al*., 2009). At the same time, the degradation and destruction of this unique natural heritage are a focus of mounting concern and increasingly urgent action. The latter encompasses national legislative and policy initiatives to expand and improve the protection of natural habitats; local, community-based conservation efforts and co-management of natural communities; the documentation and monitoring of biodiversity; and a wide range of evolutionary, ecological, and behavioral research (Goodman, 2008; Scales, 2014).

The Bezà Mahafaly Special Reserve in southwest Madagascar was established in partnership with the local community in 1986. Its founding purposes were to conserve critical, unprotected habitat, and to be a place for training and research (Richard & Dewar, 2001). Initially, the reserve protected two areas together encompassing 600 ha of riverine, dry deciduous, and spiny forest that formed part of a much broader forest. In 2006, the local community supported expansion of the reserve to 4,200 ha, including the original fully protected areas, as well as surrounding forest set aside for co-management (Richard & Ratsirarson, 2013).

The Bezà Mahafaly Monitoring Program began in 1995, with the goal of learning more about the forest and wildlife and threats to their survival, and of contributing this information to decision-making about the conservation and management of the reserve. In practice, Monitoring Team members became de facto ambassadors to and from their villages, and their contribution to conservation efforts at Bezà Mahafaly has extended far beyond the original goal (Richard & Ratsirarson, 2013). Monitoring Team members were recruited from villages around the reserve. Under the leadership of the Département des Eaux et Forêts, Ecole Supérieure des Sciences Agronomiques, Université d'Antananarivo, the team gathered systematic data on climate, biodiversity, and the demography, socio-economy, and views of the local community. Ratsirarson *et al*. (2001) reported the initial results of their activities, coupled with the findings of visiting researchers and students.

Today, the cumulative findings of the Bezà Mahafaly Monitoring Program and contributing research indicate four distinct but interacting sets of environmental pressures on endemic mammalian populations in the Bezà Mahafaly landscape: 1) destruction, fragmentation, and disturbance of the forest (Ranaivonasy *et al*., 2016a); 2) climate fluctuations, with greater amplitude and frequency predicted for the future, as well as long-term directional change in temperature and rainfall (Rasamimanana, 2011, 2014; Rasamimanana *et al.*, 2012, 2016); 3) hunting and collecting (Rasoazanabary, 2011); and 4) incursions by introduced or endemic invasive species (Youssouf, 2004, 2010; Ratsirarson, 2005). A complete list of endemic and introduced mammals at Bezà Mahafaly can be found in Richard *et al*. (2016).

Destruction, fragmentation, and disturbance of the forest

The 600 ha encompassed by the original Bezà Mahafaly Special Reserve, particularly Parcel 1, have been largely protected since the late 1970s, but surrounding forests have been extensively degraded (Ranaivonasy *et al*., 2016a). Over the last decade, the human population has expanded markedly (Ranaivonasy *et al*., 2016b). Together, these trends have reduced available habitat, and increased levels of disturbance in the forest by people, their dogs, and livestock. Ever increasing contact between people and wildlife also augments opportunities for the transmission of parasites and disease (Loudon *et al*., 2006). Zoonosis, when a pathogen leaps from a nonhuman animal into a person and succeeds in establishing itself as an infectious presence, is recognized as a globally growing risk for human populations (Quammen, 2012). Disease and parasite transmission in areas of disturbance and human-wildlife interaction may also represent a risk for animal populations. Research by Loudon *et al*. (2006) at Bezà Mahafaly indicates the potential for transmission to occur *from* people *to* wildlife; in addition, recent studies of rodents in eastern forests of the island have explored parasite transmission between introduced and endemic species (Dietrich *et al*., 2014).

Climate fluctuations and long-term directional change

Climate models for Madagascar strongly predict a continuing rise in minimum and maximum temperatures, with the greatest projected warming in the southwest (Tadross *et al*., 2008). Congruence between rainfall forecasts is weaker, with clear projections only for the southeast that indicate drier conditions by 2050. The frequency of cyclones is expected to decline, whereas their intensity may increase (Tadross *et al*., 2008). Many plant species are predicted to undergo range expansion, but with little overlap between current and future distributions (Schatz *et al*., 2008, cited in Hannah *et al*., 2008). The Bezà Mahafaly Monitoring Program has documented the impact of climate fluctuations on the diurnal lemur populations over the past 20 years, and suggests that predicted changes in the distribution of vegetation together with the direct impact of changing climate conditions will have a significant, long-term influence on the distribution and survival of these and other wildlife populations.

Hunting and collecting

In the Ankazombalala Commune, where the Bezà Mahafaly Special Reserve is located, most people identify themselves as Mahafaly. The hunting of lemurs is *fady,* or forbidden, for the Mahafaly. Recent immigrants and travelers passing through the region do not necessarily share this prohibition, however, and villagers report occasional instances of opportunistic hunting of diurnal lemurs (Monitoring Team, personal communication). Small mammals are not protected by *fady*, and the larger spiny tenrecs, in particular, are vulnerable to harvesting for food.

Introduced and invasive species

Introduced mammal species present at Bezà Mahafaly with growing impact on endemic species include two carnivorans (*Canis lupus* and *Felis silvestris*), and a rodent (*Rattus rattus*). The Carnivora are known predators of primates. *Rattus rattus* is highly invasive, particularly in disturbed habitats (Hingston *et al*., 2005), a vector for disease (Wilkinson *et al*., 2014), and inferred to compete for resources with native rodents (Goodman, 1995).

The vine *Cynanchum mahafalense* offers an interesting exception to the usual association in plants of invasive characteristics with introduced species. Endemic to southern Madagascar, it has proved highly invasive and destructive of habitat in Parcel 1 of the reserve, with potential implications for forest regeneration and resource availability (Ratsirarson, 2005).

These four sets of pressures are experienced differently by different species, and over varying time scales. This paper focuses on their effects on the large diurnal lemurs, drawing upon the work of the Monitoring Team and researchers, and presents information on other species where available.

Diurnal lemurs

Scope of data

In collaboration with researchers, the Monitoring Team has collected life history data on large samples of individually identified *Propithecus verreauxi* and *Lemur catta* in and adjacent to the riverine and dry deciduous forest protected by Parcel 1 of the Bezà Mahafaly Special Reserve. This includes the field station used by project staff and researchers which was regularly visited by *L. catta*. These data document life history patterns, demographic trends and health profiles, and provide insight into the pressures and threats confronting these populations. Sussman *et al*. (2012) have recently summarized the history of these studies and related research.

The main study population of *P*. *verreauxi* consists of groups and solitary individuals whose ranges lie completely or partly inside Parcel 1 of the Bezà Mahafaly Special Reserve (Richard *et al*., 2002). *Propithecus verreauxi* occurs at very low density in the spiny forest in Parcel 2, and has not been systematically monitored.

From 1984-2012, 751 individuals in 61 social groups were captured, measured, collared, and released. *Propithecus verreauxi* is known occasionally to chase and attack people (Richard, 1978), and the lack of aggression by others when a group member is captured has been a perplexing feature of the capture program. We note here an episode in 2012, when an unmarked adult male chased and bit one member of the capture team (J. Ratsirarson & R. Lawler, personal observation). We have no explanation for this exceptional behavior.

Between 1984 and 1993, the study population was censused annually during the August field season. Kubzdela (1997) collected detailed census information from 1993-1995. Since 1995, members of the Monitoring Team have carried out censuses at monthly intervals. Today, the population includes over 200 collared animals in or adjacent to Parcel 1, the only individuals inside Parcel 1 without collars being new immigrants or animals less than 12 months old that have not yet been captured.

Census data were transferred to electronic files, and used to compile an annual census update. Census and capture data are available to researchers with permission of the primary contributors (Peabody Museum of Natural History, Yale University & Ecole Supérieure des Sciences Agronomiques, Université d'Antananarivo, 2013). Detailed information about the database and field collection methods can be found in Richard *et al*. (1991, 2002), and in the Sifaka Data Manual at http://peabody.yale.edu/collections/vertebrate-zoology/madagascar-lemur-sifaka-database.

Methods used in genetic and parasitological analyses have been summarized by Sussman *et al*. (2012) and further details can be found in Lawler *et al*. (2001, 2009) and Sauther *et al*. (2002, 2006). PDF copies of these publications are available at www.bezamahafaly.yale.edu.

Nine groups of *L*. *catta* that ranged principally within or directly adjacent to the gallery forest of Parcel 1 of the Bezà Mahafaly Special Reserve were studied intensively between June 1987 and February 1988, and 85 of the 88 adults in the groups were captured and given collars for individual identification (Sussman, 1991). Censuses were conducted at least once annually between 1987 and 1996. When research resumed in 2001, few of the original collared animals remained (Gould *et al*., 2003), and Gould *et al*. (2005) captured and collared individuals from three groups for a hormone study. Censuses were resumed in 2003, and all remaining adult and sub-adult individuals within the gallery forest and fragmented forests south and west of the reserve were captured and collared (Cuozzo & Sauther, 2006a; Sauther *et al*., 2006). From 2003-2012 an intensive study of *L*. *catta* was carried out, and 232 individuals from 10 groups in Parcel 1 and 18 individuals from two groups in Parcel 2 were captured, measured, collared, and given a subcutaneous microchip. The size and composition of groups in Parcel 1 was monitored monthly. Census information and data on individual identification have been computerized since 2003.

Impacts of environmental pressures

Headcounts provide a crude measure of standing lemur biomass. By this measure, the populations of both diurnal lemur species are in good health. The number of individuals at least two years old in the nine marked *Lemur catta* groups with home ranges partly or completely in Parcel 1 of the reserve is similar to that of a decade ago (90 in 2003, 83 in 2013), despite wide year-to-year fluctuations. In parallel, the number of marked individuals at least one year old in the 61 *Propithecus verreauxi* groups with home ranges inside Parcel 1 is close to that recorded 15 years ago (172 in 1998, 162 in 2013). Each population is exposed to significant environmental changes, however, and a primarily qualitative assessment of their potential impact is presented below.

Forest reduction, fragmentation, degradation, and disturbance

The substantial loss of forest cover outside the reserve since the 1970s (Ranaivonasy *et al*., 2016a) has surely led to a decline in total numbers of *Propithecus verreauxi* and *Lemur catta*, although it is not documented. Less certain is whether this loss has also reduced dispersal across the landscape to remaining forested areas. *Lemur catta* and *P*. *verreauxi* are known to travel considerable distances across open areas elsewhere in Madagascar, but this has not been observed at Bezà Mahafaly. Local community members reported a collared *P. verreauxi* on the outskirts of their village 8 km from the reserve, but the individual would not have had to traverse extensive open areas to reach the site. Collared *L. catta* have been sighted 12 km from the reserve, but this too would have involved travel through a fragmented but largely forested area.

Although landscape-wide monitoring of population trends are beyond the scope of the Monitoring Program, focused monitoring and research in and around the reserve provide insight into the impact of heightened levels of disturbance and forest degradation, and associated increases in contact between lemur populations and people.

Disturbance due to the activities or passage of people and livestock through the forest has a discernible impact. In a comparative study of *P. verreauxi* in Parcel 1 of the reserve and adjacent forest outside the reserve, J. Randrianarisoa (personal communication) found that animals in unprotected forest spent more than twice as much time engaged in vigilance behavior. Vigilance behavior inside the reserve was most commonly elicited by conspecifics and birds, whereas in unprotected forest, the cause was either unidentified by the observer or a result of cattle passing by in over 50% of cases, with only 18% attributable to conspecifics and birds. Fertility and survival through the first year may also be lower in groups in unprotected forest.

Observations of the small, nocturnal primate *Microcebus griseorufus* provide additional evidence of the effects of disturbance. Rasoazanabary (2011) reported that *M. griseorufus* typically moves when disturbed and may be at greater risk of diurnal predation, particularly when individuals must move dependent young. Fish (2014) encountered *M. griseorufus* more frequently outside than inside Parcel 1 after midnight, although encounter rates were similar up to that time. Rasoazanabary's (2011) capture-recapture data suggested that *M. griseorufus* living in unprotected forest had shorter life spans than those in protected forest, with significantly lower monthly capture success rates. Rasoazanabary's findings also indicated that the harvest of particular forest products might have an adverse impact on *M. griseorufus*. She found that of the 17 plant species harvested by people, 11 were also important to *M. griseorufus* for food or nesting, and several ranked as extremely important (*Alluaudia procera*, *Terminalia fatrae*, *Albizia* spp., *Euphorbia tirucallii*, *Tamarindus indica*, and *Salvadora angustifolia*).

Greater opportunities for disease transmission add a potentially significant dimension to the impact of close contact between people and wildlife at Bezà Mahafaly. Analysis of 585 fecal samples showed that *L. catta* (n = 39 individuals) harbored six species of nematode worms and three species of protistan parasites, whereas *P. verreauxi* (n = 26 individuals) harbored only two nematodes (Loudon & Sauther, 2013). These findings confirm and extend earlier work that found few to no endoparasites in *P. verreauxi* (Raveloarisoa, 2000; Muehlenbein *et al*., 2003). Two mite species and one species of tick, *Haemaphysalis lemuris,* were collected from *L. catta*. Ticks collected from *P. verreauxi* were also identified as *H. lemuris* (D. Brockman, personal communication, cited in Loudon *et al*., 2006). *Lemur catta* ranging in disturbed forests had parasites not found in groups that lived in Parcel 1, whereas patterns of parasitism in *P. verreauxi* living in disturbed forest were not distinguishable from those studied in Parcel 1.

Figure 1. Tagged female *Lemur catta* and her infant poised to harvest any leftovers from lunch at the Bezà Mahafaly field station. (Photograph by Ed Lowther.)

Observed differences in parasite load likely result from variation in species biology, diet, and macro- and micro-habitat use, all of which mediate contact with people (Loudon *et al*., 2006; Sauther *et al*., 2006; Loudon, 2009; Loudon & Sauther, 2013). *Lemur catta* is a dietary generalist eating a wide range of foods at all levels of the forest canopy, and is the most terrestrial of extant Malagasy primates (Sauther *et al*., 1999; Fleagle, 2012), whereas *P. verreauxi* is primarily arboreal, spends much less time on the ground, and is predominantly folivorous (Richard *et al*., 1993). *Lemur catta* also forms larger and more frequently interacting social groups than *P. verreauxi*. Two social groups of *L*. *catta* included the field station in their home range, drinking water from buckets, stealing food, interacting with people almost daily, and ingesting human feces from the traditional, open-air toilet area as well as zebu and dog feces. In contrast, *P*. *verreauxi* groups crossed the camp from time to time but were never observed eating feces or human refuse, and almost never interacted with people in the same manner as *L*. *catta*.

Climate: Fluctuations and directional change

Deep historical change

The paleontological and archaeological site of Antaolambiby, located 2 km from the Bezà Mahafaly Special Reserve, provides vivid evidence of changes in the local landscape over the last few thousand years. Remains of extinct species recovered from the site include a hippo (*Hippopotamus lemerlei*), a crocodile (*Voay robustus*), at least one elephant bird (*Aepyornis* sp.), two tortoises (*Aldabrachelys abrupta* and *A. grandidieri*), and seven species of lemur (Goodman & Jungers, 2014). Together with palynological evidence of subsequent drying (Burney, 1997), these finds indicate that the southwest was wetter and supported a much more diverse fauna 3,000 years ago (Goodman & Jungers, 2014).

The roles of climate change and anthropogenic factors in faunal extinctions during the Holocene in Madagascar are much debated (Crowley, 2010; Dewar, 2014; Goodman & Jungers, 2014). Regardless of specific drivers, the catastrophic disruption of the large mammal fauna over the last several thousand years could be expected to have a historical impact on surviving populations. Research on *Propithecus verreauxi* and *Lemur catta* at Bezà Mahafaly and Tsimanampetsotsa National Park has explored whether these populations experienced a bottleneck in the last 2,000 years, by examining how patterns of genetic diversity deviate from theoretically expected equilibrium conditions and/or a neutral expectation (Lawler, 2008; Parga *et al*., 2012).

Analysis of six microsatellite loci, genotyped on more than 360 *P*. *verreauxi* at Bezà Mahafaly, revealed no evidence of a bottleneck. Indeed, one of three models used in the analysis indicated population expansion (Lawler, 2008). Analysis of seven microsatellite loci from 45 *L*. *catta* (20 from Bezà Mahafaly and 25 from Tsimanampetsotsa) indicated a potential bottleneck, with stronger evidence for Tsimanampetsotsa than Bezà Mahafaly (Parga *et al*., 2012), but even so the genetic signal was not strong.

The absence of clear bottlenecks in these populations is surprising, given the magnitude of Holocene perturbations (Dewar & Richard, 2012; Goodman & Jungers, 2014) and the evidence for bottlenecks elsewhere on the island. In dry forests in the north, genetic analyses decisively indicate a population collapse for *P*. *tattersalli* across all forest fragments sampled between 5,000 and 10,000 years ago (Quéméré *et al*., 2012). A possible explanation is that populations experiencing reductions in census size might not experience similar reductions in genetic effective population size (i.e. the number of individuals directly implicated in reproduction) (Lawler, 2008, 2011a). The effective size of the *P*. *verreauxi* population at Bezà Mahafaly is about 100, less than twice the census size. If effective population size has always been low relative to census size, the population could experience quite large reductions in census size without collapsing.

Recent fluctuations

Propithecus verreauxi and *Lemur catta* populations at Bezà Mahafaly are about the same size today as they were a decade or more ago, despite wide year-to-year fluctuations. Their resilience is well illustrated by their recovery from a severe drought during the early years of monitoring.

Demographic modeling of census data from the *P*. *verreauxi* population between 1985 and 2001 spanned three successive years of diminishing rainfall culminating in a major drought in 1991-1992. The overall population growth rate from 1985-2001 was around 0.98/year, with 95% confidence intervals >1.00 (Lawler *et al*., 2009; Lawler, 2011b), indicating that population size was about the same at the beginning and end of this period.

Fertility and survival were depressed in the population when rainfall was particularly low or the variance was high, however, with the effect of low rainfall most marked in the rate at which animals lived to sexual maturity, and in the survival of multiparous females (Lawler *et al*., 2009; Lawler, 2011b). The lowest fertility recorded was in the 1992 birth season; less than a third (27%) of reproductively active females (three years old and older) gave birth compared to a long-term average of almost half (48%), and only about a third of the few infants born survived the first 12 months. In addition, mortality rates among males and females two years old and older peaked in 1992-93, with the death of about 20% of the marked population (Richard *et al*., 2002).

The 1991-1992 drought hit the *L*. *catta* population even harder. Approximately half the adult females died and 80% of the infants born in 1992 did not survive. The population continued to decline up to 1994 but rebounded quickly thereafter, with no significant difference in population size in 2001 compared to 1987, although there was almost a complete replacement of individual animals (Gould *et al.*, 1999, 2003).

Annual rainfall strongly influences phenology (Rasamimanana, 2011, 2014; Rasamimanana *et al.,* 2012), and food scarcity probably accounts for the demographic toll taken on both populations by the 1992 drought (Sauther, 1998; Sauther *et al*., 1999). A study of seasonal fluctuations in body mass among *P. verreauxi* in relation to rainfall and subsequent reproductive success provides support for this supposition (Richard *et al*., 2000). All adults lost body mass in the dry season, with females losing significantly more than males. In years of very low rainfall, this pattern was especially pronounced. Compared to lighter females, females that were heavier during the mating season (which falls in the mid/late wet season) were more likely to give birth in the following birth season.

Analysis of the dental consequences of using fallback foods (eaten when other preferred foods are scarce) by *L*. *catta* emphasizes the indirect challenges presented by the highly variable climate conditions at Bezà Mahafaly (Sauther & Cuozzo, 2009). *Lemur catta* had two fallback foods, the fruit of *Tamarindus indica* and *Enterospermum pruinosum,* available year-round due to their highly asynchronous fruiting patterns (Rasamimanana, 2014). During the dry season, animals fed primarily on *T*. *indica*; in other months, use was not correlated with availability. Although a rich source of sugar, *T*. *indica* fruit are large, and physically and mechanically difficult to eat, with tough outer casings and fibers encasing seeds (Cuozzo & Sauther, 2006a; Yamashita, 2008). As a result, *L*. *catta* needed numerous bites to open the fruit, repeatedly exposing teeth to intense wear (Yamashita *et al*., 2012; Cuozzo *et al*., 2014). Annual dental examinations over ten years showed high levels of tooth wear and pre-mortem loss in adults, with over 20% of the study population showing tooth loss (Cuozzo & Sauther, 2006a, 2012; Cuozzo *et al*., 2014). Wear began at an early age, with sub-adults showing notable wear on deciduous teeth, and animals as young as two to four years of age displaying sometimes dramatic wear on their permanent dentition (Cuozzo & Sauther, 2006a; Cuozzo *et al*., 2014). In contrast, *L*. *catta* displayed little tooth loss at Tsimanampetsotsa National Park, 135 km from Bezà Mahafaly, where *T*. *indica* is rare (Cuozzo & Sauther, 2012).

Propithecus verreauxi at Bezà Mahafaly feeds almost exclusively on unripe *T*. *indica* fruit (Yamashita, 2008; Yamashita *et al*., 2012), and does not show the pattern of tooth loss exhibited by *L*. *catta*. Maxillary canine abscesses are more common at Bezà Mahafaly (>30% of the cranial collection housed at the reserve) than in any other *Propithecus* samples examined to date (Cuozzo & Sauther, unpublished data), however, probably linked to the processing of *T. indica* fruit with anterior teeth.

Figure 2. *Propithecus verreauxi* feeding on *Tamarindus indica* pod in Bezà Mahafaly Special Reserve, Parcel 1. (Photograph by Roshna Wunderlich.)

Lemur catta at Bezà Mahafaly responded to decreases in food processing ability due to tooth loss and severe dental wear by changing their activity patterns and feeding behavior (Cuozzo & Sauther, 2004, 2006a; Millette *et al*., 2009). Cuozzo & Sauther (2006b) also reported an increase in mandibular tooth length in the population from 1987/1988 to 2003/2004.

Projected changes

Climate models project long-term temperature and, perhaps, rainfall trends (Tadross *et al*., 2008). These will drive changes in the spatial distribution of plant communities, the plant species composition of the Bezà Mahafaly forests, and the timing of leaf, flower, and fruit production (Rasamimanana *et al*., 2016, see also Hannah *et al*., 2008). These changes in turn will shape spatial and temporal patterns of food availability for herbivorous mammals, and all mammals will experience a more extreme ambient temperature regime. Although the precise nature of these impacts on the Bezà Mahafaly landscape is uncertain, the short-term linkages between climate and phenology, and between phenology, food availability, and reproduction, are clear (Richard *et al*., 2000; Rasamimanana *et al*., 2016).

Deep historical evidence testifies to the resilience of the area's extant diurnal lemurs under changing environmental conditions, and over the short-term our data show both populations rebounding strongly from the impact of the severe drought of 1992. Yet these same data suggest that, under conditions projected for the future, the local or perhaps regional extinction of both *L*. *catta* and *P*. *verreauxi* is a real possibility.

Hunting and collecting

Most people living in or around the Bezà Mahafaly Special Reserve consider the diurnal lemurs *fady*, or understand and accept that they are protected by the presence of the reserve. As a result, hunting is not a significant pressure on these populations at this time. Spiny tenrecs (*Echinops telfairi*, *Setifer setosus*, and *Tenrec ecaudatus*) are not protected by *fady*, however. Observations of dead wood that has been broken or cut open indicate that people search for animals in these substrates, and harvest them for food (Monitoring Team, personal communication). Most of these observations have been made outside the reserve. The extent and landscape-wide impact on spiny tenrec populations of this activity has not been studied in the reserve.

Introduced and invasive species

Carnivora

Diurnal lemurs respond strongly to the suspected presence of raptors and ground predators, including introduced carnivorans, *Felis silvestris* and *Canis lupus*, and the latter two species add to predation pressure on both lemur populations. In order to provide context for reports of predation by non-native species, we first review briefly the evidence for predation by the only endemic carnivoran species at Bezà Mahafaly, *Cryptoprocta ferox*.

Richard *et al*. (1991) attributed the remains of a young adult male found in Parcel 1 of the reserve to predation by *C*. *ferox.* In 2008, *C*. *ferox* was photographed once in Parcel 1 during a 12-month camera-trapping program (Sauther *et al.*, 2011), and at that time four fresh lemur remains (two *Lemur catta* and two *Propithecus verreauxi*) were discovered in Parcel 1 over a two-week period that were consistent with the reported manner *C*. *ferox* consumes prey. In each case, the body cavity was opened up, the heart and liver removed, as was muscle from the thigh area. A large fecal specimen found buried near one *L*. *catta* kill was consistent with *C*. *ferox* scat in size and shape, and unlike felid scat (Sauther *et al*., 2011). In 2011, during a one-month study of *Microcebus*, researchers repeatedly sighted *C*. *ferox* on trails in Parcel 1 (K. Fish, personal communication).

Cryptoprocta ferox is a major predator of *Propithecus* in other forests (Wright *et al*., 1997; Wright, 1998; Dollar *et al*., 2007). Its apparently intermittent presence at Bezà Mahafaly, based on the episodic nature of tracks, direct sightings, and inferred predation, may reflect the broad ranging habits of this species. The regional population of *C*. *ferox* may also have declined, due to hunting by people in retaliation for attacks on domestic fowl in and around villages (Monitoring Team, personal communication).

Evidence for predation by *F*. *silvestris* and *C. lupus* comes primarily from the last decade (Brockman *et al*., 2008), yet *C. lupus* probably arrived in Madagascar with human settlers several thousand years ago, with *F. silvestris* introduced in the last few centuries (Goodman, 2012). Observed or inferred increases in predatory activity at Bezà Mahafaly may be real, associated with human population growth in the area (particularly in the case of the commensal *C*. *lupus*), or simply reflect a greater focus on introduced species by researchers and the Monitoring Team in recent years.

Felis silvestris has occasionally been seen in the forest since 1986 (Ratsirarson *et al*., 2001), but the

Monitoring Team reports more frequent sightings over the last decade. *Felis silvestris* is now known to breed in Parcel 1: Ratsirarson (personal observation) found a litter of five kittens in a hollow *Salvadora angustifolia* trunk in November 2004; this tree also served as a refuge for *P. verreauxi* from the midday heat during hot months (Enafa, A. Richard, personal observation) -- and a female and her kitten were camera-trapped in 2008 (Sauther *et al.*, 2011).

Felis silvestris is an opportunistic, cryptic solitary hunter, and its stalk-and-ambush hunting tactics enable it to kill diurnal lemurs close to its own body mass (Brockman *et al*., 2008). Canine puncture wounds in skulls recovered in Parcel 1 from eight *P. verreauxi* have been attributed to *F. silvestris*, with most deaths occurring since 2000 (Brockman *et al*., 2008). The known or estimated ages of these lemurs ranged from about eight months to over 25 years, and some seem to have been in their prime. (Skeletal remains are in the Bezà Mahafaly Osteological Collections housed at the Bezà Mahafaly Museum.)

Canis lupus is a human commensal, and does not occur as a feral population at Bezà Mahafaly. Individuals make forays into the forest while accompanying people along paths outside the reserve, and hunt alone and in small packs (Brockman *et al*., 2008). Several serious attacks and fatal injuries to *P*. *verreauxi* and *L*. *catta* have been linked to *C*. *lupus* in recent years (M. Sauther, F. Cuozzo, personal communication; J. Ratsirarson & A. Richard, personal observation). Growth of the population of Ankazombalala Commune (Ranaivonasy *et al*., 2016b) and surrounding areas has likely led to an increase in the local population of *C*. *lupus*.

The impact on lemur population dynamics of predation by *F*. *silvestris* and *C*. *lupus* compared to *Cryptoprocta ferox* is unknown. However, a 12-month study in 2008-2009, using camera trap and fecal sample data, indicated that *F*. *silvestris* may be the most significant predator of the three (Sauther *et al*., 2011; Bolt *et al*., 2015). Only felid fecal samples contained lemur remains, including bone fragments, toes, and even a microchip that had been implanted in a *L*. *catta*.

Rodents

Introduced to Madagascar by at least the 11th century (Rakotozafy, 1996), *Rattus rattus* is considered highly invasive even though its ability to colonize intact forest is still in question (Hingston *et al*., 2005). Youssouf (2004, 2010) investigated its distribution and penetration of forest habitats at Bezà Mahafaly in relation to those of other small mammals. Using Sherman traps and a combination of fixed and random sampling, Youssouf (2010) set 118,560 traps between October 2006 and September 2007 in three villages, the camp, and each of three forest sites: riverine forest in Parcel 1 of the reserve, spiny forest in Parcel 2, and dry forest under community management at Ihazoara. The forest sites represent a spectrum of disturbance and distance from human habitation.

The capture rate of small mammals in the study was 0.52%, with a recapture rate of 15.05%, with *R*. *rattus* the most frequently trapped rodent species overall. Statistical analyses of constancy and fidelity (the proportion of traps that captured *R*. *rattus* among all traps set) signaled that, while common in villages and the camp, *R*. *rattus* was rare in the three forests sampled, with a gradient of increasing rarity from gallery forest through spiny forest to dry forest (Youssouf, 2010). These findings mirror those reported for other western forests, where the abundance of *R*. *rattus* has been found to rise with increasing disturbance (Lehtonen *et al*., 2001; Hingston *et al.*, 2005). A direct, competitive impact of *R*. *rattus* on endemic rodents has not been established at Bezà Mahafaly, and the evidence from other forests is mixed (Hingston *et al*., 2005); it has been suggested, rather, that degradation and fragmentation create habitat mosaics suitable for *R*. *rattus* but not for most endemic rodent species (Ganzhorn, 2003).

Plants

Turning from wildlife to plants and from introduced to endemic species, the destructive capacity of the endemic vine *Cynanchum mahafalense* represents a potent, if indirect, threat to much or all of the wildlife in Parcel 1 of the reserve. The vine grows rapidly in sunlight, smothering and eventually killing trees that provide support. Unchecked, this disrupts regeneration processes in tree-fall gaps and increases gap size; *C*. *mahafalense* also encroaches on and pushes back forest edges (Ratsirarson, 2005). Livestock browse on *C*. *mahafalense* outside the reserve, a controlling role presumably played formerly by now-extinct browsers, including tortoises, elephant birds, and lemurs. Browsing inside the totally protected core areas of the reserve is not permitted in principle and is rare in practice in Parcel 1, and *C*. *mahafalense* proliferated in its absence. A successful program of regular uprooting was instigated in 2003 to control this plant in Parcel 1, after cutting it back failed to have much impact.

Conclusions

We consider the reduction of forest cover to be the single most important pressure among those confronting the endemic mammals of Bezà Mahafaly today, since all endemic species depend on the forest for survival. In the Bezà Mahafaly landscape, forest clearance and degradation are primarily the result of subsistence activities.

The presence of people brings about other environmental changes to which wildlife must respond, however, with exposure and effects that differ by species. These changes notably include increased exposure to human parasites and diseases (*Lemur catta*), increased harvesting for food (spiny tenrecs), increased abundance of human commensals as predators (*Canis lupus* for *L. catta* and *Propithecus verreauxi*) or possible competitors (*Rattus rattus* for endemic rodents), and disturbance-related reductions in reproduction (*Microcebus griseorufus*).

Madagascar's natural communities experienced profound perturbations during the course of the Holocene (Goodman & Jungers, 2014). Some combination of anthropogenic activity and climate change led to major faunal extinctions, marked reductions in forest cover, and the introduction of many non-native plant and animal species. The impact of these perturbations continues to work its way through natural communities today. The case of the highly invasive and destructive endemic vine, *Cynanchum mahafalense*, at Bezà Mahafaly illustrates how unanticipated the outcomes can be, and also poses the difficult proposition that conservation on Madagascar is more properly approached as active management or, perhaps, "gardening", in some contexts.

The positive conclusion of this review is that, based on the available evidence, the Bezà Mahafaly Special Reserve still harbors viable populations of the two diurnal lemur populations present when the reserve was founded 30 years ago. In addition, there has been no reduction in overall mammalian biodiversity over the last decade (Richard *et al.*, 2016). The population of Ankazombalala Commune, where the reserve is located, has grown sharply, however, and pressures discussed in this review will become threats to the survival of some or all species if they increase. We consider climate change to be the greatest long-term threat, but the immediate pressures are clearer, and substantial. Sustained action to continue conserving and managing the Bezà Mahafaly forests over the coming decades will be critical to their survival.

Acknowledgments

We thank members of the Ankazombalala Commune, other members of the Environmental Monitoring Team, and the staff of Madagascar National Parks for their support and involvement at all stages of this work. We are grateful for the contributions made by many Malagasy and international researchers, and we also thank generations of ESSA students who have participated in the annual field school. This paper has benefited greatly in review from the comments of Steve Goodman and Voahangy Soarimalala. We are deeply grateful for the support of the Monitoring Program since its inception by the Liz Claiborne and Art Ortenberg Foundation.

References

Bolt, L. M., Sauther, M. L., Cuozzo, F. P. & Youssouf Jacky, I. A. 2015. Anti-predator vocalization usage in the male ring-tailed lemur (*Lemur catta*). *Folia Primatologia*, 86(1-2): 124-133.

Brockman, D. K., Godfrey, L. R., Dollar, L. J. & Ratsirarson, J. 2008. Evidence of invasive *Felis silvestris* predation on *Propithecus verreauxi* at Bezà Mahafaly Special Reserve, Madagascar. *International Journal of Primatology*, 29: 135-152.

Burney, D. 1997. Theories and facts regarding Holocene environmental change before and after human colonization. In *Natural change and human impact in Madagascar,* eds. S. M. Goodman & B. D. Patterson, pp. 75-89. Smithsonian Institution Press, Washington, D.C.

Crowley, B. E. 2010. A refined chronology of prehistoric Madagascar and the demise of the megafauna. *Quaternary Science Reviews*, 29: 2591-2603.

Cuozzo, F. P. & Sauther, M. L. 2004. Tooth loss, survival, and resource use in wild ring-tailed lemurs (*Lemur catta*): Implications for inferring conspecific care in fossil hominids. *Journal of Human Evolution*, 46: 623-631.

Cuozzo, F. P. & Sauther, M. L. 2006a. Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): A function of feeding ecology, dental structure, and individual life histories. *Journal of Human Evolution*, 51: 490-505.

Cuozzo, F. P. & Sauther, M. L. 2006b. Temporal change in tooth size among ring-tailed lemurs (*Lemur catta*) at the Bezà Mahafaly Special Reserve, Madagascar: Effects of an environmental fluctuation. In *Ring-tailed lemur biology*, eds. A. Jolly, R. W. Sussman, N. Koyama & H. Rasamimanana, pp. 343-366. Springer, New York.

Cuozzo, F. P. & Sauther, M. L. 2012. The dental ecology of ring-tailed lemurs (*Lemur catta*). In *Leaping ahead: Advances in prosimian biology,* eds. J. C. Masters, M. Gamba & F. Génin, pp. 157-163. Springer, New York.

Cuozzo, F. P., Head, B. R., Sauther, M. L., Ungar, P. S. & O'Mara, M. T. 2014. Sources of tooth wear variation early in life among known-aged wild ring-tailed lemurs (*Lemur catta*) at the Bezà Mahafaly Special Reserve, Madagascar. *American Journal of Primatology*, 76: 1037-1048.

Dewar, R. E. 2014. Early human settlers and their impact on Madagascar's landscapes. In *Conservation and environmental management in Madagascar*, ed. I. R. Scales, pp. 44-64. Routledge, London.

Dewar, R. E. & Richard, A. F. 2012. Madagascar: A history of arrivals, what happened, and will happen next. *Annual Review of Anthropology*, 41: 495-517.

Dietrich, M., Wilkinson, D. A., Soarimalala, V., Goodman, S. M., Dellagi, K. & Tortosa, P. 2014. Diversification of an emerging pathogen in a biodiversity hotspot: *Leptospira* in endemic small mammals of Madagascar. *Molecular Ecology*, 23: 2783-2796.

Dollar, L., Ganzhorn, J. U. & Goodman, S. M. 2007. Primates and other prey in the seasonally variable diet of *Cryptoprocta ferox* in the dry deciduous forest of western Madagascar. In *Primate anti-predator strategies*, eds. S. L. Gursky & K. A. I. Nekaris, pp. 63-77. Springer, New York.

Fish, K. 2014. Extension of gray-brown mouse lemur (*Microcebus griseorufus*) activity period in a disturbed forest in southwestern Madagascar. *Madagascar Conservation & Development*, 9 (2): 98-101.

Fleagle, J. G. 2012. *Primate adaptation and evolution.* Academic Press, San Diego.

Ganzhorn, J. U. 2003. Effects of introduced *Rattus rattus* on endemic small mammals in dry deciduous forest fragments of western Madagascar. *Animal Conservation*, 6: 147-157.

Goodman, S. M. 1995. The spread of *Rattus* on Madagascar: The dilemma of protecting the endemic rodent fauna. *Conservation Biology*, 9: 450-453.

Goodman, S. M. ed., 2008. *Paysages naturels et biodiversité de Madagascar.* WWF, Publications Scientifiques du Muséum, Paris.

Goodman, S. M. 2012. *Les carnivora de Madagascar.* Association Vahatra, Antananarivo.

Goodman, S. M. & Jungers, W. L. 2014. *Extinct Madagascar: Picturing the island's past.* The University of Chicago Press, Chicago.

Gould, L., Sussman, R. W. & Sauther, M. L. 1999. Natural disasters and primate populations: The effects of a 2-year drought on a naturally occurring population of ring-tailed lemurs (*Lemur catta*) in southwestern Madagascar. *International Journal of Primatology*, 20: 69-84.

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

Gould, L., Ziegler, T. E. & Wittwer, D. J. 2005. Effects of reproductive and social variables on fecal glucocorticoid levels in a sample of adult male ring-tailed lemurs (*L. catta*) at the Beza Mahafaly Reserve, Madagascar. *American Journal of Primatology*, 67: 4-23.

Hannah, L., Dave, R., Lowry, P. P., Andelman, S., Andrianarisata, M., Andriamaro, L., Cameron, A., Hijmans, R., Kremen C., MacKinnon, J., Randrianasolo, H. H., Andriambololonera, S., Razafimpahanana A., Randriamahazo, H., Randrianarisoa, J., Razafinjatovo, P., Raxworthy, C., Schatz, G. E., Tadross, M. & Wilmé, L. 2008. Climate change adaptation for conservation in Madagascar. *Biology Letters*, 4: 590-594.

Hingston, M., Goodman, S. M., Ganzhorn, J. U. & Sommer, S. 2005. Reconstruction of the colonization of southern Madagascar by introduced *Rattus rattus. Journal of Biogeography*, 32: 1549-1559.

Kubzdela, K. S. 1997. Sociodemography of *Propithecus verreauxi verreauxi.* Ph.D. dissertation, The University of Chicago, Chicago.

Lawler, R. R. 2008. Testing for a historical population bottleneck in wild Verreaux's Sifaka (*Propithecus verreauxi verreauxi*) using microsatellite data. *American Journal of Primatology*, 70: 990-994.

Lawler, R. R. 2011a. Demographic concepts and research pertaining to the study of wild primate populations. *Yearbook of Physical Anthropology*, 53: 63-85.

Lawler, R. R. 2011b. Historical demography of a wild lemur population (*Propithecus verreauxi*) in southwest Madagascar. *Population Ecology*, 53: 229-240.

Lawler, R. R., Richard, A. F. & Riley M. A. 2001. Characterization and screening of microsatellite loci in a wild lemur population (*Propithecus verreauxi verreauxi*). *American Journal of Primatology*, 55: 253-259.

Lawler, R. R., Caswell, H., Richard, A. R., Ratsirarson, J., Dewar, R. E. & Schwartz, M. 2009. Demography of Verreaux's sifaka in a stochastic rainfall environment, *Oecologia*, 161: 491-504.

Lehtonen, J. T., Mustonen, O., Ramiarinjanahary, H., Niemela, J. & Rita, H. 2001. Habitat use by endemic and introduced rodents along a gradient of forest disturbance in Madagascar. *Biodiversity and Conservation*, 10: 1185-1202.

Loudon, J. E. 2009. The parasite ecology and socioecology of ring-tailed lemurs (*Lemur catta*) and Verreaux's sifaka (*Propithecus verreauxi*) inhabiting the Bezà Mahafaly Special Reserve. Ph.D. dissertation, The University of Colorado, Boulder.

Loudon, J. E. & Sauther, M. L. 2013. Verreaux's sifaka (*Propithecus verreauxi*) and ring-tailed lemur (*Lemur catta*) endoparasitism at the Bezà Mahafaly Special Reserve. *Madagascar Conservation & Development*, 8 (1): 21-28.

Loudon, J. E., Sauther, M. L., Fish, K. D., Hunter-Ishikawa, M. & Youssouf, J. I. A. 2006. One reserve, three primates: Applying a holistic approach to understand the interconnections among ring-tailed lemurs (*Lemur catta*), Verreaux's sifaka (*Propithecus verreauxi*), and humans (*Homo sapiens*) at Bezà Mahafaly Special Reserve, Madagascar. *Ecological Environmental Anthropology* (University of Georgia), 2: 54-74.

Millette, J. B., Sauther, M. L. & Cuozzo, F. P. 2009. Behavioral responses to tooth loss in wild ring-tailed lemurs (*Lemur catta*) at the Bezà Mahafaly Special Reserve, Madagascar. *American Journal of Physical Anthropology*, 140 (1): 120-134.

Muehlenbein, M. P., Schwartz, M. & Richard, A. 2003. Parasitologic analyses of the sifaka (*Propithecus verreauxi verreauxi*) at Bezà Mahafaly, Madagascar. *Journal of Zoo and Wildlife Medicine*, 34 (3): 274-277.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature*, 403: 853-858.

Parga, J. A., Sauther, M. L., Cuozzo, F. P., Youssouf, J. I. A. & Lawler, R. R. 2012. Evaluating ring-tailed lemurs (*Lemur catta*) from southwestern Madagascar for a genetic population bottleneck. *American Journal of Physical Anthropology*, 147 (1): 21-29.

Peabody Museum of Natural History, Yale University & Ecole des Sciences Supérieure Agronomiques, Université d'Antananarivo. 2013. Schwartz Database, Bezà Mahafaly sifaka. http://peabody.yale.edu/collections/vertebrate-zoology/madagascar.htm

Quammen, D. 2012. *Spillover: Animal infections and the next human pandemic.* Norton, New York.

Quéméré, E., Amelot, X., Pierson, J., Crouau-Roy, B. & Lounès, C. 2012. Genetic data suggest a natural pre human origin of open habitats in northern Madagascar and question the deforestation narrative in this region. *Proceedings of the National Academy of Sciences, USA*, 109 (32): 13028-13033.

Rakotozafy, L. M. A. 1996. Etudes de la constitution du régime alimentaire des habitants du site de Mahilaka de XIème au XIVème siècle à partir de produits de fouilles archéologiques. Ph.D. thesis, l'Université d'Antananarivo, Antananarivo.

Ranaivonasy, J., Ratsirarson, J., Rasamimanana, N., Ramahatratra & Eitroarany. 2016a. Dynamique de la couverture forestière dans la Réserve Spéciale de Bezà Mahafaly et ses environs, eds. J. Ranaivonasy, J. Ratsirarson & A. F. Richard. *Malagasy Nature*, 10: 15-24.

Ranaivonasy, J., Ratsirarson, J., Rasamimanana, N., Randrianandrasana, A. S., Ramahatratra, Razafindraibe, M. & Efitroarany. 2016b. Dynamiques socio-économiques et utilisation des ressources naturelles dans la Réserve Spéciale de Bezà Mahafaly et ses environs, eds. J. Ranaivonasy, J. Ratsirarson & A. F. Richard. *Malagasy Nature*, 10: 77-91.

Rasamimanana, N. 2011. Influence de la variabilité climatique sur la phénologie de la forêt de la Réserve Spéciale de Bezà Mahafaly. Mémoire de fin d'études, Département des Eaux et Forêts, Ecole Supérieure des Sciences, l'Université d'Antananarivo, Antananarivo.

Rasamimanana, N. 2014. Variabilité de la phénologie de la végétation de la Réserve Spéciale de Bezà Mahafaly dans le contexte de la variabilité climatique. Mémoire de DEA, Département des Eaux et Forêts, Ecole Supérieure des Sciences Agronomiques, l'Université d'Antananarivo, Antananarivo.

Rasamimanana, N., Ratsirarson, J. & Richard, A. F. 2012. Influence de la variabilité climatique sur la phénologie de la forêt de la Réserve Spéciale de Bezà Mahafaly. *Malagasy Nature*, 5: 67-82.

Rasamimanana, N., Ratsirarson, J. & Ranaivonasy, J. 2016. Variabilité et changement du climat à Bezà Mahafaly, eds. J. Ranaivonasy, J. Ratsirarson & A. F. Richard. *Malagasy Nature*, 10: 5-14.

Rasoazanabary, E. 2011. The human factor in mouse lemur (*Microcebus griseorufus*) conservation: Local resource utilization and habitat disturbance at Bezà Mahafaly, SW Madagascar. Ph.D. dissertation, The University of Massachusetts, Amherst.

Ratsirarson, J. 2005. Envahissement d'une liane endémique (*Cynanchum mahafalense*) dans la Réserve Spéciale de Bezà Mahafaly. *Forum de la Recherche 31 mars-1 avril,* MENRES, Toamasina. *https://campuspress.yale.edu/bezamahafaly/files/2015/10/Ratsirason-2005-1uxwomn.pdf*

Ratsirarson, J., Randrianarisoa, J., Ellis, E., Rigobert, J. E., Efitroarany, Ranaivonasy, J., Razanajaonarivalona, E. H. & Richard, A. F. 2001. Bezà Mahafaly: Ecologie et réalités socio-économiques. *Recherches pour le Développement, Série Sciences Biologiques*, 18: 1-104.

Raveloarisoa, A. 2000. Contribution à l'étude de la préférence alimentaire du *Propithecus verreauxi verreauxi* de la Réserve Spéciale de Bezà Mahafaly (Parcelle 1). Mémoire de DEA, Département de Biologie Animale, Faculté des Sciences, l'Université d'Antananarivo, Antananarivo.

Richard, A. F. 1978. *Behavioral variation: Case study of a Malagasy lemur*. Associated University Press, New Jersey.

Richard, A. F. & Dewar, R. E. 2001. Politics, negotiation, and conservation: A view from Madagascar. In *African rain forest ecology and conservation,* eds. L. J. T. White, A. Vedder & L. Naughton-Treves, pp. 535-544. Yale University Press, New Haven.

Richard, A. F. & Ratsirarson, J. 2013. Partnership in practice: Making conservation work at Bezà Mahafaly, southwest Madagascar. *Madagascar Conservation & Development*, 8: 12-20.

Richard, A. F., Rakotomanga, P. & Schwartz, M. 1991. Demography of *Propithecus verreauxi* at Bezà Mahafaly, Madagascar: Sex ratio, survival, and fertility, 1984-1988. *American Journal of Physical Anthropology*, 84(3): 307-322.

Richard, A. F., Rakotomanga, P. & Schwartz, M. 1993. Dispersal by *Propithecus verreauxi* at Bezà Mahafaly, Madagascar: 1984-1991. *American Journal of Primatology*, 30 (1):1-20.

Richard, A. F., Dewar, R. E., Schwartz, M. & Ratsirarson, J. 2000. Mass change, environmental variability and female fertility in wild *Propithecus verreauxi. Journal of Human Evolution*, 39 (4): 381-391.

Richard, A. F., Dewar, R. E., Schwartz, M. & Ratsirarson, J. 2002. Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). *Journal of Zoology*, 256 (4): 421-436.

Richard, A. F., Ratsirarson, J., Enafa, J., Youssouf, J. I. A., Fiorentino, I. & Ranaivonasy, J. 2016. Mammalian biodiversity at Bezà Mahafaly: An update, eds. J. Ranaivonasy, J. Ratsirarson & A. F. Richard. *Malagasy Nature*, 10: 25-36.

Sauther, M. L. 1998. The interplay of phenology and reproduction in ringtailed lemurs: Implications for ring-tailed lemur conservation. *Folia Primatologica*, 69 (Supp. 1): 309-320.

Sauther, M. L. & Cuozzo, F. P. 2009. The impact of fallback foods on wild ring-tailed lemur biology: A comparison of intact and anthropogenically disturbed habitats. *American Journal of Physical Anthropology*, 140 (1): 671-686.

Sauther, M. L., Sussman, R. W. & Gould, L. 1999. The socioecology of the ringtailed lemur: Thirty-five years of research. *Evolutionary Anthropology*, 8 (4):120-132.

Sauther, M. L., Sussman, R. W. & Cuozzo, F. 2002. Dental and general health in a population of wild ring-tailed lemurs: A life history approach. *American Journal of Physical Anthropology*, 117 (2): 122-132.

Sauther, M. L., Fish, K. D., Cuozzo, F. P., Miller, D. S., Hunter-Ishikawa, M. & Culbertson, H. 2006. Patterns of health, disease, and behavior among wild ring-tailed lemurs, *Lemur catta*: Effects of habitat and sex. In *Ring-tailed lemur biology,* eds. A. Jolly, R.W. Sussman, N. Koyama & H. Rasamimanana, pp. 313-331. Springer, New York.

Sauther, M. L., Cuozzo, F. P., Youssouf, J. I. A., Ness, J., LaFleur, M., Larsen, R. S. & Tkach, V. 2011. A season of death: Patterns of predation on wild lemurs at Beza Mahafaly Reserve, Madagascar, using multiple methods of assessment. *American Journal of Physical Anthropology*, 141 (S52): 262.

Scales, I. R. (ed.). 2014. *Conservation and environmental management in Madagascar.* Routledge, London.

Schatz, G., Cameron, A. & Raminosoa, T. 2008. Modeling of endemic plant species of Madagascar under climate change. *Assessing the impact of climate change on Madagascar's livelihoods and biodiversity. Conference January 28,* Antananarivo. *http://www.mobot.org/MOBOT/Research/climateChange/pdf/ModelingEndemicPlantSpecies.pdf*

Sussman, R. W. 1991. Demography and social organization of free-ranging *Lemur catta* in the Bezà Mahafaly Reserve, Madagascar. *American Journal of Physical Anthropology*, 84 (1): 43-58.

Sussman, R. W., Richard, A. F., Ratsirarson, J., Sauther, M. L., Brockman, D. K., Gould, L., Lawler, R. & Cuozzo, F. P. 2012. Bezà Mahafaly Special Reserve: Long-term research on lemurs in southwestern Madagascar. In *Long-term field studies of primates*, eds. P. M. Kappeler & D. P. Watts, pp. 45-66. Springer, Berlin.

Tadross, M., Randriamarolaza, L., Rabefitia. Z. & Zheng, K. Y. 2008. Climate change in Madagascar: Recent past and future. World Bank, Washington, D.C.

Thalmann, U. 2006. Lemurs: Ambassadors for Madagascar. *Madagascar Conservation & Development*, 1: 4-8.

Vences, M., Wollenberg, K. C., Vieites, D. R. & Lees, D. C. 2009. Madagascar as a model region of species diversification. *Trends in Ecology and Evolution*, 24: 456-465.

Wilkinson, D. A., Mélade, J., Dietrich, M., Ramasindrazana, B., Soarimalala, V., Lagadec, E., le Minter, G., Tortosa, P., Heraud, J.-M., de Lamballerie, X., Goodman, S. M., Dellagi, K. & Pascalis, H. 2014. Highly diverse morbillivirus-related paramyxoviruses in wild fauna of the southwestern Indian Ocean islands: Evidence of exchange between introduced and endemic small mammals. *Journal of Virology*, 88 (15): 8268-8277.

Wright, P. C. 1998. Impact of predation risk on the behaviour of *Propithecus diadema edwardsi* in the rain forest of Madagascar. *Behaviour*, 135 (4): 483-512.

Wright, P. C., Heckscher, S. K. & Dunham, A. E. 1997. Predation on Milne-Edward's sifaka (*Propithecus diadema edwardsi*) by the fossa (*Cryptoprocta ferox*) in the rain forest of southeastern Madagascar. *Folia Primatologica*, 68: 34-43.

Yamashita, N. 2008. Chemical properties of the diets of two lemur species in southwestern Madagascar. *International Journal of Primatology*, 29: 339-364.

Yamashita, N., Cuozzo, F. P. & Sauther, M. L. 2012. Interpreting food processing through dietary mechanical properties: A *Lemur catta* case study. *American Journal of Physical Anthropology,* 148: 205-214.

Youssouf, J. I. A. 2004. Bioécologie des *Rattus rattus* dans la Réserve Spéciale de Bezà Mahafaly et ses alentours. Mémoire de DEA, Option Biologie Animale, l'Université de Toliary, Toliary.

Youssouf, J. I. A. 2010. Impacts bioécologiques de la colonization de *Rattus rattus* sur les micromammifères autochtones dan la Réserve Spéciale de Bezà Mahafaly sud-ouest de Madagascar. Thèse de Doctorat, l'Université d'Antananarivo, Antananarivo.