Chapter 4
Long-Term Lemur Research at Centre Valbio, Ranomafana National Park, Madagascar

Patricia C. Wright, Elizabeth M. Erhart, Stacey Tecot, Andrea L. Baden, Summer J. Arrigo-Nelson, James Herrera, Toni Lyn Morelli, Marina B. Blanco, Anja Deppe, Sylvia Atsalis, Steig Johnson, Felix Ratelolahy, Chia Tan, and Sarah Zohdy

Please note the erratum to this chapter at the end of the book.

Abstract We present findings from 25 years of studying 13 species of sympatric primates at Ranomafana National Park, Madagascar. Long-term studies have revealed that lemur demography at Ranomafana is impacted by climate change, predation from raptors, carnivores, and snakes, as well as habitat disturbance. Breeding is seasonal, and each species (except *Eulemur rubriventer*) gives birth synchronously to be able to wean before winter. Infant mortality is high (30–70%)

P.C. Wright (✉)
Institute for the Conservation of Tropical Environments, Stony Brook University, Stony Brook, NY, USA
e-mail: patchapplewright@gmail.com

E.M. Erhart
Department of Anthropology, Texas State University, San Marcos, TX, USA
e-mail: berhart@txstate.edu

S. Tecot
School of Anthropology, University of Arizona, Tucson, AZ, USA
e-mail: stecot@email.arizona.edu

A.L. Baden • J. Herrera • A. Deppe
IDPAS, Stony Brook University, Stony Brook, NY, USA
e-mail: andrea.baden@gmail.com; jherrera84@gmail.com; deppeam@hotmail.com

S.J. Arrigo-Nelson
Department of Biological and Environmental Sciences, University of California in Pennsylvania, California, PA, USA
e-mail: arrigonelson@calu.edu

T.L. Morelli
Museum of Vertebrate Zoology, Department of Environmental Sciences, Policy and Management, U.C. Berkeley, Berkeley, CA, USA
e-mail: morellitlm@gmail.com

M.B. Blanco
Department of Anthropology, University of Massachusetts, Amherst, MA, USA
e-mail: mbblanco@anthro.umass.edu

P.M. Kappeler and D.P. Watts (eds.), *Long-Term Field Studies of Primates*,
DOI 10.1007/978-3-642-22514-7_4, © Springer-Verlag Berlin Heidelberg 2012

and partly due to infanticide in *Propithecus edwardsi,* and perhaps *Varecia variegata*. Diurnal lemurs can live beyond 30 years in the wild and most females reproduce until death. Small-bodied *Microcebus rufus* live up to 9 years without signs of senescence. *Prolemur simus* migrates in search of new bamboo and mates, and related *V. variegata* mothers park their multiple offspring in "kindergartens," protected by others while mothers forage. Interference competition among sympatric lemurs occurs. Anthropogenic factors, such as past selective logging and climate change may influence the declining density of *E. rufifrons*, *P. simus*, and *P. edwardsi* while not affecting the density of pair-living species.

4.1 Introduction

Madagascar ranks as one of the world's top biodiversity hotspots because of its high endemism and high rate of habitat degradation (Myers et al. 2000; Ganzhorn et al. 2001). For primates, Madagascar has the highest conservation priority with 5 endemic families and 15 endemic genera (Mittermeier et al. 2010). Ninety-seven lemur species are now recognized of which 41% are threatened with extinction (8 critically endangered, 18 endangered, and 15 vulnerable), while 42 species remain data deficient (IUCN 2010; Mittermeier et al. 2010). Knowledge obtained from long-term field studies, such as the ones described here, is particularly valuable compared to short-term "snapshots" because long-term data can be especially useful to conservation management efforts. For effective management, park authorities can benefit from understanding the differences between normal fluctuations in population size and real trends over time, patterns which can only be detected with decades of data.

To date there are four long-term lemur research sites in Madagascar: Kirindy Forest in the dry deciduous forest of the west (Ganzhorn and Kappeler 1996; Kappeler and Fichtel 2012), the southern spiny desert reserve Berenty Private Reserve (Jolly et al. 2006; Jolly 2012), Beza Mahafaly Special Reserve (Richard

S. Atsalis • C. Tan
San Diego Zoological Society, The San Diego Zoo's Institute for Conservation Research, San Diego, CA, USA
e-mail: satsalis55@gmail.com; ctan@sandiegozoo.org

S. Johnson
Department of Anthropology, University of Calgary, Calgary, Canada
e-mail: steig.johnson@ucalgary.ca

F. Ratelolahy
Wildlife Conservation Society, Antananarivo, Madagascar
e-mail: Jeaf_ratel@yahoo.fr

S. Zohdy
University of Helsinki, Helsinki, Finland
e-mail: sarahzohdy@gmail.com

et al. 2002; Jolly and Sussman 2006; Sussman et al. 2012), and Ranomafana National Park (RNP) in the southeastern rainforest (Wright and Andriamihaja 2002; Wright 2004). At each site, lemurs have been studied for several decades (Jolly 1966; Sussman 1974; Richard 1978; Jolly and Sussman 2006; Sussman and Ratsirason 2006; Kappeler and Fichtel 2012). In this chapter, we discuss a compilation of the findings of long-term studies of the 13 lemur species found in RNP.

4.1.1 History of Ranomafana National Park

Ranomafana National Park (RNP) is a rainforest park located in southeastern Madagascar (21°16′S, 47°20′E). The landscape is dominated by submontane rainforest, which receives a mean of 3,000 mm of rain per year during the December through March rainy season. The RNP project was initiated in 1986 with the goal of protecting the habitat of a then newly discovered lemur species, the golden bamboo lemur (*Hapalemur aureus*), and the rediscovered greater bamboo lemur (*Prolemur simus*; Meier et al. 1987). From 1986 to 1989, logging concessions were granted by the forestry department and selective logging for valuable hardwood trees was intensive. In 1991, 41,000 ha of the montane rainforest were designated as a national park (Wright and Andriamihaja 2002). The Namorona River and a parallel paved road (Route 25) bisect the park into northern and southern parcels with a third parcel on the western boundary to the north. Patricia Wright, then at Duke University, spearheaded the initial park project, an integrated conservation and development project conducted simultaneously with research on lemurs and other aspects of biodiversity (Wright 1997; Wright and Andriamihaja 2002). Management transitioned to Stony Brook University (SBU) when Wright moved there in 1991. While retaining management of research in RNP, SBU handed park management over to the Association Nationale pour la Géstion des Aires Protegées (ANGAP), the national park system, in 1998. In 2006, the System of Protected Areas of Madagascar (SAPM) replaced ANGAP and incorporated sustainable practices of resource use into park creation and management. In 2009, SAPM became Madagascar National Parks (MNP).

4.1.2 Infrastructure at Ranomafana

The first research station was built in 1989 near the entrance to RNP. This structure was a small, one-story log cabin. In 2003, the station was upgraded to a three-story stone facility adjacent to the park and overlooking the rainforest. The new research station, named the International Centre for Research and Training for the Valorization of Biodiversity (Centre ValBio), is located on Route 25 near the park entrance (Wright 2004). This hub of scientific research and education is managed by a consortium of universities headed by SBU and the Institute for the Conservation of Tropical Environments (ICTE). Founding institutions include SBU and the Universities of Antananarivo, Fianarantsoa, and Helsinki. Currently, the main building houses administrative offices, a small laboratory, a library, and a dining hall that serves 65 people. A second four-story building (15,676 square feet) will open in 2012, and will be equipped with high speed internet, modern hormone, parasite, genetics and infectious disease laboratories, an audio/visual/computer center, and living accommodations for 54 students and researchers. The Centre ValBio has authorization to do research from the Ministry of Forests and Environment of the Government of Madagascar, and works closely with the MNP, especially on conservation management.

Centre ValBio's administration oversees the Departments of Research, Biodiversity Monitoring, Logistics and Management, and Community Outreach including Health and Education. Seventy-two local staff, many trained as lemur technicians and Malagasy biodiversity experts, work at Centre ValBio and live in the villages surrounding the park. The health and education team provides training and outreach programs to 22 nearby villages. Reforestation with native species and medicinal plant gardens managed by traditional healers are two important components of Centre ValBio's outreach efforts (Wright et al. 2005a). Twenty conservation clubs foster appreciation for conservation and a cooperative of artisanal women weavers is a sustainable contributor to village economics.

4.1.3 History of Ranomafana Lemur Research

Ranomafana contains 13 lemur species of which 8 have been subjects of long-term research (Table 4.1). Seven of the 13 species have been subject to taxonomic revision during the 20-year period (Table 4.2). Five species have been redesignated based on genetics and morphology. One new species has been described (*H. aureus*), one taxon has been raised to a new genus (*P. simus*), and one remains to be identified (*Cheirogaleus* sp.).

Twenty-six PhD dissertations and 26 Masters theses on lemurs have been completed since the park's initiation, and an additional eight dissertations are currently in progress. Major foci of these long-term studies have been diurnal lemurs, including behavioral ecology, demography, life history, reproductive biology, stress and reproductive hormones, parasites, feeding and nutritional ecology, morphometrics, predation, communication, and cognition (Table 4.1). Nocturnal lemurs have been studied less intensively, with emphases on reproduction, hibernation, parasites, and vocalizations (Table 4.1). Moreover, research in ecosystem dynamics and conservation with emphasis on lemur seed dispersal, climate, and tree phenology are also ongoing (Dew and Wright 1998; Wright et al. 2005b; Dunham 2008; Dunham et al. 2008, 2010; Ganzhorn et al. 2009).

Researchers have studied lemurs at four sites, each approximately 4 km^2, within the contiguous forest of the park (Fig. 4.1). Three sites (Vatoharanana, Valohoaka, and Mangevo), each with bush camp facilities, are in undisturbed or minimally

Table 4.1 List of RNP lemur species and references to research

Species	Common name	References
Avahi peyrierasi	Peyrierasi's woolly lemur	Harcourt (1987, 1988), Roth (1996), Andriantompohavana et al. (2007a)
Cheirogaleus crossleyi	Crossley's dwarf lemur	Wright and Martin (1995), Blanco et al. (2009), Groeneveld et al. (2011)
Cheirogaleus sp.		Not yet described
Daubentonia madagascariensis	Aye–aye	Sefczek (2009)
Eulemur rufifrons	Red-fronted brown lemur	Meyers et al. (1989), Overdorff (1991, 1993, 1996), Merenlender (1993), Johnson and Overdorff (1999), Overdorff et al. (1999), Johnson (2002), Johnson et al. (2005), Erhart and Overdorff (2008a)
Eulemur rubriventer	Red-bellied lemur	Overdorff (1991, 1993, 1996), Durham (2003), Overdorff and Tecot (2006), Tecot (2008, 2010), Wright et al. (2011), Tecot in press
Hapalemur aureus	Golden bamboo lemur	Meier et al. (1987), Wright et al. (1987), Glander et al. (1992), Tan (1999, 2007), Arrigo-Nelson and Wright (2004)
Hapalemur griseus	Gray gentle bamboo lemur	Meier et al. (1987), Tan (1999), Grassi (2002), Mutschler and Tan (2003), Arrigo-Nelson and Wright (2004), Herrera et al. in press
Lepilemur microdon	Small toothed sportive lemur	Porter (1998), Louis et al. (2006)
Microcebus rufus	Brown mouse lemur	Wright and Martin (1995), Atsalis et al. (1996), Atsalis (1999a, 1999, 1999b, 2000, 2008), Louis et al. (2006), Blanco (2008), Blanco and Meyer (2009), Durden et al. (2010), Deppe (2011)
Prolemur simus	Greater bamboo lemur	Meier et al. (1987), Wright et al. (1987), Tan (1999, 2007), Bergey and Patel (2008), Wright et al. (2008b), CVB census
Propithecus edwardsi	Milne Edwards' sifaka	Hemingway (1995, 1998), Wright (1995), Erhart and Overdorff (1998), Jernvall and Wright (1998), Pochron and Wright (2003), Arrigo-Nelson and Wright (2004), Mayor et al. (2004), Pochron et al. (2004), King et al. (2005, 2011), Pochron et al. (2004, 2005), Arrigo-Nelson (2006), Lehman et al. (2006), Irwin (2007, 2008), Morelli (2008), Bailey et al. (2009), Wright et al. (2009), Wright et al. (2011)
Varecia variegata editorium	Black-and-white ruffed lemur	White et al. (1995), Balko and Underwood (2005), Overdorff et al. (2005), Ratsimbazafy (2006), Baden et al. (2008)

Table 4.2 List of RNP lemurs including recent taxonomic changes with activity pattern: nocturnal (N), diurnal (D), and cathemeral (C); weight in grams; IUCN status

Current nomenclature	Previous	Activity	Status	Weight (g)	References
Avahi peyrierasi	*A. laniger*	N	DD	960	Zaramody et al. (2006)
Cheirogaleus crossleyi	*C. major*	N	DD	350	Groeneveld et al. (2011)
Daubentonia madagascariensis		N	NT	2,500	Feistner and Sterling (1995)
Eulemur rufifrons	*E. fulvus rufus*	C	NT	2,200	Mittermeier et al. (2010)
Eulemur rubriventer	*E. rubriventer*	C	VU	2,400	Mittermeier et al. (2010)
Hapalemur aureus	*New species*	D	EN	1,800	Meier et al. (1987)
Hapalemur griseus ranomafanensis	*H. griseus*	D	NE	990	Rabarivola et al. (2007)
Lepilemur microdon	*L. mustelinus*	N	DD	990	Louis et al. (2006)
Microcebus rufus	*M. rufus*	N	LC	45	Louis et al. (2006)
Prolemur simus	*Hapalemur simus*	D	CR	2,800	Groves (2001)
Propithecus edwardsi	*P. diadema edwardsi*	D	EN	5,800	Mayor et al. (2004)
Varecia variegata editorium	*V. variegata variegata*	D	CR	3,500	Groves (2001)

From IUCN 2010 RedList Guidelines: *NE* Not Evaluated, *DD* Data Deficient, *LC* Least Concern, *NT* Near Threatened, *VU* Vulnerable, *EN* Endangered, *CR* Critically Endangered, *EW* Extinct in the Wild, *EX* Extinct

disturbed rainforest. The fourth is Talatakely located near Route 25, selectively logged by hand from 1986 to 1989, and now accessible to tourists (Wright and Andriamihaja 2002).

Ad hoc transects and surveys have been conducted throughout the park since 1987. Since 2003, researchers conducted lemur surveys along eight 2 km transects, from the edges to the interior (Fig. 4.1). The surveys have led to the identification of new social groups and discovery of new species (Irwin et al. 2000, 2005; Arrigo-Nelson and Wright 2004; Andriantompohavana et al. 2007a, b; Wright et al. 2008b).

4.2 Long-Term Data Collection and Management

4.2.1 Long-Term Research on Focal Species

Most adults from 6 of the 7 diurnal lemur species at each of the main research sites have been marked with tags and collars for individual identification (*Propithecus edwardsi, Hapalemur aureus* and *Prolemur simus, Eulemur rubriventer,*

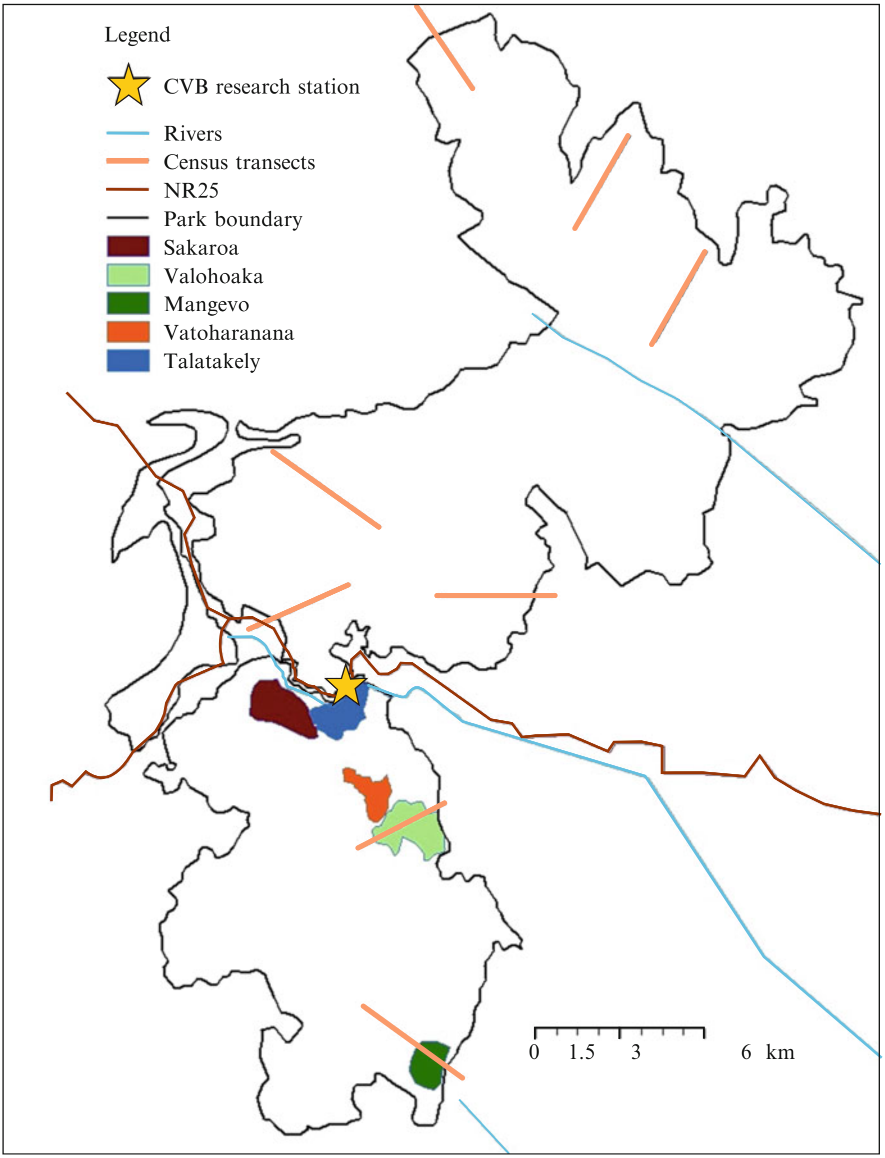

Fig. 4.1 Map of Ranomafana National Park with long-term study sites and long-term transects marked

E. rufifrons, and *Varecia variegata*). Many study groups have at least one member with a telemetry radio-collar for locating groups. Data collection on lemurs has been ongoing in Ranomafana for more than 24 years (Wright 2004; Table 4.1).

4.2.2 Weights, Measures, and Biomedical Data

Beginning in 1987, we established a protocol to obtain morphometric and health data on all seven diurnal lemur species. A trained team of Malagasy technicians capture individuals using remote injection techniques, whereby a Telinject blow gun or CO_2-powered rifle is used to tranquilize individuals with Telazol administered with lightweight darts (Glander et al. 1992; Wright 1995). Researchers, technicians, and veterinarians measure, collect samples from, and mark adult animals with a nylon collar and individual identification tags. Since 1999, captured animals also received a subcutaneous microchip (AVID, HomeAgain®) for permanent identification. While animals are tranquilized, the team uses a checklist developed to record information on general physical condition, body mass, and reproductive state (Glander et al. 1992). Dental molds are taken; physical measurements are recorded; and hair, fecal, blood, and external parasite samples are collected. We used data including body weights, canine eruption patterns, general tooth wear, female nipple length, and presence or absence of descended testes to assign age categories to all known study individuals (Johnson et al. 2005; Baden et al. 2008; Erhart and Overdorff 2008a; Wright et al. 2008a). Actual ages are known for most animals from recorded births. For individuals whose birth date is uncertain (i.e., individuals in the population since before 1986 or immigrants from other groups), Jernvall and King developed an accurate method to determine age by comparing year-to-year tooth wear (King et al. 2005). Beginning in 2003, veterinarians now also conduct detailed health evaluations, compiling biomedical profiles of all lemur individuals (Junge and Louis 2005).

Microcebus rufus and *Cheirogaleus crossleyi* have been intermittently studied since 1990 (Wright and Martin 1995; Atsalis 1999a, 2008). Beginning in 2003, subcutaneously placed microchips have allowed us to monitor individual mouse lemurs during long-term studies (Blanco 2008; Blanco and Meyer 2009; Blanco and Rahalinarivo 2010; Durden et al. 2010; Zohdy et al. 2010; Deppe 2011). Mouse lemurs are captured in Sherman traps baited with bananas, then weighed, measured, and released at the capture site. Over 300 individuals have now been marked. Dental tooth casts reveal ages, and repeated captures allow data collection on body mass fluctuations associated with torpor patterns (Atsalis et al. 1996; Atsalis 2008), reproductive status (Blanco 2008), parasite prevalence (Zohdy et al. 2010), and noninvasive behavioral experiments (Deppe and Wright 2009; Deppe 2011).

4.2.3 Long-Term Phenology, Climate, and Terrestrial Vertebrate Data

Tree phenology, daily rainfall, and temperature data have been recorded since 1987. Tree phenology began with monthly monitoring of 100 trees of 25 lemur fruit species and was expanded in 1995 with monthly monitoring of trees from more than 71 species, representing 26 genera and 19 families (Clark and Clark 2006, 2010). Initially, tree diameter measurements (diameter at breast height, DBH) were taken every 5 years, but beginning in 2004, DBH measurements are taken every 6 months (Clark et al. 2003) to correlate tree growth with rainfall. Maximum and minimum temperature and rainfall data are taken at 06:00 h each day with a team of technicians responsible for accuracy. Camera trap data are taken in distant regions of the park to monitor carnivores and terrestrial vertebrates (Gerber et al. 2010).

4.2.4 Database Management

Long-term data collection and management requires standardized protocols. The following are areas where protocols are in place: (1) permanent identification of individuals for behavioral observation and census, (2) lemur capture data including weights, measurements, and biomedical data, (3) focal lemur sampling, (4) tree phenological data, (5) daily temperature minima/maxima and rainfall, (6) ad libitum observations of predation, reproduction, and intergroup aggression, (7) GIS data for mapping, and (8) lemur fecal sample data. The phenology and climate data are archived and accessible to researchers at Centre ValBio and will soon be available on the ICTE/Centre ValBio website (http://icte.bio.sunysb.edu). Data from projects under the supervision of Dr. Wright are transcribed from field notebooks into Excel spreadsheets, by local research technicians with oversight by the CVB Chief Technical Advisor or US students at SBU with postdoctoral oversight. Data from other projects are the responsibility of the project's principal investigators. Three years after a researcher has terminated data collection, the data can be transferred into the Centre ValBio central database and made available to CVB researchers (with proper citation assured).

4.2.5 Research Highlights from Long-Term Data

Since 1986, the principal goal of primate research at Ranomafana has been to understand the factors driving the behavioral ecology of lemurs in a species-rich community. Our research has focused on particular species that have been the subjects of intensive study over 20+ years, as well as community level analyses to understand the effects of competition, predation, and habitat quality on species richness and on relative abundance. Further, the mixed history of anthropogenic disturbance has allowed comparative work to elucidate the effects of disturbance on lemur physiology, behavioral ecology, and community structure. However, for this chapter we will concentrate on population changes documented over decades of observation.

4.3 Population Ecology

4.3.1 Flexibility of Behaviors

Many social behaviors were not observed until after many years of study. Female takeovers of groups, male lethal aggression from other males, and simultaneous immigrations of related males into groups were not observed in the first 10 years of studying *P. edwardsi*, but were observed in the next decade (Morelli et al. 2009). After years of losing track of focal study groups, continuous long-term observations confirmed that *E. rufifrons* groups seasonally expand their range and travel over 4,000 m to find fruit (Erhart and Overdorff 2008a). Likewise, when *P. simus* group size began to decline in 2003, we began to observe patterns of male disappearance, as well as females' (and their offspring) migrations and wanderings for 3 months before returning to the original territory. This migration behavior was not seen in the first decade (CVB unpublished census data; Wright et al. 2008b). In addition, while breeding out of the birth peak had been observed early on in *E. rubriventer* (Overdorff unpublished data), it was not until almost 20 years of data were analyzed that it was determined that they have been observed to breed in eight different months of the year (Tecot 2010).

4.3.2 Lemur Group Size, Composition, and Social Organization

Social groupings have long been investigated in primates (Crook and Gartlan 1966; Eisenberg et al. 1972; Clutton-Brock and Harvey 1977) by correlating ecological factors to social organization (Janson 1992). For instance, it has been proposed that lemurs' relatively small group sizes may be due to nocturnal ancestry (van Schaik and Kappeler 1996) or smaller crowned fruit trees (Wright 1999). We initially reported that *P. edwardsi* have a multimale, multifemale social organization in groups of 3–9 individuals (Wright 1995). However, by 2003 we had observed every type of social grouping in this species with potential for all different types of mating systems. Moreover, we learned that group sizes can get as large as 11 (Pochron and Wright 2003). In contrast, we consistently found *E. rubriventer* in socially monogamous pairs accompanied by immature offspring (Merenlender 1993; Overdorff and Tecot 2006; Tecot 2008). Although previously described as pair-living (Tan 1999), *H. griseus* and *H. aureus* groups can contain two breeding females in habitats with abundant bamboo (Grassi 2002; Wright personal observation). Using the older mating system terminology did not reflect this flexibility and, as stated by Kappeler and van Schaik (2002), these groupings are really patterns of social organization. With that conceptual framework it makes sense that a high frequency of pair-living and small groups among lemurs may be a response to food resource scarcity and unpredictability (van Schaik and Kappeler 1996; Wright 1999), and may be linked to female dominance (Dunham 2008).

4.3.3 Dispersal

Understanding dispersal is critical to understanding population dynamics, but these data are difficult to collect. Long-term data on multiple groups make it possible to observe dispersal in long-lived primates. For *P. edwardsi,* we initially thought that only males emigrated from natal groups (Wright 1995). We have since observed emigration and immigration by both sexes (Morelli 2008), aggressive group takeovers by females (Morelli et al. 2009), and targeted aggression within and between groups (Wright 1995). Females disperse from their natal groups at a younger age than their male counterparts but male secondary dispersal is more common (Morelli et al. 2009). Male dispersal occurs in the 3–5 months before the breeding season. During this time, males visit other groups and male scent marking frequencies and testicular volume increase (Pochron et al. 2005; Pochron and Wright 2005). Testosterone levels also increase (Tecot et al. 2010). Depending on breeding opportunities, males undergo natal dispersal between 3 and 9 years of age. Most adult *P. edwardsi* males transfer at least three times in their lifetimes (Morelli et al. 2009).

In contrast, *E. rufifrons* males in Ranomafana transfer only once in their lifetimes, typically at 3–5 years old and just before the breeding season. Immigrant males are often accepted without aggression and become social partners of one adult female for 3–6 years, mating preferentially with her (Overdorff 1993, 1998; Erhart and Overdorff 1998). Female dispersal has not been seen in *E. rufifrons*, but groups may fission along matrilineal lines (Overdorff et al. 1999; Erhart and Overdorff 2008b), a behavior which differs from *Eulemur* groups in western Madagascar (Wimmer and Kappeler 2002; Ostner and Kappeler 2004).

Observations of *E. rubriventer* revealed that both sexes disperse from their natal group at 2.5–3 years of age (Overdorff and Tecot 2006). Hostile replacement of resident adult females by nongroup females has been observed, but males have not been aggressively replaced. One dispersing female was seen with a new male in an adjacent territory 15 years later (Overdorff and Tecot 2006). Our data on the genetics of *E. rubriventer* offspring revealed that the resident male consistently fathers the offspring, and there are no data that indicate extra-pair copulations (Merenlender 1993).

Molecular and behavioral data show that dispersal in *Varecia* is not sex-biased, as within-sex relatedness scores were similar for males and females (Baden 2011). Mark–recapture studies of brown mouse lemurs (*M. rufus*) have shown that male membership in the population changes at a higher rate than female membership (Atsalis 2000, 2008), and that males can disperse relatively long distances (Karanewski personal communication; Zohdy personal communication). In all species thus studied, dispersal patterns ensure heterozygosity, an advantage for conservation strategies (Merenlender 1993; Morelli et al. 2009, Bradley and Baden personal communication).

4.3.4 Reproductive Hormones

P. edwardsi, E. rubriventer, and *M. rufus* fecal hormone profiles have been developed (Tecot 2008, Tecot et al. 2009; Blanco and Meyer 2009). In *P. edwardsi* and *E. rubriventer*, estradiol, progesterone, testosterone, dihydrotestosterone, and cortisol are being measured to determine the ovarian steroid fecal metabolites that characterize reproduction. Progesterone levels can reliably indicate pregnancy in these species, and estradiol levels reliably indicate fetal sex (Tecot et al. 2009). As expected, patterns of change in fecally excreted steroid levels during the reproductive season in *M. rufus* showed estradiol (E-2) levels were elevated around estrus, whereas progesterone levels were highest during late pregnancy and around parturition (Blanco 2008; Blanco and Meyer 2009). Blanco (2008) documented moderate estrous synchrony among female mouse lemurs, with clusters of females showing strong estrous synchrony. Two females showing signs of abortion or perinatal death of offspring also showed renewed vaginal swelling in late December, suggesting that some form of polyestry (i.e., as reproductive compensation for fetal loss) exists at RNP (Blanco 2008). With these baselines and proof of concept established, we can now investigate questions associated with development, sexual relationships, and seasonal breeding.

Hormonal studies of dominance rarely investigate inter-sexual relationships. To determine whether female dominance might be mediated by hormonal levels, we investigated androgens (dihydrotestosterone and testosterone) in male and female *P. edwardsi* (Tecot et al. 2009). While DHT levels were higher in males than in females, there was no significant sex difference in testosterone levels. Similar testosterone results were found in *M. rufus*. These results differ from those found for all other mammals studied to date, in which male testosterone levels are consistently higher than female levels, with the exception of the female-dominant rock hyrax (Koren et al. 2006). In other masculinized mammals such as the hyena and ring-tailed lemur, androstenedione is elevated in females, but testosterone levels remain higher in males. This finding may have important consequences for understanding sex differences in lifespan and senescence. Maintaining high testosterone levels may explain why mammalian males frequently have shorter life expectancies than females, but testosterone burden may not explain the sex differences in lifespan in *P. edwardsi*. However, dispersal season testosterone levels increase significantly in both sexes, and if males continue to disperse throughout their lives and females do not, testosterone levels may still contribute to shorter male lifespan (Tecot et al. in prep.).

4.3.5 Reproductive Success

Obtaining lifetime reproductive success data from wild primates is possible for females who have been followed throughout their lifespans (Bronikowski et al. 2011).

By coupling life-long observations with genetic evidence, calculating male reproductive success is now possible. Currently, we have lifetime reproductive success for two females and one male *P. edwardsi*. One female, killed by a fossa at age 32, gave birth to 13 offspring (7 males and 6 females). Five of these animals lived to reproductive age with two males living to emigrate from their natal group (Pochron and Wright 2003; King et al. 2005, 2011). A second female who died at 16 had 7 offspring (3 males and 4 females). Three males and one female survived to reproductive age; the males migrated to breeding groups and the female reproduced in her natal group after her father transferred. Genetic evidence provides a measure of lifetime reproductive success for one male who produced offspring in two groups before he was killed by an immigrant male during a group takeover at age 19. He fathered 14 offspring, 9 females and 5 males, in one group with 4 male and 3 female offspring surviving to reproductive age. Following a second transfer, he sired a 15th offspring, which disappeared, a probable infanticide, after his father was killed. Without continuous long-term data collection we would not be able to have these data on lifetime reproductive success in even these few individuals.

In many primates, heavier females have more surviving offspring (Altmann 1980; Terborgh and Janson 1986). We also see this trend in lemurs. *P. edwardsi* females who were heavier during the previous mating season were significantly more likely to give birth in the following birth season than lighter females (Morelli et al. 2009). Habitat disturbance appears to have a disproportionate impact on the body mass of female *P. edwardsi*. A comparison between Talatakely (logged) and Valohoaka (unlogged) revealed that adult females but not males living within the unlogged forest weighed significantly more than those females living in the disturbed forest (Arrigo-Nelson 2006). When males and females were compared within sites, significant differences in body mass were found only at the disturbed forest site. Given the climatic and reproductive synchrony of the two study sites, and the fact that body mass is positively associated with reproductive success in some primates (Stevenson 2005), these data suggest that differences in *P. edwardsi* feeding behavior and nutrient intake may affect future reproductive success.

4.3.6 Health and Parasites

Although we follow many species daily, we rarely see signs of illness. Over the years, we have seen a wide range of effects of fighting and predation attempts. Wounds are relatively common during the breeding season and we have observed one or both testicles missing in individuals of *E. rufifrons* and *P. edwardsi*. In *P. edwardsi, E. rubriventer*, *E. rufifrons*, and *M. rufus* individuals have been found functioning with sight in only one eye (Erhart and Overdorff 2008a). Older individuals have worn teeth and in two individuals of *P. edwardsi* we have seen healed abscessed teeth (King et al. 2005; Wright et al. 2008a). In *E. rufifrons,* *E. rubriventer,* and *V. variegata* we have captured very old individuals with teeth worn to the gums.

The diversity and prevalence of parasites has been found to influence health and fitness in other mammals (Hart 2007; Price and Kirkpatrick 2009). The variation among individuals and the transfer of parasites among lemur species is presently unknown, as is the incidence of disease that parasites cause. A variety of roundworms and pinworms have been observed in lemur intestines, but further study is necessary (Junge and Louis 2005; Junge and Sauther 2006; Irwin and Raharison 2009). Our initial studies suggest that one species of parasite may be found on many species of these sympatric lemurs, but there are differences in prevalence among species. For example, *Makialges* spp., a parasitic mite, was abundant on *P. edwardsi* (80%), *P. simus* (67%), and *H. aureus* (83%), yet rare on *E. rufifrons* (3%) and *V. variegata* (14%), and absent on *H. griseus* (Wright et al. 2009; Hogg et al. in press). Large group size has been proposed as a factor for higher parasitism (Freeland 1976), but the largest groups in *E. rufrifrons* had the lowest incidence. Large body size might be more attractive for parasites than smaller body size (Freeland 1976), and indeed larger species had the most ectoparasites.

Additionally, lemurs may have species-specific parasites. For example, *M. rufus* is ecto-parasitized by three tick and one louse species. This louse, *Lemurpediculus verruculosus*, is likely a brown mouse lemur-specific parasite (Durden et al. 2010). A new species of wingless, bloodsucking hippoboscid fly, *Allobosca crassipes,* was recently described as a parasite of *P. edwardsi* and *V. variegata* (Vaughn and McGee 2009).

Parasites may increase in primates living in forests with anthropogenic disturbance and be correlated with disease and decreased fitness (Dobson and May 1986; Chapman et al. 2009). We have some evidence that this trend holds true in the Malagasy rainforest. Wright et al. (2009) found that habitat disturbance may account for high ectoparasite loads in *P. edwardsi*. Endoparasite prevalence in *M. rufus* in 2007 was higher in more disturbed habitat than in the less disturbed habitat. In 2008 and 2009 this difference disappeared, and linking habitat disturbance with lemur parasites should be done with caution. Again, long-term studies allowed us to differentiate between minor fluctuations and the consistent correlations with factors such as climate, body size, group size, or habitat disturbance factors.

4.3.7 Mortality: Adults and Infants, and Infanticide

Adult mortality is generally caused by predation, rather than by illness, wounds, or infections (see Sect. 4.4.1). Adult mortality for the lemurs at Ranomafana is low, as would be expected for long-lived primates (Erhart and Overdorff 2008a; Pochron et al. 2004). In contrast, infant mortality is high (overall approximately 50%) and food stress due to environmental unpredictability may account for some mortality (Wright 1999; Richard et al. 2002).

Long-term observations have also allowed us to document infanticides and infanticide attempts. The killing of infants of up to 2 months of age has been observed in *P. edwardsi*, with both immigrant males and females as perpetrators (Wright 1995; Erhart and Overdorff 1998; Pochron et al. 2004; Morelli et al. 2009). Over 24 years, there have been 9 infanticides out of 60 births (15%) associated with immigration in 4 groups of *P. edwardsi* (Morelli et al. 2009). These infanticides have brought the mothers back into estrus a year earlier in a species that gives birth every other year, providing males with the opportunity to improve their reproductive success (Hrdy 1977; Erhart and Overdorff 1998). A potential infanticide attempt may have also been observed when a *V. variegata* male approached and then entered an unguarded nest, knocking two young infants to the ground over 10 m below; neither infant survived the fall. To date, we have not seen infanticide in either *E. rufifrons* or *E. rubriventer* (Durham 2003; Erhart and Overdorff 2008a; Tecot 2008).

4.3.8 Lifespan

Our long-term research has allowed us to document long lifespans (over 30 years old) in individuals of all the diurnal species of wild rainforest lemurs, regardless of body mass (Erhart and Overdorff 2008a; Baden 2011; King et al. 2011). For *P. edwardsi* we documented a dramatic difference in the maximum lifespans of males and females. Since 1986, few old males have been observed whereas three females are known to have lived beyond 30 years of age. Therefore, males cease contributing genetically to the population after about 20 years, whereas we have no evidence that old females cease reproducing (Wright et al. 2008a; King et al. 2011). In *E. rufifrons*, males over 10 years old were peripheralized and replaced in breeding position by younger nonnatal males (Overdorff et al. 1999). Aged males were burdened with handicaps; one had only one eye, another only partial use of the right hand, another had lost both testicles, and two had visible limps (Overdorff et al. 1999; Erhart and Overdorff 2008a).

In *E. rufifrons* older individuals have been seen, and one functioned with only one eye. These scars and wounds are male-biased and indicate violent male–male aggression, which may account for the shorter lifespan of males as observed in many primate species (Bronikowski et al. 2011). In *E. rubriventer* older individuals have been seen, with one female a minimum of 17 years of age (Tecot 2008), though scars and wounds in this pair-bonded species are generally not evident (Tecot personal observation). In *V. variegata*, both older males and older females were observed in the population at Mangevo, suggesting that male–male aggression may not be as pronounced in this species (Baden 2011). These individual life histories add up, over time, into a better understanding of the evolution of social organization in each species.

With new dental technology that has become available in the past 5 years, Zohdy has documented that wild brown mouse lemurs survive up to 9 years of age and do not experience any of the physical symptoms of senescence that are seen in captive congeners (Bons et al. 2006). On the basis of dental wear, we have found that many brown mouse lemurs survive past 5 years (the age of the onset of senescence in captivity) and these aged individuals represent 9% of those captured. It is possible that few mouse lemurs reach old age because of high predation rates (Goodman et al. 1993; Karpanty 2006; Karpanty and Wright 2007; Sefczek 2009; Deppe 2011).

4.3.9 Nutritional Ecology

In contrast with many sympatric monkey diets, rainforest lemur diets are very diverse (Terborgh 1983; Struhsaker 1997). Studying these species over the long term and in different environments revealed the flexibility in diet within certain constraints. Many lemurs have anatomical specializations such as a large cecum or a long foregut to better digest bamboo or leaves from other plants. For example, *Avahi* and *Lepilemur* both eat leaves, but *Avahi* chooses leaves with tannins, whereas *Lepilemur* chooses leaves with alkaloids (Ganzhorn et al. 1985). The three bamboo lemurs all consume nearly 95% bamboo, but two species can tolerate large amounts of cyanide in the shoots (Glander et al. 1992; Tan 1999; Ballhorn et al. 2009). Unlike any other lemur species, *P. simus* with its strong jaws and big teeth has physical capabilities to open the tough culm of the bamboo and eat the pith (Tan 1999; Vinyard et al. 2008; Yamashita et al. 2009), and *H. griseus* eats primarily bamboo leaf petioles. *Daubentonia* eats beetle larvae extracted from dead wood, a niche taken by woodpeckers in other continents (Cartmill 1974). Recently, a comparative study of the four diurnal frugivores revealed that there is much more specialization in fruit choice than previously thought, with the fruit of entire plant families exploited by only one diurnal lemur species in the forest (Wright et al. 2011).

Our most comprehensive dietary studies have been conducted on *P. edwardsi*. Early work by Hemingway (1998) on the Vatoharanana population revealed that they ate leaves, fruits, and seeds in nearly equal proportions. More recent work by Arrigo-Nelson (2006) has added comparative data on sifaka populations at Talatakely (disturbed forest) and Valohoaka (undisturbed forest). Selective logging has altered species composition in the disturbed forest; in response, sifakas have altered their diet by consuming plant taxa in disproportion to their abundance in the forest and by relying more heavily on food from plant life forms other than trees. Disturbance limits the ability of sifakas to consume fruit and seeds, their preferred food and, as they appear to consume leaves in an effort to replace these missing foods, this creates a discrepancy in the nutrient intake of sifakas living within this habitat (Arrigo-Nelson 2006). As fruit availability was found to be lowest during the most climatologically and reproductively harsh months of the year, we hypothesize that this discrepancy may severely impact infant survival and, with it, the reproductive success of sifakas living in disturbed forest habitats.

Habitat differences in diet are evident in *E. rubriventer* as well. In a 19-month study in Talatakely and Vatoharanana, Tecot (2008) found that during the scarce season, dietary overlap decreased and the proportion of the diet composed of fruits, flowers, and leaves differed between the two sites. Seasonal changes in behavior and diet were greater in the undisturbed site, indicating more flexibility in that site. Most notably, during an entire month of the scarce season, animals in the disturbed site spent 100% of their time eating unripe fruit from the invasive Chinese guava (Tecot 2008).

Atsalis (1999, 2008) conducted a 17-month feeding study on *M. rufus* and found that this species fed on a wide variety of fruits, mistletoe berries, and insects, especially beetles. The seeds of *Bakerella* spp., epiphytic semiparasitic mistletoes high in lipids, were present in 42% of fecal samples that contained fruit and this food was consumed year-round irrespective of habitat-wide fruit availability (Atsalis 1999, 2008). This abundant mistletoe is eaten by many lemurs and has been documented to be a fallback food in both disturbed forest areas and forest fragments (Arrigo-Nelson 2006; Irwin 2006).

4.4 Community Ecology

4.4.1 Predators on Lemurs

Predation is a major selective factor in primates and major cause of mortality (Isbell 1994; van Schaik 1983; Zuberbühler 2007). Predators of Ranomafana lemurs include birds, mammalian carnivores, and snakes (Table 4.3). Two raptors,

Table 4.3 Known predation on lemurs in Ranomafana National Park

Lemur species	Carnivore	Boa constrictor	Raptor
Avahi peyrierasi	Not observed	Not observed	*Accipiter*++ *Polyboroides* ++
Cheirogaleus crossleyi	*Galidia*++	Yes	*Accipiter* ++
Cheirogaleus sp. nov.	Unk.	Unk.	Unk.
Daubentonia madagascariensis	Not observed	Not observed	Not observed
Eulemur rufifrons	*Cryptoprocta*+	Not observed	*Accipiter*++
Eulemur rubriventer	*Cryptoprocta*+	Not observed	*Accipiter*+
Hapalemur aureus	Not observed	Not observed	Not observed
Hapalemur griseus	Not observed	Not observed	*Accipiter*+++ *Polyboroides* ++
Lepilemur microdon	Not observed	Not observed	Not observed
Microcebus rufus	*Galidia*++	Yes	*Accipiter*++ *Polyboroides*++
Prolemur simus	Not observed	Not observed	*Accipiter*++
Propithecus edwardsi	*Cryptoprocta*+++	Not observed	Not observed
Varecia variegata editorium	*Cryptoprocta*++	Not observed	*Accipiter*+

Wright et al. (1997), Wright and Martin (1995), Wright (1998); Karpanty and Wright (2006), Erhart and Overdorff (2008a), Baden (2011), Deppe (2011)

+ observed once, ++ 2–14 observations, +++ 15–30 observations

Table 4.4 Changes in *Propithecus edwardsi* population size over time in relation to the observed predation events by *Cryptoprocta ferox*

Time step	Population density	# Predation events	Comments
1990–1995	7 ind/km^2	3	Two adult and three immature members of three groups
1996–2000	5 → 12 ind/km^2	0	No known predation events
2001–2005	12 → 3–6 ind/km^2	5	Two immature, two old-age and one prime-age adults from two groups
2006–2010	6 → 3 ind/km^2	6	Two immature, three old-age and one prime-age adults from four groups; extinction of two study groups in 2007

The oscillation in population size in relation to known predation events indicates that fossa predation is a major cause of population size change for *P. edwardsi*. Data are generated from one study site, Talatakely over 20 years with observations of known groups, direct observations of corpses with indications of fossa predation and long-term census data. *Arrows* within population density column indicate trends in size change within the 5-year interval

Henstii's goshawk (*Accipiter hensteii*) and the Madagascar harrier hawk (*Polyboroides radiatus*) (Karpanty and Wright 2007) eat small-bodied nocturnal (*C. crossleyi, M. rufus,* and *A. peyrierasi*) and diurnal (*E. rufifrons* and *H. griseus*) lemurs. The lemurs preferred by raptors, *A. peyrierasi* and *H. griseus*, weigh approximately 1 kg (Karpanty 2006), suggesting that the body mass, not activity cycle, account for the preference.

A major predator of lemurs is the fossa (*Cryptoprocta ferox)*, a viverrid carnivore that weighs between 8 and 12 kg, is agile in the trees, and hunts diurnally and nocturnally. The fossa has made a major impact on the population of the largest lemur in Ranomafana, *P. edwardsi* (Table 4.4; Wright 1995, 1998; Wright et al. 1997; Irwin et al. 2009) as well as on *V. variegata* in recent years (Baden personal communication). Over 20 years, it seems that predation events happen during temporally clumped periods that cut population densities by up to 50%. Fossa predation has caused the extinction of two long-term study groups and independent censuses of the study population support the tremendous impact on population density (Table 4.4; Irwin et al. 2009; see also Kappeler and Fichtel 2011). *Galidea elegans*, a diurnal mongoose weighing less than a kilogram, has been observed eating and stalking *M. rufus* and *C. crossleyi* (Wright and Martin 1995). Finally, boa constrictors (*Sanzinia madagascariensis*) have been mobbed by *Microcebus* and are known to eat *Cheirogaleus* (Wright and Martin 1995; Deppe 2011). Data on all of these rare events can only be accumulated during long-term studies.

4.4.2 Interspecific Aggression

Interference competition by close relatives has been cited as an important selective force in animal behavior (Case and Gilpin 1974; Terborgh 1983), and in a rainforest with 13 sympatric lemurs we would expect this to be the case. Results from observations over 25 years show that one strategy is for each lemur species to specialize on different fruit species (Wright et al. 2011). Yet interspecific aggression among lemurs exists, including agonistic vocalizations, chasing, and biting. These interactions occur during the season of ripe fruit availability (Overdorff and Tecot 2006; Wright personal observation). Since 88% of agonistic interactions among *E. rufifrons*, *E. rubriventer*, *P. edwardsi,* and *V. variegata* occurred over ripe fruit during the high season for fruit availability (Overdorff et al. 2005; Overdorff and Tecot 2006), interference competition for high quality fruit is the most likely driver of this agonism. *E. rubriventer* retreated in every case in the resource abundant season, but did not retreat in the few agonistic encounters which occurred with *P. edwardsi* and *E. rufifrons* during the scarce fruit season (Overdorff and Tecot 2006). *V. variegata* will often successfully defend fruit trees against all other lemur species (Balko 1998; Andrea Baden personal observation; Iris de Winter personal communication). The ruffed lemurs are most often the winner of any competition (the raucous barking of a whole group deters other species), even though the sifakas are twice their size. Congeners seem to compete most, and *E. rubriventer* and *E. rufifrons* have 0.04 aggressive interactions/hour, while *V. variegata* and *E. rubriventer* contest 0.006/h and *P. edwardsi* and *E. rubriventer* contest 0.003/h. The hierarchy established by % contests won is *V. variegata* (obligate frugivore), *E. rufifrons*, *P. edwardsi,* and *E. rubriventer* (Overdorff and Tecot 2006). During 3 months of fruit scarcity in 2010, *E. rufifrons* initiated and won 7 out of 7 contests with *E. rubriventer*, and 6 out of 7 aggressive interactions were adjacent to fruit trees (Iris de Winter personal communication).

Interference competition may also be playing a role in the population dynamics of *Eulemur* species. Across three long-term study sites, population density changes are inverse between *E. rufifrons* and *E. rubriventer*; when *E. rufifrons* population densities increase, *E. rubriventer* density decreases and vice versa (Fig. 4.2). Further evidence that competition for food resources is driving interspecific behavior, not predation, is that polyspecific associations are rare. This is contrary to observations of rainforest monkeys in Africa and South America where several species often feed together for protection against predators (Terborgh 1983; Holenweg et al. 1996).

4.4.3 Seasonal Breeding

Seasonal breeding is one female strategy to limit extra-pair copulation by males (Wright 1999). In the first decade, Ranomafana researchers suggested strict seasonality in lemur breeding (Wright 1999). Long-term results revealed that in *P. edwardsi, P. simus, V. variegata,* and *E. rufifrons* all females in a group and usually all those in the [study] population come into estrus within the same week for a day or two, with older females breeding first. In contrast, Tecot (2010) found that reproduction in *E. rubriventer* is not strictly tied to photoperiod, with births

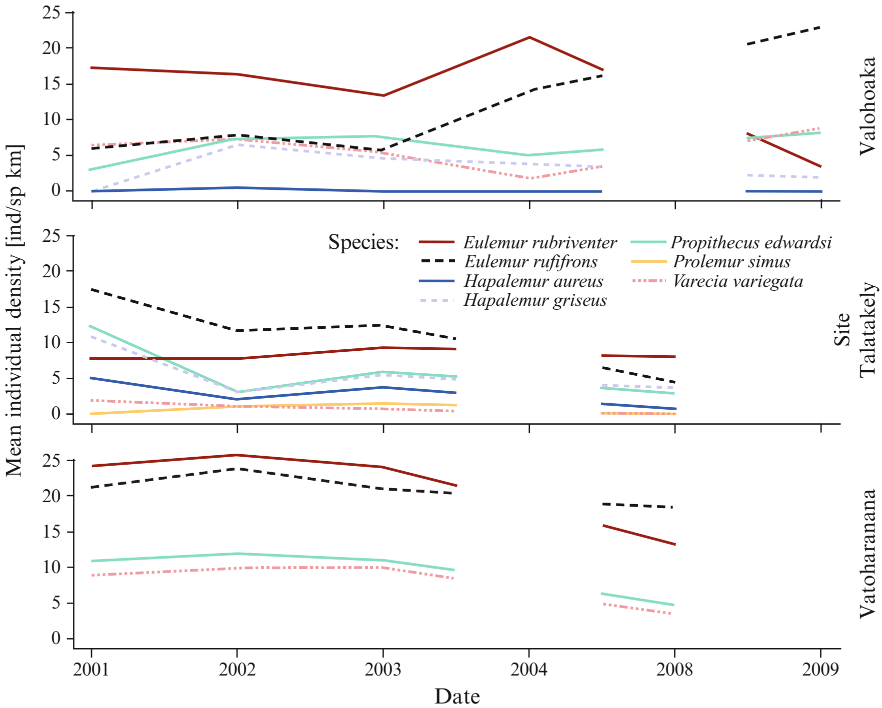

Fig. 4.2 Population densities of diurnal lemurs in Ranomafana National Park from 2001 to 2009 in three different study sites (Talatakely, Vatoharanana, and Valohoaka) within the park

occurring in eight different months. However, only infants born in the "seasonal breeding" window (with food abundance prebreeding) actually survived.

Another selective advantage to infants born at the same time is that synchronous births could be a successful strategy to satiate predators (Boinski 1987). *Varecia variegata* are strict seasonal breeders (Baden 2011) and use a boom or bust strategy (Ratsimbazafy 2006; Baden 2011). At Mangevo, a population of over 80 individuals, *V. variegata* reproduction was only observed once in 6 years of continuous observation. In 2007, 6 out of 7 adult females in the Mangevo population gave birth to twins or triplets (Baden 2011). This synchronous breeding at 6–8 year intervals has been observed in *Pongo pygmaeus* and was associated with fruit masting (Knott 1998). Preliminary analysis of plant phenological data from Ranomafana suggests that fruit availability is also the driver of *V. variegata* synchronous breeding (Wright unpublished data).

M. rufus has a breeding season from mid-October to mid-November, during which females have estrous periods of 5 days or more (Blanco 2008; Blanco and Rahalinarivo 2010), although some variation in the timing of breeding exists. Most females are gestating by mid- to late November (Atsalis 2008), although some are not gestating until December (Blanco 2008). Thus, the onset of estrus may not be completely controlled by photoperiod (Perret and Aujard 2001). There is no evidence for more than one litter a year (Atsalis 2008; Blanco 2008; Blanco and Rahalinarivo 2010).

4.4.4 Habitat Disturbance

To understand the effects of habitat disturbance on lemur demography, we compared life histories of lemurs at sites within the park with high and low levels of human disturbance. The high level disturbance site (Talatakely) was selectively logged for valuable hardwoods between 1986 and 1989, with the intrusion of invasive plant (Chinese guava) and animal (*Rattus rattus*) species (Arrigo-Nelson 2006; Brown and Gurevitch 2004; Laakkonen et al. 2003). The intermediate disturbance site (Vatoharanana) had less than 1% of the study area trees removed during the 1986–1989 period (approximately 1,000 trees; Balko 1998). The low level site (Valohoaka) is considered sacred by local villages and no known timber extraction has occurred (Herrera et al. 2009; Balko 1998). In contrast to the forests north of the park boundaries, there has been very little hunting within Ranomafana forest since the park was established (Lehman et al. 2006; Golden 2009).

The strictest frugivore, *V. variegata*, did not occur in the high disturbance level site (Talatakely) where the big canopied fruit trees were removed (Balko and Underwood 2005). Compared to forests in South America and Africa, Madagascar rainforest tree growth is slow (Struhsaker 1997; Ganzhorn et al. 1999; Clark and Clark 2010), and this delayed regeneration of the forest may impact lemur demography for decades. In the 20 years since selective logging, no one group of *V. variegata* has since arrived in the high disturbance site. Similarly, 10 years postselective logging, the effects on the physical structure of the forest, its species composition, and availability of *P. edwardsi* foods have continued at the highly disturbed site (Arrigo-Nelson 2006). Sifakas in the disturbed forest consumed foods from tree taxa in disproportion to their abundance and relied more on vines and epiphytes than counterparts at the unlogged site. As a consequence, intake of fats and sugars was lower for sifakas at the previously logged site. These differences in food availability and nutrient intake are reflected in significant differences in the body weights of female sifakas between sites and significant male–female differences in body mass in previously logged forest. Sifakas in the disturbed forest spent significantly less time interacting socially and significantly more time feeding and self-grooming than animals in the undisturbed forest. That all of these differences were greatest during lean season only makes their potential impact on the sifaka population of greater consequence. In the long term, these differences may lead to differences in group cohesion, survival, and/or reproductive success (Arrigo-Nelson 2006).

To investigate the impact of habitat disturbance on *E. rubriventer* demography, Tecot (2008, in press) collected data simultaneously on the red-bellied lemur populations in heavily logged and minimally logged sites. Results again indicate that logging has reduced the structure, species composition, abundance, and predictability of red-bellied lemur foods within the disturbed forest site. Additionally, red-bellied lemurs at the disturbed site were less active (Tecot 2008), bred out of peak season, and had higher infant mortality (Tecot 2010, in press).

High levels of cortisol have been implicated in reduced fitness (Bonier et al. 2009), and the effects of stress on lemur demography is being investigated (Tecot 2008). In a comparative study of stress hormones in adult *E. rubriventer* in selectively logged versus minimally logged sites, patterns of cortisol excretion were similar in both sites, but those in the undisturbed site showed little response to variation in food availability and rainfall. In contrast, at the disturbed site, fecal cortisol levels were significantly higher when fruit was scarce (parturition and early lactation) compared with when fruit was abundant (prebreeding season). Contrary to the Cortisol-Fitness Hypothesis (Bonier et al. 2009), cortisol levels were higher in the undisturbed site. Lower cortisol levels, minimal changes in hormones and behavior (Tecot 2008), and higher infant mortality (Tecot 2010) in the disturbed site indicate that there may be down-regulation of the cortisol stress response where environmental stress is prolonged (Tecot 2008, in press).

4.4.5 Trends in Population Densities of Lemurs

Over the past 20 years, we have documented population size changes across three sites with different histories of anthropogenic disturbance (Table 4.5; Fig. 4.2). These data allow us to determine changes, rather than trends, in population size over time. Our results indicate that changes in population size vary across sites, as

Table 4.5 Estimated population size of lemurs in Ranomafana National Park

Lemur species	Estimated density (ind/km^2) ± SE	Estimated population size ($ind/330\ km^2$ of RNP forest)	Estimated biomass ($kg/330\ km^2$)
Avahi peyrierasi	9.65 ± 1.92	3,185 ± 633	3,058 ± 607
Cheirogaleus crossleyi	13.48 ± 3.91	4,448 ± 1,291	1,557 ± 452
Daubentonia madagascariensis	rare	200 ± 50	600 ± 150
Eulemur rufifrons	6.75 ± 1.63	2,228 ± 537	4,902 ± 1,181
Eulemur rubriventer	5.46 ± 0.70	1,802 ± 231	4,325 ± 554
Hapalemur aureus	0.21 ± 0.14	69 ± 47	124 ± 85
Hapalemur griseus	2.48 ± 0.48	818 ± 159	614 ± 119
Prolemur simus	0.85–1.23 at one site in 2002–2003	20 ± 5	56 ± 15
Lepilemur microdon	0.99 ± 0.37	327 ± 128	327 ± 128
Microcebus rufus	23.52 ± 4.07	7,762 ± 1,343	233 ± 40
Propithecus edwardsi	4.73 ± 0.76	1,561 ± 251	9,366 ± 1,506
Varecia variegata	2.23 ± 0.81	736 ± 267	2,429 ± 1,082

These data are based on transect surveys from 2004 to 2009 (S.E. Johnson, F. Ratelolahy, P.C. Wright, J.P. Herrera). Species in bold are critically endangered (IUCN Redlist) would be expected of meta-populations in a varying landscape (Hanski and Gilpin 1991; Table 4.5). Oscillating population densities of *E. rufifrons* and *E. rubriventer* suggest that these changes in population density may reflect some degree of congeneric competition (Overdorff et al. 1999; Erhart and Overdorff 2008a). In comparison, in Vatoharanana, the density of *E. rubriventer* and *V. variegata* increased over the study years from 15 to 25 individuals per km^2 and from 2 to 10 individuals per km^2, respectively, while the density of *P. edwardsi* remained at 11 individuals per km^2. Similar trends have been observed in the critically endangered *V. variegata*. In the low disturbance site, their population density has oscillated but increased slightly overall. Population density in the intermediate disturbance site increased gradually between 1990 and 2003, but seems to have declined again by 2008. Overall population densities are low (2–10 ind/km^2). In *P. edwardsi* and *V. variegata*, we have seen an increase in population densities at Valohoaka, but population densities appear to be declining at the intermediate and high disturbance sites, which can perhaps be partly attributed to predation events or fruit scarcity (Arrigo-Nelson 2006; Irwin et al. 2009). Long-term data show that the species with declining populations in normal circumstances have larger home ranges and larger group sizes (Morriss et al. 2009). Theoretically this suggests that food constraints are more important than predation, as larger group size provides more eyes and ears for detecting predators (Hamilton 1964; van Schaik 1983; van Schaik et al. 1983).

4.5 Conservation

4.5.1 Successes and Ongoing Problems

RNP has been designated as a conservation priority (Kremen et al. 2008) and in 2007 was declared a World Heritage Site. We have successfully integrated education, health, and economic assistance programs with biodiversity research and habitat protection goals (Wright 1997; Wright and Andriamihaja 2002; Lovejoy 2006). An evaluation of the educational impact has shown that local people have experienced a change in attitude (Korhonen 2006). Attempts to correlate human impact on lemur populations have shown that human immigration into the park's peripheral zone is correlated with increased deforestation rates (Brooks et al. 2009). Villages which are the farthest from the road tend to encroach further into the park than do the on-road villages (DeFries et al. 2010). Moreover, the park itself has maintained edges with minimum invasion by exotic plants (Brown et al. 2009). Eco-tourism to visit the park has been a great boon to the local economy. However, the 30,000 tourists do have negative consequences on habitat and breeding birds (Razafimahaimodison 2003). Better management of tourism is in process. Satellite photos suggest that there is minimum forest destruction since 1991, when the park was gazetted, but the recent political instability is worrisome.

4.5.2 Implications of Climate Change

Long-term data enable better understanding of the effects of climate change on rainforest ecology and lemur populations. Indeed, lemur observers with long-term research projects were among the first to gain evidence of the effect of climate fluctuations on mammal populations (Gould et al. 1999; Wright 1999, 2006). Using Madagascar climate data and the Centre ValBio long-term rainfall and temperature database, we discovered that dry seasons have become longer, and cyclones more frequent (Wright 2006). In particular, the November temperatures in 2007, 2008, and 2009 were over 30°C, much higher than ever previously recorded, and the gap between minimum and maximum temperatures has increased. But does this have an effect on lemur demographics?

Long-term demographic data show that older *P. edwardsi* mothers lose infants in years with extended hot, dry seasons (King et al. 2005). Further analysis shows that the average fecundity of lemurs was over 65% lower in El Niño years (Dunham et al. 2008). As El Niño years become more erratic and frequent (Fedorov and Philander 2000) this could lead to more extreme weather and increased impacts on biodiversity. The southern oscillation (ENSO) related to El Niño is known to cause drought (Thomson et al. 2003) and changes in vegetation indices (Ingram and Dawson 2005). Dunham et al. (2010) found that cyclones, ENSO phases, and rainfall levels affected the reproductive rates of *P. edwardsi*. Overall fecundity (defined as the number of offspring per female per year surviving to 1 year of age) was negatively associated with cyclone presence during gestation, and positively associated with colder ENSO phases during the second 6 months of life and during the period faced by mothers preceding conception. Wet season rainfall and intensity during gestation was negatively related to birth rates, and the number of drought months during lactation was negatively associated with first year survival. Finally, fluctuations in lemur stress hormones show an elevation of cortisol during the dry season (Tecot 2008; Tecot in press), which may ultimately impact reproduction. Longer dry seasons in consequent years could impact lemur populations negatively (Wright 2006; Dunham et al. 2008, 2010). The effects of ENSO events on population dynamics has also been seen in many species of New World monkeys (Wiederholt and Post 2010).

4.6 Summary and Conclusions

Most of the lemur species in Ranomafana were data deficient before we initiated our first studies in 1986. The virtue and vice of long-term research is that it is never complete. Here we have compiled a list of essential findings, the product of long-term research that has many times resulted in the reevaluation of earlier findings. Thus, over the years we established the number of species residing in RNP through the rediscovery of *P. simus* and the discovery of *H. aureus* and a potentially new species awaiting description: a high altitude species of *Cheirogaleus*. We have established demographic changes through time including life history events, mortality, lifespan, and dispersal patterns for *P. edwardsi*, *E. rufifrons*, *E. rubriventer*, *V. variegata*, *H. aureus*, *H. griseus*, *P. simus,* and to a lesser extent *M. rufus*. We have documented variability of social organization in each species, and we have described how populations recover after cyclones and droughts.

Furthermore, we have confirmed that lemur population densities vary over time, and that predation by raptors and mammalian carnivores can have a major impact on local lemur populations. We know that many lemur species are important to seed dispersal and thus to forest dynamics. Monitoring and measuring the long-term effects of habitat disturbance on lemur populations, we have evidence that selective logging may negatively impact population densities of *E. rufifrons, V. variegata*, and *P. edwardsi*, even a decade after the last logging disturbance. We have also determined that fertility of *P. edwardsi* females decreased during ENSO years and infants of older *P. edwardsi* females died in years with extended dry months.

Acknowledgments This research complied with all the laws of Madagascar and was authorized by Madagascar National Parks (MNP), CAFF/CORE, and the Madagascar Ministry of the Environment. The research was approved by the IACUC animal care committees of all research host institutions. The authors thank Benjamin Andriamihaja and the MICET and ICTE staffs who have expedited the research process and made our long-term work in Madagascar possible. For funding we acknowledge the Wenner-Gren Foundation (PCW), National Geographic Society (PCW), National Science Foundation USA (PCW BCS-0721233, PCW DBI-0829761, PCW DBI-0122357, SAN BCS-0333078, SRT BCS-0424234, EME SBS-0001351, ALB BCS-0725975), Earthwatch Institute (PCW and SAN), Primate Conservation Inc (PCW, SAN, ALB, MBB, AMD, RJ, TLM, SRT), The LSB Leakey Foundation (ALB), Primate Action Fund (PCW, SAN, SRT, ALB), The University of Texas at Austin (SRT), and SUNY-Stony Brook (PCW, SAN, SRT, SJK, ALB), Fulbright Foundation (SAN and ALB), American Society of Primatologists (SRT), PEO Foundation (SRT), AAUW (SRT), Saint Louis Zoo's FRC Committee (SAN), The University of Helsinki (PCW, SZ). We would also like to acknowledge our many research technicians: Georges Rakotonirina, Raymond Ratsimbazafy, and Remi Rakotovao, Georges René Randrianirina, Paul Rakotonirina, Georges Razafindrakoto, Dominique Razafindraibe, Armand Razafitsiafazato, Bernadette (Menja) Rabaovola, Laurent Randrianasolo, Rasendrinirina Victor, Rakotonirina A. Thierry Emile (Nirina), and Rakotoniaina Jean Félix (Rakoto), Razafindravelo Zafi, Solo Justin, and Telo Albert for their expert assistance following animals and collecting phenological data. Graduate students from the University of Antananarivo: Sahoby Ivy Randriamahaleo, Rakotonirina Laingonianina, Herifito Fidèle, Ralainasolo Fidy, and Andriamaharoa Hubert. P.C. Wright is grateful to Ingrid Daubechies for assistance with the figures and Patricia Paladines for her efforts and editorial assistance.

References

Altmann J (1980) Baboon mothers and infants. Harvard University Press, Cambridge, MA

Andriantompohavana R, Lei R, Zaonarivelo JR, Engberg SE, Nalanirina G, McGuire SM, Shore GD, Andrianasolo J, Herrington K, Brenneman RA, Louis EE Jr (2007a) Molecular phylogeny and taxonomic revision of the woolly lemurs, Genus *Avahi* (Primates: Lemuriformes). Spec Publ Mus Texas Tech Univ 51:1–59

Andriantompohavana R, Morelli TL, Behncke SM, Engberg SE, Brennneman RA, Louis EE Jr (2007b) Characterization of 20 microsatellite marker loci in the red-bellied brown lemur (*Eulemur rubriventer*). Mol Ecol Notes 7:1162–1165

Arrigo-Nelson SJ (2006) The impact of habitat disturbance on the feeding ecology of the Milne-Edwards' sifaka (*Propithecus edwardsi*) in Ranomafana National Park, Madagascar. PhD thesis, State University of New York, Stony Brook

Arrigo-Nelson SJ, Wright PC (2004) Survey results from Ranomafana National Park: new evidence for the effects of habitat preference and disturbance on the distribution of *Hapalemur*. Folia Primatol 75:331–334

Atsalis S (1999) Diet of the brown mouse lemur (*Microcebus rufus*) in Ranomafana National Park, Madagascar. Int J Primatol 20:193–229

Atsalis S (1999a) Feeding ecology and aspects of life history in *Microcebus rufus* (Family *Cheirogaleidae*, Order Primates). PhD thesis, City University of New York, New York

Atsalis S (1999b) Seasonal fluctuations in body fat and activity levels in a rainforest species of mouse lemur, *Microcebus rufus*. IJP 20(6):883–910

Atsalis S (2000) Spatial distribution and population composition of the brown mouse lemur (*Microcebus rufus*) in Ranomafana National Park, Madagascar, and its implications for social organization. Am J Primatol 51:61–78

Atsalis S (2008) A natural history of the brown mouse lemur. Pearson Prentice Hall Publishers, New Jersey

Atsalis S, Schmid J, Kappeler PM (1996) Metrical comparisons of three mouse lemur. J Hum Evol 31:61–68

Baden AL (2011) Communal breeding in ruffed lemurs. PhD thesis, Stony Brook University, Stony Brook

Baden AL, Brenneman RA, Louis EE Jr (2008) Morphometrics of wild black-and-white ruffed lemurs [*Varecia variegata*; Kerr, 1972]. Am J Primatol 70:913–926

Bailey CA, Lei R, Brenneman RA, Louis EE Jr (2009) Characterization of 21 microsatellite marker loci in the Milne-Edwards' sifaka (*Propithecus edwardsi*). Conserv Genet 10:1389–1392

Balko EA (1998) A behaviorally plastic response to forest composition and logging disturbance by *Varecia variegata* in Ranomafana National Park, Madagascar. PhD thesis, State University of New York, Syracuse

Balko EA, Underwood HB (2005) Effects of forest structure and composition on food availability for *Varecia variegata* at Ranomafana National Park, Madagascar. Am J Primatol 66:45–70

Ballhorn DJ, Kautz S, Rakotoarivelo FP (2009) Quantitative variability of cyanogenesis in *Cathariostachys madagascarensis* – the main food plant of bamboo lemurs in southeastern Madagascar. Am J Primatol 71:305–315

Bergey C, Patel ER (2008) A preliminary vocal repertoire of the greater bamboo lemur (*Prolemur simus*): classification and contexts. Nexus 1:69–84

Blanco MB (2008) Reproductive schedules of female *Microcebus rufus* at Ranomafana National Park, Madagascar. Int J Primatol 29:323–338

Blanco MB, Meyer JS (2009) Assessing reproductive profiles in female brown mouse lemurs (*Microcebus rufus*) from Ranomafana National Park, southeast Madagascar, using fecal hormone analysis. Am J Primatol 71:439–446

Blanco MB, Rahalinarivo V (2010) First direct evidence of hibernation in an eastern dwarf lemur species (*Cheirogaleus crossleyi*) from the high-altitude forest of Tsinjoarivo, central-eastern Madagascar. Naturwissenschaften 97:945–950

Blanco MB (2011) Timely estrus in wild brown lemur females at Ranomafana National Park, southeastern Madagascar. Am J Phys Anthropol 145:311–317

Blanco MB, Godfrey LR, Rakotondratsima M, Rahalinarivo V, Samonds KE, Raharison J-L, Irwin MT (2009) Discovery of sympatric dwarf lemur species in the high-altitude rain forest of Tsinjoarivo, eastern Madagascar: implications for biogeography and conservation. Folia Primatol 80:1–17

Boinski S (1987) Birth synchrony in squirrel monkeys (*Saimiri oerstedi*): a strategy to reduce neonatal predation. Behav Ecol Sociobiol 21:393–400

Bonier F, Martin PR, Moore IT, Wingfield JC (2009) Do baseline glucocorticoids predict fitness? Trends Ecol Evol 24:634–642

Bons N, Reiger F, Prudhomme D, Fisher A, Krause K-H (2006) *Microcebus murinus*: a useful primate model for human cerebral aging and Alzheimer's disease? Genes Brain Behav 5:120–130

Bronikowski AM, Altmann J, Brockman DK, Cords M, Fedigan LM, Pusey AE, Stoinski T, Morris WF, Strier KB, Alberts SC (2011) Aging in the natural world: comparative data reveal similar mortality patterns across primates. Science 331:1325–1328

Brooks CP, Holmes C, Kramer K, Barnett B, Keitt TH (2009) The role of demography and markets in determining deforestation rates near Ranomafana National Park Madagascar. PLoS One 4: e5783. doi:10.1371/journal.pone.0005783

Brown KA, Gurevitch J (2004) Long-term impacts of logging on forest diversity in Madgascar. Proc Natl Acad Sci USA 101:6045–6049

Brown KA, Ingram JC, Flynn DFB, Razafindrazaka R, Jeannoda V (2009) Protected area safeguard tree and shrub communities from degradation and invasion: a case study in eastern Madagascar. Environ Manage 44:136–148

Cartmill M (1974) *Daubentonia, Dactylopsila*, woodpeckers, and klinorhynchy. In: Martin RD, Doyle GA, Walker AC (eds) Prosimian biology. Duckworth, London, pp 655–670

Case TJ, Gilpin ME (1974) Interference competition and niche theory. Proc Natl Acad Sci USA 71:3073–3077

Chapman CA, Speirs ML, Hodder SAM, Rothman JM (2009) Colobus monkey parasite infections in wet and dry habitats: implications for climate change. Afr J Ecol 48:555–558

Clark DB, Clark DA (2006) Tree growth, mortality, physical condition, and microsite in an old-growth lowland tropical rain forest. Ecology 87:2132

Clark DA, Clark DB (2010) Assessing tropical forests' climatic sensitivities with long-term data. Biotropica 43:31–40

Clark DA, Piper SC, Keeling CD, Clark DB (2003) Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. Proc Natl Acad Sci USA 100:5852–5857

Clutton-Brock TH, Harvey PH (1977) Primate ecology and social organization. J Zool Lond 183:1–39

Crook JH, Gartlan JS (1966) Evolution of primate societies. Nature 210:1200–1203

DeFries R, Rovero F, Wright PC, Ahumada J, Andelman S, Brandon K, Dempewolf J, Hansen A, Hewson J, Liu J (2010) From plot to landscape scale: linking tropical biodiversity measurements across spatial scales. Front Ecol Environ 8:153–160

Deppe AM (2011) Predator recognition in the brown mouse lemur (*Microcebus rufus*): experiments in Ranomafana National Park, Madagascar. PhD thesis, Stony Brook University, Stony Brook

Deppe AM, Wright PC (2009) Predator recognition in wild brown mouse lemurs (*Microcebus rufus*): field experiments in Ranomafana National Park Madagascar. Am J Primatol 71:67

Dew JL, Wright PC (1998) Frugivory and seed dispersal by four species of primates in Madagascar's eastern rain forest. Biotropica 30:425–437

Dobson AP, May RM (1986) Disease and conservation. In: Soulé ME (ed) Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, MA, pp 345–365

Dunham AE (2008) Battle of the sexes: cost asymmetry explains female dominance in lemurs. Anim Behav 76:1435–1439

Dunham AE, Erhart EM, Overdorff DJ, Wright PC (2008) Evaluating effects of deforestation, hunting, and El Niño events on a threatened lemur. Biol Conserv 141:287–297

Dunham AE, Erhart EM, Wright PC (2010) Global climate cycles and cyclones: consequences for rainfall patterns and lemur reproduction in southeastern Madagascar. Global Change Biol 17:219–227

Durden LA, Zohdy S, Laakkonen J (2010) Lice and ticks of the eastern rufous mouse lemur, *Microcebus rufus*, with descriptions of the male and third instar nymph of *Lemurpediculus verruculosus* (Phthiraptera: Anoplura). J Parasitol 96:874–878
Durham DL (2003) Variation in responses to forest disturbance and the risk of local extinction: a comparative study of wild *Eulemurs* at Ranomafana National Park, Madagascar. PhD thesis, University of California, Davis
Eisenberg JF, Muckenhirn NA, Rudran R (1972) The relation between ecology and social structure in primates. Science 176:863–874
Erhart EM, Overdorff DJ (1998) Infanticide in *Propithecus diadema edwardsi*: an evaluation of the sexual selection hypothesis. Int J Primatol 19:73–81
Erhart EM, Overdorff DJ (2008a) Population demography and social structure changes in *Eulemur fulvus rufus* from 1988 to 2003. Am J Phys Anthropol 136:183–193
Erhart EM, Overdorff DJ (2008b) Rates of agonism by diurnal lemuroids: implications for female social relationships. Int J Primatol 29:1227–1247
Fedorov AV, Philander SG (2000) Is El Niño changing? Science 288:1997–2002
Feistner ATC, Sterling EJ (1995) Body mass and sexual dimorphism in the aye-aye *Daubentonia madagascariensis*. Dodo 31:73–76
Freeland WJ (1976) Pathogens and the evolution of primate sociality. Biotropica 8:12–24
Ganzhorn JU, Kappeler PM (1996) Lemurs of the Kirindy Forest. Primate Report 46–1:257–274
Ganzhorn JU, Abraham JP, Razanahoera-Rakotomalala M (1985) Some aspects of the natural history and food selection of *Avahi laniger*. Primates 26:452–463
Ganzhorn JU, Fietz J, Rakotovao E, Schwab D, Zinner DP (1999) Lemurs and the regeneration of dry deciduous forest in Madagascar. Conserv Biol 13:794–804
Ganzhorn JU, Lowry PP, Schatz GE, Sommer S (2001) The biodiversity of Madagascar: one of the world's hottest hotspots on its way out. Oryx 35:346–348
Ganzhorn JU, Arrigo-Nelson SJ, Boinski S, Bollen A, Carrai V, Derby A, Donati G, Koenig A, Kowalewski M, Lahann P, Norscia I, Polowinsky SY, Schwitzer C, Stevenson PR, Talebi MG, Tan CL, Vogel ER, Wright PC (2009) Possible fruit protein effects on primate communities in Madagascar and the Neotropics. PLoS One 4:e8253. doi:10.1371/journal.pone.0008253
Gerber B, Karpanty SM, Crawford C, Kotschwar M, Randrianantenaina J (2010) An assessment of carnivore relative abundance and density in the eastern rainforests of Madagascar using remotely-triggered camera traps. Oryx 44:219–222
Glander KE, Wright PC, Daniels PS, Merenlender AM (1992) Morphometrics and testicle size of rain forest lemur species from southeastern Madagascar. J Hum Evol 22:1–17
Golden CD (2009) Bushmeat hunting and use in the Makira Forest, north-eastern Madagascar: a conservation and livelihoods issue. Oryx 43:386–392
Goodman SM, O'Connor S, Langrand O (1993) A review of predation on lemurs: implications for the evolution of social behavior in small, nocturnal primates. In: Kappeler PM, Ganzhorn JU (eds) Lemur social systems and their ecological basis. Plenum, New York, pp 51–66
Gould L, Sussman RW, Sauther ML (1999) Natural disasters and primate populations: the effects of a 2-year drought on a naturally occuring population of ring-tailed lemurs (Lemur catta) in southwestern Madagascar. Int J Primatol 20:69–84
Grassi C (2002) Sex differences in feeding, height, and space use in *Hapalemur griseus*. Int J Primatol 23:677–693
Groeneveld LF, Rasoloarison RM, Kappeler PM (2011) Morphometrics confirm taxonomic deflation in dwarf lemurs (Primates: *Cheirogaleidae*), as suggested by genetics. Zool J Linn Soc Lond 161:229–244
Groves CP (2001) Primate taxonomy. Smithsonian Institution Press, Washington, DC
Hamilton WD (1964) The genetical evolution of social behaviour, I and II. J Theor Biol 7:1–52
Hanski I, Gilpin M (1991) Metapopulation dynamics: brief history and conceptual domain. Biol J Linn Soc 42:3–16
Harcourt CS (1987) Ecology and behaviour of *Avahi laniger*. Int J Primatol 8:501
Harcourt CS (1988) *Avahi laniger*: a study in inactivity. Primate Eye 35:9

Hart D (2007) Predation on primates: a biogeographical analysis. In: Gursky SL, Nekaris KAI (eds) Primate anti-predator strategies. Springer, Chicago, pp 27–59

Hemingway CA (1995) Feeding and reproductive strategies of the Milne-Edwards' sifaka, *Propithecus diadema edwardsi*. PhD thesis, Duke University, Durham

Hemingway CA (1998) Selectivity and variability in the diet of Milne-Edwards' sifakas (*Propithecus diadema edwardsi*): implications for folivory and seed-eating. Int J Primatol 19:355–377

Herrera J, Lauterbur E, Wright PC, Ratovonjanahary L, Taylor LL (2009) Rapid assessment of lemurs in disturbed and undisturbed habitats in southeastern Madagascar 71: 90 DOI 10, 10021 Am J Primatol. 20733

Herrera JP, Wright PC, Lauterbur E, Ratovonjanahary L, Taylor LL (in press) The effects of habitat disturbance on lemurs at Ranomafana National Park, Madagascar. Int J Primatol DOI 10.1007/s10764-011-9525-8

Hogg KL, Wade S, Wright PC (in press) Parasites of nine lemur species from Ranomafana National Park, Madagascar. J Zoo Wildlife Med

Holenweg A-K, Noë R, Schabel M (1996) Waser's gas model applied to associations between red colobus and Diana monkeys in the Taï National Park, Ivory Coast. Folia Primatol 67:125–136

Hrdy SB (1977) Infanticide as a primate reproductive strategy. Am Sci 65:40–49

Ingram JC, Dawson TP (2005) Climate change impacts and vegetation response on the island of Madagascar. Phil Trans R Soc Lond A 363:55–59

Irwin MT (2006) Ecological impacts of forest fragmentation on diademed sifakas (*Propithecus diadema*) at Tsinjoarivo, eastern Madagascar: implications for conservation in fragmented landscapes. PhD thesis, Stony Brook University, Stony Brook

Irwin MT (2007) Living in forest fragments reduces group cohesion in diademed sifakas (*Propithecus diadema*) in eastern Madagascar by reducing food patch size. Am J Primatol 69:434–447

Irwin MT (2008) Feeding ecology of *Propithecus diadema* in forest fragments and continuous forest. Int J Primatol 29:95–115

Irwin MT, Raharison J-L (2009) A review of the endoparasites of the lemurs of Madagascar Malagasy. Nature 2:66–93

Irwin MT, Smith TM, Wright PC (2000) Census of three eastern rainforest sites north of Ranomafana National Park: preliminary results and implication for lemur conservation. Lemur News 5:20–22

Irwin MT, Johnson SE, Wright PC (2005) The state of lemur conservation in south-eastern Madagascar: population and habitat assessments for diurnal and cathemeral lemurs using surveys, satellite imagery and GIS. Oryx 39:204–218

Irwin MT, Raharison J-L, Wright PC (2009) Spatial and temporal variability in predation on rainforest primates: do forest fragmentation and predation act synergistically? Anim Conserv 12:220–230

Isbell LA (1994) Predation on primates: ecological patterns and evolutionary consequences. Evol Anthropol 3:61–71

IUCN (2010) IUCN red list of threatened species. Species Survival Commission

Janson CH (1992) Evolutionary ecology of primate social structure. In: Smith EA, Winterhalder B (eds) Evolutionary ecology and human behavior. Aldine de Gruyter, New York, pp 95–130

Jernvall J, Wright PC (1998) Diversity components of impending primate extinctions. Proc Natl Acad Sci USA 95:11279–11283

Johnson SE (2002) Ecology and speciation in brown lemurs: white-collared lemurs (*Eulemur albocollaris*) and hybrids (*Eulemur albocollaris* x *Eulemur fulvus rufus*) in southeastern Madagascar. PhD thesis, University of Texas, Austin

Johnson SE, Overdorff DJ (1999) Census of brown lemurs (*Eulemur fulvus* sspp.) in southeastern Madagascar: methods-testing and conservation implications. Am J Primatol 47:51–60

Johnson SE, Gordon AD, Stumpf RM, Overdorff DJ, Wright PC (2005) Morphological variation in populations of *Eulemur albocollaris* and *E. fulvus rufus*. Int J Primatol 26:1399–1416

Jolly A (1966) Lemur behavior: a Madagascar field study. University of Chicago Press, Chicago
Jolly A (2012) Berenty reserve, Madagascar: a long time in a small space. In: Kappeler PM (ed) Long-term field studies of primates. Springer, Heidelberg
Jolly A, Sussman RW (2006) Notes on the history of ecological studies of Malagasy lemurs. In: Gould L, Sauther ML (eds) Lemurs: ecology and adaptation. Springer, New York, pp 19–39
Jolly A, Koyama N, Rasamimanana HR, Crowley H, Williams GW (2006) Berenty Reserve: a research site in southern Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana HR (eds) Ringtailed lemur biology: Lemur catta in Madagascar. Springer, New York, pp 32–42
Junge RE, Louis EE Jr (2005) Preliminary biomedical evaluation of wild ruffed lemurs (*Varecia variegata and V. rubra*). Am J Primatol 66:85–94
Junge RE, Sauther ML (2006) Overview on the health and disease ecology of wild lemurs: conservation implications. In: Gould L, Sauther ML (eds) Lemurs: ecology and adaptation. Springer, New York, pp 423–440
Kappeler PM, Fichtel C (2012) A 15-year perspective on the social organization and life history of Sifaka in Kirindy Forest. In: Kappeler PM (ed) Long-term field studies of primates. Springer, Heidelberg
Kappeler PM, van Schaik CP (2002) Evolution of primate social systems. Int J Primatol 23:707–740
Karpanty SM (2006) Direct and indirect impacts of raptor predation on lemurs in southeastern Madagascar. Int J Primatol 27:239–261
Karpanty SM, Wright PC (2007) Predation on lemurs in the rainforest of Madagascar by multiple predator species: observations and experiments. In: Gursky SL, Nekaris KAI (eds) Primate anti-predator strategies. Springer, New York, pp 77–99
King SJ, Arrigo-Nelson SJ, Pochron ST, Semprebon GM, Godfrey LR, Wright PC, Jernvall J (2005) Dental senescence in a long-lived primate links infant survival to rainfall. Proc Natl Acad Sci USA 102:16579–16583
King SJ, Morelli TL, Arrigo-Nelson SJ, Ratelolahy FJ, Godfrey LR, Wyatt J, Tecot S, Jernvall J, Wright PC (2011) Morphometrics and pattern of growth in wild sifakas (*Propithecus edwardsi*) at Ranomafana National Park, Madagascar. Am J Primatol 73:155–172
Knott CD (1998) Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. Int J Primatol 19:1061–1079
Koren L, Mokady O, Geffen E (2006) Elevated testosterone levels and social ranks in the female rock hyrax. Horm Behav 49:470–477
Korhonen K (2006) The rocky road of social sustainability: the impact of integrated biodiversity conservation and development on the local realities in Ranomafana National Park, Madagascar. PhD thesis, University of Helsinki, Finland
Kremen C, Cameron A, Moilanen A, Phillips SJ, Thomas CD, Beentje H, Dransfield J, Fisher BL, Glaw F, Good TC, Harper GJ, Hijmans RJ, Lees DC, Louis EE, Nussbaum RA, Raxworthy CJ, Razafimpahanana A, Schatz GE, Vences M, Vieites DR, Wright PC, Zjhra ML (2008) Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. Science 320:222–226
Laakkonen JT, Lehtonen JT, Ramiarinjanahary H, Wright PC (2003) Trypanosome parasites in the invading *Rattus rattus* and endemic rodents in Madagascar. In: Singleton GR, Hinds LA, Krebs CJ, Spratt DM (eds) Rats, mice and people: rodent biology and management. Australian Centre for International Agricultural Research, Canberra, pp 37–39
Lehman SM, Ratsimbazafy J, Rajaonson A, Day S (2006) Decline of *Propithecus diadema edwardsi* and *Varecia variegata variegata* (Primates: Lemuridae) in south-east Madagascar. Oryx 40:108–111
Louis EE Jr, Engberg SE, Lei R, Geng H, Sommer JA, Randriamampionona R, Randriamanana JC, Zaonarivelo JR, Andriantompohavana R, Randria G, Prosper RB, Rakotoarisoa G, Rooney A, Brenneman RA (2006) Molecular and morphological analyses of the sportive lemurs (Family Megaladapidae: Genus *Lepilemur*) reveals 11 previously unrecognized species. Spec Publ Mus Texas Tech Univ 49:1–47

Lovejoy TE (2006) Protected areas: a prism for a changing world. Trends Ecol Evol 21:329–333
Mayor MI, Sommer JA, Houck ML, Zaonarivelo JR, Wright PC, Ingram C, Engel SR, Louis EE Jr (2004) Specific status of *Propithecus* spp. Int J Primatol 25:875–900
Meier B, Albignac R, Peyriéas A, Rumpler Y, Wright PC (1987) A new species of *Hapalemur* (Primates) from southeast Madagascar. Folia Primatol 48:211–215
Merenlender AM (1993) The effects of sociality on the demography and genetic structure of *Eulemur fulvus rufus* (polygamous) and *Eulemur rubriventer* (monogamous) and the conservation implications. PhD thesis, University of Rochester, Rochester
Meyers DM, Rabarivola C, Rumpler Y (1989) Distribution and conservation of Sclater's lemur: implications of a morphological cline. Prim Conserv 10:77–81
Mittermeier RA, Louis EE Jr, Richardson M, Schwitzer C, Langrand O, Rylands AB, Hawkins F, Rajaobelina S, Ratsimbazafy J, Rasoloarison RM, Roos C, Kappeler PM, Mackinnon J (2010) Lemurs of Madagascar 3 rd edn. Tropical field guide series. Conservation International, Arlington/VA
Morelli TL (2008) Dispersal, kinship, and genetic structure of an endangered Madagascar primate, *Propithecus edwardsi*. PhD thesis, Stony Brook University, Stony Brook
Morelli TL, King SJ, Pochron ST, Wright PC (2009) The rules of disengagement: takeovers, infanticide, and dispersal in a rainforest lemur, *Propithecus edwardsi*. Behaviour 146:499–523
Morriss DH, Arrigo-Nelson SJ, Karpanty SM, Gerber BD, Wright PC (2009) Ranging behavior flexibility in response to habitat disturbance by Milne-Edwards' sifakas (*Propithecus edwardsi*) in Ranomafana National Park, Madagascar. Am J Phys Anthropol 138(48):194
Mutschler T, Tan CL (2003) *Hapalemur*, bamboo or gentle lemurs. In: Goodman SM, Benstead JP (eds) The natural history of Madagascar. University of Chicago Press, Chicago, pp 1324–1329
Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858
Ostner J, Kappeler PM (2004) Male life history and the unusual adult sex ratios of red-fronted lemur, *Eulemur fulvus rufus*, groups. Anim Behav 67:249–259
Overdorff DJ (1991) Ecological correlates to social structure in two prosimian primates, *Eulemur fulvus rufus* and *Eulemur rubriventer* in Madagascar. PhD thesis, Duke University, Durham
Overdorff DJ (1993) Similarities, differences, and seasonal patterns in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana National Park, Madagascar. Int J Primatol 14:721–753
Overdorff DJ (1996) Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. Am J Primatol 40:327–342
Overdorff DJ (1998) Are *Eulemur* species pair-bonded? Social organization and mating strategies in *Eulemur fulvus rufus* from 1988–1995 in southeast Madagascar. Am J Phys Anthropol 105:153–166
Overdorff DJ, Tecot SR (2006) Social pair-bonding and resource defense in wild red-bellied lemurs (*Eulemur rubriventer*). In: Gould L, Sauther ML (eds) Lemurs: ecology and adaptation. Springer, New York, pp 235–245
Overdorff DJ, Merenlender AM, Talata P, Telo A, Forward ZA (1999) Life history of *Eulemur fulvus rufus* from 1988–1998 in southeastern Madagascar. Am J Phys Anthropol 108:295–310
Overdorff DJ, Erhart EM, Mutschler T (2005) Does female dominance facilitate feeding priority in black-and-white ruffed lemurs (*Varecia variegata*) in southeastern Madagascar? Am J Primatol 66:7–22
Perret M, Aujard F (2001) Regulation by photoperiod of seasonal changes in body mass and reproductive function in gray mouse lemurs (*Microcebus murinus*): differential responses by sex. Int J Primatol 22:5–24
Pochron ST, Wright PC (2003) Variability in adult group compositions of a prosimian primate. Behav Ecol Sociobiol 54:285–293
Pochron ST, Wright PC (2005) Testes size and body weight in the Milne-Edwards' sifaka (*Propithecus edwardsi*) of Ranomafana National Park, Madagascar, relative to other strepsirhine primates. Folia Primatol 76:37–41

Pochron ST, Tucker WT, Wright PC (2004) Demography, life history, and social structure in *Propithecus diadema edwardsi* from 1986–2000 in Ranomafana National Park, Madagascar. Am J Phys Anthropol 125:61–72

Pochron ST, Morelli TL, Scirbona J, Wright PC (2005) Sex differences in scent-marking in *Propithecus edwardsi* in Ranomafana National Park, Madagascar. Am J Primatol 66:97–110

Porter LM (1998) Influences on the distribution of *Lepilemur microdon* in the Ranomafana National Park, Madagascar. Folia Primatol 69:172–176

Price TD, Kirkpatrick M (2009) Evolutionarily stable range limits set by interspecific competition. Proc R Soc Lond B 276:1429–1434

Rabarivola C, Prosper P, Zaramody A, Andriaholinirina N, Hauwy M (2007) Cytogenetics and taxonomy of the genus *Hapalemur*. Lemur News 12:46–49

Ratsimbazafy J (2006) Diet composition, foraging, and feeding behavior in relation to habitat disturbance: implications for the adaptability of ruffed lemurs (*Varecia variegata editorium*) in Manombo Forest, Madagascar. In: Gould L, Sauther ML (eds) Lemurs: ecology and adaptation. Springer, New York, pp 403–422

Razafimahaimodison JC (2003) Biodiversity and ecotourism: impacts of habitat disturbance on an endangered bird species in Madagascar. Trop Biodiv 4:12–23

Richard AF (1978) Behavioral variation: case study of a Malagasy lemur. Bucknell University Press, Lewisburg, PA

Richard AF, Dewar RE, Schwartz M, Ratsirarson J (2002) Life in the slow lane? Demography and life histories of male and female sifakas (*Propithecus verreauxi verreauxi*). J Zool Lond 256:421–436

Roth O (1996) Ecology and social behaviour of the woolly lemur (*Avahi laniger*), a nocturnal Malagasy prosimian. Master thesis, University of Basel, Basel

Sefczek TM (2009) Diurnal evidence of a nocturnal feeder: using feeding traces to understand aye-ayes feeding strategy in Ranomafana National Park, Madagascar. PhD thesis, San Diego State University, San Diego

Stevenson PR (2005) Potential keystone plant species for the frugivore community at Tinigua Park, Colombia. In: Dew JL, Boubli JP (eds) Tropical fruits and frugivores: the search for strong interactors. Springer, Netherlands, pp 37–57

Struhsaker TT (1997) Ecology of an African rain forest: logging in Kibale and the conflict between conservation and exploitation. University of Florida Press, Gainsville

Sussman RW (1974) Ecological distinction in sympatric species of lemur. In: Martin RD, Doyle GA, Walker AC (eds) Prosimian biology. Duckworth, London, pp 75–108

Sussman RW, Ratsirason J (2006) Beza Mahafaly Special Reserve: a research site in southwestern Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana HR (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 43–51

Sussman RW, Richard AF, Ratsirarson J, Sauther ML, Brockman DK, Gould L, Lawler R, Cuozzo FP, Mahafaly B (2012) Special reserve: long-term research on Lemurs in Southwestern Madagascar. In: Kappeler PM (ed) Long-term field studies of primates. Springer, Heidelberg

Tan CL (1999) Group composition, home range size, and diet of three sympatric bamboo lemur species (Genus *Hapalemur*) in Ranomafana National Park, Madagascar. Int J Primatol 20:547–566

Tan CL (2007) Behavior and ecology of gentle lemurs (Genus *Hapalemur*). In: Gould L, Sauther ML (eds) Lemurs: ecology and adaptation. Springer, New York, pp 369–381

Tecot SR (2008) Seasonality and predictability: the hormonal and behavioral responses of the red-bellied lemur, *Eulemur rubriventer*, in Ranomafana National Park in southeastern Madagascar. PhD thesis, University of Texas, Austin

Tecot SR (2010) It's all in the timing: birth seasonality and infant survival in *Eulemur rubriventer*. Int J Primatol 31:715–735

Tecot SR (in press) Variable energetic strategies in disturbed and undisturbed rain forest habitats: fecal cortisol levels in southeastern Madagascar. In: Leaping Ahead: Advances in Prosimian

Biology. Developments in Primatology series. Master J, Gamba M, Genein F (eds) Springer, New York
Tecot S, King SJ, Jernvall J, Wright PC (2009) Lemur pregnancy in the wild: Noninvasive monitoring of reproductive function in Milne-Edwards' sifaka, *Propithecus edwardsi*, in Ranomafana National Park, Madagascar. Am J Phys Anthropol S44:393
Tecot S, Zohdy S, King S, Wright PC, Jernvall J (2010) Wimpy males and formidable females: Testosterone levels in *Propithecus edwardsi*. Am J Phys Anthropol S50:228
Tecot SR, Wright PC (2010) Primate conservation efforts. In: Hill McGraw (ed) Yearbook of science and technology. McGraw Hill, New York, pp 310–315
Terborgh J (1983) Five New World primates: a study in comparative ecology. Princeton University Press, Princeton
Terborgh J, Janson CH (1986) The socioecology of primate groups. Annu Rev Ecol Syst 17:111–135
Thomson MC, Abayomi K, Barnston AG, Levy M, Dilley M (2003) El Niño and drought in South Africa. Lancet 361:437–438
van Schaik CP (1983) Why are diurnal primates living in groups? Behaviour 87:120–144
van Schaik CP, Kappeler PM (1996) The social systems of gregarious lemurs: lack of convergence with anthropoids due to evolutionary disequilibrium? Ethology 102:915–941
van Schaik CP, van Noordwijk MA, Warsano B, Satriono E (1983) Party size early detection of predators in Sumatran forest primates. Primates 24:211–221
Vaughn SE, McGee EM (2009) Association of *Allobosca crassipes* (Diptera: *Hippoboscidae*) with the black and white ruffed lemur (*Varecia variegata variegata*) and Milne-Edwards' sifaka (*Propithecus edwardsi)* in southeastern Madagascar. Pan Pac Entomol 85:162–166
Vinyard CJ, Yamashita N, Tan CL (2008) Linking laboratory and field approaches in studying the evolutionary physiology of biting in bamboo lemurs. Int J Primatol 29:1421–1439
White FJ, Overdorff DJ, Balko EA, Wright PC (1995) Distribution of ruffed lemurs (*Varecia variegata*) in Ranomafana National Park, Madagascar. Folia Primatol 64:124–131
Wiederholt R, Post E (2010) Tropical warming and the dynamics of endangered primates. Biol Lett 6:257–260
Wimmer B, Kappeler PM (2002) The effects of sexual selection and life history on the genetic structure of redfronted lemur, *Eulemur fulvus rufus*, groups. Anim Behav 64:557–568
Wright PC (1995) Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. Int J Primatol 16:835–854
Wright PC (1997) The future of biodiversity in Madagascar: a view from Ranomafana National Park. In: Goodman SM, Patterson BD (eds) Natural change and human impact in Madagascar. Smithsonian University Press, Washington, DC, pp 381–405
Wright PC (1998) Impact of predation risk on the behaviour of *Propithecus diadema edwardsi* in the rain forest of Madagascar. Behaviour 135:483–512
Wright PC (1999) Lemur traits and Madagascar ecology: coping with an island environment. Yearb Phys Anthropol 42:31–72
Wright PC (2004) Centre ValBio: long-term research commitment in Madagascar. Evol Anthropol 13:1–2
Wright PC (2006) Considering climate change effects in lemur ecology and conservation. In: Gould L, Sauther ML (eds) Lemurs: ecology and adaptation. Springer, New York, pp 385–401
Wright PC, Andriamihaja BR (2002) Making a rainforest national park work in Madagascar: Ranomafana National Park and its long-term research commitment. In: Terborgh J, van Schaik CP, Davenport L, Rao M (eds) Making parks work: strategies for preserving tropical nature. Island Press, Washington, DC, pp 112–136
Wright PC, Martin LB (1995) Predation, pollination and torpor in two nocturnal prosimians: Cheirogaleus major and Microcebus rufus in the rainforest of Madagascar. In: Alterman L, Doyle GA, Izard MK (eds) Creatures of the dark: the nocturnal prosimians. Plenum Publishing, New York, pp 45–60

Wright PC, Daniels PS, Meyers DM, Overdorff DJ, Rabesoa J (1987) A census and study of *Hapalemur* and *Propithecus* in southeastern Madagascar. Primate Conserv 8:84–88

Wright PC, Heckscher SK, Dunham AE (1997) Predation on Milne-Edward's sifaka (*Propithecus diadema edwardsi*) by the fossa (*Cryptoprocta ferox*) in the rain forest of southeastern Madagascar. Folia Primatol 68:34–43

Wright PC, Andriamihaja BR, Raharimiandra SA (2005a) Tanala synecological relations with lemurs in southeastern Madagascar. In: Paterson JD, Wallis J (eds) Commensalism and conflict: the human-primate interface. Kluwer Press, New York, pp 118–145

Wright PC, Razafindratsita VR, Pochron ST, Jernvall J (2005b) The key to Madagascar frugivores. In: Dew JL, Boubli JP (eds) Tropical fruits and frugivores. Springer, Netherlands, pp 121–138

Wright PC, King SJ, Baden A, Jernvall J (2008a) Aging in wild female lemurs: sustained fertility with increased infant mortality. In: Atsalis S, Margulis SW, Hof PR (eds) Primate reproductive aging: cross-taxon perspectives. Karger, Basel, pp 17–28

Wright PC, Johnson SE, Irwin MT, Jacobs R, Schlichting P, Lehman SM, Louis EE Jr, Arrigo-Nelson SJ, Raharison J-L, Rafalirarison RR, Razafindrasita V, Ratsimbazafy J, Ratelolahy FJ, Dolch R, Tan CL (2008b) The crisis of the critically greater endangered bamboo lemur (*Prolemur simus*). Primate Conserv 23:5–17

Wright PC, Arrigo-Nelson SJ, Hogg KL, Bannon B, Morelli TL, Wyatt J, Harivelo AL, Ratelolahy F (2009) Habitat disturbance and seasonal fluctuations of lemur parasites in the rain forest of Ranomafana National Park, Madagascar. In: Chapman C, Huffman M (eds) Primate parasite ecology: the dynamics and study of host-parasite relationships. Cambridge University Press, Cambridge, pp 311–330

Wright PC, Tecot SR, Erhart EM, Baden AL, King SJ, Grassi C (2011) Frugivory in four sympatric lemurs: implications for the future of Madagascar's forests. Am J Primatol 73:585–602

Yamashita N, Vinyard CJ, Tan CL (2009) Food mechanical properties in three sympatric species of *Hapalemur* in Ranomafana National Park, Madagascar. Am J Phys Anthropol 139:368–381

Zaramody A, Fausser J-L, Roos C, Zinner DP, Andriaholinirina N, Rabarivola C, Norscia I, Tattersall I, Rumpler Y (2006) Molecular phylogeny and taxonomic revision of the eastern woolly lemurs (*Avahi laniger*). Primate Report 74:9–23

Zohdy S, Tecot S, Rakotoarinivo TH, Carag J, King SJ, Jernvall J, Wright PC (2010) Wild brown mouse lemurs live long and prosper. Am J Phys Anthropol 141(suppl 50):251

Zuberbühler K (2007) Predation and primate cognitive evolution. In: Gursky SL, Nekaris KAI (eds) Primate anti-predator strategies. Springer, Chicago, pp 3–26