THE HUMAN FACTOR IN MOUSE LEMUR (*MICROCEBUS GRISEORUFUS*) CONSERVATION: LOCAL RESOURCE UTILIZATION AND HABITAT DISTURBANCE AT BEZA MAHAFALY, SW MADAGASCAR

A Dissertation Presented

by

EMILIENNE RASOAZANABARY

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Approved as to style and content by:

Laurie R. Godfrey, Chair

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This dissertation is dedicated to the late

Berthe Rakotosamimanana and Gisèle Ravololonarivo
(Both Professors in the DPAB)

Claire
(Cook at Beza Mahafaly)

Pex and **Gyca**
(Both nephews)

Guy and **Edmond**
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All of my grandparents

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(Grandpa)

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WE WILL TAKE CARE OF YOU AND YOURS!

ABSTRACT (ENGLISH)

THE HUMAN FACTOR IN MOUSE LEMUR (*MICROCEBUS GRISEORUFUS*) CONSERVATION: LOCAL RESOURCE UTILIZATION AND HABITAT DISTURBANCE AT BEZA MAHAFALY, SW MADAGASCAR

FEBRUARY 2011

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Directed by: Professor Laurie R. Godfrey

Gray-brown mouse lemurs (*Microcebus griseorufus*) are able to survive in the most stressful environments of Madagascar. Between 2003 and 2007, I collected data on threats to the survival of *M. griseorufus* at Beza Mahafaly and how various factors impact their behavior. Individuals can survive ~5 years, but few do. Females give birth to multiple young in single litters; furthermore, polyestry exists at Beza. Population turnover rates are higher than they are for other mouse lemurs, which also live longer.

The morphology and behavior of *M. griseorufus* in three populations (protected gallery and spiny forests; unprotected forest at Ihazoara) at Beza are influenced by differences in vegetation. Gallery-forest mouse lemurs have hook-like hands and feet while those in the spiny forest have more "clamp-like" cheiridia. Differences in feeding and nesting behavior may explain these differences, as mouse lemurs in the different habitats use small branches in high canopy vs. larger supports close to the ground to different degrees. Morphology and behavior also vary by sex. Reverse sexual canine dimorphism is strong in *M. griseorufus* at all three forests. The greater canine height of females likely relates to female dominance. Females have greater access to exudate-producing trees and to tree-holes for nesting. They undergo seasonal torpor more frequently than males, and this may give them a survival advantage.

Mouse lemurs are not hunted for food but their habitats are disturbed. In the most highly-disturbed (unprotected) forest, I recorded the highest population turnover rate and shortest maximum lifespan. Ihazoara mouse lemurs here cannot fatten or hibernate. But even in "protected" forests where they do hibernate, mouse lemurs suffer from the felling of trees and herding of cattle.

The Mahafaly people are cattle herders and faithful to their culture. The externally-imposed prohibition against resource extraction in protected forests engenders local hostility toward conservation. Education has minimally affected these attitudes. Building a more healthy relationship between conservationists and local people is of paramount importance; the views of local people must be considered and more of an effort made to involve local communities in constructing effective conservation strategies.

ABSTRACT (MALAGASY)

NY SEHATRA MAHAOLONA AMIN'NY FIAROVANA NY SONGIKY (*MICROCEBUS GRISEORUFUS*): FITRANDRAHANA NY SOMPITRA AO AN-TOERANA SY NY FAHASIMBAN'NY ALA, BEZA MAHAFALY, ATSIMO-ANDREFANA MADAGASIKARA

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Ny songiky (*Microcebus griseorufus*) dia afaka miaina amin'ny tontolo sarotra eto Madagasikara. Nandritra ny dimy taona (2003-2007) no nanaovana asa fikarohana mikasika ny songiky ao Beza Mahafaly. Hita ary fa ny songiky iray dia manana taham-pahavelomana dimy taona farafahakeliny saingy vitsy amin'izy ireo no manana izany fahafahana izany. Ambony be ny tahan'ny songiky vaovao azo ao Beza Mahafaly raha mitaha amin'ireo songiky any amin'ny faritra hafa.

Misy fiantraikany amin'ny fiainan'ny songiky ny fahasamihafan'ny zava-maniry ao Beza Mahafaly (ala mandomando, ala feno tsilo, ary ny ala tsy voaaro ao Ihazoara). Ny ratsambatan'ny songiky ao amin'ny ala mandomando dia lavalava kokoa miohatra amin'ny an'ireo izay ao amin'ny ala feno tsilo. Nahafahana nanamarika izany ny fihetsiny eo am-pisakafoanana sy ao am-patoriana. Ratsan-kazo kely, manify ary avo no

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Voamarika amin'ny vavy sy ny lahy ihany koa ny fahasamihafana ara-batana sy ara- pihetsika. Lava vangy ny songiky vavy ary misy ifandraisany amin'ny fanjakazakany izany. Manjaka amin'ny hazo misy gaoma "dity" hohanina ary ny hazo misy lavaka hatoriana ny songiky vavy. Miteraka fahafana milevina ho azy ireo mandritra ny fotoana sarotra izany ary tombotsoa manokana ihany koa amin'ny fahafahana miaina maharitra.

Hita fa mijaly ny songiky na dia tsy hazaina hohanina aza satria voakorontana ny ala onenan'izy ireo. Miohatra amin'ny ala roa hafa voaaro, dia marobe ireo songiky vaovao azo ao Ihazoara isaky ny fihazana. Ny songiky ao Ihazoara koa anefa no manana taham-pahaveloma ambany indrindra, tsy mety matavy ary noho izany tsy afaka milevina. Na ny songiky ao amin'ny ala voaaro, izay afaka milevina aza dia mbola misedra olana ihany koa, hazo tapaka sy ny arakandro.

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CHAPTER 1

INTRODUCTION

1.1 Introduction

The smallest Malagasy lemur species belong to the genus *Microcebus* (the "mouse" lemurs, in the family Cheirogaleidae. Eighteen species of mouse lemurs (*Microcebus* spp.) are recognized today from all regions of Madagascar, from the northern to the southern tips, and from the eastern to the western coasts (Schmid and Kappeler, 1994; Zimmermann et al., 1998; Rasoloarison et al., 2000; Yoder et al., 2002; Andriantompohavana et al., 2006; Roos and Kappeler, 2006; Louis et al., 2006, 2008; Olivieri et al., 2007; Radespiel et al., 2008). Field studies have shown them to live in a great variety of environments, from extremely arid, "spiny" forests (Génin, 2008) to dry deciduous forests (Radespiel et al., 1998; Schmid and Kappeler, 1998), eastern rain forests (Atsalis, 1999; Blanco, 2010), and high-altitude montane forests (Blanco, 2010). They are often the last primates to disappear from forests undergoing habitat loss due to climatic and anthropogenic effects. While their densities may reach 400 individuals per km^2 (Hladik et al., 1980, 1998; Harcourt and Thornback, 1990), giving them the appearance of ecological health, their populations may not be self-sustaining (Ganzhorn and Schmid, 1998).

Southeastern and southwestern Madagascar are home to two mouse lemur species, including one which has been described in the riverine or gallery forests of the south (*Microcebus murinus*, Yoder et al., 2002), and a second, *Microcebus griseorufus*, which lives in some of the most arid and hostile environments in all of Madagascar.

Microcebus murinus has been studied at Mandena, a littoral rain forest in the southeast (Hapke, 2005; Lahann et al., 2006; Gligor et al., 2009; Schmid and Speakman, 2009) and in a dry deciduous forest at Kirindy (Schmid and Kappeler, 1998; Rasoazanabary, 2006). *M. griseorufus* has been studied in the spiny forest at Berenty, a private reserve in the southeast (Génin, 2008) in the drought-prone cliffs of Tsimanampetsotsa National Park near Lake Tsimanampetsotsa on the southwest coast (Mittermeier et al., 2006, 2008; Kobbe and Dausmann, 2009; Bohr et al., submitted) and in the forests within and near the Beza Mahafaly Special Reserve (BMSR) near Betioky, in the interior (Rasoloarison et al., 2000; Rasoazanabary, 2004; this thesis) (Figure 1.1).

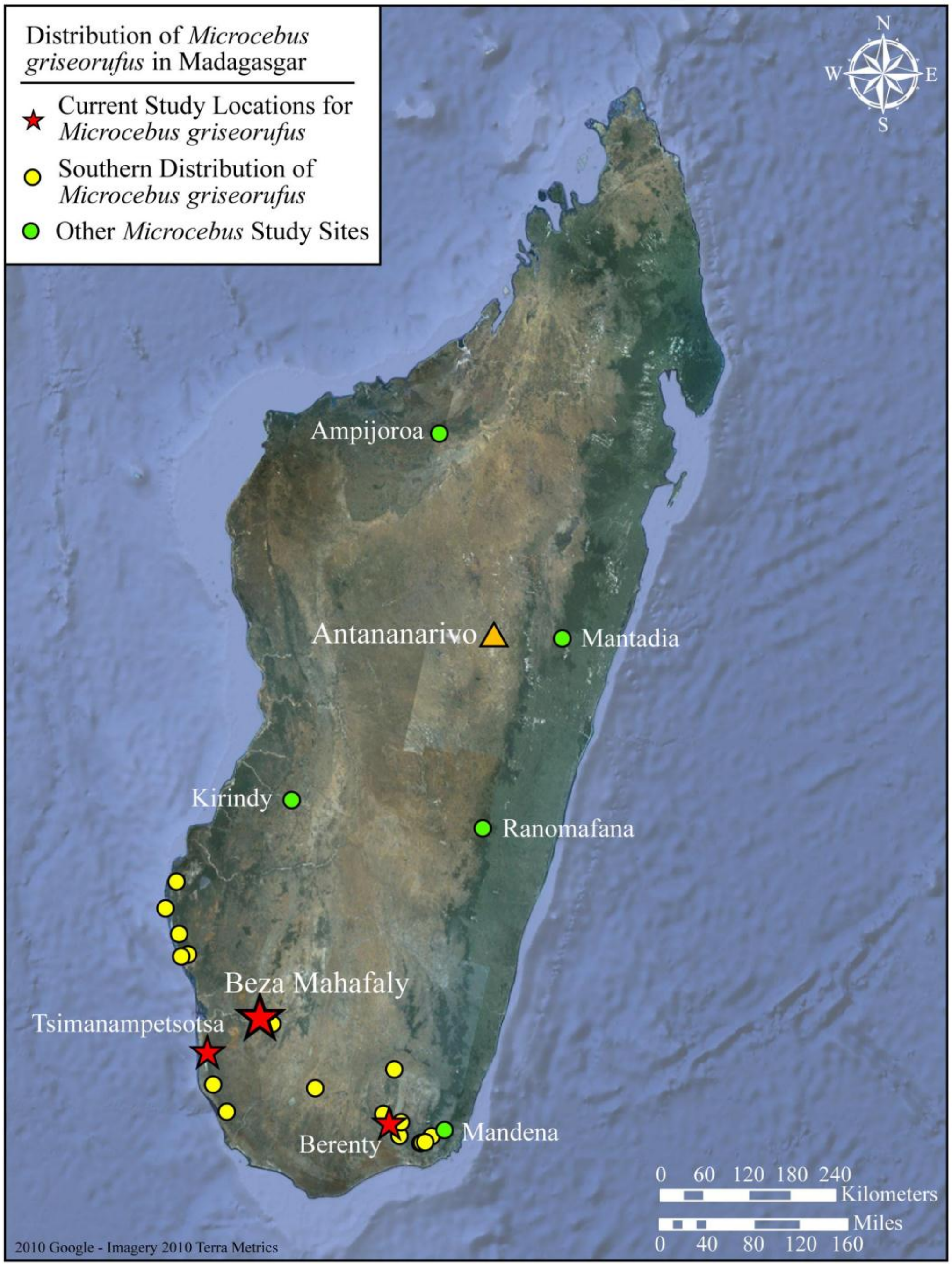


Figure 1.1: Map of Madagascar showing the distribution of sites at which *M. griseorufus* has been found.

All of these forests, with the exception of Kirindy, are within the Spiny Thicket Ecoregion of Madagascar (Burgess et al., 2004). The mouse lemurs in museum collections from localities in the arid south, even when originally identified as *M.*

murinus, are largely if not entirely *M. griseorufus* (Cuozzo et al., in press), although hybridization of the two species has been reported in the forested corridors connecting the humid littoral forest at Mandena and the dry spiny forest to the west (Gligor et al., 2009). At Berenty, the two species were identified in entirely different habitats – *M. murinus* in the gallery forest and *M. griseorufus* in the adjacent spiny forest (Yoder et al., 2002).

Given their high densities, broad distribution, and given the diversity of habitats in which they live, mouse lemurs are generally considered the least endangered of Malagasy lemurs (www.iucnredlist.org). However, nobody knows in which habitats they reproduce best and maintain the largest breeding populations. Nobody knows the limits to their habitat flexibility. Despite the perception that mouse lemurs are common, it is recognized that many mouse lemurs may become endangered due to deforestation, and for that reason they are protected under CITES (www.cites.org) regulations. The mouse lemurs in the region of Beza Mahafaly were poorly studied prior to my research, which began in the year 2003. In 1996-97, Rodin Rasoloarison captured some mouse lemurs at Ihazoara, a forest near the Beza Mahafaly Special Reserve (BMSR), which he identified as *M. griseorufus* (Rasoloarison et al., 2000). However, a lower jaw of one individual *M. murinus* was identified along with many bones of *M. griseorufus* in the owl pellets collected by Steven Goodman and colleagues along the road near Ambinda, another village close to the research camp at the reserve (Goodman et al., 1993).

Thus, when I first went to Beza Mahafaly Special Reserve in April to August of 2003, I expected to find two species of mouse lemurs living in this region. Indeed, remarkable variation in coat color convinced me that as many as three species (one gray, one gray-brown, and one red) might live in the area (see Figure 1.2). If prior ecological distinctions held, I would have expected to see different species in the different habitats that exist at Beza, with *M. murinus* (the common gray mouse lemur) living in gallery forests, and *M. griseorufus* (the gray-brown mouse lemur) living in drier forests, including the spiny thickets (Rasoazanabary, 2004).

Figure 1.2: Two morphotypes collected at Beza Mahafaly. On the left is 0659-D2FC (the "all-red" variant), and on the right is 0659-CE82 (with "typical" *M. griseorufus* coloration). Both of these individuals were found in the gallery forest. Photo credits: Laurie R. Godfrey, 2005.

My preliminary study of mouse lemurs at Beza in 2003 and 2004 confirmed the existence of individuals with very distinct coat coloration. Some were gray, with little or no dorsal stripe or markings above the eyes – very like the *Microcebus murinus* that I had previously studied at Kirindy (Rasoazanabary, 2006). A few individuals were red from head to tail. Most were gray-brown with a dorsal stripe, reversed “V” on the head, and red tail. These are typical *M. griseorufus*. I was initially convinced that Rasoloarison et al. (2000) were correct in identifying multiple species at Beza, despite the rarity of individuals deviating in their coat characteristics from the typical *M. griseorufus* pattern (Rasoazanabary, 2004).

However, both genetic and morphometric research brought these initial conclusions into question. First, in a study of variation in the morphology of the teeth of mouse lemurs that I conducted with Drs. Frank Cuozzo, Laurie Godfrey, and Michelle Sauther, significant dental morphological variation was found. Traits presumed to typify *Microcebus murinus* occur in populations comprising only *M. griseorufus* (Cuozzo et al., in press). Secondly, a genetic analysis of the DNA of mouse lemurs (based on ear clip samples that I collected in 2003 at Beza and surrounding forests) demonstrated the very close relationship of all individuals there, regardless of coat coloration. All were *M. griseorufus* (Heckman et al., 2006). This was very interesting, because it implied that (1) intraspecific variation in dental and coat color in mouse lemur species is much greater than had been previously understood; (2) far from being confined to spiny forests, *Microcebus griseorufus* lives in very different habitats at Beza Mahafaly, at least in the absence of other mouse lemur species; and (3) if Rasoloarison et al. (2000) were correct in identifying one individual in the owl pellet samples as *M. murinus*, then this species has apparently very recently disappeared from this Reserve.

M. murinus is believed to be the most broad-niched species of mouse lemur; it is certainly among the most widespread, living in sympatry with its congeners from Ampijoroa in northwest Madagascar to Mandena in the extreme southeast (Schmid and Kappeler, 1994; Zimmermann et al., 1998; Rasoloarison et al., 2000; Yoder et al., 2002; Mittermeier et al., 2008). But here at Beza Mahafaly, we found *M. griseorufus* to exhibit apparently broad ecological tolerance. This single species, despite its common name (i.e., the "gray-brown" mouse lemur), had red, gray and gray-brown variants, all living in a variety of habitats, including the gallery forest bordering the Sakamena River within the special reserve proper, and the very arid spiny and dry forest habitats far from any river.

M. griseorufus had never before been reported to live in gallery forests. One possibility was that its occurrence there was the result of a recent invasion, following a local extirpation of *M. murinus* from gallery forest. Heckman et al. (2006) used MIGRATE genetic analysis to estimate population size in the spiny and gallery forests; that work demonstrated consistently higher population size in the spiny forest habitat (0.024) than in the dry forest (0.004) and in the gallery forest (0.0006) (see below). But whether or not an invasion of the gallery forest by *M. griseorufus* was a recent phenomenon, it was clear that the current distribution of this species may have been influenced by recent changes in the primate community composition (e.g., a recent loss of *M. murinus*) in those forests. What was not clear, however, was exactly how endangered *Microcebus griseorufus* may be in its different habitats at Beza Mahafaly. In some habitats, the numbers of individuals appeared to be critically low, despite the fact that there was no evidence that mouse lemurs were being eaten by the local people.

My preliminary research on mouse lemurs at Beza Mahafaly spanned a discontinuous period comprising in total 12 months (during the years 2003-2005). An important goal of that preliminary work was to understand the pressures that may threaten their existence. It was clear that the activities of humans, whose populations had been growing in this region at a rapid rate, might have influenced the distribution of small nocturnal lemur species, whether or not these species were targeted for food. To capture their ecological diversity, I decided to study mouse lemurs in three habitats: (1) a gallery forest surrounded by a barbed fence (Parcel 1, well protected); (2) a spiny forest (Parcel 2, poorly protected, not fenced, but part of the reserve); and (3) a dry, deciduous, unfenced forest (Ihazoara, unprotected) located across the Sakamena River, and not part of the reserve (Figure 1.3). A botanical survey published by Sussman and Rakotozafy in 1994 demonstrated microhabitat variation even within the gallery forest (Parcel 1); thus, I expected to see great microhabitat differences across these three forests.

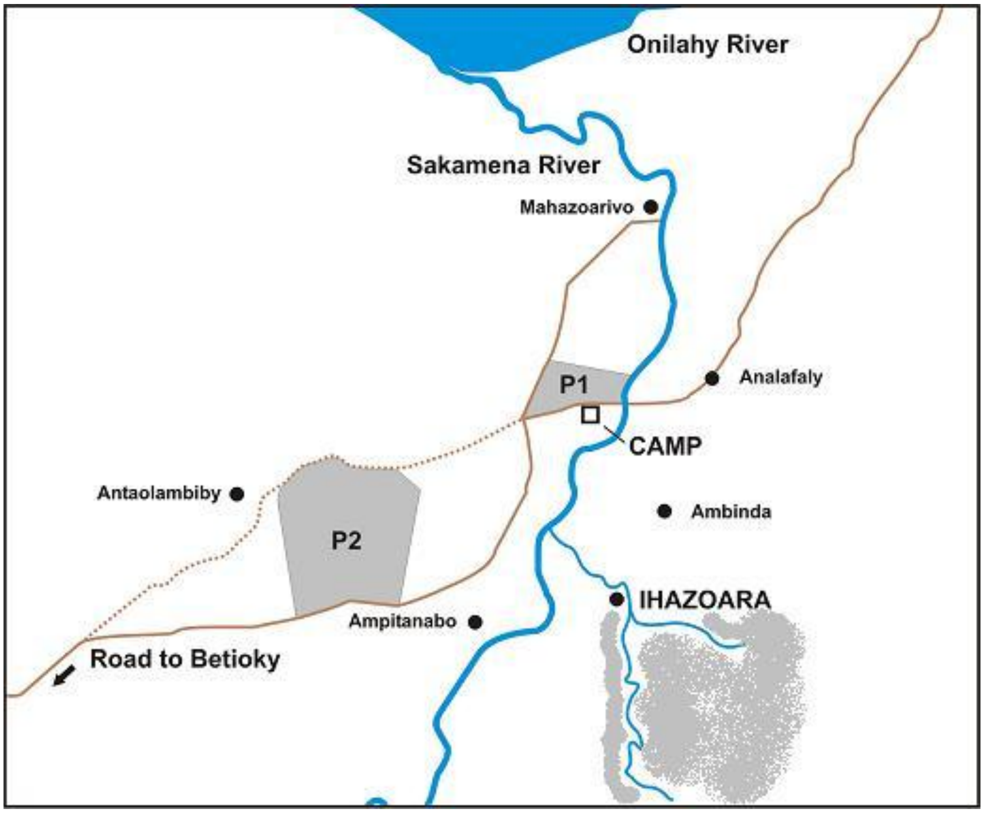


Figure 1.3: Map of the Beza Mahafaly area, showing my three study sites, Parcels 1 and 2 (gray) and the forest near the village of Ihazoara. Photo credits: Darren Godfrey, 2004.

The goal of my dissertation study was to discover, first: does *M. griseorufus* prefer the spiny and dry forest habitats at Beza Mahafaly? What is the level of human disturbance of the spiny and dry forests as opposed to the gallery forest at Beza? How do mouse lemurs respond to human disturbance in these habitats? What are the ecological consequences of disturbance for mouse lemurs of living in different habitats? Finally, how do the local people view the local conservation efforts, and how are these views dependent on the economic circumstances, education, needs or proximity to the forests of the people themselves? Understanding the needs of forest-dependent villagers, as well as the ecological flexibility of the mouse lemurs themselves, is critical to developing a workable conservation strategy. This would become the subject of my dissertation research. The ultimate goal of my work at Beza was to establish a long term monitoring program for mouse lemurs living there, and to gather the information sufficient to build a conservation policy on the basis of a true understanding of their ecological requirements and threats to their survival, as well as an understanding of the needs of the local people.

With these goals in mind, and with my preliminary research behind me, I began my year-long field study in October 2006. This dissertation project was, effectively, a continuation of the pilot research that I had conducted in 2003-2005, but the research itself was far more intense. The entire field project focused on the behavior of mouse lemurs during two different seasons (the rainy season from October 2006 to March 2007, and the dry season, from April 2007 to September 2007) and in three different forests (the gallery forest bordering the Sakamena River, the spiny forest, and the dry forest at Ihazoara) that differ in microhabitat, degree of protection, and degree of human disturbance. Each forest has segments that exhibit differing degrees of disturbance as well as minor differences in natural vegetation; these factors may affect mouse lemur distribution within the forests. These factors may also affect mouse lemur behavior.

The research plan was also motivated by the realization that conservation of biodiversity typically fails for two main reasons: (1) lack of cooperative partnership between conservationists and local people; and (2) failure to identify the true conservation needs of the species in jeopardy. While it is true that local people stand to gain as much in the long term from conservation efforts as does the academic community, it is also true that they often consider each other bitter adversaries (Hill, 2002). When Beza Mahafaly was first designated as a protected area in the 1970s, there was a hostile response from the local villagers. They killed a number of sifakas (the largest of the lemur species at Beza) and suspended their bodies in the middle of the road to register their anger at having been prohibited from using their traditional forests (Richard and Dewar, 2001; Primack and Ratsirarson, 2005). While such extreme incidents have not reoccurred in more recent decades, neither has local resentment entirely dissipated. In the spiny forest, trees used by mouse lemurs are regularly cut by local villagers, because they are also valuable sources of honey or wood for house construction (Rasoazanabary, 2004). In addition, 'protected' habitat is cut and burned for maize agriculture, and killing weeds such as lianas that attract cattle are spreading. Documenting the specific effects of disturbance on the health and population dynamics of mouse lemurs is imperative if new conservation measures are to be implemented.

1.2. Chapter goals

What follows is a brief description of the plan for this dissertation – specifically, the goals for each of the chapters.

1.2.1 Chapter 2

Mouse lemurs live in many habitats in the southwest and are considered by IUCN "of least concern". How do they manage? Are they really unthreatened, or is that an illusion? What is the life expectancy of individuals? In captivity, mouse lemurs can live up to ~ 18 years and reproduce multiple times during the year, but in the dry West (Kirindy), they have been shown to have a single reproductive season per year. Wild mouse lemurs in the east (Ranomafana) have been reported to live up to 9 years (Zohdy et al., 2010). Is this also true of mouse lemurs, *Microcebus griseorufus*, living in the arid region of Beza Mahafaly, south of the Onilahy River? Does *M. griseorufus* experience polyestry? Are they slow-reproducing "bet hedgers" or are they living their lives "in the fast lane?"

In Chapter 2, I will present the results of the first study on reproductive profiles of the gray brown mouse lemurs at Beza Mahafaly. Basic data on the seasonality of reproduction, from conception and gestation to lactation, as well as the growth of infants and juveniles, will be presented. Evidence of polyestry at Beza Mahafaly within the context of variation among mouse lemurs across Madagascar will be explored in this chapter.

1.2.2 Chapter 3

M. griseorufus is known to thrive in spiny forest habitats. Yet at Beza Mahafaly, it occupies gallery forests as well as spiny forests and other dry habitats. How different are these habitats? This chapter documents differences in plant species and phenological characteristics among three forests at Beza Mahafaly, and asks how mouse lemurs living in the three habitats differ morphologically and behaviorally. How do those differences reflect variation in available resources (nesting sites, food resources) and differences in forest structure?

In Chapter 3, I show that mouse lemurs living in the three forests differ consistently in the relative proportions of the digits of the hands and feet. I also quantify differences in the feeding and nesting behavior of mouse lemurs living in the three sites. The morphological differences (with more clamp-like hands and feet in the spiny forest and more hook-like hands and feet in the gallery forest) appear to be related to differences in the characteristics of the trees themselves, and in the utilization of high canopy sites for nesting and feeding.

1.2.3 Chapter 4

In different parts of Madagascar, males and females belonging to various species of mouse lemurs exhibit different behavior patterns. In some cases, they differ markedly in their propensities to enter seasonal torpor; in other cases, they do not. *Microcebus* females are reported to be dominant over males, but what this means, exactly, varies across species. Fluctuating body size dimorphism has been described for *M. murinus* at Kirindy. Does it exist in *M. griseorufus*? How do male and female *M. griseorufus* survive in the harsh habitats of southwestern Madagascar? This chapter will document and attempt to explain differences between *M. griseorufus* sexes, with special attention to morphometric and behavioral traits. The goal is to further understand coping strategies of the sexes within this variable genus.

In Chapter 4, I show that fluctuating body size dimorphism does not exist in *M. griseorufus* at Beza Mahafaly. On the other hand, I provide evidence of strong reverse sexual dimorphism in canine height, as well as marked differences in the behavior and activities of adult males and females (especially in terms of access to resources). I attempt to explain these differences within the context of survival and reproduction in the harsh environment of the arid southwest.

1.2.4 Chapter 5

Southwestern Madagascar has a rapidly growing human population that depends greatly on resources gleaned from forested habitats. How widespread is human disturbance in "protected" and "unprotected" areas in the southwest? How does that disturbance affect mouse lemurs?

In Chapter 5, I investigate human activities in the three forest habitat at Beza Mahafaly and quantify disturbance levels. Villagers' attitudes towards conservation are documented through interviews and observations. I present evidence that the populations of mouse lemurs in unprotected forests are shrinking while those in protected forests may be stabilizing or growing. Finally, I explore barriers to and the potential for successful conservation through expanded participation of local people ("bottom-up" conservation practices).

1.2.5 Chapter 6

Chapter 6 summarizes the main conclusions of the other chapters.

CHAPTER 2

POPULATION DYNAMICS OF MOUSE LEMURS IN THE REGION OF THE BEZA MAHAFALY SPECIAL RESERVE, SW MADAGASCAR

2.1 Introduction

The forests of southern and southwestern Madagascar can be described as the harshest of all forest habitats in the country. This can be quantified in a number of different ways, but most convincingly through a comparison of temperature and rainfall data collected over prolonged periods of time at various weather stations. Dewar and Richard (2007) compare *P* ("predictability of periodic phenomena," following Colwell, 1974) values for monthly rainfall at 15 weather stations on Madagascar and 15 on continental Africa, to demonstrate that Madagascar in general exhibits higher unpredictability. Predictability is defined as the sum of *C* (constancy) + *M* (contingency) where constancy is the extent to which rainfall (in this comparison) is constant from month to month, and contingency is the extent to which rainfall in any selected month is similar from year to year. Contingency measures the frequency of extreme years – years, for example, marked by drought or by cyclones. *P* varies from 0 (low predictability) to 1 (high predictability). The formulae for C and M are based on the mathematics of information theory, and are explained in detail by Colwell (1974). *P* values for 15 weather stations in Madagascar vary from 0.281 to 0.438 while 15 weather stations matched for mean annual rainfall on continental Africa range from 0.371 to 0.652 (Dewar and Richard, 2007). The weather station closest to Beza Mahafaly, Betioky, for example, has a *P* value of 0.320, which is extremely low.

Two conclusions can be drawn from these climate data – first that southwestern Madagascar exhibits unusually low constancy combined with moderate contingency for rainfall, while rainfall in eastern Madagascar shows high constancy but unusually low contingency. Secondly, overall predictability is significantly lower in Madagascar than in matched weather sites on continental Africa. Thus, it is not surprising that Madagascar has been singled out as one of the most "hypervariable" places on Earth (Wright, 1999; Dewar and Richard, 2007).

One can argue, furthermore, that the southwest experiences the greatest hypervariability within Madagascar. Additional weather station data compiled by Kamilar and Muldoon (2010) demonstrate that those sites at which *Microcebus griseorufus* lives exhibit extreme seasonality (i.e., very low constancy) not merely for rainfall but also for temperature (Ratsirarson, 2003; Fenn, 2003), coupled with low annual rainfall. Annual rainfall can be less than 500 mm at Beza Mahafaly (Ratsirarson, 2003), but averages ~750 mm (Sussman and Ratsirarson, 2006). Normally, rains fall only between November and March, but there can be occasional storms even at the height of the dry season (July and August, pers. obs.). Beza Mahafaly is also extremely hot during the short "rainy" season (with maximum daily temperatures regularly in excess of 42°C, and up to 48°C), and very cold, particularly at night when these animals are active (with minimum daily temperatures regularly lower than 5°C, and sometimes as low as 3°C), during the prolonged dry winter (Ratsirarson, 2003). Mean annual temperature is 25°C. Because rainfall is limited even in good years at Beza (the Sakamena River is usually wet for only a few weeks in any given year), drought years are punishing for virtually all species. Nevertheless, periodically, cyclones hit the forests at Beza, carrying whole trees downstream. In effect, *M. griseorufus* experiences higher "seasonality" than virtually any other lemur species (including other mouse lemur species), as demonstrated using weather records.

Wright (1999) and Dewar and Richard (2007) have suggested that Madagascar's hypervariability has been instrumental in shaping the adaptations of its endemic fauna. The latter authors, particularly, have argued that the reproductive strategy called 'bet hedging' has evolved repeatedly (and in very different taxa on Madagascar) because of its climatic unpredictability (see also Godfrey and Rasoazanabary, in press). Bet hedgers maximize adult survivorship at the expense of infant and juvenile mortality; they depend on high iteroparity (the production of offspring multiple times within the reproductive lifetime) to counteract the negative effects of bad years with exceptionally high infant and juvenile losses. Dewar and Richard (2007) suggest that many of Madagascar's extant lemurs are bet hedgers, and they showcase the Verreaux's sifaka (*Propithecus verreauxi*) as a perfect example. Indeed, they maintain that a number of non-primates endemic to Madagascar can be similarly described. The Malagasy jumping rat (*Hypogeomys antimena*), in sharp contrast to rodents in most other parts of the world, reproduces slowly. Madagascar's endemic carnivores (belonging to the euplerid group) are also bet hedgers, giving birth once a year to a single offspring.

Bet hedging, however, would not appear to describe mouse lemurs, and indeed Dewar and Richard (2007) single them out (referring specifically to data collected on *M. murinus*) to suggest that a reproductive strategy very different from bet hedging also works well in hypervariable environments. At ~60 g, *Microcebus griseorufus* is among the smallest-bodied of Madagascar's lemurs. Its reproductive profile stands in stark contrast to those of larger-bodied, “bet-hedging” lemurs (such as the three-kilogram sifaka, *Propithecus verreauxi*); indeed, it may lie at the “fast” extreme of species within its own genus. Effectively, Dewar and Richard (2007) maintain that mouse lemurs survive in hypervariable environments by being able to reproduce very rapidly; they maximize reproduction at the expense of adult survivorship. Thus hypervariable environments (as are found in Madagascar) favor species at both reproductive extremes – i.e., those (like sifakas) that reproduce slowly but spread reproductive effort over a prolonged life spans, and those (like mouse lemurs) that concentrate reproductive effort over a very short period of time. Moreover, “fast” reproduction may work better than “slow” reproduction in very hostile environments; as we will see, there are forests in southwestern Madagascar where, of all remaining lemur species, only the mouse lemurs survive (Godfrey and Rasoazanabary, in press).

In some ways, however, mouse lemurs do not fit the reproductive profile typical of species that grow quickly, reproduce rapidly and die young. First, in captivity, mouse lemurs can live long lives; indeed life spans of 18 years in captivity have been described (Weigl, 2005). Secondly, mouse lemurs can enter prolonged torpor, and such patterns tend to typify species with prolonged life spans, and slow reproduction (Blanco, 2008; Zohdy et al., 2010). Cheirogaleids (the family to which mouse lemurs belong) are the only primates for which some species experience obligate hibernation; mouse lemurs themselves exhibit flexible patterns of seasonal torpor (Fietz, 1998; Schmid and Kappeler, 1998; Rasoazanabary, 2006). Finally, few data exist on the life spans of mouse lemurs in the wild, and their actual reproductive profiles are only beginning to be understood. If there is a relationship between torpor and reproductive life span in mouse lemur species, that relationship is poorly understood. If there is a relationship between climatic hypervariability and reproductive life span in mouse lemur species, that relationship is poorly understood, as well.

The goal of this chapter is to document the reproductive and population dynamics of the mouse lemurs, *M. griseorufus*, living in the region of the BMSR, and to compare their reproductive profiles with those of mouse lemurs living in less seasonal habitats. To sample the wide variety of habitats in which *M. griseorufus* survives at Beza Mahafaly, I studied their populations at three sites: 1) a gallery forest; 2) a spiny forest; and 3) a dry forest. To understand the seasonality of reproduction, reproductive profiles of mouse lemurs should be studied within the context of their activity patterns throughout the year, as seasonal torpor may affect the length of the reproductive season. Thus, using capture data, I also documented activity patterns of adult males and females. Comparative data were culled from the literature, allowing me to compare Beza mouse lemurs to populations of *M. griseorufus* at other southern sites, and to other mouse lemur species living in less seasonal environments (Mandena, Ranomafana).

Various authors have sought to understand how seasonality ought to relate to reproductive characteristics of mouse lemurs. Lahann et al. (2006) argued that species in highly seasonal habitats will be strongly constrained by that seasonality to have a strictly controlled and short reproductive season without polyestry. They might adapt to strong seasonality by entering prolonged periods of seasonal torpor during the season of scarce resources. They should have relatively long life spans, and high iteroparity over their prolonged life spans (effectively behaving like bet hedgers going for multiple opportunities for reproductive success). On the other hand, populations or species living in habitats with low seasonality can take advantage of the opportunity to reproduce repeatedly during a single year; they should therefore forgo seasonal torpor, exhibiting instead several litters in single reproductive seasons (or polyestry) and greater reproductive success over a shorter period of time. This would result in shorter life spans, and high population turnover. In sharp contrast, Génin (2008) argued that populations and species living in highly seasonal habitats may be challenged to reproduce quickly because high seasonality can lead to high mortality due to resource deprivation. Individuals should therefore exploit whatever resources allow for survival during harsh periods, and they should compensate for higher mortality due to resource deprivation by reproducing over a prolonged period of time during a single reproductive season. They should exhibit high population turnover, and short life spans.

The critical questions I sought to address are: Do the mouse lemurs living at Beza (with its exceptionally high seasonality of temperature and rainfall, as well as its prolonged dry season) exhibit special adaptations that allow them to survive in these stressful habitats? Do they conform to the expectations of either Génin's (2008) or Lahann et al.'s (2006) models?

2.2 Methods

To address the above questions, I collected field data over a period spanning several years (beginning in 2003 and ending with intensive sampling for a whole year, from October 9, 2006 to September 30, 2007). These observations were supplemented by data collected on skeletons of *Microcebus griseorufus* found at Beza Mahafaly (and currently housed in the research center at the main camp site, Parcel 1, Beza Mahafaly Osteological Collection) as well as on skeletons in museum collections in the USA (particularly those at the Field Museum, Chicago, of specimens collected in the field at Ambinda, a village between Ihazoara and the research camp at Parcel 1, as well as at Ihazoara; see Figure 2-2). Comparative data were drawn from the literature; unpublished data for *Microcebus rufus* at Ranomafana were generously supplied by Dr. Marina Blanco (University of Massachusetts, Amherst, Massachusetts).

2.2.1 Study sites

Beza Mahafaly (literally, "the place where many baobab trees bring joy to people") is located 35 km northeast of Betioky (literally, "the place of the big wind") in Southwestern Madagascar. Like any other southwestern area, this area has two seasons, rainy and dry, but the "rainy" season brings little relief from a long dry season, as the total annual rainfall at Beza Mahafaly averages under 500 mm (Ratsirarson, 2003). The "rainy" season can be described as extending from October to March, but heavy rains generally occur only between December and February, when the local riverbed (the Sakamena), otherwise dry, can fill and even flood in a matter of one or two days (Ratsirarson, 2003). During the dry season, from April to September, the temperature drops to <5° C at night and increases to >32° C during the day (Richard et al. 1991). Forest types vary in the region, as does the degree of conservation protection. I sampled three forests at Beza Mahafaly: 1) the protected gallery forest near the Sakamena River (Parcel 1 of the Special Reserve); 2) the protected (but with minimal enforcement) spiny forest (Parcel 2 of the Special Reserve); and 3) the unprotected dry deciduous forest bordering the village of Ihazoara. Sampling sites were selected following initial census transects conducted in 2003 and 2004 in each of these three forests. No mouse lemurs were located in the densest gallery forest very close to the riverbed; thus, I selected a main sampling area in the drier western portion of Parcel 1. For Parcel 2, I selected an area approximately 200 m from the road to Betioky. In addition to the main sampling sites, random sampling sites were selected at each of the three forests.

2.2.2 Capture-recapture methods

Capture-recapture methods were used to sample *M. griseorufus* at Beza Mahafaly between 2003 and 2007 (five months, April to August, in 2003; four months, September to December, in 2004; three months, February, April, and July, in 2005; three months, October to December, in 2006; and nine months, January to September, in 2007). The total number of sampling months over the entire research period was 24, of which 14 were in the "non-reproductive" "dry" season (April to September) and 10 in the wet season (October to March), which includes the beginning of the reproductive season in early October. During the 2003, 2004, and 2005 sessions, I sampled each forest in successive weeks, and then repeated the sequence. In 2006-2007, more rigorous sampling was conducted simultaneously in all three forests by three teams of three people each. These are the main data from which my conclusions are drawn, with contributions from the previous years. Note that the total number of traps used each year was not the same.

2.2.2.1 Trapping procedures

Aluminium Sherman live traps (7.7 x 7.7 x 30.5 cm) were used to capture mouse lemurs. At dusk (between 5 and 6 p.m.), traps baited with bananas were set both on the ground and in trees at heights of about 1-2 m and they were checked in the morning between 5 and 7 a.m. (at dawn). Traps that did not have mouse lemurs in them had the uneaten bananas removed and they were then closed for the day. All traps containing captured animals were collected for cleaning at the campsite, and were cleaned before reuse. While they were transported to the camp, the animals were left in the traps. At this hour of the morning, most were in a state of torpor, particularly in the cold, dry season. In the rainy season, they are awake and active. Before handling captured animals, animal handlers used gloves to prevent the transmission of diseases. Before taking measurements, each animal received a safe dosage of Telazol (usually 0.001 mg). I inserted microchips (Transponder ID 100) for individual identification using the Trovan detector system. Animals were monitored and fed, if necessary, while in the camp during the daylight hours, and each was returned to the exact location where it had been captured at dusk of the same day.

2.2.2.2 Capture schedule

Trapping occurred on a regular basis between October 9, 2006 and September 30, 2007. I used two trapping schedules ("intensive daily sampling," and "reduced sampling"), depending on the month. Four months were selected for intensive daily sampling (30 days in a row, at the main sampling areas) – October, January, May, and September. Two of these intensive sampling sessions were conducted during the "rainy" season, the first at the beginning (October) and the second during the middle (January). Two were conducted during the "dry" season, the first during the middle (May) and the second at the end (September). "Reduced sampling" was conducted for each of the other eight months. This included 5 days per week for three weeks each month at random sampling areas and 3 days at the end of the fourth week at the main sampling area (for a total of 18 days per month). The same sampling procedures were conducted simultaneously at each of the three study sites (gallery forest, Ihazoara, and spiny forest).

Every evening when sampling was conducted at a main sampling area (including the three days at the end of each reduced sampling period), 180 traps were set (120 in the trees and 60 on the ground). Main sampling areas were about 6.20 ha, and divided into grid systems of 25 m x 25 m.

When sampling was conducted at random sampling areas, only 60 traps were set (45 in the trees and 15 on the ground). These random sampling areas were selected outside the main sampling areas; every forest had a minimum of four random sampling sites. Each random sampling grid measured approximately 20 m x 20 m. On any given week during reduced sampling months, a single random sampling site was selected. During any single such month, therefore, three random sampling sites would be sampled at each forest. In total, my assistants and I set 33,120 traps in each forest (or 99,360 traps in all 3 forests) over the entire year.

During the years 2003-2005, standard sampling methods were employed, encompassing only 3 days at the end of each month per study site (following Kappeler and Schmid, 1994; Radespiel, 1998; Rasoazanabary, 2004). Whereas each of the same three forests was sampled, sampling sessions were sequential and not simultaneous. No random plots were sampled, but the same main sampling areas that were used in 2006-2007 were also employed in each of the earlier years. Sampling months in earlier years were April to August (2003), September to December (2004), February and April (2005).

2.2.3 Data collection

2.2.3.1 Morphometric measurements

All animals captured were identified by sex and weighed with a spring scale balance (±1g); for every first capture, a full set of morphometric measurements was taken with digital calipers (Appendix 2-1). All appendicular measurements were taken on both right and left sides; all axial measurements (head, trunk, and tail) were taken once.

2.2.3.2 Identifying youngsters

Because I wanted to describe the pattern of development, I needed to separate immature individuals from adults. This is easy to do when one recognizes that certain traits grow rapidly and others slowly. By the time youngsters are weaned and potentially trapped, they will have nearly adult measurements for the rapidly growing traits, but immature measurements for traits that grow slowly. Immature individuals will also tend to be small in overall mass; however, mass can be low in adults, and is strongly affected by health and reproductive state; it should never be used as the sole criterion for identifying youngsters (although typically, it is used in exactly this manner). Linear traits that grow slowly will typically have larger coefficients of variation (standard deviation divided by the mean) than traits that grow quickly and reach near-adult size in young individuals, simply because a greater portion of their developmental schedule is being sampled. To identify those traits that are most useful in determining age, I examined the coefficients of variation for each. Three traits stood out as most informative (i.e., with the highest coefficients of variation) – two linear (upper arm or humerus length and body length) and body mass. Individuals with body masses of 28 g or less, arm lengths of <14 mm, and body lengths of <80 mm, were clearly immature (no such individuals had been micro-chipped the year before) and I adopted these values as cut-points for separating immature individuals from others. This system was also used to check the utility of body mass as a sole criterion, as researchers in the past have used body masses of 35-40 grams the sole criterion (e.g., Lahann et al., 2006). I did find some individuals with adult measurements for arm and trunk length at weights of 35-40 g. However, I found 28 g to be "safe" – i.e., no individual weighing 28 g or less had adult measurements for other body parts, or adult proportions. I also checked for differences between left and right sides and found none; unless there was an injury and one side was abnormal, only the left side was used for statistical analysis.

Skeletal data were available to confirm the pattern of growth and development of Beza Mahafaly region mouse lemurs, and these data helped me to age individuals. The skeletal remains of individuals killed by owls and preserved in owl pellets, previously collected at my study sites (Goodman et al., 1993a, b), were donated to the Field Museum of Natural History in Chicago (FMNH). These specimens were measured by Dr. Laurie Godfrey, who made her data available to me. The bodies of four individuals that I found in the forest (two in 2005 and two in 2007) also were collected, cleaned and added to the skeletal collection at the research laboratory in the Beza Mahafaly camp site (Beza Mahafaly Osteological Collection, BMOC). Two of these individuals were micro-chipped and estimated to be 11 months old. Two were victims of owl predation and lacked microchips. Finally, I examined data collected by Dr. Godfrey on mouse lemur skulls and skeletons (apparently *M. griseorufus*; see Cuozzo et al., in press) that were collected by H. Bluntschli in November 1931 at Amboasary. These specimens are housed in various museums, the largest collection of which is at the American Museum of Natural History in New York.

2.2.3.3 Reproductive observations recorded for females

At each capture, I recorded the status of the reproductive organs (morphology of the vagina [sealed, swollen, and open], development of the nipples [invisible, swollen]) of all females, to categorize their reproductive state (not pregnant or lactating, pregnant, or lactating). The abdomens of females were also palpated to determine any enlargement of the uterus, and their changes in body mass over time provided additional useful information. Body mass increases during gestation, remains high during the initial phase of lactation, and then gradually decreases (Randrianambinina et al., 2003).

2.2.4 Data analysis

2.2.4.1 Inferring activity patterns, survival, longevity, and population turnover

To make the capture data comparable across months, and to facilitate comparisons to other studies (e.g., at Mandena and Ranomafana) where different sampling procedures were followed, I converted numbers of individuals captured to monthly capture success rates (total captures/total traps set), taking into account the number of traps set in each month at each of the three study sites. The monthly pattern of capture success was documented for each study site and for males and females. Following Lahann et al. (2006), I also calculated, again for each study site, the percent of individuals captured in any one year that were recaptured in the following year, two years hence, etc. Finally, I calculated the time intervals from first to last capture date for each individual. The longest intervals provide a minimum value for longevity.

2.2.4.2 Inferring the timing of birth, and polyestry

The status of female reproductive organs was examined to determine variation in the timing of estrus, birth, and weaning. To determine whether polyestry is manifested at Beza Mahafaly, I examined the reproductive profiles of individual females and recorded whether any individuals had open vaginas at least twice in any reproductive season, and whether the timing of those openings indicated the plausibility of "regular" (following weaning), rather than "rebound" (following fetal or infant death), polyestry. I also examined our morphometric data to determine the presence or absence of immature individuals (identified as indicated above) at different times of the year. Skeletons in owl pellets were particularly useful as many of them were from immature animals, and they had associated collection dates (usually within a few days of the death of the individuals). Because the owl pellets had collection information (month, day, year, place), and because their presence was checked regularly, we could be certain that the collection dates were close to the actual kill dates. Furthermore, because the reproductive season of mouse lemurs has a predictable beginning, skeletons of mouse lemurs found in them can be arranged into rough ontogenetic series. Thus, skeletons from owl pellets could be used to generate ontogenetic growth curves for *M. griseorufus*, and to determine the timing of births in the population.

2.3 Results

2.3.1 Survival and population turnover

During the period of systematic capture (October 2006-September 2007), the three field teams captured a total number of 249 individual mouse lemurs (117 females and 132 males) within the three study forest sites, gallery (116), Ihazoara (65), and spiny (68). At each of the study forests, monthly capture success was low throughout the year. The highest monthly capture success rates were observed during the dry season (May to September; figure 2-1). Note that the highest monthly capture success rate (during the month of July, in the gallery forest) was under 10%, and this pertained only to one of the three forests sampled.

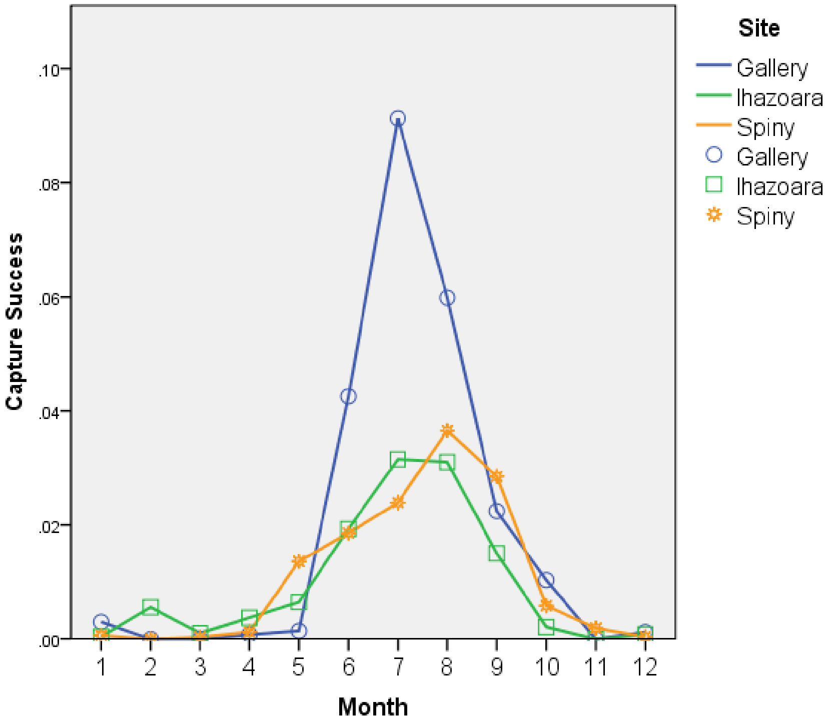


Figure 2.1: Monthly capture success for *Microcebus griseorufus* at three sites at BMSR (see key), October 2006 – September 2007. Capture success rates = # successful captures (including recaptures) / total # of traps set.

Female *M. griseorufus* enter bouts of torpor during the dry season significantly more often or for longer periods than males at Beza Mahafaly (see Chapter 4).

Nevertheless, it is important to note that females as well as males were captured during the dry season.

The annual distribution of the *number of individuals* captured from 2003 to 2007 is summarized in Table 2.1; Table 2.2 shows the capture success rates for each year by site. During the five-year extended period, we captured a total number of 435 individual mouse lemurs, with 164 in the gallery forest, 118 in the dry forest at Ihazoara, and 153 in the spiny forest. Overall, from 2003 to 2007, capture success declined (Table 2.2). In addition, very few individuals captured in the previous year were recaptured in the following year. All capture rates are very low; few exceed 1.0% and the capture success rate percentages are particularly low in 2006 and 2007. Table 2.3 gives the % of individuals known to be alive in at least 2, then 3, and then 4 consecutive years.

Table 2.1: Number of individuals captured in each year during the extended five-year period, with number of months sampled per year. Note that some individuals captured in any one year may have been recaptured in subsequent years; thus the row sums are not the total number of individuals captured per forest site.

Site	2003 # months = 5	2004 # months = 4	2005 # months = 3	2006 # months = 3	2007 # months = 9
Gallery	21	28	17	14	108
Ihazoara	23	20	14	7	60
Spiny	45	28	32	14	63
Total	89	76	63	35	231

Table 2.2: Capture success rates (% of traps with mouse lemurs, including recaptures) by forest and year. Unequal numbers of traps were set in the three forests prior to 2006-2007.

Site	2003	2004	2005	2006	2007
Gallery	0.58	1.0	1.08	0.15	0.34
Ihazoara	0.78	0.79	1.94	0.07	0.19
Spiny	1.3	0.93	0.77	0.15	0.18
All sites	0.92	0.92	1.12	0.10	0.24

Table 2.3: Percentage of *Microcebus* individuals recaptured over extended periods, with numbers of individuals indicated in each cell.

Forest	Total number of individuals captured per site (2003-2007)	Known to be alive in at least two consecutive years	Known to be alive in at least three consecutive years	Known to be alive in at least 4 consecutive years
Ihazoara Dry deciduous forest	N = 118	5.1% N = 6	0	0
Parcel 1, Gallery forest	N = 164	14.6% N = 24	1.8% N = 3	1.2% N = 2
Parcel 2, Spiny forest	N = 153	13.7% N = 21	5.2% N = 8	1.3% N =2

By examining the intervals between first and last captures for each individual caught since 2003, I was able to estimate the life span for mouse lemurs at Beza Mahafaly. The individual with the longest interval was a male from the gallery forest (063C-0A91), first captured in June 1, 2003 with a body mass of 44 g, a skull length of 34.5 mm, and a body length of 90 mm. This individual had his full adult dentition at first capture. Minimally, he was six months old at that time (~183 days). The same individual was recaptured on October 28, 2006, 1245 days after the first capture. Thus, this individual was minimally 1428 days old when last captured, or 3.92 years old. Given that these animals reproduce in their first year, he would likely have survived at least four reproductive seasons. In 2007, we did not recapture this individual. Very few individuals exhibited such longevity, and indeed only one other individual had an interval of more than 1000 days from first to last capture – a female (0659-C153) from the gallery forest whose exact interval was 1047 days. Two additional individuals had intervals greater than 900 days; these were Transponder ID numbers 0627-92C8 and 063B-F118, both females from the spiny forest. Only five individuals (two females and three males) had a first-to-last capture interval of more than 800 days (see Table 4.3 for further discussion).

The mean values and standard deviations for the intervals from first to last capture by forest were 51.5±107.1 days for Ihazoara, 92.7± 206.8 days for the spiny forest, and 94.7±183.9 days for the gallery forest (Figure 2.2).

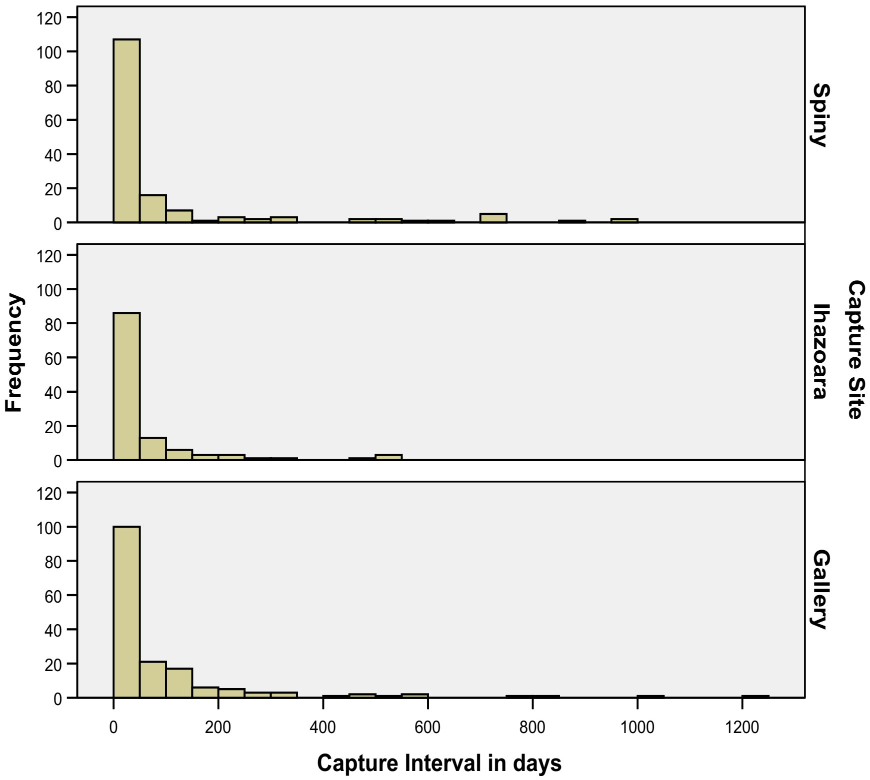


Figure 2.2: Histograms showing the relative frequencies of intervals between first and last captures for individuals from each of the three forest sites.

2.3.2 Reproductive timing and polyestry

A total of 117 females were captured during the 2006-2007 field season. During the months of May through August, no female showed any signs of reproduction (e.g, vaginal swelling, open vaginas, pregnancy, or lactation). This encompassed most of the dry season (April through September). All females had sealed vaginas and showed no indication of swollen nipples as occurs during gestation and lactation.

This state changed at the end of the dry season. First (usually in September, but possibly as late as the end of October), the vulvae began to swell (in *M. griseorufus*, this can occur over an extended period of up to four weeks). Two individuals (Transponder ID#s 0659-D356 and 0659-D600) repeatedly captured in the gallery forest during the month of September 2007 exhibited swollen vaginas for periods of 20 and 28 days, respectively. Swelling could have lasted longer, as the sampling period ended when they were still in this state. One individual (ID 0658-57B6) captured at Ihazoara displayed a swollen vagina over a period of 14 days. At the end of the period of swelling the vagina opens. An open state can exist for up to eight days.

During the month of September 2007, 32 females were captured in all three forests combined. Of these, 19 (59.4%) showed reproductive activity. Seventeen had swollen vaginas during this month (two of whom passed from a swollen to open state during this same month). An additional female was recorded as having a sealed vagina, but on later captures in the same month, her vagina was open. Finally, one female was only captured when her vagina was open. All of the females with open vaginas (n = 4) were scored as likely to have conceived. In several cases, this was obvious from their observed pattern of weight gain and nipple swelling immediately following the open vaginal state (see below). Unfortunately, pregnancy cannot be palpated at this stage, and we collected neither hormonal nor vaginal smear data to confirm the exact timing of conception. In October, 2006, 16 females were captured, 15 of which (93.8%) showed reproductive activity. Of these, 8 showed swelling only, 4 showed open vaginas, and 3 showed both conditions, passing from swelling to open state during the month of October. Again the seven with open vaginas were deemed to have conceived on the basis of weight gain and in some cases, swelling of the nipples. This record did not include the full month of October, as capture-recapture did not begin until 10 October in 2006. During November 2006, only 5 females were captured; of these five, one had an open vagina and was likely pregnant, three were obviously pregnant (discernable via palpation), and only one was reproductively inactive, with a sealed vagina. In summary, swelling occurs in September and October, copulation occurs mostly in October, but can occur in November, by which time most females are pregnant. Given that 15 of the 16 females captured in October were reproductively active, and given that this group must include individuals that are younger than one year old, one can infer that reproduction begins in the first year of life.

Because most of the females were captured only once, it is difficult to develop full reproductive profiles for single individuals. Several individuals, however, were recaptured repeatedly and these provide the most information about the duration of swelling and opening. One such individual (ID 065A-3342) was captured several times in early September with a swollen vagina (September 2, 4, 5, 7, 8, 9, 11, 12, and 17). Then she was recaptured on September 25 and 29 with an open vagina but no nipple development. During this interval, from early to late September, her body mass increased from 55 to 69 g and she was judged to have conceived in late September. Her body mass remained low, fluctuating between 49 and 55 grams between September 2 and September 11, when it began to rise dramatically. On September 25, she weighed 60 g, and on September 29, her weight was 69 g. The duration of vaginal opening in this female was minimally five days, but she was undoubtedly pregnant during the last few days of opening. In general, pregnant females weigh more than non-pregnant females (excluding lactating females). Their means are 45.8±8.5 g (non-pregnant or lactating) vs. 65.1±14.7 g (pregnant); this is significant ($t = 4.5$, $df = 11.3$ with equal variances not assumed, $p = 0.001$; note that equal variances cannot be assumed because the Levene’s test for equality of variances gives a highly significant F values, which is not surprising, as pregnant females are highly variable in body mass).

Another individual (ID 0659-D356) was first captured with her vagina open on October 20. She was recaptured on October 26 and 27, still with her vagina open. Vaginal opening in this female lasted minimally eight days. From October 20 through 27, she remained at the low body mass of 42-43 g. Yet another individual was recorded as having an open vagina for a minimum of five days.

The ranges of the documented dates on which vaginal swelling and opening were observed at the three forests at Beza varied. Without considering outliers (individuals with vaginal openings in February), the last individual observed with vaginal opening (ID 065A-17A9) was from the spiny forest. When she was captured on November 21, 2006 her vagina was still open. However, she weighed 57 grams and showed signs of nipple swelling, suggesting that she had already conceived. The dates for vaginal opening imply that conception usually occurs in mouse lemurs at Beza Mahafaly between mid-September and late November. This can be considered the "regular" breeding season for this species in the SW. There were two individuals with later vaginal openings – one on December 2 (ID 0659-D0EF the gallery forest) and another on January 7 (ID 0659-D3A5 at Ihazoara) (Table 2.5). Other data suggestive of reproductive activities outside the "regular" breeding season comes in the form of outlier pregnancies, and newly weaned infants appearing in the population at the wrong time.

Table 2.4: Recorded dates for first and last swollen vaginas during the "regular" breeding season in each of the three forest sites during the year of systematic capture.

Gallery	Ihazoara	Spiny
Sept 2 – Sept 29	Sept 16 – Sept 30	Sept 27 – Sept 30
Oct 16 – Oct 22	Oct 20 – Oct 23	Oct 14 – Oct 29

Table 2.5: Recorded dates of first and last vaginal opening during the “regular” breeding season in each of the three forest sites during the year of systematic capture.

Gallery	Ihazoara	Spiny
Sept 22 - Sept 29	January 7	---
Oct 18 - Dec 2	Oct 27 - Oct 29	Oct 28 - Nov 21

As stated above, conception likely occurs in some individuals in late September. However, females in advanced stages of pregnancy were observed only from the month of November onward. Pregnant females were also recorded in the months of December (two of the three females captured in December 2006, one of which exhibited vaginal opening on December 2 and was judged, because of her swollen nipples, to have recently conceived), January (2 of the 13 females captured), February (4 of the 8 females captured) and April (1 of the 5 females captured). Only one female was captured in March (and she was not pregnant), and, as stated above, none of the females captured in May showed reproductive activity.

The total number of adult female captures in the months of October through April is very low; in March, only one female was captured. The months of October and January were heavily sampled (intensive capture) and despite this fact, relatively few individuals entered the traps. Furthermore, the percentage of females that were found to be pregnant increased to a high in November, then decreased to a low in January, which resembled September. The percentage of females found to be pregnant in February resembled that in October. It is unfortunate that trapping failed in March. If in fact there were two consecutive breeding seasons, we would expect the percentage of pregnant females to peak again in March.

Table 2.6: Pregnant females captured by month.

Month	Most Common Reproductive State(s) Observed	# Likely Pregnant	# Adult Females Captured	Percentage of Females Captured That Were Likely Pregnant
September	Swollen vulvae	4	32	12.5
October	Open vaginas/ Pregnant	7	16	43
November	Pregnant	4	5	80
December	Pregnant/Lactating	2	3	67
January	Lactating/Weaning	2	13	15
February	Pregnant	4	8	50
March	--	0	1	---
April	--	1	5	20

Génin (2008) estimated gestation length for *M. griseorufus* at Berenty to be 52 days. Other species of mouse lemurs generally have slightly longer gestation periods (Eberle and Kappeler, 2004; Blanco, 2008) of around 60 days. If the gestation period is really 52 days, and conception first occurs anywhere between September 22 and November 21, then births should occur between November 14 and January 19. If gestation is actually 60 days, then births should occur between November 22nd and January 27.

The percentage of females captured that were pregnant increased dramatically from January (15.4%) to February (50.0%) (Table 2.6). The relatively high percentage of females that were caught pregnant in February requires special explanation. It is noteworthy that an incidence of copulation was observed on February 12, 2007 (ID 0659-2687) in the gallery forest. The same individual was previously captured on October 16, 19 and 22, when her vagina was swelling and then on October 26, 27 and 28 when her vagina was open and her body mass was 35, 39 and 36 g, and then twice in January (January 6 and 17) when she was lactating and weighed 58 g. Three infants were repeatedly observed in her nest. If she conceived on October 28 she would have given birth on December 20 or shortly thereafter, and on January 17 her infants would have been almost ready to be weaned.

It is difficult to document reproduction in February, March, and April because few individuals entered traps during this time in the year 2007. Thus, in March, only one female was captured and she was not pregnant. In April, only five females were captured, of which one was pregnant. Many more females (21 adults) were captured in May but none was pregnant or lactating. If the first breeding season was September, October, November, it appears that a second breeding season, beginning in February and ending in April, occurs at Beza. Certainly the individual that was caught pregnant on April 21 falls outside the “regular”or “first” breeding or mating season. The existence of a second mating season suggests that regular polyestry (comprising two reproductive cycles in a single extended reproductive season) occurs.

Lactation was recorded first in January (9 of the 13 females captured, or 69.2%). In January, 11 of the females captured showed reproductive activity, as two were pregnant and 9 lactating. Lactating females were quite variable in body mass (52-83 g). No lactating females were captured in February, March, or April. Lactation itself generally lasts approximately one month. Thus, with females giving birth from mid or late November to mid or late January, and weaning their offspring from mid or late December to mid or late February, they should be ready to conceive again shortly thereafter – perhaps anywhere from mid or late January through mid or late March – perhaps even later.

Ideally, to demonstrate the existence of regular (as opposed to rebound) polyestry, one would like to follow single individuals through successful pregnancy, birth, and weaning twice in a single extended reproductive season. Such evidence is hard to come by when capture rates are so low. However, one individual may fit the bill, although there are some gaps in the data. A female with ID 0659-B7F2 from the spiny forest was pregnant when she was captured on November 21, 2006. Her body mass of 55 g, and the swelling of not a single but of two pairs of nipples demonstrated that her pregnancy was well established at that time. Unfortunately, this individual was not recaptured until April 21, 2007, when she was again pregnant, but at an earlier stage. Her body mass was 51 g, and only the proximal pair of nipples were well developed while the distal pair were in an incipient stage of swelling. The same individual was recaptured yet again in September, 2007 (13 times), and showed no sign of vaginal swelling during this entire period. Her last capture was September 30. Given the time interval between her November and April pregnancies, however, it is plausible that her first litter was brought successfully through weaning.

Interestingly, data collected in 2005 corroborate the inference that regular polyestry exists at Beza Mahafaly. In this year, 6 adult females were trapped in February and 27 in April. (There were five additional relatively young females captured in April, ranging in body mass from 28 to 33 g, (with a mean of 30.6 g and a likely age of around four to five months). None of these five individuals were captured prior to April, 2005).

In February, 2005, three of the six adult females captured had open vaginas, including one from Parcel 1 captured on February 17, another from Ihazoara captured on February 2, and another from Parcel 2 captured on February 11. The latter had a sperm plug in her vagina indicating recent copulation and likely pregnancy. The female from Ihazoara may have had a miscarriage, as there was blood on her vagina. The other individuals showed no sign of miscarriage, however. The additional three females had sealed vaginas but swelling nipples, possibly indicative of pregnancy.

None of the five young females and 28 adult females captured in April had open vaginas. However, five of the 27 (i.e., 19%) captured adult females had swelling breasts and tended to have unusually high body mass (averaging 69.1 g). Twelve of the adults (43%) had both proximal and distal pairs of nipples well developed, and somewhat lower body masses (averaging 59.8 g); these were judged to be possibly lactating. Ten adult females (37%) were neither pregnant nor lactating; they averaged 45.4 g in body mass, ranging from 36.5 to 54 g.

In summary, 50% of the females captured in February, 2005, had open vaginas and the other 50% may have been pregnant, while 19% of the females captured in April, 2005, were probably pregnant, and an additional 43% probably lactating. The percentage of adult females judged to be pregnant in April, 2005 (19%) is quite similar to the percentage of adult females judged to be pregnant in April, 2007 (20%).

Captures of immature (likely freshly weaned, or almost weaned, and mobile) individuals in 2006 and 2007 occurred in two periods – December/January, and

May/June. Their temporal distribution in the population is clearly bimodal. These data offer additional indirect evidence of polyestry. Morphometric data (Figure 2.5) demonstrate that the captured individuals include youngsters that fit this description. Very young individuals can be identified because they are not merely low in body mass, but also have relatively short arms and short trunks (and thus, exhibit the body proportions of immature individuals; see Methods). Accordingly, we suggest that there are two distinct two-month periods when very young but weaned individuals are present in the population and entering traps. The first is December through January; the second is May through June. Figure 2.6 shows the frequencies of immature individuals trapped in December, January, May and June. The peaks are in January and May. The smallest immature individual captured (transponder ID number 065A-2923) weighed only 18 g when she was captured on December 22 at Ihazoara. This individual was never captured again and was likely separated from his mother prematurely.

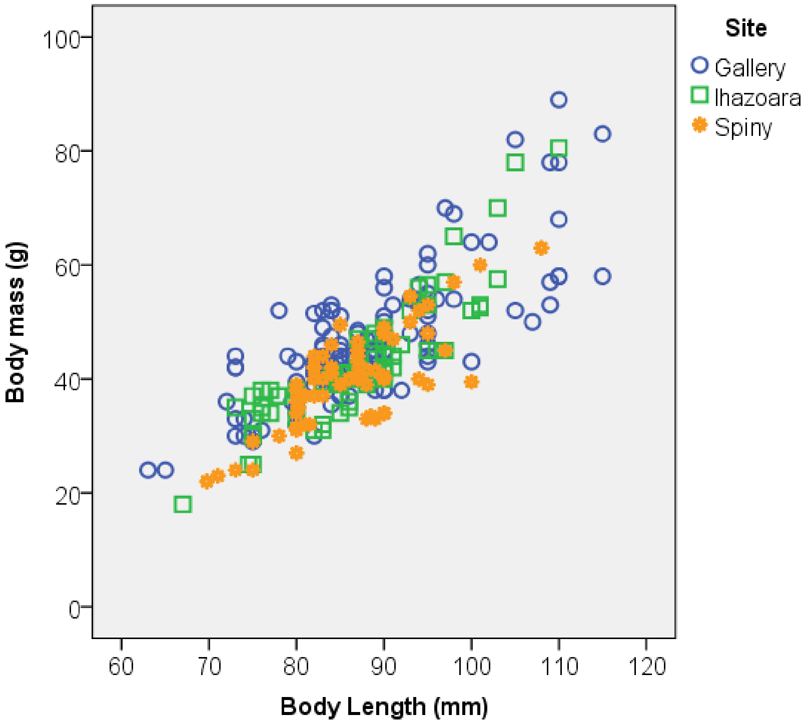


Figure 2.3: Growth and development of *M. griseorufus*. Individuals in the lower left corner of this plot (with body masses lower than 28 g) have body proportions and limb lengths characteristic of immature individuals. They were either freshly weaned or they were mobile and trapped while traveling with their likely mother. Key for capture site: circle = gallery forest; square = Ihazoara, and star = spiny forest.

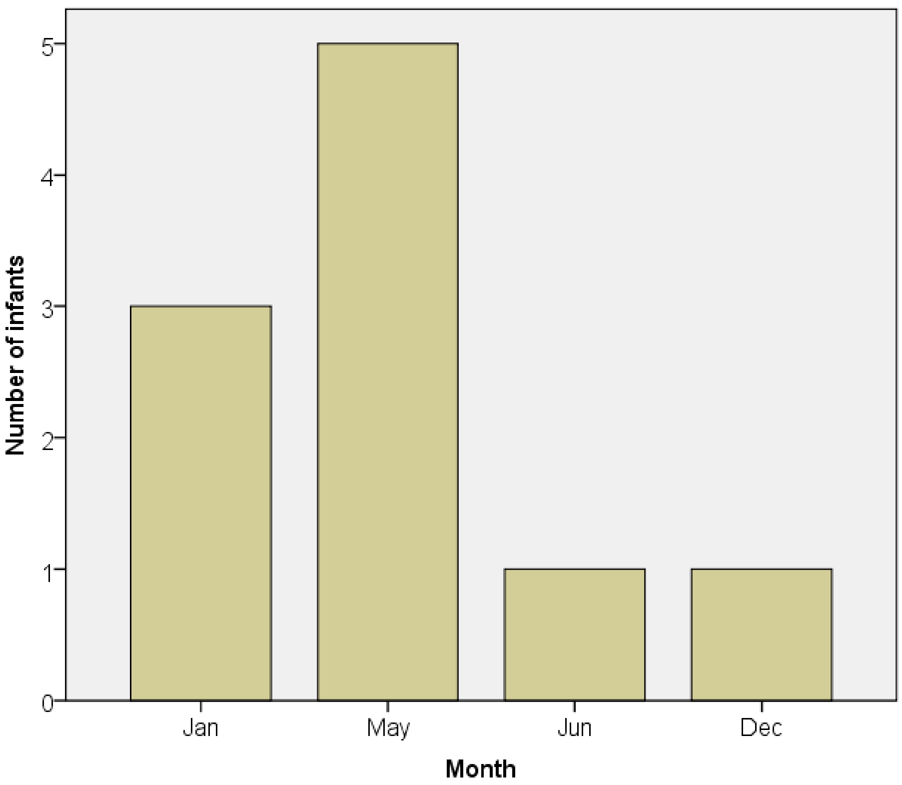


Figure 2.4: Total number of very young individuals captured by month, from October 2006 to September 2007. For criteria (e.g., body mass lower than 28 g) for designating immature individuals, see text. Very young individuals were captured only during the months of December, January, May, and June.

Unweaned infants were occasionally observed in open nests at each of the three sites sampled. During the 2006-2007 year of systematic capture, infant sightings occurred in the months of December through March; older infants sometimes remain with their mother even after weaning has occurred (see Chapter 3). Nests containing three infants were observed at Parcels 1 and 2. At Ihazoara, three infants were never observed in a nest; the maximum observed here were two. In the spiny forest in 2004, a collared female with transponder ID 063B-CC60 (frequency 150.044) was observed with four infants.

Finally, Table 2.7 shows evidence of polyestry in *M. griseorufus* at Beza Mahafaly in skeletal data collected by Dr. Laurie Godfrey, in an unpublished study of skeletons of mouse lemurs. These skeletons were found in owl pellets that were collected by Dr. Steve Goodman between November 1990 and November 1991 at a forest near the village of Ambinda (Goodman et al, 1993a, b); see Figure 1.2. Here too is evidence of the existence of two mouse lemur birth periods, with very young individuals (judged to be around one month in skeletal age) appearing in the population in December and equally young individuals appearing in the months of April and May when older immature individuals (also found in owl pellets) are in the population.

Table 2.7: Very young *M. griseorufus* individuals in skeletal collections, with collection dates, including those found in owl pellets at Ambinda and Ihazoara, and now housed at the Field Museum of Natural History in Chicago (FMNH), and one shot at Ambovombe, and now housed at the Museum of Comparative Zoology (MCZ) at Harvard.*

Date Owl Pellet or Specimen was Collected	**Skeletons of Very Young Wild Individuals (with Inferred Ages of ~ One Month or Younger)**	**Notes**
December 6, 1990	FMNH 1557a, b, e, f, Humeral diaphysis short (12.5-13.7 mm), deciduous dentition present but adult toothcomb erupted, M1 and m1 erupted, M2 erupted, M3 and m3 in crypt, p2 erupting, distal humerus unfused or fusing, no other humeral or femoral epiphyses fused.	Four individuals, no older infants or juveniles in pellet
December 20, 1990	FMNH1569, Skull and mandible with milk teeth, permanent incisors and toothcomb erupting, upper and lower first and second molars erupted; humerus and femur with unfused epiphyses; diaphysial lengths 17.3 mm (femur) and 13.4 mm (humerus).	One individual, ~ one or two months.
March, 1990	FMNH 1574 a, b, c, No postcrania, milk dentition, M1 erupted, M2 erupting, toothcomb erupting, m1 and m2 erupted. Third molars in crypt.	Three individuals, 1-2 months
April 6, 1991	FMNH1571a Humeral diaphysis12.2 mm in length with only the distal epiphysis beginning to fuse	One individual ~ 1 month
May 20, 1991	FMNH1559a, Humerus and femur with unfused epiphyses; diaphysial lengths 17.6 mm (femur) and 12.1 mm (humerus). FMNH1572, Partial skull (no mandible) with milk teeth, upper and lower first and second molars erupted.	Two individuals ~ 1 month.
June, 1931	MCZ 44844, Skull and mandible with milk dentition, upper incisors erupted, C1 just beginning to erupt, M1 and M2 erupted, toothcomb erupted, p2 erupting, m1 and m2 erupted.	One individual, ~ 2 months

*Data collected by Laurie Godfrey on samples collected by Steven Goodman and others.

2.4 Discussion

I found that, during the year of systematic capture and recapture (October 2006 to September 2007) at Beza Mahafaly, there were more *M. griseorufus* captured during the dry season than during the rainy season. The relatively high capture success from May to September was unexpected because this is the season of scarce resources, and, in other mouse lemurs, activity levels for both sexes decrease markedly beginning in May (e.g., see Rasoazanabary, 2006, on Kirindy). The presence of young individuals is not unexpected particularly if polyestry exists and the reproductive season is long (with lactation ending in May or June). The presence of adult males and females during the dry months suggests that many individuals remain active at least periodically through the dry season, and may be more tempted by baited traps than at other times of year.

Mouse lemurs at Beza differ from mouse lemurs belonging to certain other species in this characteristic, as researchers studying *M. murinus* at Kirindy (Schmid and Kappeler, 1998; Rasoazanabary, 2006) and elsewhere have found that females particularly enter a prolonged period of seasonal torpor during the dry season of scarce resources. When exposed to shorter day lengths, captive mouse lemurs show a significant decrease in behavioral activities and increase in fattening and lethargy (Perret, 1997). This situation was also expected for wild mouse lemurs but hardly characterizes all of them. Thus, for example, Génin (2008) reported no dry season decrease in general activity and capture success for a population of *M. griseorufus* at Berenty (southeast Madagascar), and Radespiel et al. (1998) observed the same for *M. ravelobensis* at Ampijoroa (northwest Madagascar). Atsalis (2000) shows a general tendency for greater activity levels in male than female *M. rufus* at Ranomafana through much of the year, with females entering apparent torpor towards the end of the dry season. More recent research at this site, however, suggests a more complex pattern of variation in activity levels (Atsalis, 1999, 2000).

Nowhere except at Beza has a marked *dry-season* increase in the activity levels of mouse lemurs (ascertained through focal individual sampling) or in capture success rates (ascertained through capture, mark and release) been observed. This regional difference in dry season activity levels may relate in part to the strong seasonality of the habitat at Beza, where individuals may have difficulty attaining sufficient food to enter prolonged torpor (or where torpor bouts themselves may be reduced in length) (but see Chapter 4, for a consideration of other factors influencing torpor). If females are entering torpor late, the reproductive season may be extended in this species. Adult females with lighter body mass cannot hibernate because they cannot survive the non-reproductive season without additional foraging effort. Seasonal torpor may be facultative in mouse lemurs (Schmid, 1997) but may require high pre-hibernation body masses, which are more easily attained in captivity than in the harshly seasonal environments of southwestern Madagascar.

Higher activity levels during the dry season may have negative consequences, as they may expose more individuals to predation by owls, particularly since individuals in leafless trees can be easier for predators to spot. Extremely high owl predation rates on adult as well as young mouse lemurs at Beza have been documented (Goodman et al. 1993a, b; see below).

It is interesting that one of the fitness advantages of hibernation is presumed to be an increase in reproductive success (Michener, 1992; Kunz et al., 1998). However, under certain conditions, reproductive success may require the opposite – i.e., extended reproductive effort into the dry season. In other words, for mouse lemurs to enter seasonal torpor, they must be able to gain sufficient weight to support hibernation after the reproductive season. If they must also have multiple litters in any single year to counter the effects of high infant mortality, they must also be able to gain that extra body mass in a limited amount of time (for the mouse lemurs of Beza, this is the month of May – part of the dry season). They must have access to sufficient food during that limited time to allow pre-hibernation fattening to occur. Certain individuals may be able to do this (indeed, in Chapter 4, I review evidence that this does occur); others may have only one litter, and use the extra non-reproductive time to gain access to resources. The mouse lemurs at Beza Mahafaly suffer very high mortality and exhibit high population turnover, making prolonged torpor a luxury that many individuals cannot afford. I will return to this question in Chapter 4, where I reveal that despite the difficulties in obtaining food in this hostile environment, at least some females do succeed in this endeavor.

The critical question posed at the beginning of this chapter was the extent to which extreme seasonality might predict population turnover rates and capture success rates at different locations in Madagascar. Table 2.3 presents the data I collected from 2003 to 2007 at the three forests at Beza. The question becomes, is the population turnover rate at Beza higher than at sites with relatively low temperature and rainfall seasonality? Is the capture success rate lower than at sites with relatively low temperature and rainfall seasonality? Is there greater polyestry at Beza than at sites with relatively low temperature and rainfall seasonality?

I used data collected during my systematic sampling year (2006-2007) and other sources to assess the degree to which females in the mouse lemur population in the region of the Beza Mahafaly Special Reserve vary in their reproductive characteristics. In particular, I can affirm that *M. griseorufus* in these forests show evidence of an extended reproductive season, with likely polyestry. That evidence is sometimes indirect, and sometimes direct. Together, the different lines of evidence converge to present a convincing case.

Table 2.8 compares population turnover data for Beza (the means for the three sites sampled here) to that of other forest sites in Madagascar. In particular, it compares percentages of mouse lemurs captured, marked and then recaptured over periods of at least two, at least three and at least four consecutive years at Beza and at: (1) Mandena littoral forest in Southeast Madagascar and (2) Ranomafana in the East. Figure 2.5 compares capture success rates at Beza Mahafaly and one of these forests – Ranomafana.

Table 2.8: Percentage of *Microcebus* individuals recaptured over extended periods at other forests.*

Species, sampling period, and forests	Climate conditions	Known to be alive in at least 2 consecutive years	Known to be alive in at least 3 consecutive years	Known to be alive in at least 4 consecutive years
M. griseorufus 2003-2007 Beza Mahafaly N = 435	Mean Annual T = 25°C Total annual RF = 750 mm	10.1% N = 51	1.7% N = 11	0.4% N = 4
M. murinus 2000-2003 Mandena N = 127	Mean annual T = 23°C Total annual RF = ~1600 mm	13%	1.8%	0%
M. rufus 2004-2008 Ranomafana N = 131	Mean annual T = 21°C Total annual RF = 3200 mm	45.0%	25.2%	6.9%

*For Mandena, see Lahann et al., 2006. For Ranomafana, Marina Blanco, unpublished

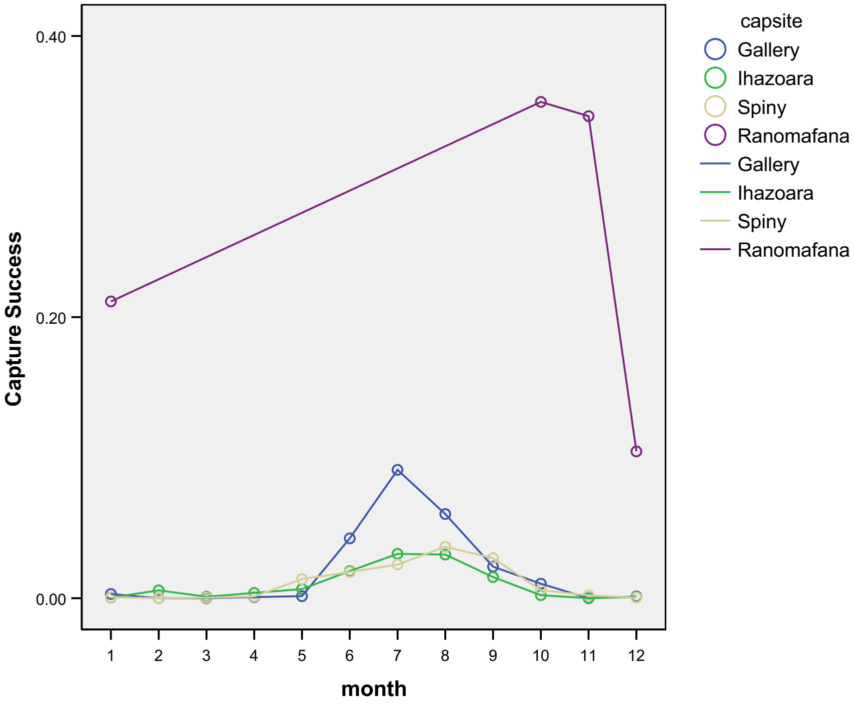


Figure 2.5: Capture success (successful captures divided by total traps set) at Ranomafana and the three forests at Beza Mahafaly during the year 2006-2007. Capture success at Beza never exceeded 10% (= 0.10) and regularly fell below 1% at all three forests. Capture success at Ranomafana, in contrast, climbed to nearly 40% during the reproductive season and never fell much below 10%. Note that captures at Ranomafana only occurred during the months October, November, December, and January. No traps were set during the other months.

Both Mandena and Ranomafana have climates that are considerably less seasonal than that of Beza Mahafaly. If seasonality is a factor that affects population turnover rates strongly, then they should both differ from Beza Mahafaly in a consistent direction. Under the premise that high seasonality increases mortality, then population turnover should be highest at Beza Mahafaly. Interestingly, Lahann et al. (2006) argue that high population turnover should be correlated with low seasonality, on the grounds that there are few constraints on polyestry when seasonality is lower, and strong constraints when seasonality is higher. Lahann et al. (2006) use this argument to explain the higher mouse lemur population turnover rates at Mandena than at Kirindy, which, while experiencing a climate that is generally milder and less seasonal than at Beza, with slightly higher mean annual rainfall (~800 mm cf. 750 mm at Beza, see Figure 2.6a-d), also experiences high temperature and rainfall seasonality and low mean annual rainfall in comparison to eastern rainforest sites.

Lahann et al. (2006) report a mean annual temperature of 23°C and mean annual rainfall of 1600 mm for Mandena. Rainfall seasonality is very low at Mandena; there is no distinct dry season. Average temperatures per month vary from 20 to 26°C, so temperature seasonality is also low. Mandena is an evergreen coastal forest (5 to 20 m above sea level).

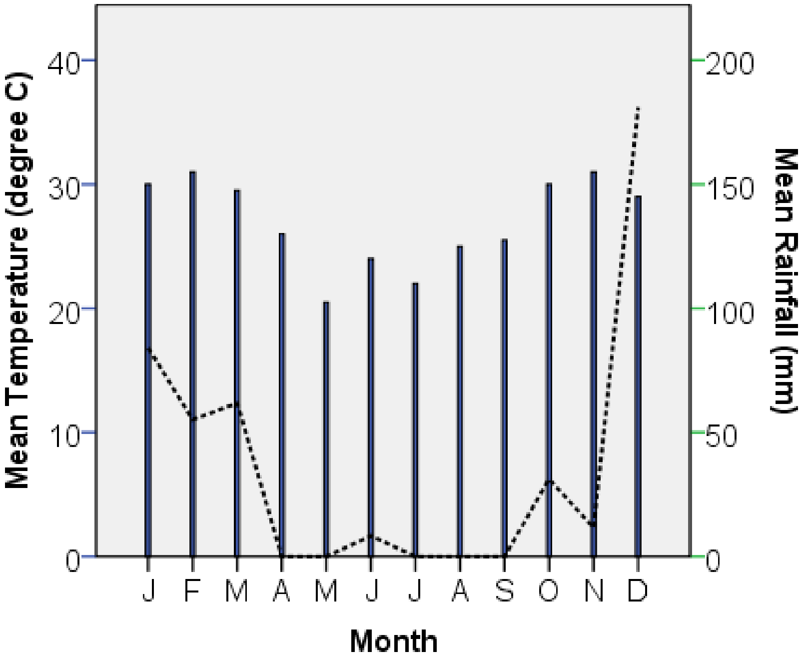


Figure 2.6a: Climate variation at Beza Mahafaly (Year 2004)

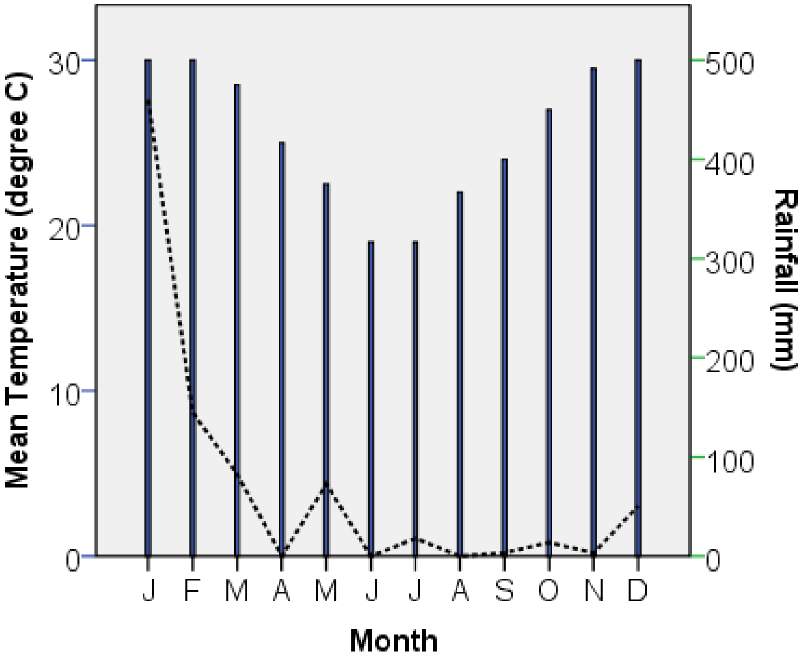


Figure 2.6b: Cimate variation at Beza Mahafaly (Year 2005)

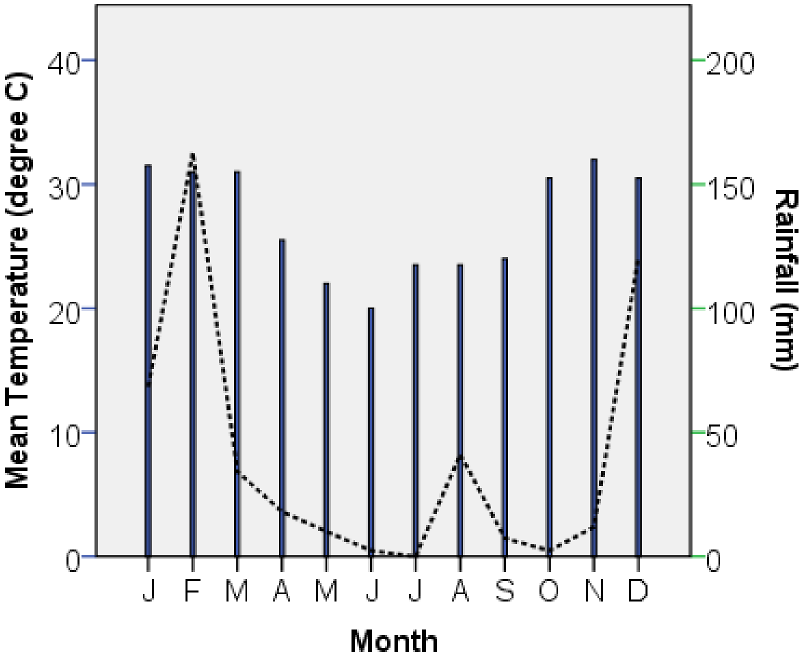


Figure 2.6c: Climate variation at Beza Mahafaly (Year 2006)

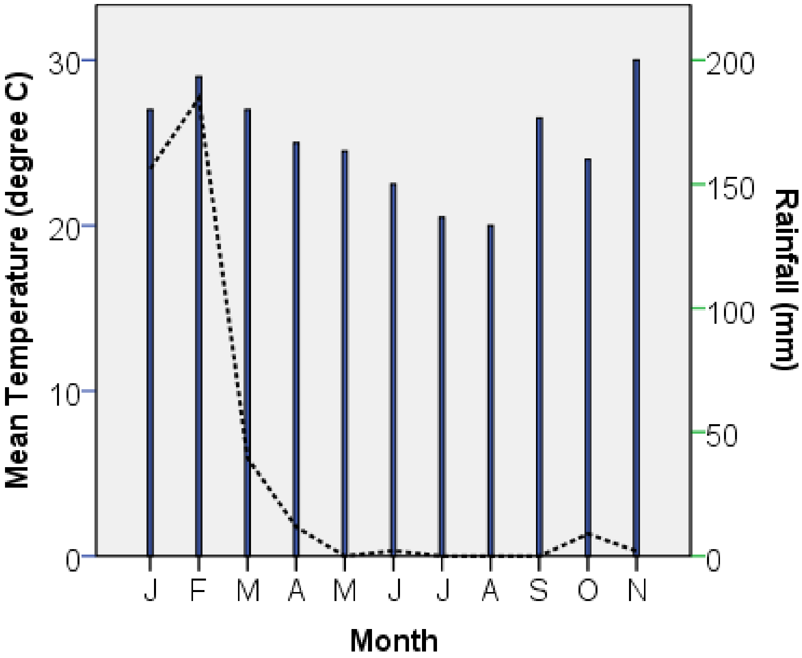


Figure 2.6d: Climate variation at Beza Mahafaly (Year 2007)

Mouse lemurs (*M. rufus*) were studied by Blanco (2010) at Ranomafana, a mid-altitude rainforest on the eastern escarpment of Madagascar. Annual rainfall was reported by Atsalis (1999) at 4485 mm; the range is 1500 to over 4000 mm, and Wright (1999) gives an average of 3200 mm. No month experiences zero rainfall. During the year recorded by Atsalis (1999), monthly means for maximum temperature ranged from 15.8 to 26.9°C, and monthly mean minima ranged from 9.1 to 16.7°C. In comparison to Beza Mahafaly, rainfall and temperature seasonality at Ranomafana are moderately low; however, there is clearly more variability here than at a littoral rainforest site such as Mandena. Thus, in terms of rainfall seasonality, Mandena scores the lowest, followed by Ranomafana, and then Beza Mahafaly.

Table 2.8 demonstrates no correlation between seasonality and population turnover or apparent life span. Over the extended five-year period during which I studied mouse lemurs at Beza, population turnover for *M. griseorufus* was very similar to that of *M. murinus* at Mandena. Compared to that of Ranomafana (with moderate seasonality), population turnover at both Beza Mahafaly (with high seasonality) and at Mandena (with low seasonality) is very high. Apparent life span at both Beza Mahafaly and at Mandena is quite low, judging from the percentages of individuals captured over periods of two, three and four consecutive years. Less than one percent of individuals at Beza Mahafaly is known to have survived beyond age 4, whereas almost 7% is known to have done the same at Ranomafana. [On the basis of a study of dental wear, Zohdy et al. (2010) calculated a maximum life span for wild *M. rufus* at Ranomafana of at least 9 years.]

Capture success rates are more than an order of magnitude higher at Ranomafana than at Beza Mahafaly (Figure 2.5); months with "low" success at Ranomafana well exceed the months with "high" capture success at Beza. Differences among the three forests at Beza are dwarfed by differences between any of the forests at Beza and Ranomafana. Blanco (2008) described some equivocal evidence in favor of opportunistic polyestry at Ranomafana, and Lahann et al. (2006) defended its regular occurrence at Mandena. We observed apparent polyestry at Beza Mahafaly, and would argue that evidence in favor of its regular occurrence here is at least as strong as evidence for polyestry at Mandena (Lahann et al., 2006) or at Ranomafana (Blanco, 2008, 2010).

These results match neither the predictions of Génin's (2008) hypothesis that *high seasonality* should correlate with high population turnover, short life spans, and a long reproductive season with individuals giving birth at different times, nor the predictions of Lahann et al.'s (2006) hypothesis that *low seasonality* should correlate with high population turnover, short life spans, and individuals giving birth repeatedly during a single reproductive season (or regular polyestry). Perhaps other factors affect population turnover rates, life span, the length of the reproductive season, and the occurrence of polyestry.

Goodman et al. (1993a) inferred high predation on mouse lemurs by the long-eared owl *Asio madagascariensis* at Ihazoara on the basis of high occurrence of mouse lemur bones in owl pellets. Mouse lemurs comprised 21.2% of the total prey biomass; only the introduced *Rattus* (at an incredible 72.1%) was higher. This was deduced from remains in regurgitated owl pellets collected on three occasions in 1990, mid June, early November, and March through April. Percentages varied by month, however, from low in November (7.8% of the total prey biomass) to moderate in March through April (24.9% of the total prey biomass) and high in June (40.3% of the total prey biomass). Goodman et al. (1993b) reported a similar mean percentage of total prey biomass for mouse lemur victims of two barn owls, *Tyto alba*, perched in a tree along the bank of the Ihazoara tributary to the Sakamena River, on the path to the village of Ambinda. These percentages also varied by month, and were especially high in May (65.8%) and June (81.7%) and much lower from July to November. Note that May and June are two of the four months in which we captured recently-weaned individuals at Beza, and that individuals born in November through January should be fully weaned and active from March onward. Godfrey (unpublished) observed that young individuals comprise a high percentage of the bones of mouse lemurs in the owl pellets that Goodman and his colleagues collected, and that no youngsters are present in the pellets collected in November.

Microcebus falls victim to many predators, both aerial and on the ground. Multiple incidents of direct predation were witnessed by me and by my assistants in all three forests at Beza Mahafaly. We also observed indirect evidence of predation. For example, during the dry season of 2003, we observed an arboreal snake (fandrefiala, *Stenophis* sp.) targeting an infant *M. griseorufus* in the gallery forest. Two adult female *M. griseorufus* were raising two infants in a single sasavy tree hole (*Salvadora angustifolia*). My assistant and I heard the sound of a mouse lemur crying in the tree hole, and when we looked at the hole we saw that one of the infants had fallen out and the snake was emerging from the hole with the other infant in its mouth. The two adult females (who had remained in the hole) waited until after the snake had retreated with its victim before descending to the ground to retrieve the remaining infant, whom they brought to another tree hole.

During the rainy season of 2007, another assistant and I located a radiocollar of one of our focal animals in the gallery forest. The collar was beeping inside a large snake hole (likely belonging to a *Boa dumerili*) on the ground. We found mouse lemur fur near the entrance to the hole, and we inferred that the collared individual (frequency 150.293, adult female) had been consumed by the snake. During the same year but at Ihazoara forest, we often observed hawks (*Accipiter francesii*, Frances' sparrowhawks and *Polyboroides radiatus*, the Madagascar Harrier-hawk) taking mouse lemurs out of their tree holes, most of which were not very high off the ground (see Chapter 4). On August 9, 2007, my assistant and I found a partial cadaver (lacking its head) of an adult male *Microcebus* (transponder ID 0659-9FC3, with radiocollar 150.885) at the entrance to a hole in a "tsiongake" (*Rhopalocarpus lucidus)* tree that was located 3.5 m from the ground in the gallery forest. The radiocollar had fallen several feet below the remainder of the cadaver. In addition to the head, the hands and feet of this individual were missing. Eight additional cadavers were found at Ihazoara and Parcel 1. Likely victims of bird predation found during my year of systematic capture are listed in Table 2.9. Bird predation is responsible for a very high percentage of deaths of mouse lemurs at Beza Mahafaly, affecting immature and mature individuals of both sexes. Eighty percent of observed mouse lemur predation attempts (successful and unsuccessful) involved birds. During the entire field study (2003-2007), up to ten species of predators including birds and snakes were recorded; some were nocturnal and others diurnal (see Table 2.10).

Table 2.9: List of individuals apparently killed by bird predators during the year of systematic capture-recapture (October, 2006- September, 2007) with transponder ID and Beza Mahafaly Osteological Collection (BMOC) numbers, when available.

Transponder and BMOC IDs, when available	Date and place found	Victim sex and age	Forest	Notes
BMOC 167 0658-5D67	7/09/2007	Adult female	Gallery	Partial skeleton
BMOC 168 0659-D129, collar 150.283	6/17/2007	Adult male	Gallery	Partial skeleton, no skull, no innominate; trunk and limb bones present
BMOC 179 0659-DB18	9/2/07 Ground	~ year old male	Ihazoara	Partial skeleton; No skull or mandible; no scapula, no innominate; partial skin
BMOC 185 0659-9FC3	8/9/07 Tree hole	Adult male	Gallery	Partial skeleton, no skull, no mandible; skin present
BMOC 187 No microchip	8/22/07 Vegetation tangle	Immature	Gallery	Partial skull and skeleton; scapula, innominate, femur, humerus
BMOC 188 065A-27CC	8/30/07 Tree hole, dead fatra	Adult male	Ihazoara	Partial skeleton, no skull, no mandible; skin and postcranial skeleton present
BMOC 190 0659-E883	8/9/07 Ground	Immature female	Ihazoara	No skull, no mandible, no scapula; other postcrania present
BMOC 189 no microchip	8/15/07	Immature	Ihazoara	Partial skull (piece of cranium) and partial skeleton; postcrania, femur, humerus, 1 scapula, 1 innominate

Table 2.10: List of mouse lemur predators recorded during the entire field study (2003-2007).

Predators	Malagasy names	Scientific names	Sites
Nocturnal	Pitsy (bird)	*Copsychus albospecularis*	Ihazoara
	Fihiake (bird)	*Polyboroides radiates*	Ihazoara
	Vorondolo (bird)	*Ninox duperciliaris*	Gallery, Spiny
	Torotoroke (bird)	*Asio madagascariensis*	Gallery, Spiny
	Refario (bird)	*Tyto alba*	Gallery, Spiny
	Boa (snake)	*Boa dumerili*	Gallery, Spiny
Diurnal	Firaokibo (bird)	*Accipiter madagascariensis*	Ihazoara
	Fandrefiala (snake)	*Stenophis* sp.	Gallery
	Hitsikitsika (bird)	*Falco newtoni*	Gallery, Ihazoara, Spiny
	Papango (bird)	*Milvus aegiptius*	Gallery, Ihazoara, Spiny

In summary, high seasonality may limit reproductive options but other factors (such as predation) may have a greater influence on mortality. It is possible that such factors have a greater impact than seasonality on population turnover rates. In comparing population turnover rates at the various forests of Madagascar, therefore, greater attention must be paid to collecting data on predation and other factors that influence mortality. The point is that the high population turnover observed at Beza Mahafaly may be related to high infant and juvenile mortality, and that mortality may not be correlated with seasonality in any simple manner (see Blanco et al., in prep.).

2.5 Conclusions

The study of capture and recapture rates of individual mouse lemurs and of the timing of reproduction allows us to better understand the population dynamics of *M. griseorufus* at Beza Mahafaly, and to compare those dynamics to those of mouse lemurs living in less seasonal habitats. We found that capture success rates at Beza Mahafaly are very low in comparison to that at the less seasonal Ranomafana. We also found that annual recapture rates (the percentages of individuals captured in one year that were recaptured in successive years) are low at Beza Mahafaly and at the much less seasonal Mandena forest, and relatively high at Ranomafana, with its moderate seasonality. The pattern observed does not fit the predictions of prior theoretical frameworks (e.g., Lahann's 2006 hypothesis that population turnover should be inversely correlated with seasonality, and Génin's 2008 hypothesis that population turnover should be positively correlated with seasonality). We offer potential alternative explanations (e.g., population turnover rates are correlated with mortality, which may or may not relate to seasonality), and urge further analysis of the data along those lines. We further stress that proper comparisons will depend not merely on an analysis of capture success rates, but on a demographic analysis of birth and death rates.

To conclude, *M. griseorufus* at Beza Mahafaly is able to reproduce rapidly and repeatedly during single reproductive seasons in order to meet the challenge of high mortality, apparently affecting both infants and adults. As a species, *M. griseorufus* does indeed appear to live its life in the fast lane, with individuals reproducing fast and dying young. Therefore, we suggest that *M. griseorufus* at Beza Mahafaly are not "bet hedgers".

CHAPTER 3

THREE HABITATS, ONE SPECIES, *MICROCEBUS GRISEORUFUS*: SEASONAL AND BEHAVIORAL ADAPTATIONS TO RIVERINE AND XERIC FORESTS IN SW MADAGASCAR

3.1 Introduction

Mouse lemurs live today in a wide variety of habitats, from the littoral, mid-altitude, and high altitude rain forests of the east (Atsalis, 1999; Lahann et al., 2006; Gligor et al., 2009; Radespiel et al., 2008; Blanco, 2010) to the xeric "spiny" and gallery or riverine forests in the south and southwest (Yoder et al., 2002; Rasoazanabary, 2004; Génin, 2008, Kobbe and Dausmann, 2009) and the dry deciduous forests of the west and north (Ganzhorn and Schmid, 1998; Schmid and Kappeler, 1998; Zimmermann et al., 1998).

Among the western (or dry-loving) mouse lemur species, *Microcebus murinus* is the best studied. It has a broad geographic distribution, and has been hailed as broad-niched – adapting to a wide variety of environments. It lives in sympatry with other mouse lemur species that appear to have much narrower habitat preferences, including *M. ravelobensis* in the northwestern dry deciduous forest of Ampijoroa (Zimmerman et al., 1998) and *M. berthae* in the western dry deciduous forest of Kirindy (Schmid and Kappeler, 1994; Schwab and Ganzhorn, 2004). It also lives in sympatry with *M. griseorufus* in the southern dry forest of Berenty (Yoder et al., 2002). There is evidence of hybridization between *M. griseorufus* and *M. murinus* in the transitional forest corridor connecting the dry spiny forests (with *M. griseorufus*) located west of Ampihamy to the wetter littoral forests (with *M. murinus*) located east of Sarikady (see Gligor et al, 2009). At Mandena and other sites (located along the eastern extreme of the southern coast of the island), there exist populations of *M. murinus*. However, *M. murinus* does not inhabit the very dry (xerophilic) forests of the extreme south and southwest. And whereas it had been reported to exist in the gallery or riverine forests of the south and southwest, only one individual was captured at Berenty (Yoder et al., 2002) and no individuals belonging to this species were present in the gallery forest at Beza Mahafaly when I arrived there in 2003 (see Heckman et al., 2006) even though I had expected to find them there. *M. murinus* has also been reported to tolerate very disturbed forests (Ganzhorn, 1995; Ganzhorn and Schmid, 1998; Radespiel and Raveloson, 2001; Hapke, 2005). However, its tolerance for disturbed habitats may be limited, and it has never been reported in the most hostile habitats of all of Madagascar – the extremely dry spiny thickets of the south. The population of mouse lemurs captured in 1931 in a spiny forest at Amboasary (and housed at many museums under the name *M. murinus*) is actually *M. griseorufus* (Cuozzo et al., in press), and it is the latter species that may be the most tolerant of habitat variation of all mouse lemurs. Rasoloarison et al. (2000) reported one mouse lemur jaw from Ihazoara (found initially by Steve Goodman in an owl pellet collected in 1990 or 1991) that identified as *M. murinus*. The rest were identified as *M. griseorufus*. If *M. murinus* lived in the vicinity of Beza Mahafaly in 1990, it appears to have disappeared since. Alternatively, the single jaw may have been misidentified.

M. griseorufus has a broad geographic distribution in the south and southwest of Madagascar (the Spiny Thicket Ecoregion of Burgess et al., 2004 – known for its unique flora with a dominance of members of several plant families, including the Didiereaceae and the Euphorbiaceae; see Fenn, 2003), from Lamboharana south of Toliara to the forests in the eastern part of the southern quadrant of Madagascar (e.g., Berenty, Amboasary, and likely Andrahomana on the eastern part of the southern coast). *M. griseorufus* has been described in spiny forests at Berenty (notably outside the gallery forest there; Yoder et al., 2002; Génin, 2008), Tsimanampetsotsa (Kobbe and Dausmann, 2009), formerly at Amboasary (Cuozzo et al., in press), and in the easternmost spiny forests of Mahavelo and Ampihamy, as well as in the transitional forests (Sarikady, Ankilivalo, and Anjà) between the littoral forest of the east (at Mandena) and the easternmost spiny forests mentioned above (Gligor et al., 2009). It has also been identified in surveys conducted at Mikea, Itampolo, Vohombe, Behara, and Namoroka along the western coast of Madagascar (Wilmé et al., 2006); Namoroka is well north of Toliara. Interestingly, *M. murinus* has been found in the extreme southeast (at Mandena, east of Andrahomana), so at some point in the past this species must have been widely distributed across the south. This does not mean that it necessarily tolerated very dry habitats, however. It is possible that there was a more mesic (or water-loving) forest corridor that spread west to east across the central highlands of the south (Goodman and Rakotondravony, 1996; Goodman and Rakotozafy, 1997; Goodman and Ramanamanjato, 2007) – a dispersal route for species that may not tolerate very xeric (or dry-loving) habitats. Note that at Kirindy (in the west), *M. murinus* prefers the moister forest habitats of the reserve, bordering the Kirindy River (Yoder et al., 2002; Rasoazanabary, 2006). At Berenty Private Reserve, *M. murinus* was not captured in the spiny forest (Yoder et al., 2002). When conducting surveys at Berenty in 2000, Génin captured one mouse lemur (*M. murinus*) in the gallery forest and many *M. griseorufus* in the spiny forest. The latter species may prefer spiny forest.

At Beza Mahafaly, *M. griseorufus* lives in three forest habitats: the gallery forest, dry deciduous forest of Ihazoara and other villages, and the spiny forest. This chapter focuses on the patterns of behavior and differences in morphology of *M. griseorufus* living in those different forest habitats at the Beza Mahafaly Special Reserve and its surrounding areas. The data presented for this chapter were collected from October 9, 2006 to September 30, 2007. The goals of this chapter are: 1) to document the physical environments, structure and phenology (i.e., the timing of periodic events such as leafing, fruiting, etc.) of the three selected forest habitats inhabited by *M. griseorufus* at Beza, focusing particularly on the plant resources used by *Microcebus*; 2) to investigate the physical (morphometric) differences between adults in populations of *M. griseorufus* in the three habitats, and their behavioral plasticity in selecting food resources and nesting sites (by site and season); and 3) to study the relationship between the morphological/behavioral differences among mouse lemur populations and the differences in their habitats and available resources. Ultimately I hope to better understand how *M. griseorufus* copes with variation in its environment in space and time.

3.2 Methods

Animal trapping procedures (capture-recapture) and the general characteristics of the study area are described in Chapter 2. Figure 1-3 shows a map of the study locations. Here I describe the methods that I used to collect (1) field data on the plants and (2) behavioral data on focal individual animals. The latter were used to document variation in feeding and nesting patterns. Climate data (including daily rainfall in mm and temperature minimums and maximums in °C) were also collected by team members at the research camp site. This site is located close to the main entrance to gallery forest, and approximately 5-7 km away from the other forests that I studied.

3.2.1 Botanical survey

A total of 11 plots (each 10 x 100 m) were established in the three habitats at Beza Mahafaly: gallery forest (n = 4), dry deciduous forest of Ihazoara (n = 3), and spiny forest (n = 4). [Four plots were initially established at Ihazoara, but children removed about three quarters of the tags in one of these plots, rendering it useless for further analysis.] At each forest, two botanical plots were located within the main animal study area (see Chapter 2). At the gallery and spiny forests, the other two plots were located outside the main animal study area, while at Ihazoara, the remaining one plot was located outside the main animal study area. In November, 2006, I tagged all trees with diameters at breast height (dbh, ~ 4.5 feet from the ground) >5 cm at each of the 11 plots, and collected data on tree height, and the depth and diameter of the crowns of each tree. A total of 1313 individual trees were recorded in all of the three forests (see Appendix B for a complete species list). Plants are considered excellent indicators of the nature of habitats and of seasonal variation because they react quickly to changes in rainfall and temperature (Chen, 2003).

Plant phenology must be documented to understand the impact of changing resource availability on animals that depend on plants for feeding and nesting (van Schaik et al., 1993; Wright et al, 2005; Wright 2006). To do so, I conducted monthly plant surveys (beginning in November) tracking changes in each tagged plant in each of the 11 plots. The status of the leaves, flowers, and fruit of each tree was recorded. The botanical survey teams recorded absence, presence, and maturity of leaves, flowers, and fruit for each plant. Scoring was as follows: For leaves, 1 = emergent, 2 = mature, 3 = senescent, 4 = shed; for flowers, 0 = none, 1 = budding and 2 = mature; for fruit, 0 = absent, 1= present, including "bouton fruit" or fruit buds, unripe and ripe fruit.

3.2.2 Radiotracking and focal individual observations

In order to study the feeding and nesting behavior of mouse lemurs, I hoped to capture, at each of the three forests, six adult males and six adult females for fitting with radio collars. During the reproductive (rainy) season, adult females that were either pregnant or lactating were targeted for focal individual sampling. Because the radio collars that I used (TW4-button cell tags, Biotrack, Wareham, UK, each weighing 2 g and accommodating the antenna within the collar band itself, to be least obstructive), and that are suitable for use on very small animals, only last up to three months, the capture and fitting of individuals for focal individual sampling was conducted twice, once in November, 2006, and a second time in May, 2007. Given the constraints of (1) the number of nights available for focal-individual sampling, (2) the high human investment required for such night sampling, (3) our desire to sample adult females in multiple reproductive states, and (4) our desire to sample as many individuals as possible to obtain statistically robust results, we set a goal of radio-collaring 6 males and 6 females per season per forest. Our ideal projected total was thus 12 individuals x 2 seasons x 3 forests (or 72). Because mouse lemur captures were infrequent in November 2006, we could not attain this ideal. Our choice of individuals to collar depended on daily capture success rates in each forest. It was sometimes necessary to collar subadults to obtain sufficient numbers of males and females. Given also the premature loss of individuals or collars, the number of focal animals watched on any given day in each forest was not constant. During this period, I collared a total number of 57 individuals of *M. griseorufus*; three of whom were lost just few days after the collars were installed (Table 3.1).

Table 3.1: Number of collared individuals followed during the entire one-year period (October 2006-September, 2007), by sex, age, and forest.

Focal individuals	First sampling period			Second sampling period		
	Gallery	Ihazoara	Spiny	Gallery	Ihazoara	Spiny
Total number of individuals	8	8	8	12	10	11
Adult females	2	4	4	6	3	4
Adult males	6	3	1	4	2	6
Subadults (with sex as indicated)	none	1 male	2 females and 1 male	2 males	2 females and 3 males	1 female
Total	24			33		
Starting date	11/22/06	01/09/07	12/24/07	05/19/07	05/27/07	05/21/07
Ending date	04/01/07	05/20/07	04/04/07	08/24/07	08/18/07	08/26/07

Because I wanted to document the differences in mouse lemur feeding and nesting behaviors by forest without differences in the timing of data collection affecting the results, focal-individual-follows were made simultaneously by teams working in each forest. I assigned three teams of three people each to collect data in each of the three habitats. We conducted focal observations at night to document the feeding behavior of mouse lemurs. We also conducted focal observations during the day to study mouse lemur nesting patterns. Focal individuals were located by their distinct radio frequencies, and nesting locations as well as the properties of nests (see below) were recorded. All radio-collared individuals were followed by using a portable device TR-4 receiver (Telonics, Impala, AZ). The daily sampling schedule (starting time, ending time) depended on the season (see "Feeding behavior," below), but follows were conducted in the same manner (i.e., same starting time, same duration) whenever possible. A summary of the focal sampling periods for each individual is provided in Table 3.1.

3.2.2.1 Nesting behavior

Beginning on the morning of the very first day of focal individual observation, we followed collared individuals' radio signals to the nests where they slept. We recorded the observation date, and identified, flagged, and numbered the individual plants used as nests. On every focal-individual sampling day, we confirmed the location of the nest to determine whether or not the individual had moved. We collected data on the height of the nest above the ground, type of nest (in open, tangled vegetation or in tree holes), as well as animal grouping patterns in nests whenever possible.

3.2.2.2 Feeding behavior

On every focal individual sampling night, at each forest, two radio-collared individuals were followed. For each, observations began as soon as the individual left its nest (or, if the individual was already active, as soon as the individual could be found). Overall, nocturnal feeding observations on active individuals were conducted for 788 hours during the first focal individual sampling period (the reproductive or rainy season, from November to whenever the radio collars ceased functioning, see Table 3.1), and for 1129 hours during the second focal individual sampling period (June through August, see

Table 3.1). Focal observations were made between 18h30 and 02h00 (first sampling period, rainy season) and between 17h30 to 02h00 (second sampling period, dry season). We made feeding observations (not feeding, feeding on leaves, fruit, flowers, insects including insect secretions, gums, water; feeding on the ground or on a particular plant) every two minutes, following (Altmann, 1974). Features of the plants on which animals fed were also recorded (species, height above the ground and trunk diameter at feeding location).

3.2.3 Data analysis

The general characteristics of the plants in the three forests were assessed using standard ecological descriptors (species richness or the total number of tree species sampled at each forest, species richness as a percentage of the total number of tree species sampled at all locations, Simpson's Index, or D, which measures the probability that two individual plants randomly sampled from a forest will belong to the same species, and Simpson's Index of Diversity, or 1-D, which captures the probability that two individual plants sampled from a forest will NOT belong to the same species and thus gives an indication of species diversity). ANOVA was used to test the differences between forests in general structural characteristics. Habitat differences in the frequencies of the various tree species in the botanical plots were tested using $\chi2$; separate analyses were made of plant species used by mouse lemurs for feeding and nesting. Discriminant function analysis was used to determine whether the three forests could be distinguished by their general phenological (timing of leafing, fruiting, flowering) and structural (crown heights, crown diameters, tree heights, dbh) characteristics, and to determine which forests differed most in these characteristics.

Cluster analysis of Euclidean distances among the eleven botanical plots (based on plant species presence and absence data) was used to determine whether the individual plots belonging to single forests would cluster together, or with plots in other forests.

Feeding and nesting behavioral differences between mouse lemurs by forest and season were analyzed using the $\chi 2$ test. For feeding behavior, I was interested in differences in the tree species on which they fed, as well as plant parts eaten. Feeding on insects, insect secretions, and water on particular plants was also noted. For nesting behavior, I was interested in the tree species in which they nested and nest type (hole or open). Open nests are considered poorer in quality than tree holes because they are generally more vulnerable to predation. Finally, I used Discriminant Function Analysis in order to determine whether and how mouse lemurs in the three forest habitats differ in their morphological traits, including body mass, limbs, hands and feet (see measurement list, Appendix A). Only measurements taken from the left side were used since I did not find any differences between the two sides. Additionally, immature individuals (see methods in Chapter 2) were excluded from the analysis to control for ontogenetic changes in size and proportions.

In combination, these methods allow me to make the following comparisons: 1) plant species composition and characteristics in the three forest habitats; 2) plant usage patterns for diet and shelter by mouse lemurs; 3) morphology of the populations of *M. griseorufus* in the three forests; and finally 4) the relationship between variation in mouse lemur behavior and morphology and the characteristics of the forests in which it lives. The goal is to quantify morphological variation and behavioral flexibility of *M. griseorufus* at Beza Mahafaly, and to determine whether morphological differences between mouse lemurs living in the different forests are related to the differences in forest characteristics, or to the ways in which they use those forests. If relationships between mouse lemur morphology and habitat characteristics can be demonstrated, it would behoove us to study their genetic and developmental basis – i.e., their degree of developmental plasticity – although this is beyond the scope of this dissertation. The existence of such relationships would confirm, in any case, that habitat differences do influence the biology of mouse lemurs in a non-trivial manner, and they would underscore the adaptive plasticity of *M. griseorufus* (whether or not those adaptations relate to developmental plasticity or have a genetic basis).

3.3 Results

Figure 3-1 shows photos of each of the three forests. Ground cover is thin or absent in many parts of the spiny forest and Ihazoara, but present, even during the dry season, in the gallery forest. The soil of the gallery forest tends to be moist, even during the dry season, because of its proximity to the Sakamena River; the water table is sufficiently high to maintain a fairly dense forest throughout the year, particularly in the eastern half of the gallery forest, nearest the river, despite the fact that the river is dry most of the year. The ground is noticeably more shaded in the gallery than the other forests due to the width of mature tree crowns. The terrain of the gallery forest and of the forest at Ihazoara is flat, whereas the spiny forest floor is steep in places and there are lots of rocky outcrops. At each forest, one can find deciduous broad-leafed trees that are bare during the dry season, as well as a few species that are evergreen throughout the year. Succulent, dry-loving endemic plant species belonging to the families Didiereaceae and Euphorbiaceae dominate the spiny bush, but the vegetation of the southwest is not uniformly spiny. Rather, it is a mosaic of different habitats, including dry and riverine forest, and the vegetation can change over short distances. Indeed, within the Parcel 1 gallery forest, the vegetation of the western portion can be considered “transitional forest” – and not gallery at all.

Figure 3.1a: The gallery forest, showing barbed fence. Photo credits: Emilienne Rasoazanabary.

Figure 3.1b: The dry deciduous forest of Ihazoara. Photo credits: Emilienne Rasoazanabary.

Figure 3.1c: The spiny forest. Photo credits: Emilienne Rasoazanabary.

3.3.1 Differences in forest habitats

3.3.1.1 Habitat structure, tree density, and tree diversity

In all of the 11 botanical plots surveyed (i.e., an area of 1.1 ha combined), I recorded a total of 1313 individual trees with dbh ≥ 5 cm. Compared to the gallery and the forest at Ihazoara, tree density (number of individuals per hectare) is highest in the spiny forest. Differences between the three forests were found in average tree height (one way ANOVA F=107.53; df = 2,1304; $p < 0.001$), dbh (F=8.05; df = 2,1303; $p < 0.001$), crown height (F=82.27; df = 2,1082; $p < 0.001$), and crown diameter (F=105.17; df = 2,1021; $p < 0.001$). Tukey's post hoc tests of Honestly Significant Differences (HSD) confirm that the trees of the gallery forest are significantly taller, and larger in crown height and crown diameter than the trees in the other two forest habitats (with $p < 0.001$ in each case). Diameter at breast height is significantly larger in the gallery forest than in the spiny forest ($p < 0.001$); however there is no significant difference in dbh between the trees of the gallery forest and Ihazoara. The spiny forest and Ihazoara differ only in crown diameter, with those in the spiny forest being smaller than those at Ihazoara ($p = 0.001$). In general, tree measurements for Ihazoara are intermediate between those in the gallery and spiny forests, but Ihazoara is more similar to the spiny forest than it is to the gallery forest. Table 3.2 summarizes the physical characteristics of all three forest habitats.

Table 3.2: Physical characteristics of the three forest habitats

Measurement	Gallery	Ihazoara	Spiny
Number of individual trees in the selected plots	362 (4 plots)	342 (3 plots)	609 (4 plots)
Tree Density (total number per ha)	905	1140	1522
Mean Tree Height (m) and SD	8.47 (±3.19)	6.07 (±2.39)	5.94 (±2.64)
Mean DBH (cm) and SD	12.51 (±9.07)	11.79 (±6.67)	10.67 (±5.87)
Mean Crown Height (m) and SD	3.17 (±2.15)	1.88 (±0.87)	2.00 (±1.00)
Mean Crown Diameter (m) and SD	2.68 (±1.69)	1.76 (±1.01)	1.47 (±0.64)

3.3.1.2 Habitat diversity and forest composition

The sampled trees comprise 47 species (see Appendix B). Because the trees on average are bigger and taller in the gallery forest than at the spiny forest or Ihazoara, there are fewer individual trees per plot in the gallery forest. The total number of tree species found at each forest was greater than 50% of the total number of tree species found in all three forests. To estimate tree diversity, I used Simpson's D and 1-D (formula given in Table 3.3). Simpson's "D" was calculated to ascertain the probability of randomly selecting the same species of tree twice in a row from all trees in the sample. Higher values of D (which ranges from 0 to 1) reflect lower diversity. Simpson's Index of Diversity, shown here in Table 3.3, is 1-D; it reflects the probability that different species will be sampled twice in a row in random picks. Now, higher values mean higher diversity. The values of Simpson's Index of Diversity show that, despite the smaller number of trees in each plot, the gallery forest is actually more diverse than the spiny forest which is in turn more diverse than Ihazoara.

Table 3.3: Species richness and diversity of the forest habitats

Sites	**Gallery (4 plots)**	**Ihazoara (3 plots)**	**Spiny (4 plots)**
Average number of individual trees per plot	90.5	114	152.25
Species Richness, N: Total number of tree species sampled at forest	26	30	28
N as percentage of total number of tree species sampled at Beza Mahafaly	53%	61%	57%
Simpson' Index of Diversity, 1-D, where D $= \frac{\sum_{i=1}^{S} n_i(n_i - 1)}{N(N-1)}$	0.91	0.84	0.87

I created a plant presence-absence similarity matrix to capture similarities and differences in plant species composition of the eleven sampling plots. This matrix was used to calculate Euclidean distances between pairs of sampling plots, which in turn were used in a cluster analysis (using average linkages) to determine whether plots belonging to single forests are more similar to each other in tree species composition than plots belonging to different forests. I also wanted to see whether the cluster analysis would recognize three clusters matching the three forests, and whether the clustering would indicate a greater similarity for plots from two of the three forests. Results of the cluster analysis are provided in Figure 3.2. Plots are labeled by site (1 = gallery, 2 = Ihazoara, and 3 = spiny forest) and plot number (1 through 3 or 1 through 4). The plot numbers themselves are simply plot identifiers, and have no additional significance.

Figure 3.2 shows that all four gallery forest plots form a single cluster that is distant to all other plots. Within the gallery forest, plots 2 and 3 (SP12 and SP13) are very similar to each other, but these two link to plots 1 and 4 to form a single distinct cluster. Distinctions between plots in the spiny forest and Ihazoara are less sharp in that one of the three Ihazoara plots (SP21) actually clusters with the four spiny forest plots. However, this cluster links to the other two Ihazoara plots, and all seven form a cluster distinct from that of the gallery forest. This indicates that, in terms of presence and absence of particular plant species, Ihazoara and the spiny forest have much more in common than does either with the gallery forest.

Simple frequency counts provide a similar message; the frequencies of individuals belonging to each species differ enormously by forest, with no two alike ($\chi2 = 1399.39$; df = 92; $p < 0.001$). Looking, however, at species composition (presence-absence data only), the similarities between Ihazoara and the spiny forest are evident. The following counts are informative: Only 21% (n=10) of the 47 tree species recorded are common to the three forest habitats. However, more than 70% (20/28) of the tree species recorded in the spiny forest are present in the forest of Ihazoara. Up to 53.85 % (14/26) of the tree species recorded in the gallery forest are also found in the dry deciduous forest of Ihazoara. Similarly, 50% (13/26) of the gallery tree species are present in the spiny forest. The data are provided in Appendix B.

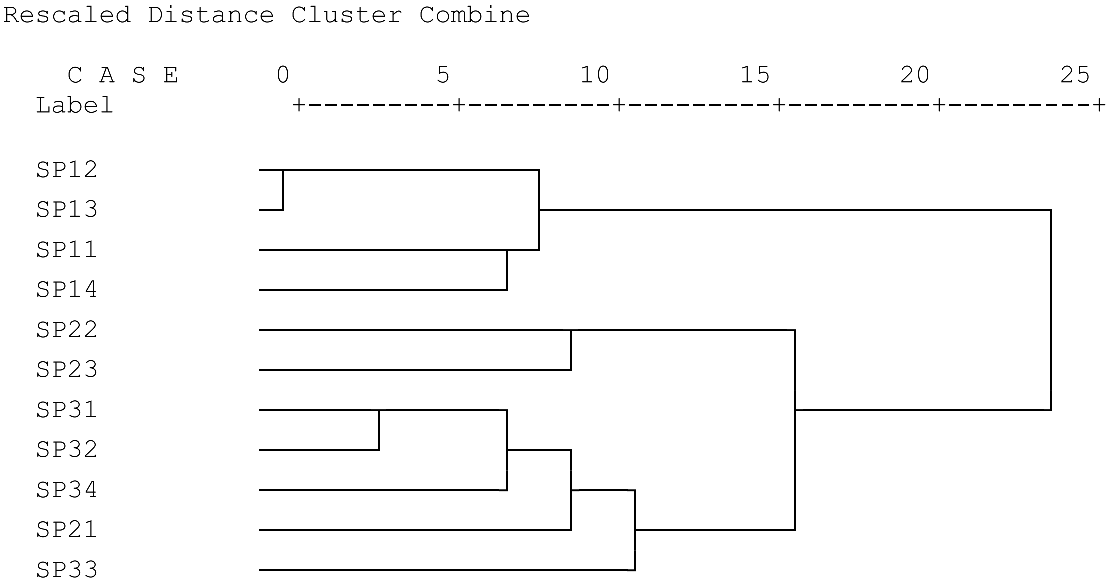


Figure 3.2: Dendrogram created using Average Linkage (Between Groups). S indicates site (S1, gallery forest; S2, forest of Ihazoara; S3, spiny forest); P indicates plot. Thus, for example, SP21 means plot #1 in the forest of Ihazoara); 1, 2, 3, and 4 indicate the number of plots in the forest habitat.

Another way to quantify similarities and differences among forests is to do a discriminant function analysis (DFA) of both physical characteristics and phenology (Figure 3.3). In this analysis, each tree is treated as an individual with height, dbh, crown characteristics, and phenological characteristics measured every month (i.e., leaf, fruit, and flower status represented as monthly scores). This analysis asks how the forests cluster when only the phenological and physical characteristics of individual plants are considered in the analysis. Does the gallery forest separate from Ihazoara and the spiny forest on this basis alone, and, if so, which phenological characteristics distinguish it?

The first function of this DFA does indeed distinguish the gallery forest (whose plants tend to have high negative scores) from both spiny forest and Ihazoara (whose plants tend to have positive scores on this axis), while the second function polarizes

Ihazoara (with positive scores) and the spiny forest (with negative scores). The first function accounts for 74.5% of the total variance and the second function accounts for the remaining 25.5% of the variance, but both functions capture significant differences between polar extremes (Wilks' Lambda test of significance, $p < 0.001$ for each). The percentage of trees that could be classified correctly as belonging in the gallery forest, spiny forest, or Ihazoara on the basis of the data used in this analysis alone was 88.3, signaling excellent separation of the three forests by phenological characteristics. Success rates for the gallery and spiny forests were both very high (89.9 and 91.1% correct classification respectively) while that for Ihazoara was 81.7%.

One can decipher which of the original, measured variables correlate most strongly with Functions 1 and 2 by examining the "structure" (or correlation) matrix. Interestingly, variables such as tree height, crown height, crown width, etc., do not correlate most strongly with either function. Instead, the first function captures differences among the three forests in leafing phenology, which are strongest towards the end of the dry season (July, August, and September), when the leaves of the trees in the two drier forests have senesced and shed more of their leaves than those in the wetter gallery forest. From November through February (generally the most humid or wettest months of the year), there are no differences between the gallery and other forests in leafing phenology; thus leafing scores during these three months are uncorrelated with scores on Function 1. In general, the correlation between scores on Function 1 and leafing phenology scores increases from March ($r = 0.10$) until September ($r = 0.82$), and then decreases dramatically in November. [Unfortunately, we have no data for October.] This means that the leaves of the trees in the gallery forest tend to move from "emergent" to “shed” more slowly than in the other forests. Correlations with tree height (-0.20), crown height (-0.21) and crown diameter (-0.21) affirm that the gallery forest (with negative scores) have trees that are taller, and larger in crown height and diameter. Interestingly, the differences in fruiting and flowering phenology are small. In general, the gallery forest is slightly more advanced than the spiny forest or Ihazoara in its flowering trajectory (with correlations of -0.10 to -0.20), except in December, January, February, and June, when the correlations are zero. The correlations of scores on Function 1 with fruiting never exceed -0.11 (November). Throughout the year (except in December through April, when the differences are trivial), fruiting in the gallery forest is slightly ahead of the other two forests.

The second function, which accounts for 25.5% of the variance, captures phenological differences between the spiny forest and Ihazoara. Of greatest importance, once again, are differences in leafing phenology. In April, *Gyrocarpus americanus*, which is abundant at both Ihazoara and the spiny forest, sheds its leaves at Ihazoara while leaves remain abundant (mature or senescent) at the spiny forest. The same pattern characterizes species of *Commiphora*. The correlation between scores on “April Leaves” and Function 2 is 0.67. In contrast, in September at the spiny forest, there are still leaves on *Albizzia* at Ihazoara while leaves on this plant are entirely shed at the spiny forest. During most of the wet season (November through February), phenological differences between Ihazoara and the spiny forest are trivial. During this period, leaves of trees emerge and mature. In addition, the structure matrix for Function 2 reveals few differences in the fruiting and flowering schedules of the trees at these two sites (all correlations are very low).

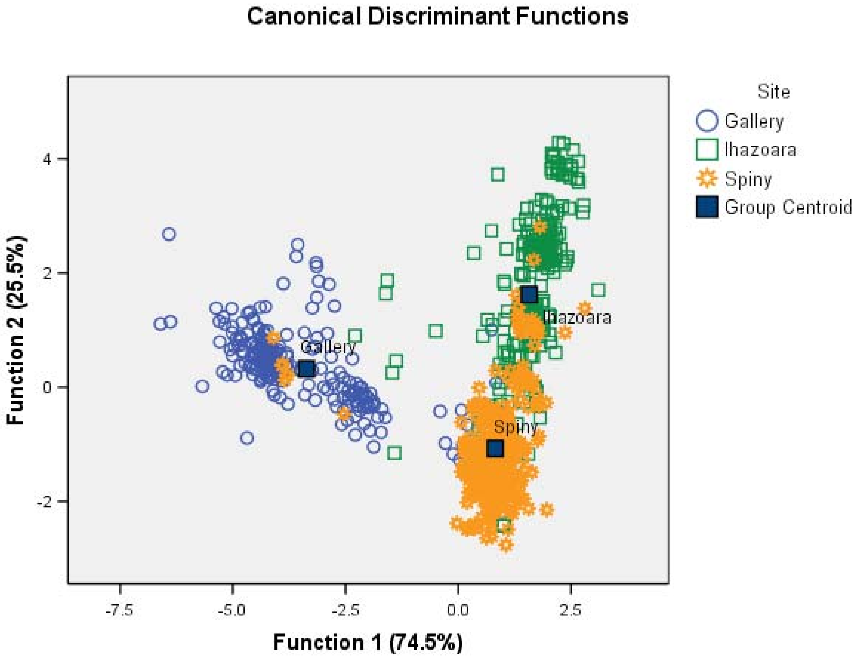


Figure 3.3: Discriminant Function Analysis of three forests based on the physical characteristics (tree height, tree crown diameter) and phenological trajectories (leafing, flowering, and fruiting) of individual trees.

Figure 3.4 underscores the similarities in the fruiting schedules not merely of Ihazoara and the spiny forest, but of all three forest habitats at Beza Mahafaly. It also underscores the pronounced seasonality in fruiting schedules of the trees of the southwest. High fruit production occurred during the rainy season, with a peak in November at each of the three forest habitats (as reflected in the mean fruiting scores for each month). Fruit production dropped dramatically during the month of December and remained low from January to April. No fruiting occurred in the spiny forest during the rest of the year, from May to September, and trivial fruiting occurred during this time at Ihazoara. In the gallery forest, fruiting occurred throughout the year, but below 2% during the very dry months. During the month of November, a higher percentage of trees were fruiting in the gallery forest (producing a higher peak) than in the spiny forest or Ihazoara.

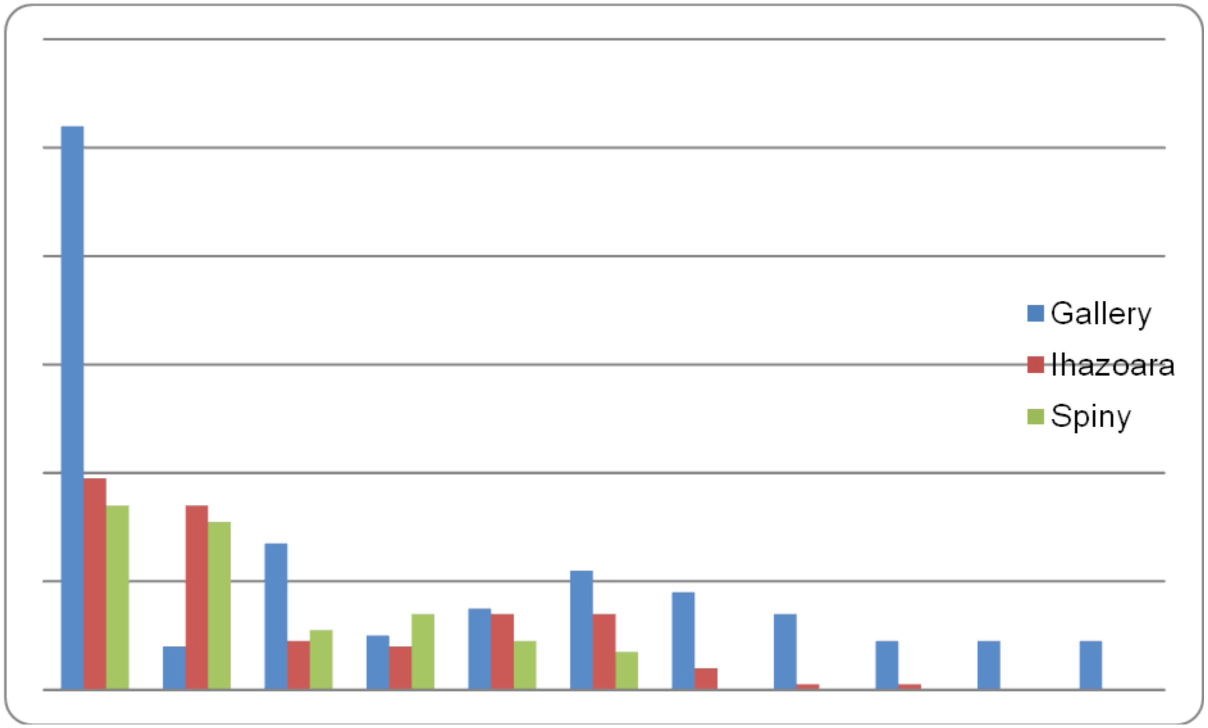


Figure 3.4: Percentage of trees that are fruiting, or that display some combination of emerging (i.e., “bouton fruit” or “fruit bud”), unripe and/or ripe fruit.

In summary, the three forests differed in species composition and structural characteristics, with the gallery having trees that were, on average, taller and with larger crowns (both in terms of crown diameter and height). Tree density was poorest in the gallery forest because of the size of individual trees; however tree species diversity was highest there. Because of the size of the crowns and proximity to the Sakamena riverbed, the ground remained moist in the gallery forest throughout the year, and fruiting persisted through the dry season only in the gallery forest.

The three forest habitats of Beza Mahafaly differ in both tree species present and the relative proportions of individual trees representing each species. Based on absence and presence of tree species, it is clear that the spiny forest and Ihazoara forest are much more similar to each other than is either to the gallery forest. Shared species at the spiny forest and Ihazoara include *Pachypodium* sp., Mahafanogne, *Opercuyarium decaryi*, etc. (see Appendix B). The gallery and spiny forests have dominant plant species – for example, *Tamarindus indica* in the gallery forest and *Alluaudia procera* in the spiny forest. The species most common at Ihazoara, *Gyrocarpus americanus*, also occurs in abundance at the spiny forest. A few other dominant species at Ihazaora, e.g., *Terminalia fatraea*, also occurs at the spiny forest and to a much lesser extent, in the gallery forest. *Fernandoe madagascariensis*, *Strychnos madagascariensis*, and *Tallinella grevei*, occur at Ihazoara and the gallery forest, but in low numbers at each.

3.3.2 *Microcebus* morphology and habitat usage patterns

3.3.2.1 Morphological traits

Overall, between October 2006 and September 2007, we captured a total of 249 individual *M. griseorufus* within the three forest habitats. Of individuals captured, 200 were adult, 145 of which were first caught in the dry season and 55 first in the rainy season. One hundred and two were captured in the gallery forest, 49 in Ihazoara, and 49 in the spiny forest. These individuals were weighed, measured and compared; the full set of measurements appears in Appendix A. The number of individuals caught per hectare was very low. I calculated "relative density" by taking the mean of individuals captured/ha during each of four months of intensive capture (October, January, May, and September); these values varied from 0.29 individuals per ha (Ihazoara in January) to 6.15 individuals per ha (gallery in May). The averages for the four months were 3.54/ha (gallery), 1.72/ha (Ihazoara) and 2.54/ha (spiny forest). The maximum relative densities were 6.15/ha (gallery), 3.58/ha (Ihazoara) and 5.86/ha (spiny forest), all in May.

Total counts of individuals captured per forest during the year October 2006 to September 2007 were 116 (gallery), 65 (Ihazoara), and 68 (spiny forest). If these counts represent the entire population at each site, then the densities would be 16.59/ha (gallery), 9.30/ha (Ihazoara), and 9.73/ha (spiny forest). It is clear that the density is higher in the gallery forest than at the other two sites. One can justify these estimates on the basis of the fact that by September 2007, 91% of captured individuals were recaptures. Between October 2006 and May 2007, the percentage of individuals recaptured was much lower (0% to 22%); the recapture rate began rising in June (to 51%), July (66%), August (71%), and finally September (91%).

Analysis of the morphometric data revealed site differences for adults of both sexes. Mean body mass of adult *M. griseorufus* at Beza Mahafaly was about 10% higher in the gallery forest than in the spiny forest; a one way Analysis of Variance of body mass differences across all three forests demonstrated strong significance (ANOVA, F = 5.162; df = 2, 197; $p = 0.007$). Tukey's post hoc test of honestly significant differences, however, showed that this difference is entirely driven by individuals in the spiny forest being smaller than individuals in the gallery forest. Neither the gallery forest population nor the spiny forest population differed significantly from the population at Ihazoara, which fell between the two. The average body mass by site was 49.3±10.6 g at the gallery forest, 46.6±10.1 g at Ihazoara, and 44.0 ±6.1 g in the spiny forest. Maximum mass was considerably smaller in the spiny forest (63 g) than in either Ihazoara (80.5 g) or the gallery forest (89 g).

Other morphometric traits differed significantly by forest habitat. These are summarized in a discriminant function analysis, which successfully distinguished among individuals in the three forests on the basis of their measurements alone (post hoc classification success = 99%). Figure 3.5 graphically shows the scores of individuals from the three forest habitats on the first and second functions. The structure matrix shows the correlations of the original traits with scores on these functions, allowing simple interpretation of the differences. The strongest correlations for Function 1 (which captured 89.1% of the variance) were with the lengths of digits 1, 3, 4, and 5 of both the manus and pedis (hand and foot) (Figure 3.6). Individuals with negative scores on Function 1 (primarily from the gallery forest) have relatively long digits 3, 4, and 5 of the foot and hand and relatively short hallux and pollex (and thus a hook-like hand and foot), while individuals with positive scores on Function 1 (primarily from the spiny forest) have relatively short digits 3, 4, and 5 of the foot and hand, and relatively long hallux and pollex (and thus a clamp-like hand and foot). Function 1 clearly separates individuals from the gallery and spiny forests (Wilks' Lambda test of significance, $\chi^2 = 585.7$, df = 52, $p < 0.001$). Function 2 accounts for 10.9% of the variance and distinguishes individuals from Ihazoara (who, with negative scores on this axis, have relative short hind limbs – in particular, the legs and feet) from individuals inhabiting either of the other forests. This function is also significant (Wilks' Lambda test of significance, $\chi^2 =$ 147, df = 25, $p < 0.001$).

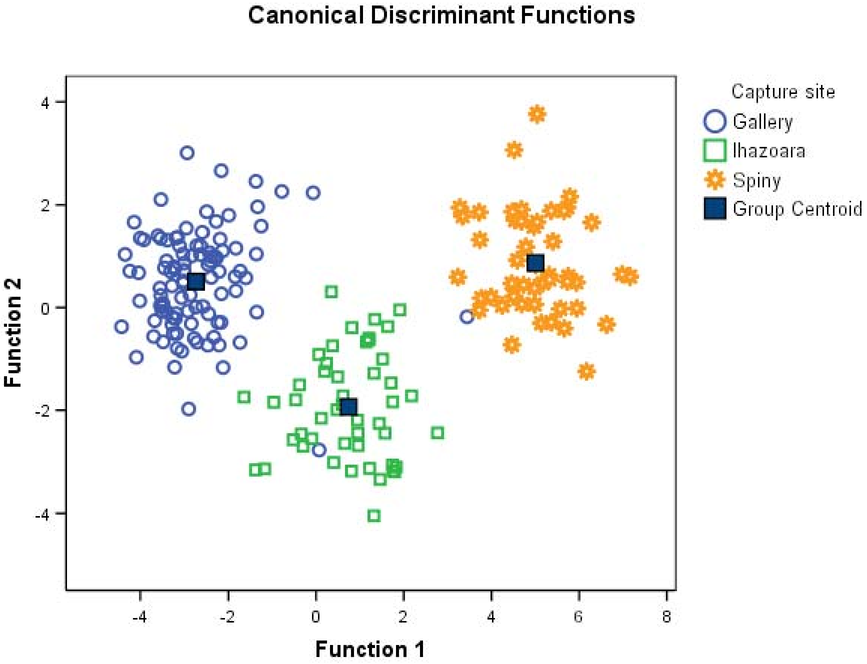


Figure 3.5: Discriminant Function Analysis of morphometric traits.

Figure 3.6: Hands and feet of *M. griseorufus* showing the relative lengths of the digits. (The digits of a total of 200 individuals were measured.) Photo credits: Emilienne Rasoazanabary

3.3.2.2 Behavioral patterns

3.3.2.2.1 Habitat use – Feeding behavior

Individual mouse lemurs were found feeding on plant parts belonging to 48 tree species during the two focal individual sampling periods (42 for the rainy season and 28 for the dry season, with some overlap). A list of plants used for food is presented in Appendix C. Differences in the frequencies of different plants consumed were significant by season ($\chi^2 = 570.80$, df = 47, $p < 0.001$). Trees that are differentially preferred in the rainy season include *Bridelia* sp. (family Euphorbiaceae), *Grewia leucophylla* (family Tiliaceae), *Operculicarya decaryi* (family Rubiaceae), and *Scutia myrtina* (family Rhamnaceae); these trees are exploited largely for their fruit. Trees that are differentially preferred in the dry season include *Acacia bellula* (family Mimosaceae), *Mimosa delicantuta* (family Mimosaceae), and *Rhopalocarpus lucidus* (family

Rhopalocarpaceae); these trees are exploited largely for their gums. The number of species exploited was greater in the wet season than in the dry season; up to 88 % of the tree species providing food were eaten in the wet season, while this percentage dropped to 58% during the dry season. Up to 46% of the tree species were used during both seasons.

Pooling data from both wet and dry seasons, and selecting only tree species that provided food for mouse lemurs in at least one of the forests, I found significant differences in tree species eaten by forest ($\chi^2 = 1919.51$, df = 94, $p < 0.001$). The number of species used for food differed little (23 in the gallery forest, 21 in the forest of Ihazoara, and 25 in the spiny forest) but the species were different. Tree species that were particularly important food resources in the gallery forest included *Rhopalocarpus lucidus* (20.9% of all focal feeding records in the gallery forest), *Acacia bellula* (19.9%), *Grewia leucophylla* (14.2%), *Bridelia* sp. (13.8%), and *Euphorbia tirucalli* (5.8%). Tree species that were particularly important food resources at Ihazoara included *Terminalia fatraea* (family Combretaceae, 26.0% of all focal feeding records at Ihazoara), *Albizzia* sp. (family Mimosaceae, 21.9%), *Commiphora brevicalyx* (14.5%), *Grewia grevei* (6.2%), and *Operculicarya decaryi* (4.1%). Tree species that were particularly important food resources in the spiny forest included *Terminalia fatraea* (33.8% of all focal feeding records at the spiny forest), *Albizzia* sp. (20.5%), *Cedrelopsis grevei* (7.3%), *Mimosa delicantuta* (5.2%) and *Operculicarya decaryi* (4.5%). Note the reliance on *Terminalia fatraea* and *Albizzia* sp. in the spiny forest (54.3% of all feeding observations combined) and at Ihazoara (47.9% of all feeding observations combined), but not in the gallery forest, where the frequency of *Terminalia* is very low and *Albizzia* does not exist.

Albizzia sp. and *Terminalia fatraea* are favored for gum feeding in the spiny forest and *Acacia bellula* and *Rhopalocarpus lucidus* are favored for gum feeding in the gallery forest.

Mouse lemurs were found feeding in different heights in the trees, according to forest site. An ANOVA test confirmed significant differences in the heights of feeding locations across forest type (F = 445.59; df = 2, 1828; $p < 0.001$). Mouse lemurs in the gallery forest tended to feed at higher locations, within the canopy, with a mean height of 6.70 m (SD = ±3.33). Mouse lemurs Ihazoara fed closer to the ground (at a mean height in the trees of 3.90 m; and SD = ±1.16). Those in the spiny forest fed even closer to the ground (at a mean height of 3.15±1.46 m). Differences in feeding height were confirmed for all site comparisons using Tukey's post hoc test of HSD. The differences in feeding height correspond to the differences I found in tree heights in the botanical sampling plots.

A second ANOVA test confirmed differences across forests in the diameters of the branches or supports on which the mouse lemurs fed (F = 16.755, df = 2, 2825; $p < 0.001$). Diameter support for feeding was not predicted by dbh. While feeding, mouse lemurs in the gallery and the spiny forests tended to utilize wide supports at around 5.32 and 5.84 cm respectively (these values do not differ significantly), whereas those in the forest of Ihazoara utilized supports averaging 4.05 cm (Table 3.4) (a value significantly smaller than those of spiny and gallery forest feeding supports).

Table 3.4: Characteristics of plants selected for feeding at the three forests, compared to mean values of trees sampled in the botanical plots.

Measurement (with F values and significance of differences across forests)	**Gallery**	**Ihazoara**	**Spiny**
Height at feeding (m) and SD (F = 445.59, $p < 0.001$)	6.70 (±3.32)	3.90 (±1.16)	3.15 (±1.46)
Mean Tree Height (m) and SD (F = 107.5, $p < 0.001$)	8.47 (±3.19)	6.07 (±2.39)	5.94 (±2.64)
Diameter of feeding support (cm) and SD (F = 16.76, $p < 0.001$)	5.32 (±4.96)	4.00 (±2.59)	5.84 (±4.74)
Mean DBH (cm) and SD (F = 8.05, $p < 0.001$)	12.51 (±9.07)	11.79 (±6.67)	10.67 (±5.87)

Mouse lemurs in the region of Beza Mahafaly have omnivorous diets, mainly comprised of insects, fruit, and gums. Food selection (i.e., insects, fruit, gums, leaves, flowers) varies significantly by season ($\chi^2 = 752.600$; df = 5; $p < 0.001$). During the rainy season, mouse lemurs ate mostly insects and fruit. They fed on the fruit of 23 tree species, three of which (*Bridelia* sp., *Grewia leucophylla*, and *Terminalia fatraea*) were frequently visited. Leaves and flowers were consumed in very small quantities (see Appendix C). Eleven tree species were visited for leaf consumption, only one (*Salvadora anguistifolia*, Salavadoraceae) of which was visited repeatedly (and then only when leaves were very young, during the rainy season). *M. griseorufus* fed on gums throughout the year but dependence on gums increased dramatically during the dry season, when gum consumption almost doubled. Plant species utilized for gum consumption also differed by season ($\chi^2 = 247.19$; df = 39; $p < 0.001$). *Acacia bellula* was used for gums preferentially in the dry season, as it is one of the few tree species in the gallery forest that provides gums when other foods are not available (this species does not occur in the other forests). Also preferred in the dry season for gum consumption are

Terminalia fatraea and *Rhopalocarpus lucidus*. The tree species used preferentially for gum consumption in the rainy season was *Albizzia* sp.

Gum consumption was very high during the dry season (77.8% of dry season feeding observations cf. 27.3% of rainy season feeding observations), whereas fruit (29.8% of rainy season feeding observations) and insect (40.4% of rainy season feeding observations) consumption were relatively high during the rainy season. Forty tree species were visited by mouse lemurs for gums, but most of these were brief encounters. Three tree species were commonly used by mouse lemurs for this purpose, including *Albizzia* sp., *Rhopalocarpus lucidus*, and *Terminalia fatraea*. Variation in diet by season is presented in Figure 3.7. Gums comprise 46.3% of the diet of *M. griseorufus* at Beza Mahafaly; gum consumption is highest in the spiny forest (52.5%), next highest in the gallery forest (42.0%), and lowest at Ihazoara (39.9%).

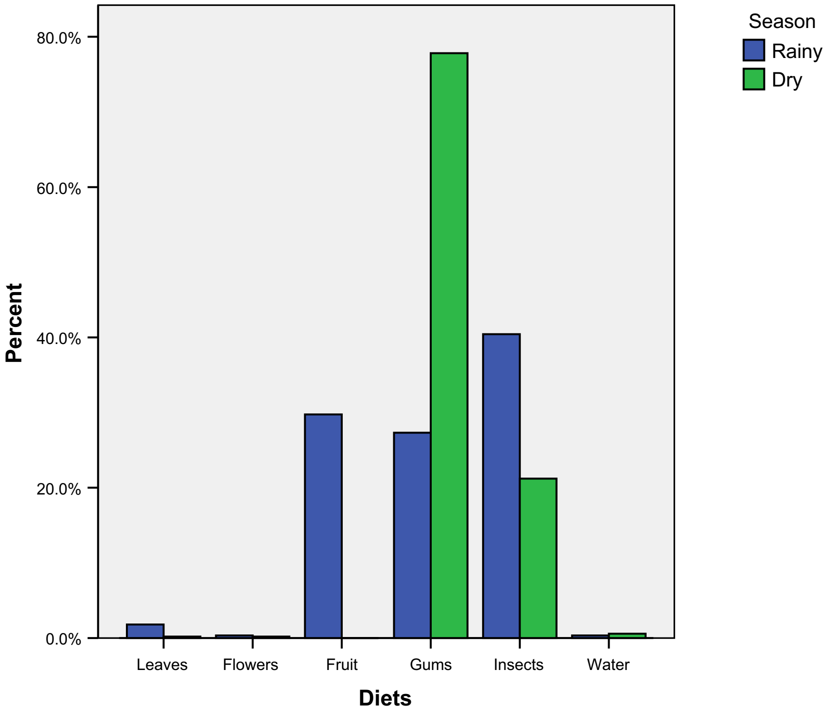


Figure 3.7: Differences in diets (in % feeding observations per season) of *M. griseorufus*

Diets varied significantly by forest habitat ($\chi^2 = 204.311$; df = 10; $p < 0.001$). Mouse lemurs in the gallery forest fed more on fruit and less on insects; mouse lemurs in the spiny forest consumed gums and insects to a greater than "expected" degree, and they consumed much less fruit than "expected" (Figure 3.8). A somewhat similar pattern was manifested at Ihazoara, where insects were consumed more than "expected"; however, gums were consumed slightly less than "expected" at Ihazoara. Figure 3.9 combines season and site feeding data, so that the % of total feeding observations across season by site can be visualized.

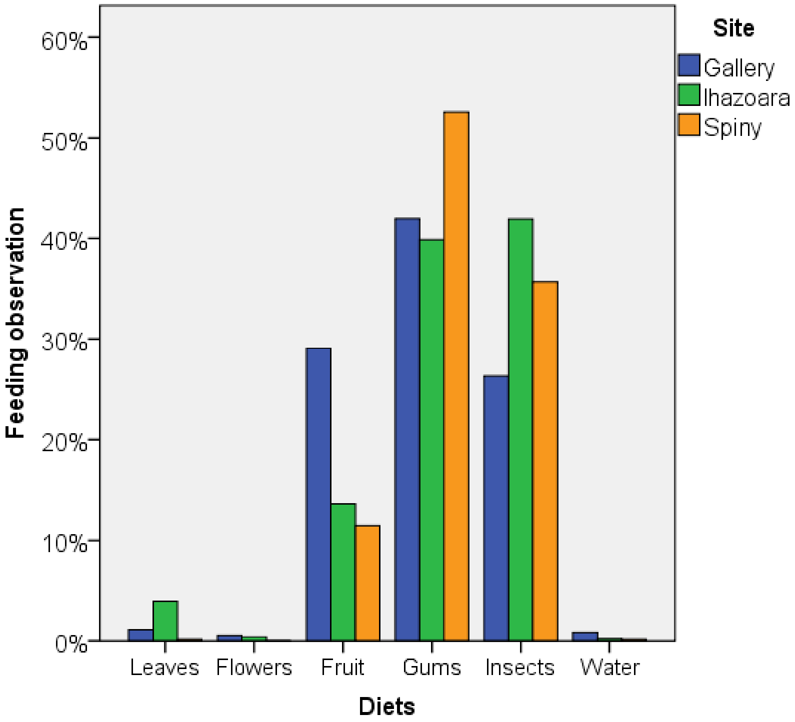


Figure 3.8: Differences in diets of *M. griseorufus* across three sites.

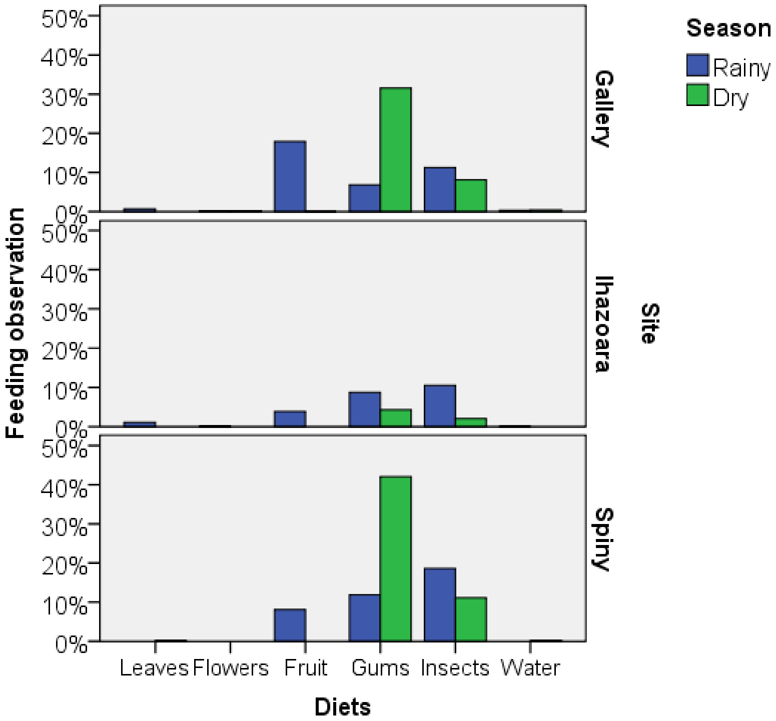


Figure 3.9: Dietary differences in % total feeding observations on different food types during the dry and wet seasons, broken down by site.

The shift from fruit and insects being staple foods to gums being the staple food occurs during the month of April (Figure 3.10). Diets differed significantly by month ($\chi^2 = 1519.597$; df = 40; $p < 0.001$). Leaves and flowers are trivial components of the diet of mouse lemurs. In February and March, fruit and insects are more often eaten than gums. Insect consumption peaks in March. A slight secondary increase in insect consumption occurs during the months of June, July, and August, but this reflects an increased availability of insect secretions and not insects per se. From April to August, gums are the primary resource. Gum consumption peaks in June.

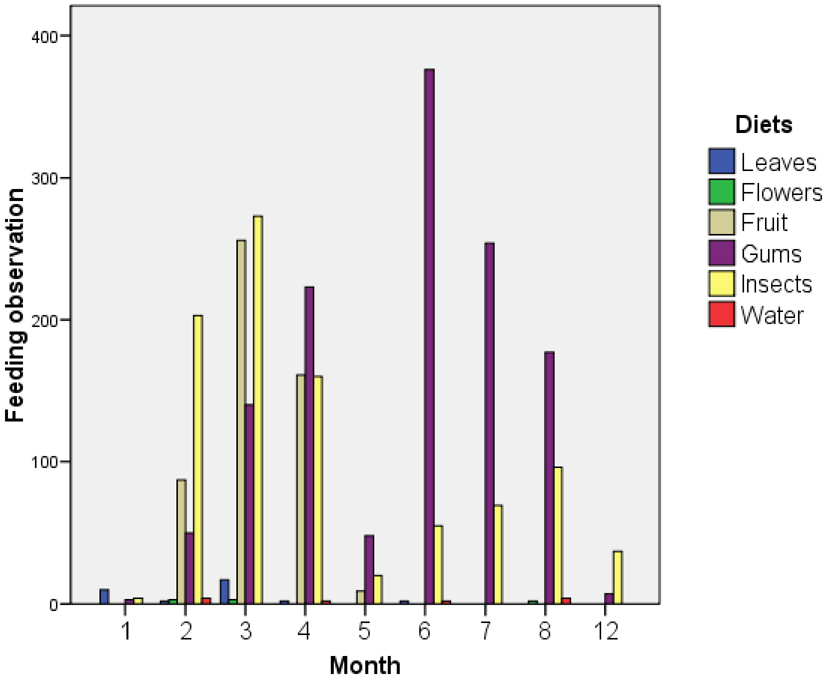


Figure 3.10: Dietary profiles of *M. griseorufus* across months.

3.3.2.2.2 Habitat use – Nesting behavior

Mouse lemurs at Beza Mahafaly were found nesting in 58 tree species, 50 during the rainy season and 39 during the dry season. Appendix E provides a complete list of tree species used as nests. Seasonal preference was strong, as large tree holes that are preferred during the dry season and exist only in certain tree species may hold rain during the rainy season, rendering them useless for nesting at that time. Thus 20.5% of the 39 species used in the dry season are abandoned during the wet season. Conversely, 38% of the 50 species used as nests during the rainy season are abandoned in the dry season, and six new tree species, or 15% (n = 6/39), are added. There are significant differences in frequencies of species used as nests between the two seasons ($\chi^2 = 1161.103$, df = 58; $p <$

0.001), and in the frequencies of species used as nests at the three forest sites (χ^2 = 4559.503, df = 116; $p < 0.001$). Site differences hold when controlled for season (χ^2 = 2485.469; df = 100; $p < 0.001$, during the rainy season, and χ^2 = 2583.923; df = 78; $p < 0.001$, during the dry season). In the gallery forest, 13 tree species were selected for nesting, while 19 species were used at each of the other forests.

During the hot, rainy season, mouse lemurs selected nests that were higher in the trees (mean height = 3.47 m, SD = ±1.67) than those used during the dry season (mean height = 2.67±1.56 m) (t =14.2, df = 3333, $p < 0.001$). Mouse lemurs may prefer to spend the day closer to the ground during the cold dry season for thermoregulatory reasons, as low tree holes are less exposed to chilling morning winds and may provide a thermoregulatory advantage. (Conversely, during the hot wet season, higher tree holes or open nests that are more exposed to the winds may provide relief from the very high midday temperatures that mouse lemurs encounter while they sleep.) Differences in nest height were also found by forest (ANOVA, F = 320.9; df = 2, 3332; $p < 0.001$); Tukey's post hoc tests of significance confirmed significant pairwise comparisons across the board. Mouse lemurs in the gallery forest used higher nests (3.91 ±2.15m) than those in the other two forests (mean height = 2.82±1.16m for the spiny forest and 2.33±0.82m for the dry deciduous forest of Ihazoara). Site differences hold when corrected for season. Thus, during the rainy season, mouse lemurs in the gallery were found sleeping at the height of 4.45±2.26 m; those in the spiny forest at 3.36±0.98 m), and those at Ihazoara forest at 2.58±0.69 m (ANOVA, F = 217.902; df = 2, 1620; $p < 0.001$). During the dry season, the mean tree height used by gallery mouse lemurs was 3.46±1.95m, at Ihazoara it was 2.07±0.87m, and at the spiny forest it was 2.30±1.07m (ANOVA, F = 164.461; df

= 2, 1709; $p < 0.001$). Figure 3.11 shows the differences in the distributions of heights of nests selected by mouse lemurs in the three forest habitats. Note that nest sites, like feeding sites, have a higher mean in the forest with the taller trees. However, it is interesting to compare median and modal heights above the ground for the nests. At all three forests, the annual mode is 2 m. The median (or 50% mark) is identical (3.0 m) for both the gallery and the spiny forest; Ihazoara has a median of 2.0 m. Breaking this down by season, an interesting pattern emerges. During the rainy season, the modal nest heights are 3 m (gallery), 3 m (Ihazoara), and 4 m (spiny forest) – thus highest in the spiny forest. The median values are identical to the modes. During the dry season, the modal nest heights are 2 m at all forests, and the median values are 3 m (gallery), 2 m (Ihazoara), and 2 m (spiny forest). The largest seasonal shift in nest height occurs in the spiny forest.

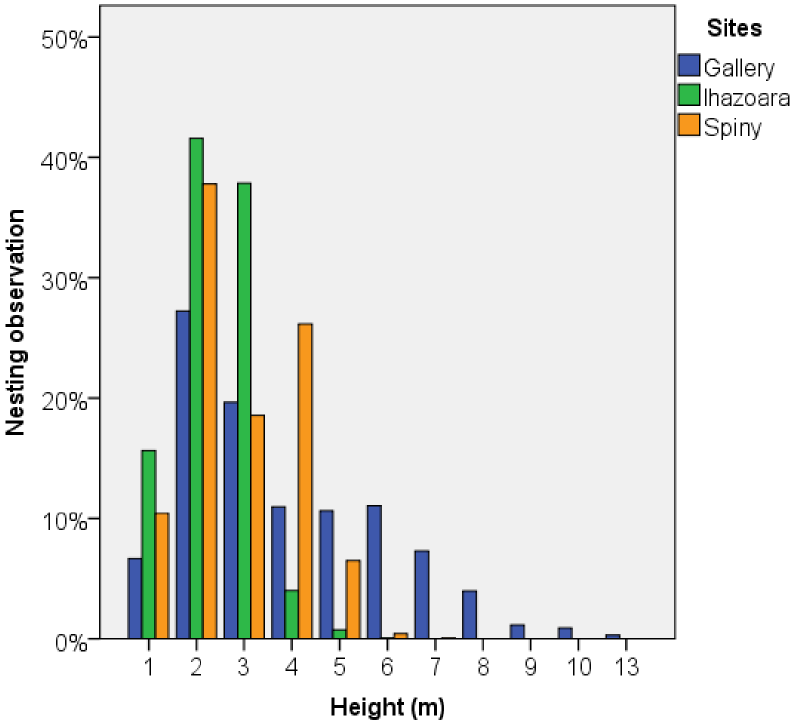


Figure 3.11: Distribution of nest heights used by mouse lemurs in the three forests.

Types of nests (open vs. tree holes) also differ by season ($\chi^2 = 1177.196$; df = 1; $p < 0.001$). Open nests are strongly preferred during the rainy season, whereas tree holes are preferred during the dry season. This seasonal shift is associated with a decrease (from wet to dry season) in the number of individual trees used for nesting, as not all trees have holes appropriate for such purposes (compare Tables 3.5a and 3.5b). There is a significant difference in the frequencies of nest types across months ($\chi^2 = 1398.315$; df = 9; $p < 0.001$), as displayed in Figure 3.12. The seasonal shift holds for all forests, as is illustrated in Figure 3.13.

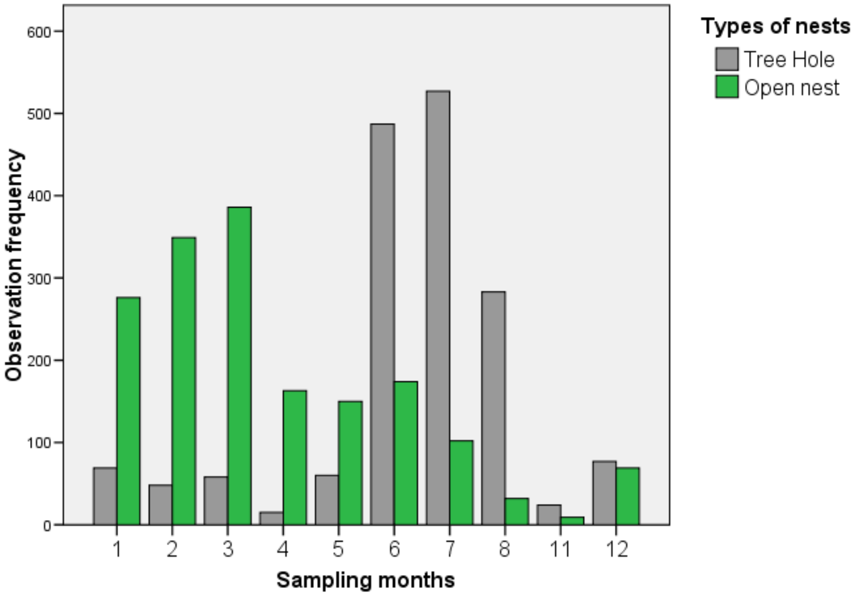


Figure 3.12: Shift in nesting preference, across months

Table 3.5a: Distribution of nest preference during the rainy season

Seasons	Trait	Gallery	Ihazoara	Spiny
Rainy	# Nests	174	122	157
	Mean height (m)	4.45 (±2.26)	2.58 (±0.7)	3.36 (±0.98)
	# Tree species	28	24	17
	# Open nests	147	117	114
	# Tree holes	32	6	34
	# Tree species with Both nests	5	1	9
	Tree species with Frequency ≥40	*Euphorbia tirucallii* *Tamarindus indica* *Acacia bellula*	*Gyrocarpus americanus* *Operculicarya decaryi* *Terminalia fatraea* *Mahafanogne*	*Phyllanthus decoryanus* *Euphorbia stenoclada* *Cedrelopsis grevei* *Alluaudia procera*

Table 3.5b: Distribution of nest preference during the dry season

Seasons	Trait	Gallery	Ihazoara	Spiny
Dry	# Nests	105	55	45
	Mean height (m)	3.46 (±1.95)	2.07 (±0.86)	2.30 (±1.07)
	# Tree species	13	19	19
	# Open nests	51	21	7
	# Tree holes	54	33	36
	# Tree species with both nests	3	1	2
	Tree species with Frequency ≥40	*Grewia leucophylla* *Euphorbia tirucallii* *Salvadora angustifolia* *Tamarindus indica* *Rhopalocarpus lucidus* *Acacia bellula*	*Hildergadia erythrosiphon* *Gyrocarpus americanus* *Commiphora brevicalyx* *Terminalia fatraea*	*Rhigozum madagascariensis* *Terminalia fatraea* *Alluaudia procera* *Albizzia* sp.

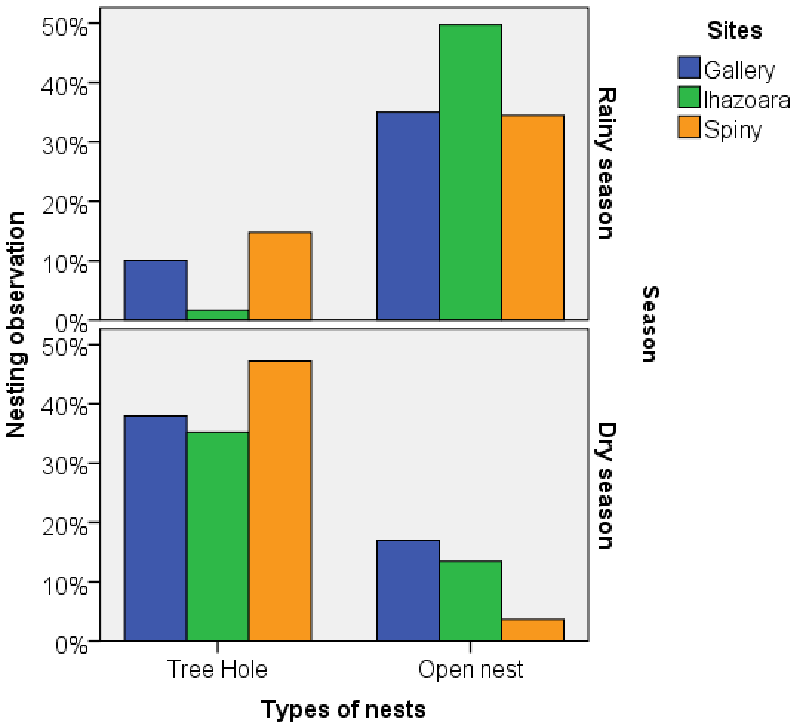


Figure 3.13: Types of nests, by season and site.

That the seasonal shift in nest type is significant at each forest is confirmed by chi square tests. During the rainy season, open nests are preferred: at the gallery forest, χ^2 =525.080 (df = 173; $p < 0.001$); at Ihazoara, χ^2 = 388.398 (df = 121; $p < 0.001$); at the spiny forest, χ^2 = 494.817 (df = 156; $p < 0.001$). During the dry season, tree holes are preferred: at the gallery forest, χ^2 = 615.967 (df = 104; $p < 0.001$); at Ihazoara forest, χ^2 = 503.850 (df = 54; $p < 0.001$); and at the spiny forest, χ^2 = 531.496 (df = 44; $p < 0.001$).

Table 3.6: Characteristics of plants selected for nesting at the three forests, with mean heights of trees sampled in the botanical plots.

Measurement	**Gallery**	**Ihazoara**	**Spiny**
Percentage of total nests used (focal individual nest observations) that are open	52.5%	62.8%	38.1%
Height of nest (m) and SD for trees with open nests	4.12 (±2.15)	2.60 (±0.7)	3.32 (±1.02)
Height of nest (m) and SD for trees with holes used for nesting	3.67 (±2.13)	1.87 (±0.81)	2.52 (±1.13)
Mean Tree Height (m) and SD	8.47 (±3.19)	6.07 (±2.39)	5.94 (±2.64)

The characteristics of nests are influenced to some extent by the characteristics of the forests themselves (Table 3.6). In particular, both open nests and tree-hole nests are located higher in the gallery forest, where the mean height of trees is also greater. The mean heights of trees at Ihazoara and the spiny forest are virtually identical; differences here in the location of open nests vs. nests in tree holes are not dictated by tree height, but may depend on the particular trees with available tree holes. In all forests, mouse lemurs select open nests that are higher than the tree holes, likely because they must use the canopy for these nests.

There are significant differences in the types of nests chosen by forest (χ^2=135.5, df = 2, $p < 0.001$), with mouse lemurs in the spiny forest using more tree holes, independently of season. If tree holes are what *M. griseorufus* prefers, then it is nesting in less than ideal conditions at Ihazoara and the gallery forest, particularly in the dry season, when tree holes are preferred regardless of habitat. In the spiny forest, 61.9% of all nesting locations were tree holes, whereas that percentage decreased to 48.0% in the gallery forest and 36.9% at Ihazoara.

Finally, there are enormous differences in the trees selected for nesting by forest ($\chi^2 = 4514.8$, df = 114, $p < 0.001$). At the gallery forest, the most commonly exploited trees are *Euphorbia tirucallii* (26.6% of all focal nesting records at this forest), *Albizzia* sp. (20.6%), *Acacia bellula* (13.2%), *Tamarindus indica* (11.4%), and *Salvadora angustifolia* (8.6%). At the spiny forest, the most commonly exploited nesting trees are *Alluaudia procera* (34.4%), *Terminalia fatraea* (16.4%), *Cedrelopsis grevei* (5.4%), *Albizzia* sp. (4.5%), *Euphorbia tirucallii* (4.0%), and *Salvadora angustifolia* (3.8%). At Ihazoara, the most commonly exploited nesting trees are *Terminalia fatraea* (18.9%), *Commiphora brevicalyx* (7.4%), Mahafanogne (5.9%), *Hildegardia erythrosiphon* (5.8%), *Operculicarya decaryi* (4.9%) and *Euphorbia tirucallii* (3.9%). The overlap is minimal, and at least in terms of percentages, primarily between the spiny forest and Ihazoara (e.g., *Terminalia fatraea* at 18.9% at Ihazoara and 16.4% in the spiny forest). Only *Euphorbia tirucallii* (the famata tree) is used for nesting at all three sites, and much more so in the gallery forest than at the other two forests. The favored tree at the spiny forest, *Alluaudia procera*, does not exist at the other two forests (Figure 3.14a and Figure 3.14b).

Figure 3.14: The two most favored tree species, *Alluaudia procera*, Family Didieraceae (left), and *Euphorbia tirucallii*, Family Euphorbiaceae (right). The mouse lemurs on the right are nesting in an “open nest” in the famata tree. Photo credits: Emilienne Rasoazanabary.

3.3.2.2.3 Relationship between behavior, morphology and habitat characteristics

To better understand how mouse lemur feeding and nesting behavior, as well as morphology, relate to habitat characteristics, I will now examine the differences between the populations in the two most distinctly different forests – the spiny forest and the gallery forest. Such a comparison eliminates potentially confounding factors relating to disturbance (as Ihazoara is located next to a village and is highly disturbed; see Chapter 5) and it also focuses our attention on those mouse lemur populations which differ the most morphologically.

In general, the differences in mouse lemur habitat use in the gallery and spiny forests can be summarized as follows: In the gallery forest, mouse lemurs eat more fruit, feed and use nests that are higher in the canopy, and sleep more often in open nests. In the spiny forest, mouse lemurs eat more gums, sleep more often in tree holes, and feed and use nests that are lower in the canopy. One can also specify particular tree species that are most important to mouse lemurs in each of these habitats. Table 3.7 lists only those species that comprise more than 10% of focal individual observations for nesting or feeding at either the gallery or spiny forest. The table indicates at which forest the species is particularly important, and provides the relative abundances of each plant species within each of those forests (% of trees recorded in the botanical plots). It also provides basic metric data for these selected species. Table 3.8 gives the % of focal observations for feeding and nesting on each of these plant species in the gallery and spiny forests. Finally, Table 3.9 gives summary descriptive statistics for characteristics of these most important tree species (three in the spiny forest and five in the gallery forest). It is clear that the gallery forest species used most often by the mouse lemurs are taller, have larger crowns (in both height and diameter), and have wider trunks at breast height. T-tests comparing these measurements for individual trees measured in the botanical plots in the gallery and spiny forests confirm that each of these differences is highly significant.

Table 3.7: Characteristics of tree species in which focal individuals in the spiny or gallery forests were observed feeding or nesting more than 10% of the time, with relative abundances (percentages of individuals in the botanical sampling plots) and metric data for these species.

Species	Site	Rel. Abund. Gallery	Rel. Abund. Spiny	Height (m)	Crown Height (m)	DBH (cm)	Crown diameter (m)
Albizzia sp.	Spiny	0	0.3	5.36	1.27	6.65	1.23
Alluaudia procera	Spiny	0	20.9	6.67	2.04	13.92	0.86
Terminalia fatraea	Spiny	0.3	2.3	4.59	1.78	6.57	1.65
Euphorbia tirucallii	Gallery	14.9	2.1	7.59	2	11.97	2.26
Acacia bellula	Gallery	7.2	0	11.5	4.42	20.59	3.38
Rhopalocarpus lucidus	Gallery	9.9	0	7.12	8.77	8.77	1.36
Tamarindus indica	Gallery	14.6	0	10.8	5.09	20.97	3.81
Grewia leucophylla	Gallery	5.2	0	8.02	2.83	7.87	1.58

Table 3.8: The tree species most favored for food or nesting by focal individuals in the gallery or spiny forests at Beza Mahafaly.

Species	% of focal observations in specified forest on specified plant			
	Food		Nest	
	Gallery	Spiny	Gallery	Spiny
Albizzia sp.	0	20.5	1.1	4.5
Alluaudia procera	0	0	0	34.4
Terminalia fatraea	0	33.8	0	16.4
Euphorbia tirucallii	5.8	0	26.6	4
Acacia bellula	19.9	0	13.2	0
Rhopalocarpus lucidus	20.9	0	5.4	0
Tamarindus indica	0	0	11.4	0
Grewia leucophylla	14.2	0	17.1	0

Table 3.9: Descriptive statistics for the group of 8 plant species (107-155 individuals belonging to three tree species in the spiny forest, and 136-189 individuals belonging to five species in the gallery forest)* used by focal individuals >10% of time for either feeding or nesting.

Variable	Gallery			Spiny			t value, df, and p**
	Mean	SD	SE	Mean	SD	SE	
Height (m)	9.03	3.36	0.25	6.55	3.93	0.32	6.3, 342,$p < 0.001$
Crown height (m)	3.57	2.58	0.21	2.22	1.27	0.11	2.8, 314, $p = 0.005$
DBH (cm)	14.98	9.82	0.72	12.55	5.93	0.48	5.58, 217, $p < 0.001$
Crown diameter (m)	3.09	1.91	0.16	1.33	0.53	0.05	10.3, 161, $p < 0.001$

* Sample sizes vary because not all of the individual trees could be measured for all traits.

** When the Levene's F test of equality of variances demonstrated that the variances of the two samples being compared were significantly different, I did not pool the variances in testing the significance of differences of the means. This affected the degrees of freedom but in no case did it affect the significance of the result.

These comparisons have implications for substrate use by mouse lemurs. When mouse lemurs are in the high canopy, they are generally using branches that are smaller in diameter. When they are feeding more often on fruit, they are using the most peripheral branches, which are also the smallest in diameter. In the gallery forest, where mouse lemurs sleep more often in high, tangled vegetation in wide and tall crowns, they must use smaller branches. In the spiny forest, where mouse lemurs spend more time in secure tree holes closer to the ground, and feed more often at lower heights, and more often on gums, they are more frequently using larger branches. The contrast between nesting in a tree hole in a fork on an *Alluaudia* tree (spiny forest) vs. nesting in an open tangle of *Euphorbia tirucallii* ("famata") branches (see Figure 3.14a and Figure 3.14b) is a case in point. Another is the difference between feeding on gums on a relatively large trunk (where spreading the digits, and using the fingers and toes as a clamp is advantageous) vs. feeding in peripheral branches on fruit and insects (where having relatively longer digits 3-5 increases prehensility, and is therefore advantageous).

Thus it is not surprising that the hands and feet of gallery forest mouse lemurs are more hook-like (with relatively longer digits 3-5 and shorter thumbs and big toes) while those of spiny forest mouse lemurs are more clamp-like (with relatively larger thumbs and big toes). Whether these differences are genetic or merely developmental is unclear; it is clear, however, that they are adaptive in their respective forests. The morphological differences between mouse lemurs living in the different forests do indeed appear to reflect differences in the way they use their habitats.

We can finally ask to what extent mouse lemurs are selective in their use of trees in their habitats. To address this question, I ran a correlation between the relative abundances of the eight species featured in Tables 3.7 through 3.9 in botanical plots in the spiny and gallery forests and in the focal observation databases for nesting and for feeding. The relative abundances of the 8 species in each forest were strongly correlated with the percentages of focal individual observations of nesting ($r = 0.75$ for the gallery forest, $N = 8$, $p = 0.03$; $r = 0.93$ for the spiny forest, $N = 8$, $p = 0.001$ for the spiny forest) but not feeding behavior (not significant for both). Thus, mouse lemurs appear to be selective in their feeding behavior (selecting trees that are not necessarily abundant in the forest) but not in their nesting behavior. Instead, they nest in some of the most abundant tree species in their respective forests. Thus, to some extent, mouse lemur behavior and morphology do indeed relate to differences in the plant composition and structure of the forests.

3.4 Discussion

In this chapter, I explored how *M. griseorufus* copes with very different habitats in the vicinity of Beza Mahafaly. This species lives today in spiny thickets throughout southern and southwestern Madagascar, including some forests devoid of any other lemur species. It lives in highly disturbed habitats as well as pristine spiny forest habitats. The Beza Mahafaly region is an ideal place to study its adaptability because it lives here in gallery forest as well as dry and spiny forest habitats. Indeed, despite its absence from gallery or wet forests at other sites in southern Madagascar, *M. griseorufus* seems to thrive in the riverine forest at Beza (possibly because there are no *M. murinus* in that forest). Here, I documented the differences in plant composition and phenology in the three habitats in which *M. griseorufus* lives at Beza. I then examined morphometric variation in the mouse lemur populations at the three sites. Finally, I documented the differences in the feeding and nesting behavior of the mouse lemurs in those forests (by season, and across all those sites), and how these differences are related to variation in mouse lemur morphology, and to the plant composition and structure of the forests themselves. The mouse lemurs at Beza Mahafaly are flexible in their diets and use of different types of nests. Indeed, there are strong seasonal differences in both food resources and preferred nest type, and these differences occur at each of the three forests. Nevertheless, there are highly significant differences in diet and nest use across the three forests, which are related to some extent at least to the differences in available plants. Remarkably, the mouse lemurs of the gallery forest differ from those at the two drier forests (particularly the spiny forest) morphologically as well as behaviorally, and the differences appear to correlate with differences in the substrates they must use to feed and to get to their nesting sites.

Several inferences can be drawn in comparing my results to observations of mouse lemurs in other parts of Madagascar. I will pay special attention to variation in mouse lemur feeding and nesting behavior at Beza within the context of the broader literature on mouse lemurs; little can be said about variation in mouse lemur hands and feet as nobody has examined this in other species. Clearly, there is a need for further research here.

Sussman and Rakotozafy (1994) had previously reported the existence of two microhabitats within one of the three forests that I studied – i.e., the gallery forest. The gallery forest derives its moisture largely from the water table of the Sakamena River (which is dry for more than 11 months every year). Sussman and Rakotozafy (1994) reported an ecological gradient from east to west, along a trajectory moving from the

Sakamena River (to the east) westward towards the transitional forest outside the reserve. They noted that the soil becomes drier as one moves further away from the Sakamena River. They also noted that the drier soil supports denser vegetation than does the wetter soil closer to the Sakamena River, but that the wetter soil supports trees with larger trunks and a higher canopy. In effect, the western portion of the "gallery forest" (or Parcel 1) can be described as transitional forest, but it is nevertheless quite different in character from forests even further from the Sakamena River.

My results show that similar habitat differences occur on a larger scale – i.e, that the even drier (and higher) forest sites of Ihazoara and the spiny forest have yet denser vegetation, and yet lower canopies. Tree diversity but not density is greatest at the gallery forest, whereas the vegetation at Ihazoara and in the spiny forest is less diverse but denser. The dry deciduous forest of Ihazoara is similar in many ways to the spiny forest, but slightly less diverse. My analysis of the presence and absence of various tree species in the three forests underscored the big differences between the gallery forest and the other two.

Although there are differences in vegetation between the forests in the region of Beza Mahafaly, the pattern of phenology documented here shows that fruit production is highly seasonal, and that fruit production is synchronous, in the three habitats. The high peak of fruit production occurs in November in the three forest habitats. Generally, rainfall is believed to trigger fruit production (Sorg and Rohner, 1996; Morellato, 2000), but fruiting begins at Beza Mahafaly suddenly, during a month that normally experiences little or no rain, and well prior to the peak in rainfall (between December and February; Sussman and Ratsirarson, 2006). Fruit production then extends over a prolonged period (longer in the gallery forest than in the spiny forest or Ihazoara), and doesn't end until May (or even later in the gallery forest). The schedule of fruit production at Beza Mahafaly is similar to that of Ranomafana, a rain forest in eastern Madagascar (Atsalis, 1999), as well as Kirindy, a dry deciduous forest in the west (Dammhahn and Kappeler, 2008). The difference is that the climate at Beza is hotter, drier, and more seasonal than the climate at either Ranomafana or Kirindy. During the dry season at Beza there is no fruit – none whatsoever – and the relative abundance of insects depends on the relative abundance of fruit. Mouse lemurs at Beza must feed on other items in order to compensate for the scarcity of fruit and insects during the dry season, and at Beza, gums become the preferred resource at that time. Whereas the timing of peak fruit and insect consumption is similar in *M. griseorufus* to that of *M. rufus* in Ranomafana (Atsalis, 1999) and *M. murinus* at Kirindy (Dammhahn and Kappeler, 2008), the relative abundance of these various food resources is not the same. Thus, whereas it has been reported that insects constitute the preferred resource for mouse lemurs (e.g., Harste et al., 1997), in fact, at Beza, insects comprise a relatively small part of the total diet.

Everywhere, mouse lemurs are flexible omnivores, and insect secretions, flowers, and leaves (very few), are consumed in addition to insects, fruit and gums (see Martin, 1972, 1973; Barre et al., 1988; Corbin and Schmid, 1995; Génin, 2001, 2003; Lahann, 2007; Dammhan and Kappeler, 2008). *M. griseorufus* at Beza is no exception. For western mouse lemurs (not merely *M. griseorufus*), gums are an important keystone food. When available, they are consumed all year round. Many primates living in dry habitats rely on gums in a similar manner (Nash, 1986; Isbell, 1998; Heymann and Smith, 1999; Peres, 2000; Radespiel et al., 2006). Schulke (2003) reported that the diet of *Phaner* *furcifer* is mainly made of gums. Competition for access to gum trees between *M. murinus* and *Phaner furcifer* has been reported at Kirindy forest (Génin, 2003). In a short study (March-April, during the early dry season) of *M. murinus* at Kirindy, Génin (2003) reported that gums comprised up to 75% of the diet. The mouse lemurs, *M. ravelobensis*, at Ampijoroa in northwest Madagascar fed mainly on gums and insect secretions during the late dry season (Radespiel et al., 2006). Thus, gum feeding is widespread, and occurs at forests that experience greater or lesser degrees of seasonality (seasonality is greatest at Beza, less so at Kirindy, and even less so at Ampijoroa). It appears to be a favored resource for western mouse lemurs belonging to different species. My results support the inference that gums are a critical resource for *M. griseorufus*, and that they remain important even when gum-producing tree species that are favored in one habitat are absent in another. Mouse lemurs can be quite flexible in their choice of species from which they extract gums. However, in certain habitats, they can be quite selective. Thus in the spiny forest, very few tree species were used for gum feeding, while in the gallery forest, many were used. The gum trees of choice in the spiny forest (*Terminalia fatraea* and *Albizzia* sp.) are rare in the gallery forest. The spiny forest trees used for gum feeding are not terribly common in that habitat, and thus are specifically targeted for gum feeding. In the gallery forest where tree species diversity is high, mouse lemurs are less selective in their choice of trees for exudate feeding. They also have a more diverse diet, relying less on gums than individuals in the spiny forest. Whether or not this explains the significantly higher adult body mass of individuals in the gallery forest than individuals in the spiny forest is at present unclear, although it is a possibility.

One fascinating observation was the seasonality of preference for open vs. tree-hole nests, and its universality across sites. When mouse lemurs sleep during the day, the choice of sleeping nests is crucial for their survival. Ganzhorn and Schmid (1998) as well as Radespiel et al. (1998, 2003) argued that choosing "high quality" nests can be very important for mouse lemurs as they are exposed to high predation risks (e.g., Goodman et al., 1993a, b). Ganzhorn and colleagues assumed that: (1) tree holes provide better protection against predators than do open nests; (2) holes that are high in trees are safer than holes that are closer to the ground; and (3) well-insulated tree holes are better than poorly-insulated tree holes. Thus nest "quality" could be ascertained using these criteria. Other researchers have embraced the same set of assumptions (Radespiel et al., 1998; Rasoloarijaona et al., 2003, 2008). However, Lutterman et al. (2010), in a study of *Microcebus murinus* at Ampijoroa, found that the choice of nest depends strongly on season and relates more to thermoregulatory factors than to protection against predators. My results offer strong confirmation of the inference that there is no universal preference for tree holes over open nests, but that nest-type selection depends on season (with tree holes being preferable in the colder dry season, and open nests preferable in the hot, rainy season). I was also able to document a seasonal shift in nest height off of the ground, with nests closer to the ground preferred during the dry season and higher nests (which would be cooler) preferred during the hot, rainy season. Another consideration is whether or not tree holes fill with water during the rainy season. If they do, their inhabitants must temporarily leave the nests during heavy rains, and open nests would again be preferable. The point is that nests cannot be assessed in terms of overall "quality," when their utility varies seasonally with ambient temperature.

If nest height provides safety from predators, then nest height should shift in relation to seasonal variation in predation risk. Predation risk may vary seasonally (particular predators may be more active when feeding their young); it is said to increase during the dry season, when food is scarce and visibility is high (with the shedding of leaves), particularly in dry deciduous and spiny forests. Indeed, I witnessed predation events on mouse lemurs only during the dry season. If predation risk does increase during the dry season, and if predation were the main factor influencing nest height, then mouse lemurs should select higher nests during the dry season.

Instead, at Beza, higher nests are selected during the rainy season, when the ambient temperature can be extremely high in the middle of the day when mouse lemurs are sleeping. During the hot, rainy season, the temperature inside well-insulated nests described by Schmid (1998) may be intolerable, rendering them less desirable at that time of year.

The fact that Beza mouse lemurs select tree holes that are closer to the ground during the cooler dry season and nests that are higher in the trees during the rainy season makes sense only in terms of a thermoregulatory advantage. Bird predators have no difficulty attacking mouse lemurs in low tree holes; in the deciduous forest of Ihazoara, I witnessed mouse lemurs being taken by bird predators (*Copsychus albospecularis*, the Pitsy bird, *Polyboroides radiates*, the Fihiake bird, and *Accipiter madagascariensis*, the Firaokibo bird) from very low tree holes (~2 m from the ground). These predators use their long legs as clawed probes to extract the mouse lemurs.

Many researchers have witnessed direct predation on nocturnal lemurs sleeping in tree holes (Schmelting, 2000; Schulke and Ostner, 2001; Fietz and Dausmann, 2003).

For example, Biebouw et al. (2009) witnessed predation on the hairy dwarf lemur, *Allocebus trichotis*, sleeping in tree holes; these predators (including the herpestid *Fossa fossana* and the snake *Ithycyphus perineti*) entered the holes by climbing from the ground, even though the tree holes were located high in the trees, and were occupied during the rainy season (median height 7m). The notion that higher tree holes are "safer" is questionable, and would require much more documentation. However, a pattern is beginning to emerge, and it characterizes mouse lemurs living in very different parts of Madagascar (and certainly living in all three forests at Beza Mahafaly), and appears to support the thermoregulatory hypothesis. The thermoregulatory hypothesis may also explain why the largest seasonal shift in nest height occurs in the spiny forest; due to the lack of canopy shading, this forest can be extremely uncomfortably hot in the rainy season and uncomfortably cooler in the dry season.

Finally, if in fact open nests are preferable to tree holes during the hot, rainy season, then the greater use of tree holes in the spiny than gallery forest or Ihazoara cannot be explained as a matter of preference, but rather must relate to the availability of acceptable nesting sites. The fact is that there are many *Alluaudia* trees in the spiny forest, and they may provide tree holes, but they certainly do not provide open nests. Alternatively, the gallery forest and Ihazoara may provide fewer acceptable tree holes during the cool, dry season, making the spiny forest the better place to live during this time of year.

3.5 Conclusions

In this chapter, my goal was to examine how mouse lemurs at Beza Mahafaly differ in feeding and nesting behavior in different habitats, and to investigate whether those differences correlate with morphology. Beza Mahafaly is special in that a single species of mouse lemur inhabits a wide variety of habitats, including one that is apparently not utilized by the same species, *M. griseorufus*, in other parts of Madagascar. This is of particular interest because there are stark differences in the plant species composition, species richness, species diversity, and tree characteristics (height, dbh, and crown height and depth) across the three forest habitats, with two of them (the spiny forest and Ihazoara) are more similar to each other than the third (the gallery forest). My analysis shows that the spiny and gallery forests differ the most, and that the mouse lemurs living in these two forests also differ the most in terms of morphology and certain aspects of their behavior. Those morphological differences do indeed appear to reflect differences in the way they use their habitats.

In particular, I found that the hands and feet of gallery forest mouse lemurs are more hook-like (with relatively longer digits 3-5 and shorter thumbs and big toes) while those of spiny forest mouse lemurs are more clamp-like (with relatively larger thumbs and big toes). These differences appear to be correlated with the amount of time mouse lemurs in the different forests spend negotiating small branches in the high canopy (higher in the gallery forest), vs. large tree trunks and larger supports closer to the ground (higher in the spiny forest). Behavioral differences in both feeding and nesting are implicated in the explanation developed here. It does appear that habitat differences influence the biology of mouse lemurs in a non-trivial manner.

These data raise more questions than they address. Population-specific data on hand and foot proportions are very rare. At issue are the developmental or genetic basis for these differences; little is known about the developmental plasticity of digit proportions (or indeed, more generally, how genes and environments interact in producing adult shape; for a recent review, see Klingenberg, 2010). What is clear is that natural selection favors shapes with fitness-related functions, and that environments are more important in determining the direction of evolutionary change than is often admitted (development mediates the complex interactions between genes and environments, and it is the product of development upon which natural selection acts). The question of serial homology is also of interest, given that the proportional differences in the hand and foot of mouse lemurs from the gallery and spiny forests are virtually identical. Unfortunately, factors affecting the co-evolution of the fore and hind limb in mammals are also poorly understood. On the one hand, there is evidence in favor of some kind of developmental constraint; indeed, Rolian et al. (2010) have argued that such constraints explain the hand proportions (long thumbs, short lateral digits) of humans. However, research on birds and certain other vertebrate groups demonstrates that the fore and hind limb develop and are regulated as independent modules (Kathy Kavanagh, pers. comm.); the extent to which those of mammals share regulatory elements is yet to be fully elucidated.

My data underscore the behavioral plasticity of *M. griseorufus* at Beza Mahafaly. Some of the behavioral differences observed in the three forests can be related to differences in the plant species available in the three forests, or to the characteristics of the plants as revealed by my analysis of botanical plots. However, there are particular plants that are specifically targeted, particularly for feeding, in particular habitats. For example, the spiny forest trees used for gum feeding are not common in the spiny forest, so these become objects of possible competition. In the gallery forest where tree species diversity is higher, mouse lemurs are less selective in their choice of trees for exudate feeding.

In summary, the mouse lemurs at Beza Mahafaly are flexible in their diets and use of different types of nests. Mouse lemurs at Beza Mahafaly are more selective with regard to feeding behavior (selecting trees that are not necessarily abundant in the forest) than they are with regard to their sleeping behavior. Instead, they nest in some of the most abundant tree species in their respective forests. They are selective, however, in their choice of nest type and nest height within the trees.

One of my more interesting (and unanticipated) discoveries was that mouse lemurs in all three forests have no universal preference for tree holes over open nests, but rather that nest-type preference depends on season. There is also a seasonal shift in nest height off of the ground, with a preference for nests closer to the ground during the dry season and for higher nests during the hot, rainy season. I argue that the notion that higher tree holes are “safer” from predators is questionable, but that the differences are consistent with the hypothesis that the driving factor is thermoregulation. The thermoregulatory hypothesis may also explain why the largest seasonal shift in nest height occurs in the spiny forest.

What is most remarkable is the ability of *M. griseorufus* to survive in very different forests at Beza Mahafaly. This is all the more remarkable in light of the fact that *M. griseorufus* does not occupy riverine forests in other parts of Madagascar, but appears to be doing relatively “well” in the gallery forest at Beza. I will explore this further when I examine disturbance in the forests of Beza. For now it is sufficient to point out that the apparent density of mouse lemurs at Beza is greatest in the gallery forest, and that differences in behavioral patterns are indeed influenced by both habitat and climate.

My general conclusion is that *Microcebus griseorufus* may have the highest habitat-tolerance of the eighteen mouse lemur species in all of Madagascar. No other mouse lemur species has been observed in habitats as distinct as the three forests studied here. *M. griseorufus* also lives in some of Madagascar’s harshest, most seasonal environments. One may ask how or whether they differ from other species of mouse lemurs in other characteristics. Mouse lemur species vary in the activity patterns and behavioral characteristics of males and females, but these differences are difficult to understand within an adaptive framework. I will address this question in the next chapter.

CHAPTER 4

SEXUAL DIMORPHISM IN THE SOUTHWESTERN MOUSE LEMUR, *M. GRISEORUFUS*, IN THE REGION OF BEZA MAHAFALY, SW MADAGASCAR

4.1 Introduction

In the previous chapter, I described how the nesting and feeding behavior of *Microcebus griseorufus* varies according to habitat. While I found relative digit lengths to distinguish most strongly mouse lemurs living in the three forest habitats (the gallery forest, Ihazoara, and spiny forest) at Beza Mahafaly, other traits also contributed to their separation. The differences appeared to reflect adaptations to differences in habitat structure and plant composition at the three forests. However, my prior analysis paid no attention to whether males and females differ in the way they use their habitats. Here, I turn to the latter question, specifically addressing differences in those traits that typically vary in other primates by sex – most importantly, canine height, skull length, and body mass. Some lemurs are sexually dichromatic, but as colleagues and I have demonstrated elsewhere (Heckman et al., 2006), the mouse lemurs of Beza Mahafaly, while exceptionally variable in coat coloration, are not. Most lemurs are not sexually dimorphic in other characteristics (e.g., skeletal traits), but as we will see below, the cheirogaleids are an exception.

If canine, body mass, or skull length dimorphism can be demonstrated for mouse lemurs, that dimorphism must be not merely described, but understood. It behooves us to understand the dimorphism in terms of differences in the behavior of males and females.

Can it be that some of the smallest-bodied of the lemurs of Madagascar are the only ones to exhibit skeletal (canine or skull length) dimorphism? If so, why so?

This chapter will first explore sexual differences in the standard morphological traits listed above, and then it will explore differences in male and female activity patterns (including seasonal torpor), apparent longevity, feeding and nesting patterns. Sexual differences in activity patterns of mouse lemurs during the dry season have been reported (e.g., Schmid and Kappeler, 1998; Schmid, 1997, 1999; and Rasoazanabary, 2006, on *M. murinus* at Kirindy; Schmid and Ganzhorn, 2009, on *M. murinus* at Mandena; Randrianambinina et al., 2003, on *M. rufus* at Mantadia; Atsalis, 2008, on *M. rufus* at Ranomafana). Sexual differences in nesting behavior have been reported only for *M. murinus* at Ampijoroa (Radespiel et al., 1998) and Kirindy (Rasoazanabary, 2006), with females preferring tree holes over open nests. Perhaps sexual differences in morphology relate to nesting or activity patterns? However, little has been published regarding the degree to which male and female *M. griseorufus* differ in activity patterns, and nothing has been published on differences in nesting or feeding. Kobbe and Dausmann (2009) report both sexes (one male and two female *M. griseorufus*) entering hibernation over periods of up to 77 days at Tsimanampetsotsa (totaling three out of sixteen individuals studied during the dry season), while all other males and females entered much shorter torpor bouts, if any. No difference between the sexes was observed. Génin (2008) reported daily torpor in *M. griseorufus* at Berenty, but he observed no seasonal torpor during the dry season, and thus, once again, no difference between males and females. His trapping schedule, however, was not adequate to pick up patterns of torpor, however, as he only sampled between one and six nights per month.

The literature on sexual dimorphism in primates tends to focus on its relationship to mating systems and differential agonism of males and females, with polygynous species tending towards higher dimorphism and greater intrasexual competition among males than pair-living and polyandrous species (Plavcan and van Schaik, 1992; Plavcan, 1994; Plavcan et al, 1995; Plavcan, 1998; 2001; Plavcan and Ruff, 2008). What is stunning about lemurs is that they do not fit this model; not even the most polygynous lemur species exhibits strong dimorphism or male dominance over females. Indeed, among lemurs, females tend to be dominant over males, and, when dimorphism exists, it is minor. Curiously, the lemurs for which "reverse" dimorphism (with females larger than males) is most strongly manifested appear to be the smallest in body size – i.e., the cheirogaleids. Patterns of agonism vary tremendously across cheirogaleids, and both males and females engage in severe agonistic bouts in some species (e.g., Kappeler, 1997). It would appear that any differences in male and female body measurements would need to be understood in terms of the differences in male and female behavior. However, any parallels with anthropoids in this realm cannot be assumed. The literature on anthropoids highlights variation in the probability of successful access to reproductive females by competing reproductive males. Other variables may be more important to lemurs living in harsh, unpredictable environments – e.g., access by reproductive females to resources that may increase the probability of survival of their young. Critical variables may include access to the best nesting sites or to the best feeding sites. The ability to enter prolonged periods of inactivity (seasonal torpor or hibernation) prior to the breeding season may be another critical factor.

Perhaps the best studied cheirogaleid with regard to sexual dimorphism is the mouse lemur. Kappeler (1991) studied body mass dimorphism in captive *M. murinus*, and later, Schmid and Kappeler (1998) examined body mass dimorphism in the same species at Kirindy, concluding that there is a seasonal fluctuation – effectively a flip in who is heavier than whom that correlates with reproduction. This was contested by Fietz (1998) who interpreted the body mass fluctuation as related to differences in male and female activity patterns. Rasoazanabary (2006) affirmed sex differences prior to the season of scarce resources (with females larger than males, and more ready for prolonged torpor), but contested the notion that males gained weight specifically to enhance their reproductive success prior to the breeding season.

Kappeler (1996) analyzed canine dimorphism in a skeletal population from Amboasary that he thought belonged to *M. murinus* but that actually belongs to *M. griseorufus* (Cuozzo et al., in press). He also measured a few *M. rufus.* Jenkins and Albrecht (1991) studied skull length dimorphism in the Amboasary skeletal population (again misidentified as *M. murinus*). These authors reached different conclusions with regard to the presence of skeletal dimorphism in mouse lemurs, but all affirmed greater manifestation of reverse dimorphism in mouse lemurs than in most other prosimians. Nobody has come up with a satisfactory explanation of why dimorphism of any sort should be more pronounced in mouse lemurs than in other lemur species.

This chapter will document differences between male and female *M. griseorufus* at Beza Mahafaly, with special attention to factors that may impact the survival of young. This is the first study of sexual dimorphism in mouse lemurs that specifically combines an analysis of field morphometrics with an analysis of differences in nesting, feeding, and resting (or activity) patterns (including prolonged torpor) by males and females. It is also the first study to examine these differences in both the rainy and dry season. The goal of the study is two-fold: 1) To explore whether sexual dimorphism in skeletal characteristics such as canine height and skull length exists in mouse lemurs at Beza Mahafaly, and to explore variation in body mass over the year, to test Schmid and Kappeler's fluctuating dimorphism hypothesis; and 2) To investigate what aspects of behavioral patterns differentiate male and female *M. griseorufus* at Beza Mahafaly. Activity patterns, longevity, nesting, and feeding behavior will all be examined.

4.2 Methods

I studied gray-brown mouse lemurs, *Microcebus griseorufus*, at Beza Mahafaly from 2003 to 2007 (435 individuals, 200 females and 235 males). During a systematic capture year beginning in October 2006 and ending in September 2007, simultaneous focal individual (28 females and 29 males) and capture-recapture data (249 individuals, including 83 adult females and 117 adult males, as well as immature individuals) were collected in three different forests. Both capture-recapture and focal individual data were collected on individuals during each of the other years, but less systematically, and never simultaneously. Animal trapping procedures (capture-recapture) are described in Chapter 2; on first capture, a full set of morphometric data was collected for each individual, and the measurements taken are listed in Appendix A. Thus, each individual was measured only once, at first capture. The general characteristics of the three sampling forest sites, and how these forests were sampled, are described in Chapter 3. Behavioral data were collected using focal individual sampling; the methods used to collect these data were described in Chapter 3. Particular behaviors analyzed here include the following: **for**

nesting, nest height, nest type [tree holes vs. open vegetation]; **for feeding**, feeding height, food type [fruit, gums, insects or insect secretions, and other]; **for activity**, inactive [i.e., remaining in the nest] vs. active [emerging from the nest some time during the first three hours of focal observation per night]; **for social contacts,** alone or in close contact with at least one other individual.

Here, I analyze (1) capture-recapture data collected during the entire five years of study; and (2) a subset of the morphological data (i.e., body mass, canine height, and skull length) collected during the year of systematic capture (2006-2007) and (3) all of the focal individual behavioral data collected during that same year. For each analysis, adult males and females are compared. Appendix E provides the age, sex, weight, and microchip information for focal individuals as well as the sampling intervals and other pertinent data for each individual.

Capture-recapture data were used to estimate the following information for males and females: minimum longevity (in years), average interval (in days) from first to last capture, location fidelity (maximum distance in meters for individuals between trapping locations), and average capture frequency. In order to estimate a minimum longevity, I calculated the intervals from first to last capture date for each individual. The longest intervals, adjusted for likely age at first capture, provided a minimum value for longevity for males and females. To quantify sexual dimorphism in morphological traits (using standard t tests), only mature individuals (identified as described in Chapter 2) were considered. For body mass, I analyzed sexual differences by season and month. To quantify canine height and skull length dimorphism, I analyzed sexual differences by site to verify patterns observed in the entire population. To determine differences in behavior (activity pattern, nesting behavior, and feeding behavior) by sex, I utilized the chi square (χ^2) test of the significance of differences in the frequencies of particular focal individual observations. Student's t-tests were also used to test for differences in nest height and height at feeding by sex.

4.3 Results

4.3.1 Variation in morphology

4.3.1.1 Sexual differences in body mass

I found significant differences in body mass between adult male and female *M. griseorufus* at Beza Mahafaly (t = 3.37, df = 105, *p* = 0.001) captured during the year October 2006 to September 2007, with females heavier than males. The mean body mass was 45.2 ± 5.8 g for males and 50.3 ± 13.0 g for females. Adult female body mass varies significantly by month (ANOVA, F = 8.28, df = 12, *p* < 0.001). Female body mass is highest in December (83.5 g), January (71.0 g), and February (62.7 g). Mean body mass for all other months varies from 38.0 to 51.0 g. The pattern of body mass fluctuation is shown in Figure 4.1 (top panel).

Fluctuations across months in adult male body mass were of much lower magnitude but nevertheless significant across months (ANOVA F = 2.6, df = 11, 105, *p* = 0.005), with males somewhat higher in September (mean = 53.5 ± 2.1 g), February (55.0 ± 2.6 g), and March (53.0 with an N of 1) than in other months. Adult males in the rainy season (October to March) are significantly higher in body mass (mean = 49.0 ± 6.3 g, n = 22) than in the dry season (mean = 44.3 ± 5.4 g, n = 95) (t = 3.5, df = 115, *p* = 0.001). The pattern of body mass fluctuation is shown in Figure 4.1 (bottom panel).

I did not observe the pattern of fluctuating body mass dimorphism reported by Schmid and Kappeler (1998) for *M. murinus* (see Figure 4.2). These authors reported males to be significantly heavier than females in September and October, and presumably non-pregnant females to be significantly heavier in February, March and April. We found no difference in body mass of adult males and females in September and October (t test, t = 0.04, df = 31, NS). In fact, taking each month one at a time, there was no significant difference in average body mass between males and females except during the months of December (t=3.5, df = 3, *p* = 0.038) and January (t=3.76, df = 10, *p* = 0.004), during which time, females were significantly heavier than males. These were also months during which very few individuals were captured. In December, the average body mass of females was 83.5 ± 7.8 g (n = 2) and that of males was 49.7 ± 11.6 g (n = 3). In January, females were heavier than males (71.0 ± 11.1g, n = 7, vs. 49.0 ± 7.9 g, n = 5, respectively). Of course, females in December and January were also likely to be pregnant or lactating. In fact, all of January captures of adult females were lactating, and all of the December captures of adult females were pregnant.

I did, however, observe a seasonal shift, with males being slightly heavier than *non-pregnant females* in the rainy season, and with there being no body mass difference in the dry season. The mean body mass of non-pregnant adult females during the rainy season was 44.1 ± 4.6 g (n = 17, range = 37.0 - 53.0 g), which is actually significantly lower than that of adult males (49.0 ± 6.3 g, n = 22) during the rainy season (t = -2.6, df = 37, *p* = 0.01). This difference disappears entirely during the dry season, when active adult male and active non-pregnant adult female body masses are virtually identical (for females, the mean is 46.5 ± 9.0 g, n = 50; for males, the mean is 44.3 ± 5.4 g, n = 95; t = 1.6, df = 68, NS).

For females, data presented in Chapter 2 support the existence of polyestry. It is clear from the body mass data presented here that females tend to gain more weight with the pregnancy and lactation cycle at the beginning of the reproduction season (which coincides with the middle of the rainy season) than with the second cycle (which begins near the end of the rainy season, and extends into the beginning of the dry season). Low-weight adult females (between ~ 40 and 50 g) can be found at all times of the year, with the exception of December and January (Figure 4.2).

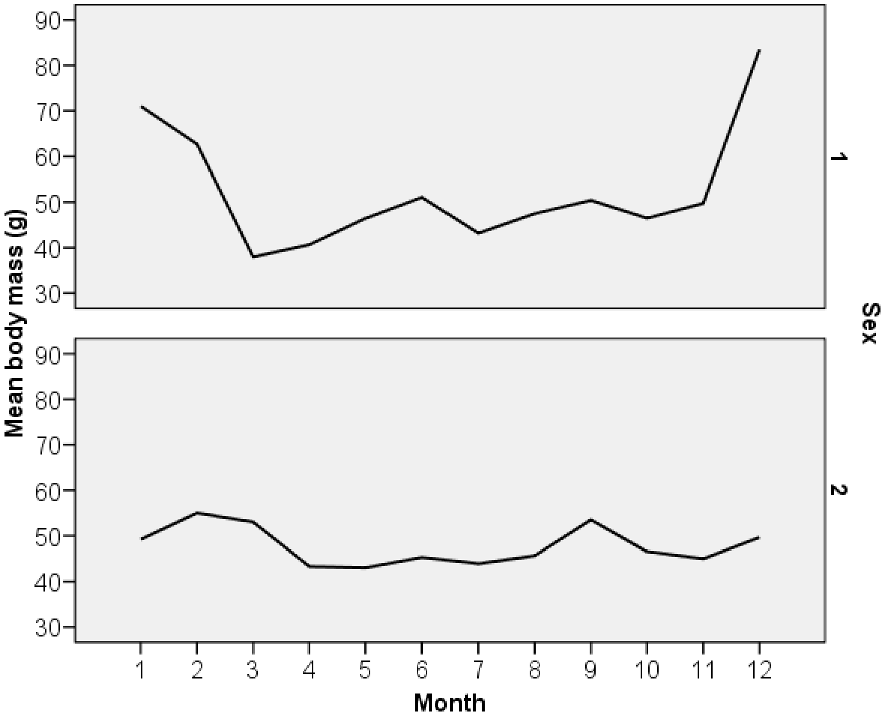


Figure 4.1: Average body mass of individual adult males and females (including pregnant and lactating individuals) across months. Top panel (1) = females. Bottom panel (2) = males.

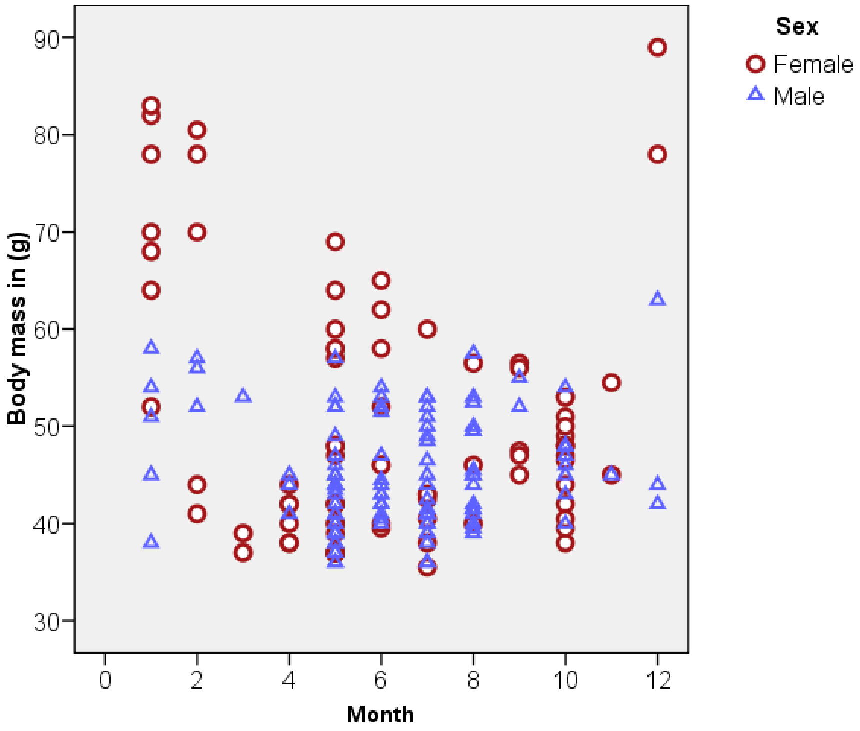


Figure 4.2: Comparison of body masses of individual adult males and females captured by month. (Recaptures are excluded.)

4.3.1.2 Sexual differences in skull length and canine height

I found sexual differences in canine height to be stunningly significant and unrelated to differences in body mass. For both *skull length* (t = 6.49, df = 128, $p <$ 0.001) and *canine height* (t = 13.67, df = 198, $p < 0.001$), females are significantly larger than males. The difference in skull length was relatively small (33.25 ± 1.77 mm for females and 31.81 ± 1.13 mm for males). Mean canine height was 1.80 ± 0.15 mm for adult females and 1.54 ± 0.11 mm for adult males. This amounts to an average dimorphism value (male canine height divided by female canine height) of 0.86.

I tested each forest separately to determine whether these dimorphism patterns hold universally at Beza. In fact, with one exception, they do. Importantly, that exception *only* involves skull length in the spiny forest. Canine dimorphism is strong at every site, as is shown in Table 4.1 and graphically in Figure 4.3. Indeed, the canine dimorphism values are much stronger than has ever previously been reported for any lemur species.

Note that, to see this dimorphism pattern clearly, it is important that immature individuals be excluded from the sample. Fortunately, the upper canine comes into full occlusion relatively early in mouse lemurs (it erupts with the upper and lower third molars, and prior to the eruption of the adult premolars, in other words, by ~ age 2-3 months; pers. comm., L. Godfrey, based on skeletal research). By using body proportions and body mass to eliminate immature individuals (see Chapter 2), I am likely measuring canine dimorphism in individuals that have adult values for canine height. Skull length, in contrast, matures more slowly, and individuals with fully erupted canines may not be fully grown. Thus, measures of skull length dimorphism may be affected by the inclusion of individuals who are not completely grown, but treated as adults. It is clear that canine dimorphism is not merely a correlate of variation in skull size in mouse lemurs, as I found canine dimorphism to be strongest in the spiny forest, the only site lacking skull dimorphism entirely.

Table 4.1: Summary of significance of sexual dimorphism in skull lengths and canine heights across site

Site	**Trait (mm)**	**♀ n, Mean±SD**	**♂ n, Mean±SD**	**t**	**df**	**Sig. (*p*)**	**Dimorphism ♂/♀**
Gallery	Skull length	41, 34.3±1.2	61, 32.5±0.7	8.4	55	<0.001	0.95
	Canine height	41, 1.8±0.1	61, 1.6±0.1	8.0	100	<0.001	0.89
Ihazoara	Skull length	22, 33.5±0.9	27, 31.1±0.8	9.0	47	<0.001	0.93
	Canine height	22, 1.7±0.1	27, 1.5±0.1	7.1	47	<0.001	0.88
Spiny	Skull length	20, 30.9±1.0	29, 30.9±1.1	-0.3	47	NS	1.00
	Canine height	20, 1.9±0.1	29, 1.5±0.1	10.3	47	<0.001	0.79

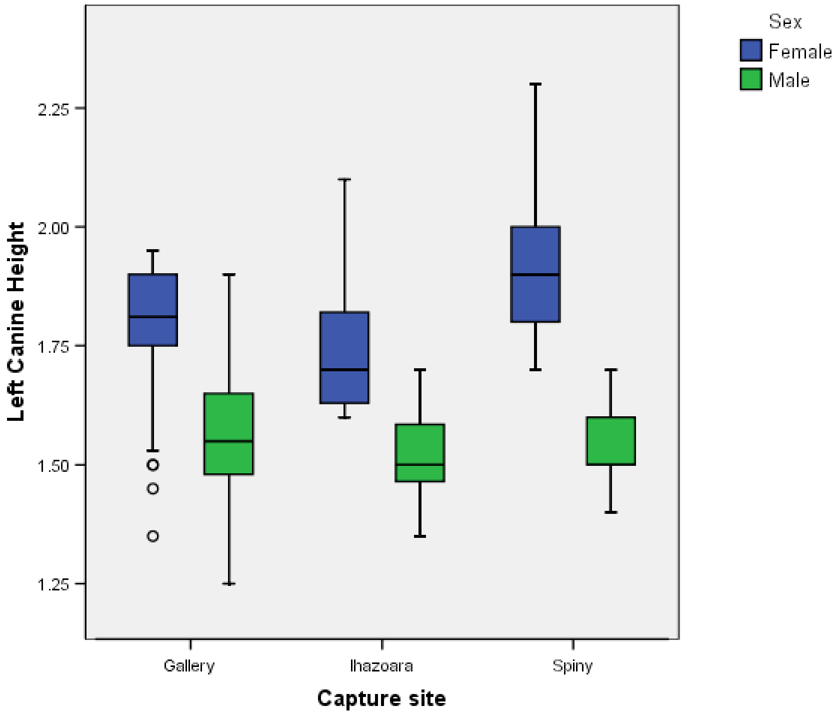


Figure 4.3: Canine dimorphism: average canine height of males and female by sites. Open circles represent sample outliers.

4.3.2 Variation in capture patterns

4.3.2.1 Sexual differences in capture frequency

Of the 200 adult individual mouse lemurs first captured during the year of systematic capture, there were more males than females (117 vs. 83). This was mainly due to a bias in capture frequency of males and females during the dry season. Overall, there were significantly more females first captured during the rainy (early reproductive) season (33 females vs. 22 males) and more males first captured during the dry season (50 females vs. 95 males; $\chi^2 = 10.7$, df = 1, $p = 0.001$), when, as we will see, mouse lemurs are more likely to enter prolonged bouts of torpor. The sex-ratio for first captures was male-biased during the months of May (# ♂: # ♀= 36/21 = 1.7), June (15/8 = 1.9), July (22/7 = 3.1), and August (17/3 = 5.7), and the sex ratio was female-biased during the rest of the year. The same pattern emerges if we include all adult individuals, first captures and recaptures, counting each as either captured or not during any particular month (Table 4.2) . Note that the exception (December) is one for which very few adult individuals were captured.

Table 4.2: Sex ratios for adult individuals captured by month

Sex	Frequencies of adult individuals captured by month											
	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	March	April
♂	40	26	47	45	30	9	1	3	5	3	1	2
♀	38	20	28	26	29	15	5	2	11	6	2	8
Ratio ♂: ♀	1.1	1.3	1.7	1.7	1.0	0.6	0.2	(1.5)	0.5	0.5	0.5	0.3

4.3.2.2 Sexual differences in capture interval (first to last capture dates)

When I analyzed the interval between the first and last capture dates for all individuals captured from April 2003 to September 2007, I found sexual differences in the average interval from first to last capture (t = 3.05, df = 359, *p* = 0.002). The average interval for males was 59.6 ± 148.0 days, and that of females was much longer, i.e., 112.3 ± 202.0 days. Capture frequency did not differ by sex across years; the mean for females was 5.0 (SD = 6.1) while the mean for males was 4.4 (SD = 5.4); t = 1.1, df = 429, NS. The frequency of capture for females varied from 1 to 43, and for males from 1 to 29. However, for individuals who were captured repeatedly (e.g., more than 5 times), the mean frequency of capture *per unit time* was higher in males than females (t = -2.1, df = 107, *p* =0.035). In a nutshell, for individuals who were captured repeatedly, males were captured more often but over shorter periods of time. This may result from a higher degree of activity on the part of males (or more sedentary behavior on the part of females). It may also reflect larger ranges on the part of males (they simply move out of the sampling area), or greater location fidelity on the part of females.

4.3.2.3 Sexual differences in minimum longevity, and location fidelity

Minimum lifespan for males and females could be estimated by selecting those individuals with the longest interval between their day of first capture and their day of last capture (Table 4.3). Only five individuals (two males and three females) exceed 800 days. The longest interval (1245 days) belonged to a male with transponder number 063C-0A91. To derive age at last capture (and thus minimum longevity), I estimated age at first capture. My first question was, was it possible that the individual was in the first year of his or her life at first capture (body mass less than 50 g), and if so, was he or she too heavy to have been born toward the end of the reproductive season – i.e., in the early dry season? I assumed that individuals were born either in the first or second cycle of the reproductive season (see Chapter 2), and used the midpoints of likely conception dates in each cycle (November 28 for cycle 1 and April 28 for cycle 2) and an estimated gestation length of 52 days, to derive possible birth dates (Génin, 2008) to estimate time since birth. For each individual, I used the most conservative estimate (i.e., the estimate that would yield the youngest longevity). Mouse lemurs tend to reach 40 g in body mass some time between ages 3 and 6 months, but few exceed 50 g in their first year. (Two mouse lemurs that were found dead in the spiny forest in November 2004 were judged to be 10 months old at death. They had their full adult dentitions but incomplete growth and epiphyseal fusion of their humerus and femur. They weighed 40 and 40.5 g each when they were first captured in mid-October, at ~ 9 months) Thus, to take an example, male 063C-0A91 was first captured on June 1 2003, with a body mass of 44 g, and a minimum estimated age of 6 months at first capture. On this basis, I calculated a minimum longevity of 3.92 years for this individual and a similar minimum of four years for two additional individuals. The maximum was 4.37 years for a female from the gallery forest (transponder ID# 0659-C153).

Table 4.3: Estimate of minimum longevity for the individuals with the longest capture intervals (first to last capturedate)

Trait	063C-0A91 Male	0659-C153 Female	063B-F118 Female	0627-92C8 Female	0659-6ECC Male
First capture date	06/01/03	10/10/04	9/16/04	9/16/04	10/01/04
Body mass (g) at first capture	44	58.5	40.5	53.5	51
Estimated age at first capture	6 months	18 months	5 months	17 months	17 months
Forest	Gallery	Gallery	Spiny	Spiny	Gallery
Interval between first to last capture	1245	1047	983	975	829
Minimum survival in days	1431	1596	1134	1494	1348
Minimum longevity in years	3.92	4.37	3.11	4.09	3.69
Maximum distance between trapping locations in the main study area	250 m	35 m	90 m	105 m	25 m

Taking only those individuals that had the longest capture intervals (from first to last), the maximum distance between capture locations was higher for males than for females. The mean distances were 76.7 m for three females, and 137.5 m for two males. One of those males was only captured twice. Eliminating him from consideration, the male distance was 250 m. Next, I sampled all individuals with capture frequencies exceeding 20, and calculated the maximum distance between capture locations for individuals trapped in the main study areas, as well as the frequency of captures per unit time for all (Table 4.4). The male mean for this sample was 139 ± 98.4 m, and the female mean was 101 ± 32.6 m. Whereas the sample is too small to yield significance, the direction of the difference is the same as that observed in the sample of individuals with the longest interval between first and last capture. For this sample, male relative frequency of capture (number of captures per unit time) (0.23 captures per day) is much higher than that for females (0.14 captures per day), suggesting again greater activity for males.

The pattern is consistent whether we sample all individuals captured with a frequency greater than 5, all individuals captured over an interval of time greater than 800 days, or all individuals captured with a frequency greater than 20. It appears that females are more anchored to a particular location (they have smaller ranges), and that males are more active, and travel greater distances for shorter periods of time. Males drop out of the population more rapidly than females.

Table 4.4: Maximum distance between trapping locations for individuals captured more than 20 times

Transponder ID	Sex	First to last capture (days)	Number of captures	Frequency per unit time	Maximum distance between trapping locations in the main study area (in meters)
063B-C82F	M	730	21	0.03	206
063B-E8FF	M	571	29	0.05	Random sampling area*
0659-9698	M	72	21	0.29	35
0659-ACE1	M	95	27	0.28	80
0659-C38D	M	127	29	0.23	175
0659-F4A0	M	109	23	0.21	55
0682-9468	M	46	24	0.52	285
064C-A58C	F	135	23	0.17	Random sampling area*
064C-C80D	F	81	21	0.26	Random sampling area*
064C-E061	F	134	21	0.16	125
0658-656F	F	171	26	0.15	145
0659-BA7D	F	208	22	0.11	90
0659-D3A5	F	260	20	0.08	112
0659-D42D	F	174	22	0.13	55
0659-D600	F	798	43	0.05	80

*Individuals trapped in random sampling areas were not included in the distance analysis.

4.3.3 Variation in behavior patterns

4.3.3.1 Sexual differences in feeding behavior

At Beza Mahafaly, male and female *M. griseorufus* tend to feed in different tree species ($\chi^2 = 223.38$, df = 47, $p < 0.001$). Of the 48 tree species used for food by mouse lemurs, only 24 were used by both sexes. Eighteen tree species were used only by females while six were used only by males. Among the tree species most visited for feeding by both sexes were *Terminalia fatraea* (25.6% of all feeding observations), *Albizzia* sp (15.8%), *Rhopalocarpus lucidus* (10.8%), *Acacia bellula* (9.2%)*, Bridelia* sp. (8.4%), and *Grewia leucophylla* (7.4%). Feeding in these trees comprised 77.3% of all feeding observations. Females tended to favor *Terminalia fatraea* (29.5% of all female feeding observations), *Albizzia* sp. (17.3%), and *Bridelia* sp (10.2%) while males favored *Grewia leucophylla* (11.8%), and *Rhopalocarpus lucidus* (16.1%). The two sexes spent similar proportions of their feeding time in *Acacia bellula* (8.8 % for females and 9.8 % for males).

During the rainy season, tree species selected by male and female mouse lemurs for feeding also differed significantly ($\chi^2 = 311.06$, df = 41, $p < 0.001$). Of the forty tree species used for feeding in the wet season, 20 were used exclusively by females while only six were used exclusively by males. Sixteen species were used by males and females, including the species most commonly utilized by each sex: *Terminalia fatraea*, *Albizzia* sp., *Bridelia* sp., *Grewia leucophylla*. During the dry season, 28 tree species were selected for feeding, and once again, there were significant differences in tree species selection by sex ($\chi^2 = 97.31$, df = 27, $p < 0.001$). Eight tree species were used exclusively by males and seven by females, while thirteen were shared. Among the tree species used by both sexes were *Terminalia fatraea*, *Rhopalocarpus lucidus*, *Albizzia* sp., *Acacia bellula*, and *Mimosa delicantuta*. The highest percentages of all feeding observations for both males and females during the dry season were in *Terminalia fatraea* (28.1% for females and 26.2% for males). Other foods tended to be preferred by one sex over the other. Males in particular fed in *Albizzia* sp. and *Rhopalocarpus lucidus* while females preferred *Acacia bellula*.

The tree species listed above were selected mainly for fruit and gums. The third important element in the diet of *M. griseorufus* was insects, which were consumed mainly in the rainy season. During the rainy season, these three elements – i.e., insects

(40.4% of all focal individual rainy season feeding observations), fruit (29.8%), and gums (27.3%) – comprised 97.5% of the diet of *M. griseorufus*, but flowers and young leaves were also consumed in small amounts. Breaking these down by sex, however, reveals highly significant differences ($\chi^2 = 48.91$, df = 5, $p < 0.001$) (Figure 4.4). During the rainy season, females consumed more gums than males (31.3% vs. 16.5%) while males consumed more fruit than females (39.2% vs. 26.3%). Males and females consumed insects in roughly similar proportions (42% and 39.9%, respectively).

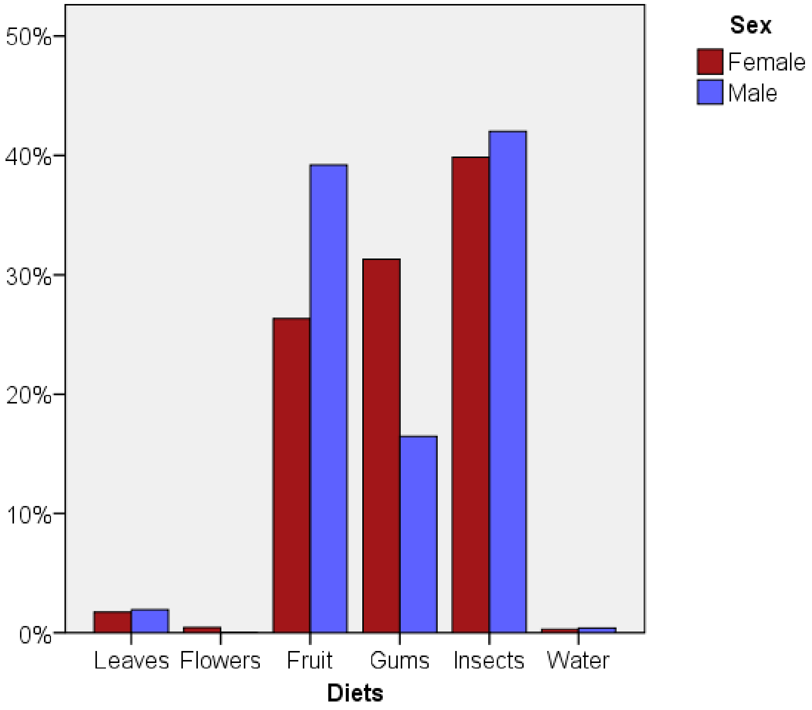


Figure 4.4: Percentages of rainy season focal individual feeding observations devoted to different dietary elements, broken down by sex.

During the dry season, no fruit, flowers, or young leaves were consumed by mouse lemurs, so 100% of their diet comprised insects and gums. Again, I found significant differences in items consumed by males and females ($\chi^2 = 17.09$, df = 4, $p = 0.002$) (Figure 4.5). Individual males fed more on insects than females did (24.1% vs.

15.7%), and females consumed a higher proportion of gums (82.6% for females and 75.3% for males).

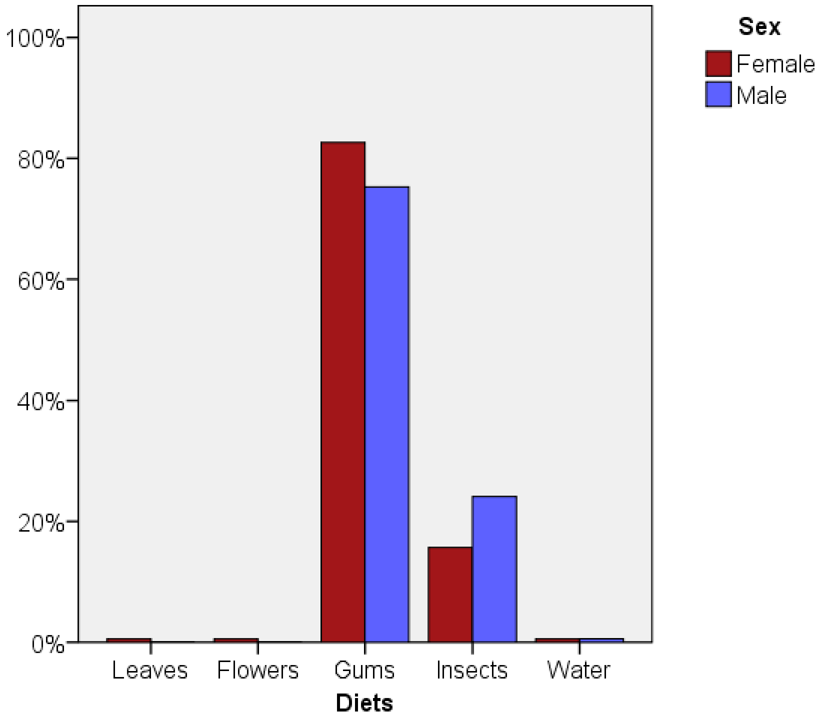


Figure 4.5: Percentages of dry season focal individual feeding observations devoted to different dietary elements, broken down by sex.

The question arises – are males or females more selective in their choice of trees for gum feeding? In other words, which sex depends more on the most abundant gum trees in the forests? Do the sexes differ in their choice of gum trees during the wet and dry seasons?

In doing the botanical surveys, I recorded a total of 48 tree species, of which 28 were visited by focal individuals for gum feeding. Twelve additional tree species that were not recorded in the botanical surveys were also visited for gum feeding, but rather infrequently. Of the 40 tree species on which mouse lemurs consumed gums, 32 were used during the rainy season, 28 during the dry season, and 20 during both seasons. There were a few tree species that were only used during each season (12 in the rainy season and 8 in the dry season). These tree species were visited for gum tree less than 12 times during the focal observation period, and included all of the species not represented in the botanical surveys.

Overall, females used 36 tree species for gum feeding while males used 24 tree species, and they both used 20 tree species in common. Females and males showed significant differences in the tree species used for gum feeding ($\chi^2 = 126.4$, df = 39, $p < 0.001$). Table 4.5 lists the eight tree species most used for gum extraction by males and females, along with the relative abundances of these species across all forests (as determined through botanical surveys). Analyzing the frequencies of focal observations on males and females extracting gums from the various tree species in the two seasons, I found significant differences between males and females (rainy season: $\chi^2 = 150.3$, df = 31, $p < 0.001$ and dry season: $\chi^2 = 97$, df = 27, $p < 0.001$).

With regard to the selectivity of gum tree species by males and females, I found no correlation for either sex between the relative percentages of the top eight species of gum producing trees in the botanical plots and the relative percentages of trees used for extracting gums. The correlations between the relative percentages of trees used and relative percentages of trees in the botanical plots were consistently low (females, rainy season, r = -0.03, n = 8, NS; females, dry season, r = 0.18, n = 8, NS; males, rainy season, r = -0.16, n = 8, NS, males, dry season, r = 0.19, n = 8, NS). This indicates strong selectivity for the trees used for gum extraction by both sexes in both dry and rainy seasons. Neither sex can be called more selective than the other. There was no correlation between male and female tree choice during the rainy season (r = 0.08, n = 8, NS); however, the two were strongly correlated during the dry season (r = 0.78, n = 8, p = 0.02), suggesting high intersexual competition for gum trees during the dry season. During the dry season, the trees most preferred for exudate feeding by both sexes are *Terminalia fatraea*, *Rhopalocarpus lucidus*, *Acacia bellula* and *Albizzia* sp. During the rainy season, females prefer *Albizzia* sp. and *Terminalia fatraea*, while males prefer *Acacia bellula* and *Rhopalocarpus lucidus*.

Table 4.5: Relative abundance of the main gum producing trees at Beza Mahafaly, and relative frequencies of focal observations of gum feeding by males and females in the preferred tree species

Tree species	Percentage of trees in the botanical surveys, all sites combined	Rainy season		Dry season	
		Percentage of total female focal observations in particular tree species	Percentage of total male focal observations in particular tree species	Percentage of total female focal observations in particular tree species	Percentage of total male focal observations in particular tree species
Acacia bellula	1.2	4.1	32.9	25.1	10.0
Albizzia sp.	0.9	33.2	11.8	10.8	18.9
Commiphora brevicalyx	3.9	5.1	0.0	1.0	1.6
Mimosa delicantuta	0.3	0.0	1.3	2.0	6.1
Operculycaria decaryi	1.1	8.9	3.9	0.3	2.1
Rhopalocarpus lucidus	2.8	6.8	18.4	15.6	21.1
Terminalia fatraea	3.1	20.8	6.6	28.5	26.2
Terminalia serygii	2.0	1.0	0.0	4.7	5.3

The mean heights in trees at which individuals fed also varied by sex and season (Figure 4.6). Females were found feeding at significantly lower heights (mean height of 4.53 ± 1.92 m) than males (7.06 ± 3.61 m) during the rainy season (t = -14.33, df = 559, *p* < 0.001). This is likely a function of males feeding on significantly more fruit and insects at that time. The mean heights of feeding locations reversed during the dry season, but maintained statistical significance (t = 4.8, df = 604, *p* < 0.001). Now males fed at lower heights, decreasing on average 56.4% to 3.98 ± 2.62 m, whereas females fed at higher locations, increasing 9.05% (to 4.94 ± 3.23 m).

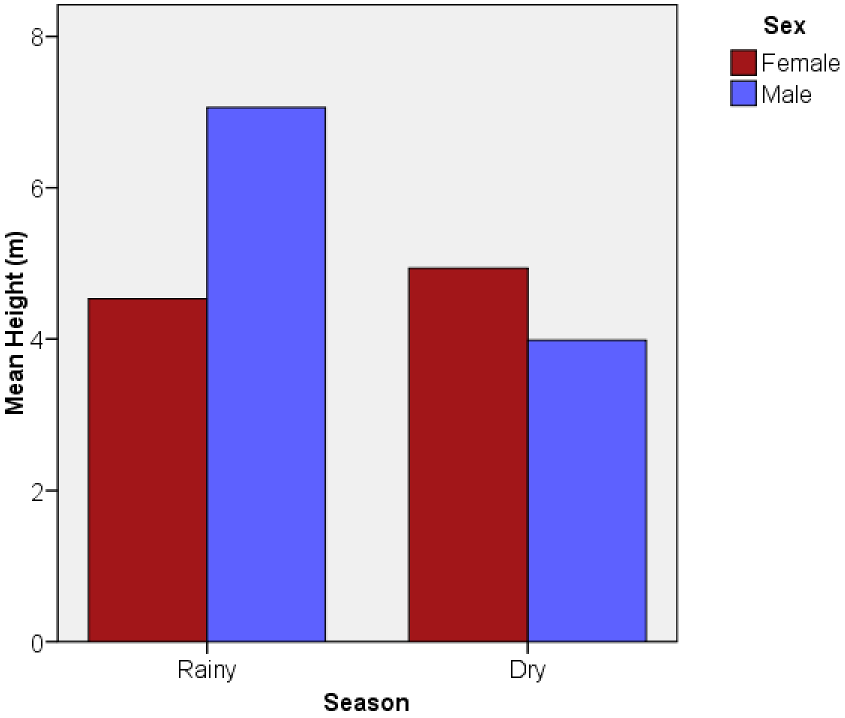


Figure 4.6: Mean height at feeding location across season.

Breaking down this pattern by forest (Figure 4.7) reveals that the differences in feeding height between sexes are mainly due to differences in the gallery forest. These differences are significant for the rainy season (t = -12.4, df = 451.9, *p* < 0.001), males used mean height of 8.68 ± 3.77 m and females did at 5.39 ± 2.56 m, and the dry season (t = 4.96, df = 410, *p* < 0.001), Females used mean height of 7.46 ± 2.7 m and males 6.01 ± 3.05 m in the same direction as revealed in the overall pattern. At Ihazoara, there are no differences in feeding height by sex in either season (rainy season t = -.72, df = 417, NS; dry season t = -0.22, df = 59, NS). And in the spiny forest, males feed at greater heights again in the rainy season (t = -5.2, df = 664, *p* < 0.001), males used a mean height of 4.92 ± 1.4 m and females did 4.15 ± 1.5 m, but there is no difference during the dry season (t = -1.9, df = 552, NS). Both sexes used similar feeding height at 2.51 m (females) and 2.75 m (males).

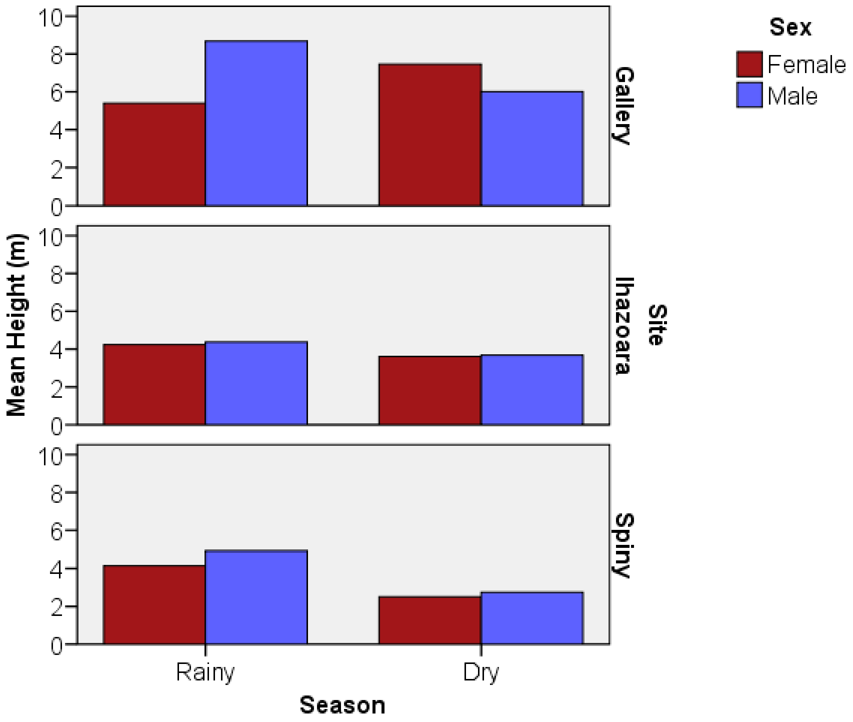


Figure 4.7: Mean height at feeding location by site and by season

4.3.3.2 Sexual differences in nesting behavior

Microcebus griseorufus focal individuals were found nesting in 58 tree species, 49 of which were used for nesting by females and 46 by males. I found significant differences in the tree species used for nesting by males and females ($\chi^2 = 706.48$, df = 58, $p < 0.001$). Nineteen tree species were used only by females, and eight only by males. Males and females used 31 tree species in common, nine of which were frequently selected, including *Euphorbia tirucallii* (12.1% of all focal individual nesting observations), *Alluaudia procera* (11.3%), *Acacia bellula* (5.3%), *Terminalia fatrae* (11.3%), *Grewia leucophylla* (6.2%), *Salvadora angustifolia* (5.2%), *Gyrocarpus americanus* (5.2%), and *Tamarindus indica* (4.1%). While the first four of these species were used roughly as frequently by both sexes, there was differential use of the latter four, with males preferring *T. indica* for nesting, and females preferring *Grewia leucophylla* and *Gyrocarpus americanus*.

Sexual preferences for nesting tree species also held for the seasons (for the rainy season, $\chi^2 = 300$, df = 49, $p < 0.001$; for the dry season, $\chi^2 = 562.75$, df =39, $p < 0.001$). During the rainy season, 50 tree species were used as nests, of which 17 were used only by females and 7 only by males. Males and females used 26 tree species in common, including *Euphorbia tirucallii* (16.5% of all focal individual nesting observations during the rainy season), *Alluaudia procera* (15.0%), *Gyrocarpus americanus* (7.0%), *Euphorbia stenoclada* (5.5%), and *Acacia bellula* (4.8%).

During the dry season, 39 tree species were selected for nesting. Eleven tree species were used exclusively by males, while nine were used only by females. Nineteen tree species were used by both sexes, including *Terminalia fatraea* (18.87% of all focal individual nesting observations during the dry season), *Grewia leucophylla* (10.47%), *Euphorbia tirucallii* (7.88%), *Alluaudia procera* (7.83%), *Salvadoria angustifolia* (6.96%), *Acacia bellula* (5.7%), *Tamarindus indica* (4.66%) and *Commiphora brevicalyx* (4.49%).

I analyzed sexual preferences for nest types (open vs. tree holes) by season and by site. While there were strongly significant differences in nest type preference by season across all sites (see Chapter 3), nest preferences by males and females were more subtle; they varied by season, and sometimes by site.

During the rainy season, when both males and females prefer open nests, I found significant differences in nest use by males and females over all sites ($\chi^2 = 9.68$, df =1, $p = 0.002$). The ratio of open nests to tree holes used by males was 86.4 to 13.6, while the ratio of open nests to tree holes used by females was 79.7 to 20.3. Focal males used relatively more open nests, and females used relatively more tree holes. During the rainy season, combining all three sites, there were no differences in the height of nests used by males (3.4 ± 1.8 m) and females (3.5 ± 1.6 m).

Taking each site singly during the rainy season, I found the following: In the gallery forest, sexual differences in nest type preference were highly significant ($\chi^2 = 13.4$, df = 1, $p < 0.001$), with males using a greater percentage of open nests (86.9%) than females (73.1%). In the dry deciduous forest of Ihazoara, males and females differed in nest use ($\chi^2 = 5.52$, df = 1, $p < 0.019$). Males used open nests 100% of the time while females used open nests 95.9% of the time. In the spiny forest, while males used open nests more than did females (72.3% for males vs. 69.4% for females), the difference was not statistically significant ($\chi^2 = 0.4$, df = 1, NS).

To determine why females select tree holes during the rainy season more than males, I tested the differences in rainy-season nest type preference for non-pregnant, pregnant, and lactating females. The differences here again are highly significant ($\chi^2 = 53.26$, df = 2, $p < 0.001$). During the rainy season, pregnant females used tree holes more often (46.4% of all pregnant female focal observations) than non- pregnant females (20.8% of all non-pregnant female focal observations) or lactating females (17.1% of all lactating female focal observations) (Figure 4.8). I also observed highly significant differences in nest height used by females that were pregnant, non-pregnant or lactating during the rainy season (ANOVA F = 74.77; df = 2, 1178; $p < 0.001$). Nest heights were greatest for pregnant females (5.13 ± 1.84 m), lower for lactating females (3.38 ± 1.53 m), and lowest for non-pregnant females (3.02 ± 1.09 m).

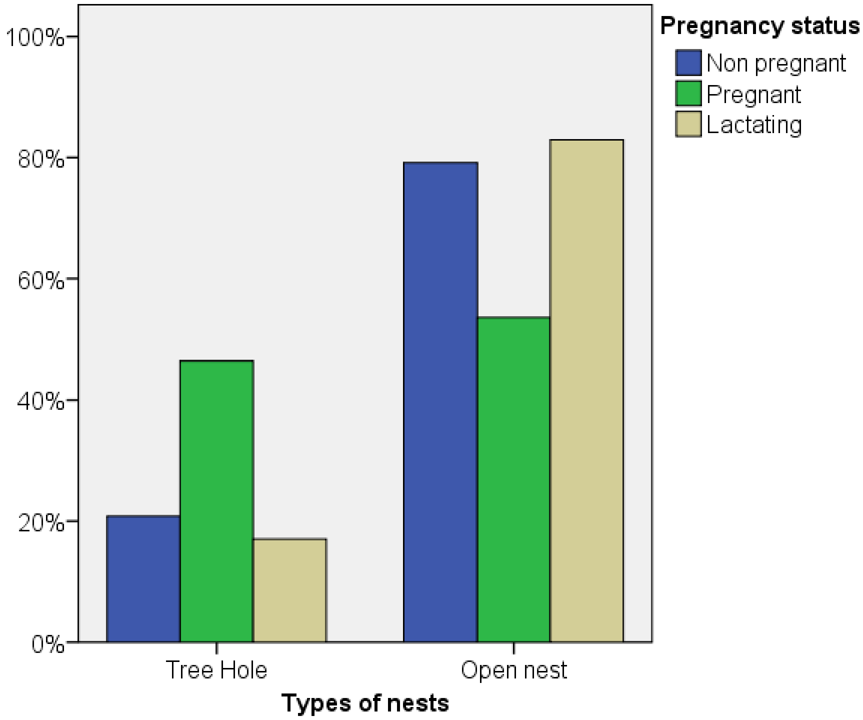


Figure 4.8: Nesting profiles of females during the rainy season.

During the dry season, I also found significant differences in nest type use by males and females ($\chi^2 = 17.53$, df = 1, $p < 0.001$), again with females using tree holes relatively more than males (Figure 4.9). Among the nests used by females, 82% were tree holes and 17.9% were open nests. Males used 73.7% tree holes and 26.3% open nests. During the dry season, males and females differed in height used for nesting ($t = -6.1$, df = 1677, $p < 0.001$); the mean height of nests used by females was 2.4 ± 1.3m while males nested higher at 2.9 ± 1.7 m.

When nests used by male and female mouse lemurs during the dry season were analyzed by site separately, the mouse lemurs in the gallery forest showed significant differences ($\chi^2 = 16.8$, df = 1, $p < 0.001$). Again, the relative percentage of tree hole (vs. open nest) use was higher in females (76.7%) than males (62.0%). The pattern in the spiny forest paralleled the pattern in the gallery forest, whereby males and females differed significantly in nest type use ($\chi^2 = 17.89$, df = 1, $p < 0.001$), and females used tree holes significantly more than did males (98.0% vs. 88.7%). However, there were no significant differences in nest type use between sexes in the dry deciduous forest of Ihazoara ($\chi^2 = 0.2$, df = 1, NS), where both males and females preferred tree holes to open nests in similar proportions (73.3% for females vs. 71.6% for males).

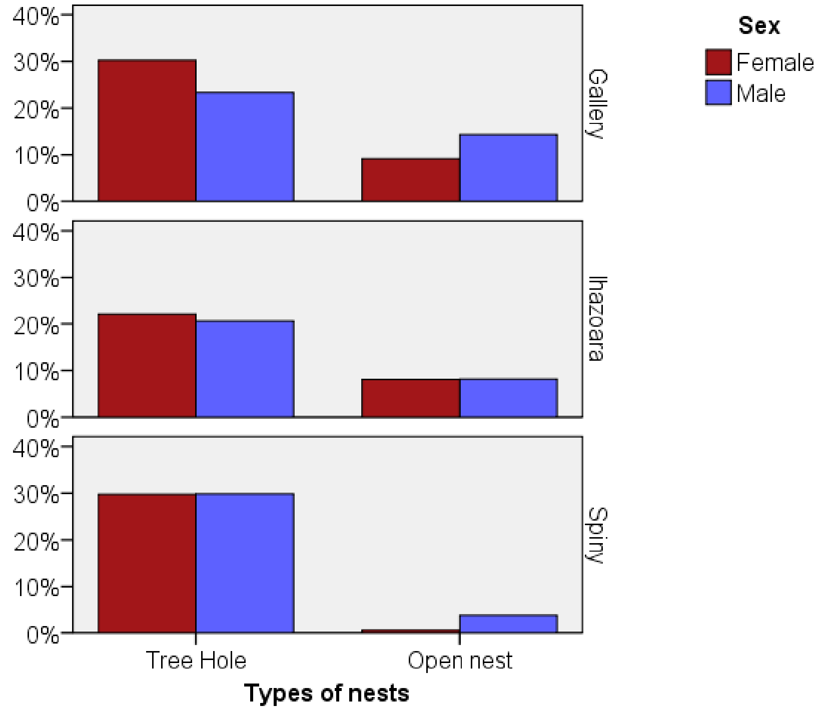


Figure 4.9: Type of nest used during the dry season, by sex and site (% of all focal nesting observations for each sex)

I now turn to the question of the relationship between nest choice by males and females and the relative abundance in botanical plots of trees used for nesting, to determine whether one sex is more selective than the other. A total of 48 tree species were recorded in the botanical plots, of which only 26 were used by focal individuals for nesting. A total of 32 additional tree species, not recorded in the botanical plots, were also used for nesting (58 in all); however, the 32 additional species were rarely used. Table 4.6 shows the percentages of the trees that were most commonly used for nesting, and their relative use by focal males and females during the rainy and dry seasons.

Correlations between tree species use and relative abundance in the botanical plots were all very low for both sexes in both seasons (female, rainy, r = 0.51, n = 14, NS; female, dry, r = 0.1, n = 14, NS; male, rainy, r = 0.38, n = 14, NS; male, dry, r =

0.10, n = 14, NS), suggesting that tree species choice is selective and not dependent simply on the abundance of the trees in the plots. On the other hand, male and female tree species choices were strongly correlated especially in the rainy season (r = 0.92, n = 14, $p < 0.001$) but also in the dry season (r = 0.54, n = 14, $p = 0.05$). This suggests strong intersexual competition for particular nesting trees, particularly in the rainy season (i.e., the beginning of the reproductive season).

Table 4.6: Relative abundance of the main tree species used for nesting at Beza Mahafaly, and relative frequencies of male and female focal nesting observations in the preferred tree species

Tree species	Percentage of 1313 trees in the botanical surveys, all sites combined	Rainy season		Dry season	
		Percentage of total female focal observations in particular tree species	Percentage of total male focal observations in particular tree species	Percentage of total female focal observations in particular tree species	Percentage of total male focal observations in particular tree species
Acacia bellula	1.2	5.0	4.3	6.2	5.2
Albizzia sp.	0.9	0	2.9	1.1	4.5
Alluaudia procera	9.7	14.7	15.6	6.8	8.7
Commiphora brevicalyx	3.9	2.4	2.0	0.2	8.3
Euphorbia stenoclada	0.5	5.0	7.0	0.6	0
Euphorbia tirucallii	5.1	15.1	20.3	4.9	10.6
Grewia leucophylla	1.5	1.9	0.9	16.2	5.3
Gyrocarpus americanus	19.7	7.5	5.6	5.1	2
Hildegardia erythrosiphon	0	0	0	6.6	0.8
Mahafanogne	1.5	3.8	1.4	1.1	0.2
Operculicarya decaryi	1.1	4.2	0	0.1	0
Salvadora angustifolia	1.4	3.9	1.8	6.5	7.4
Tamarindus indica	4.0	3.0	5.0	2	7.1
Terminalia fatraea	3.1	3.2	3.4	26	12.5

4.3.3.3 Sexual differences in grouping behavior

An attempt was made at determining the relative frequencies of social nesting (or sleeping in nests with multiple individuals) by males and females. This was sometimes difficult, as many tree holes were high, and it was not possible always to ascertain whether or not multiple individuals occupied them (given that only one may have been radio collared). During the 2006-2007 sampling period, focal individuals rarely interacted with one another. The only observed interactions of focal individuals were between two adult females in the gallery forest, and these were females with infants sharing an open nest intermittently for a number of days. In 2003, two other radio-collared females were observed together in a tree hole in the gallery forest, again with infants. When collared individuals are seen at a distance interacting with other individuals, it is often impossible to tell the sex of the individuals with which the focal individual is engaged.

When it was impossible to verify the presence or absence of other individuals at a nest site, data on social grouping were not collected. Therefore when individuals were recorded as being alone, it was because no other individual was observed over an extended period.

Unsurprisingly, females were more often observed nesting in groups than were males. Some of these groups clearly comprised their own young, but co-sleeping also occurred when infants were not present. Taking both seasons together, differences between male and female focal individuals were strongly significant ($\chi^2 = 172.1$, df = 1, $p < 0.001$); females were observed with co-sleepers (25.9% of all female focal individual nesting observations) far more than were males (7.8% of all male focal individual nesting observations). In actuality, this pattern holds for the rainy season only. During the rainy season, females were found nesting with co-sleepers 37.7% of the time, while males were found in groups only 15.6% of the time ($\chi^2 = 72.3$, df = 1, $p < 0.001$). During the dry season, there was no difference in the relative frequency of co-sleeping for females (4.1% of female focal individual nesting observations) and males (3.9%) ($\chi^2 = 0.01$ df = 1, NS).

4.3.3.4 Sexual differences in activity pattern

Finally, I investigated whether males and females differ in the degree to which they are likely to emerge from nests at night. When mouse lemurs enter seasonal torpor, they do not emerge from their sleeping nests at night (or rather, they emerge only occasionally, when changing nest sites). During the rainy season, both males and females emerge every night from their nests. During the dry season, I found a highly significant difference, with radio-collared females remaining inactive (not emerging from their nests, when watched for a period of at least three hours) far more often than radio-collared males ($\chi^2 = 301.8$, df 1, $p < 0.001$). Females were scored as "inactive" on 40.6% of their focal individual sampling nights, while males were "inactive" only 5.9% of dry season sampling nights. This sexual difference holds for both the gallery forest and the spiny forest (gallery: 48.0% vs. 8.7% for females vs. males respectively, $\chi^2 = 128.9$, df = 1, $p < 0.001$; spiny forest: 68.1% vs. 6.5% for females vs. males respectively, $\chi^2 = 233.4$, df = 1, $p < 0.001$).

Interestingly, this pattern does not hold for Ihazoara, where very few individuals entered prolonged torpor in the dry season (3.2% of female focal observations vs. 1.5% for males; $\chi^2 = 1.7$, df = 1, NS). I will return to this point in Chapter 5.

If females enter bouts of prolonged torpor during the dry season when food is scarce, they may need to increase their fat reserves prior to entering torpor. Females emerging from extended periods of torpor at the end of the dry season may need to increase their body mass in preparation for the reproductive season. To determine whether or not this occurs, I examined the pattern of weight change in adult, non-pregnant females over the course of the year. Mean female weights were highest in May (46.5 g), June (51.1 g), and September (50.4 g). Whereas these weights do not differ markedly from the annual mean for non-pregnant females (45.2 g), they differ from the mean for all other months combined (43.6 g). Thus, I conclude that the modest increases in body mass in May and June indeed may be correlated with preparation (through an increase in fat reserves) for seasonal torpor and the modest increase in September may signal preparation for the first reproductive cycle. If this interpretation is correct, however, the pattern of weight change should track temporal changes in activity patterns and other behaviors. Thus, we should consider the temporal pattern of shifts in behavior in greater detail. In the next section, I examine the behavioral differences between the sexes on an annual time line, probing further possible correlations among changes in activity pattern, nest use, diet, and co-sleeping.

4.3.3.5 Temporal pattern of shifts in activity, nest use, diet, and co-sleeping

Tables 4.6-9 show differences in activity patterns, nest type choice, co-sleeping, and exudate feeding by month for both sexes. Figures 4.10-13 depict these patterns graphically. Note that, for these figures, the values for each condition (e.g., inactive and active for Activity; tree holes and open nests for Nest Type, etc.) sum to 100%.

I begin in the month of May, which is the beginning of the season of prolonged torpor in many mouse lemurs, including *M. griseorufus*. For each of the tables, I highlighted the pattern (or "sign") of sex differences – i.e., the direction of differences between females and males, regardless of whether or not the differences were significant. Thus, for example, despite the fact that females and males differ significantly in nest type selection in only two of the nine months of focal individual sampling, it is significant that females use tree holes more than males in eight of the nine months sampled. These patterns are indicated in the last rows of Tables 4.7 to 4.10, which correspond to each of the above-listed figures.

Females and males differ sharply in activity patterns for four months, from May to August, during the dry season. During this time, females tend to enter prolonged torpor (or inactivity at night) in much higher percentages than males, although some females remain active, and a few males enter torpor at this time, but beginning in June rather than May (Table 4.7, Figure 4.10).

During the season of scarce resources and increased inactivity particularly by females (June, July, and August), tree holes are preferred by both sexes, but females increase tree hole occupancy earlier than males, and generally occupy more tree holes than do males, even when open nests are preferred by both sexes (Table 4.8, Figure 4.11). In effect, the males appear to be "catching up" to females in tree-hole use throughout this period.

For both females and males, nesting alone is more common than nesting with others in every month; however, females show a distinct preference in comparison to males for co-sleeping (Table 4.9, Figure 4.12). This is especially true from February to

May, when the sex differences are significant, and the percentage of female focal observations showing co-sleeping can increase to ~ 50%. A markedly different pattern occurs when some females enter prolonged torpor (June, July, and August) while males remain active. During this time (the season of scarce resources), co-sleeping is rare for everyone, but males co-sleep more often than females. The difference is significant in August. It appears that hibernating individuals do not sleep in groups.

Thus far, we see that females and males differ strikingly in June, July, and August, when females are less active, use more tree holes, and co-sleep less often than males. Females also have relatively greater access to exudates during this period. They begin preferring exudates earlier than males (in March, April, and May) and this pattern continues through the peak of the dry season. In seven of the eight focal individual sampling months females feed on exudates more than males (Table 4.10, Figure 4.13). The exception is the month of February, during which time females feed significantly more on insects (61.7% vs. 50.0% of respective focal individual feeding behavior samples) and less on gums than males ($\chi^2 = 4.3$, df = 1, $p = 0.04$). Unfortunately, I don't have data for January. But it is clear that females gain access to gums earlier than do males.

Table 4.7: Percentages of focal observation nights during which female focal individuals or male focal individuals remained inactive (did not emerge from nest for an observation period of at least three hours)*

Month	May	June	July	August
♀	6.2	31.7	47.5	69.7
♂	0	3.8	8.7	5.6
χ^2	5.2	81.5	124.6	145.5
df	1	1	1	1
p	= 0.02	< 0.001	< 0.001	< 0.001
Pattern	♀>♂	♀>♂	♀>♂	♀>♂

*During all unlisted months, all individuals were active.

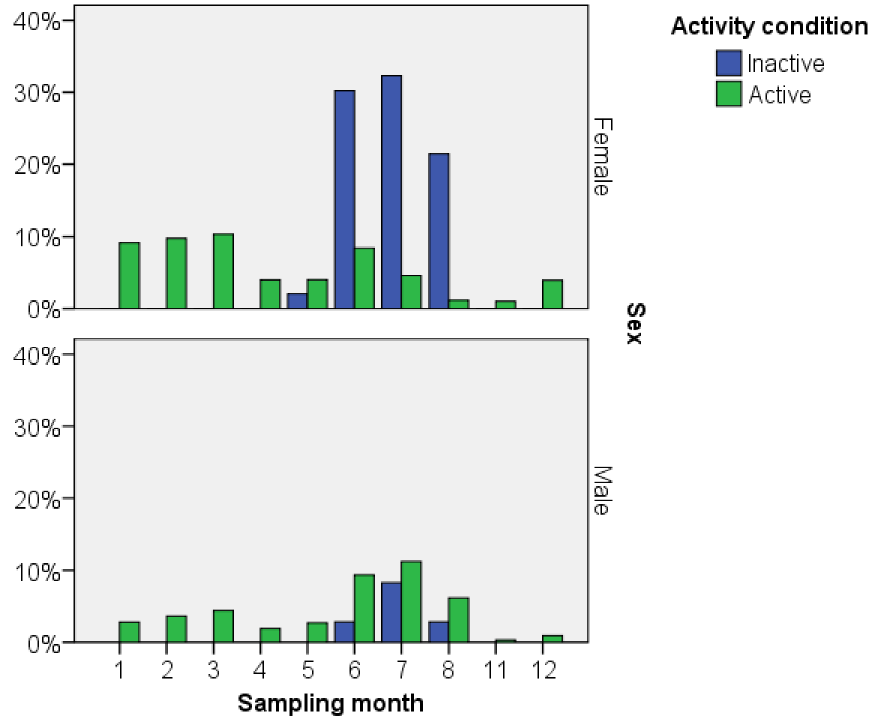


Figure 4.10: Activity condition by month for females and males.

Table 4.8: Percentages of focal observation days during which female or male focal individuals selected tree holes as sleeping sites

Month:	May	June	July	August	November	December	February	March	April
♀	31.8	83.7	84.2	93.3	78.3	55.9	13.9	15.1	6.7
♂	23.5	61.0	83.5	87.9	60	39.3	7.3	8.3	12.1
χ^2	1.7	43.6	0.1	2.5	1.5	2.5	3.2	3.2	1.5
df	1	1	1	1	1	1	1	1	1
p	NS	< 0.001	NS	NS	NS	NS	NS	= 0.05	NS
Pattern	♀>♂	♀>♂	♀>♂	♀>♂	♀>♂	♀>♂	♀>♂	♀>♂	♀<♂

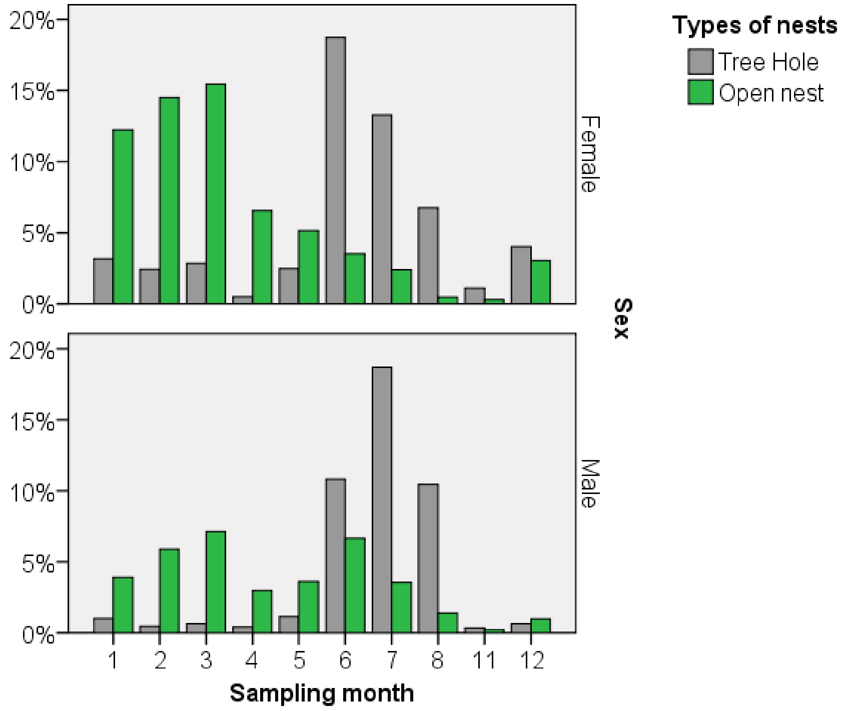


Figure 4.11: Types of nests used by focal females and males, by month.

Table 4.9: Percentages of focal individual nesting observations during which the focal individual was in social contact with a co-sleeper (sometimes infants), by month and sex.

Month:	May	June	July	August	November	December	February	March	April
♀	31.6	3.6	0	0	8.7	10.2	49.3	33.4	25.0
♂	12.3	4.5	1.4	4.1	0	0	22.9	9.8	10.3
χ^2	9.7	0.3	2.7	4.6	0.9	3.1	22.6	26.5	5.2
df	1	1	1	1	1	1	1	1	1
p	0.002	NS	NS	0.03	NS	NS	<0.001	<0.001	= 0.02
Pattern	♀>♂	♀<♂	♀<♂	♀<♂	♀>♂	♀>♂	♀>♂	♀>♂	♀>♂

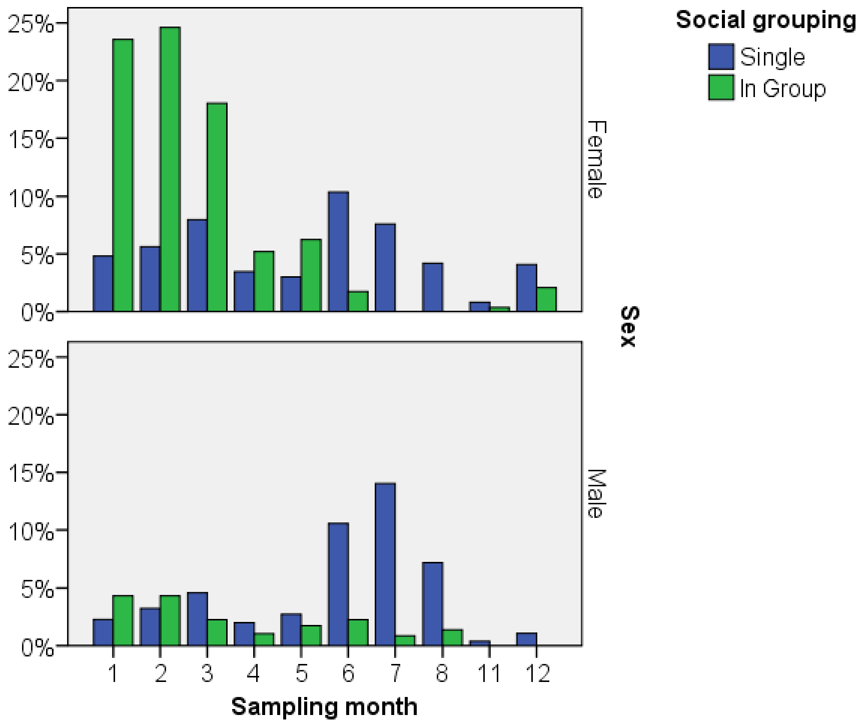


Figure 4.12: Co-sleeping (or grouping pattern) by month, for females and males.

Table 4.10: Percentage of focal individual feeding observations during which the focal individual was feeding on gums (by month and sex)

Month:	May	June	July	August	December	February	March	April
♀	65.2	88.0	94.8	64.6	20.0	11.1	22.2	52.4
♂	37.5	85.1	75.1	62.8	0.0	21.1	13.9	14.7
χ^2	2.3	0.8	11.0	0.09	2.1	6.2	5.2	69.0
df	1	1	1	1	1	1	1	1
p	NS	NS	0.001	NS	NS	0.01	0.02	<0.001
Pattern	♀>♂	♀>♂	♀>♂	♀>♂	♀>♂	♀<♂	♀>♂	♀>♂

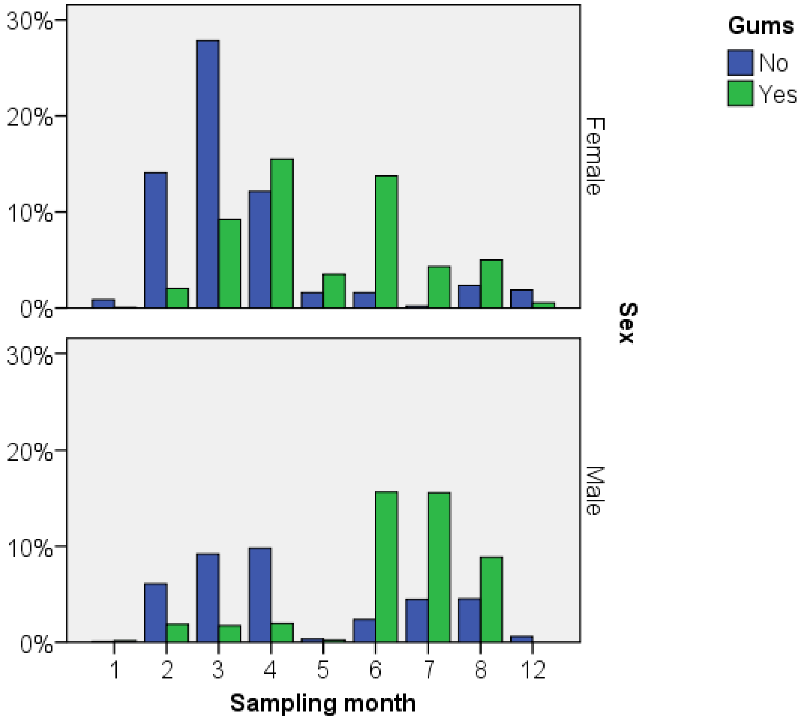


Figure 4.13: Gum feeding by month, for females and males.

With regard to heights in trees for nesting or feeding, there are no consistent temporal changes in feeding heights and the heights of nesting sites characterizing either males and or females. Feeding heights and nesting heights are correlated in the gallery forest (where males feed and nest at higher locations during the rainy season, and females feed and nest at higher locations during the dry season). There are no differences in either season between feeding and nesting heights for males and females at Ihazoara. However, in the spiny forest, males feed at significantly higher locations in the rainy season but use significantly lower nests, while during the dry season, the sexes do not differ in feeding height, but females nest at significantly higher locations than males.

4.4 Discussion

I was able to confirm that strong canine dimorphism occurs at each of the three very different sites that I studied. These results raise several questions, which I address in three separate sections of the following discussion. First, I ask why canine height dimorphism is so strong in *Microcebus griseorufus* when it has not been reported in other lemurs. Next, I compare my torpor results to results of other studies of populations or species of mouse lemurs, and ask why females of some enter seasonal torpor while others do not. Finally, I address the question of body mass dimorphism – i.e., are mouse lemurs dimorphic in body mass, and if not, why not (especially in light of their strong dimorphism in canine height).

4.4.1 Interpreting variation in canine height dimorphism: Why is it so strong in *Microcebus griseorufus*?

I have demonstrated that *M. griseorufus* at Beza Mahafaly exhibits exceptional reverse canine dimorphism, relatively weak reverse skull length dimorphism, and no body mass dimorphism once we control for pregnancy and lactation. Females are heavier than males only by virtue of pregnancy or lactation. Most lemur species are not dimorphic in any feature, and when reverse dimorphism occurs, it is generally very weak. Thus the strong reverse dimorphism in canine height documented here came as a surprise. It stands out, not only in relation to other traits, but also in relation to larger-bodied lemurs that do not exhibit reverse canine dimorphism, even though, in many species, females are dominant over males. Generally, in anthropoid primates, it is the larger-bodied species that have the strongest dimorphism. Here we have the strongest canine dimorphism in lemurs manifested in one of the smallest-bodied species. The question is, how can this phenomenon be explained? Under what circumstances might we expect primate species to exhibit strong reverse canine dimorphism?

Sexual dimorphism in primates is usually interpreted within the context of variation in mating systems (Kappeler, 1991, 1996; Plavcan, 2001). Larger canines serve as weapons in intrasexual (male-male) competition for access to female mates (Greenfield, 1992, 1998; Plavcan and van Schaik, 1992, 1994, 1997; Plavcan, 1993, 1994, 1998, 2001; Plavcan et al., 1995 Plavcan and Ruff, 2008); thus, the degree of sexual dimorphism is correlated with the degree of intrasexual competition among males for mates. This theoretical framework fails in lemurs, which generally are sexually monomorphic, regardless of the degree to which mating is polygynous and there is strong intrasexual competition among males for mates. Monomorphism in body size and other characteristics has been generally interpreted as a by-product of female dominance, but it isn't clear why females should not be larger than males, given that dominance (Dunham, 2008). Habitat and diet have been more or less dismissed as factors affecting body and canine size dimorphism in primates (Leutenegger and Cheverud, 1982; Plavcan and van Schaik, 2001), contra Clutton-Brock and Harvey (1977). The non-primate literature is not as dismissive. Ecological factors are considered very important in explaining size dimorphism, particularly in species for which females are larger than males. In general, males are larger than females in birds and mammals, and females are larger than males in virtually all other taxa (especially invertebrates). Exceptions occur in both birds and mammals, however. In particular, among birds of prey, females are regularly larger than males (Wheeler, 1983). In the broad literature on sexual dimorphism, dimorphism is understood in terms of costs and benefits; the benefits (in terms of increased reproductive advantage) must outweigh the costs (in terms of increased mortality) for any particular sex that is larger, has larger canines, or is more colorful than the other (Andersson, 1994). Three selective processes are generally considered: (1) sexual selection influencing mating success; (2) fecundity selection operating on females; and (3) intersexual resource division or competition (e.g., Lislevand et al., 2009). When females are larger than males, it is usually because there is a selective premium on female fecundity or survival, with females contributing more to the next generation than males. Parental care may play a role. However, Shreeves and Field (2008) show that, among bees and wasps, the presence or absence of male parental care is not the only factor. Of species in which males assume no parental role, females are generally larger than males only when they must also gather and transport very heavy resource loads to their nests, provisioning their young, and not merely laying the eggs. It is essential to consider the specific roles of males and females in ensuring their own survival and the production and survival of infants.

With these considerations in mind, we can now return to the question of why strong reverse canine dimorphism, but not body size dimorphism, might occur in the mouse lemurs of southern Madagascar. In this section of the discussion, I will consider first canine height dimorphism. Later I will discuss body size.

First, it behooves us to consider carefully the resource needs of males and females – how might they differ? Why or how might those differences in mouse lemurs exceed those of other primates? Under what circumstances might selection favor adult female access to particular resources or female dominance over males? The following factors may play a role:

a. **High weight gain in association with pregnancy/lactation, resulting in high reproductive costs to females.** The relative cost of reproduction in males and females may differ in relation to how much body mass females must gain to support their pregnancies and suckling infants.

b. **Adult mortality rates are high (e.g., due to predation).** A selective premium for producing large numbers of infants in a short period of time should occur if a population is subjected to high adult mortality rates, in which case there should also be high population turnover and short life spans.

c. **Scarcity of resources.** If favored resources are limited there may be strong intersexual competition for particular resources, particularly if the ability to gain weight rapidly helps females to successfully reproduce, and the resources that are limited are exactly those that help females gain weight rapidly.

d. **The species lives in a highly unpredictable environment, in which exceptionally high mortality occurs periodically in very bad years.** Bad years will exacerbate the need for rapid population reproductive resilience, and may increase the burden on females. Dewar and Richard (2007) argue that the extremes of opposite reproductive strategies will occur under high environmental or climatic unpredictability. The first strategy is bet-hedging and the second involves extremely rapid reproduction. The choice of strategy depends on the pattern of mortality. Bet hedgers maximize adult survivorship at the expense of infant and juvenile mortality; they depend on high iteroparity (the production of offspring multiple times within the reproductive lifetime) to counteract the negative effects of bad years with exceptionally high infant and

> juvenile losses. For bet hedging to work as a reproductive 'strategy,' reproductive rates can be low and interbirth intervals long, but reproductive life spans must also be long and adult mortality must be relatively low. Bet hedging works well *as long as adult mortality is low*. When adult mortality is high, the opposite strategy prevails – maximizing reproduction at the expense of adult mortality. Animals with very short generation times and multiple births per litter are better able to withstand high adult mortality rates. Under either extreme, the ability of females to access resources and support their young is of paramount importance. The combination (high infant and high adult mortality) places a strong selective premium on rapid, successful reproduction.

The question is, do any or all of the above apply to *Microcebus griseorufus*? I argue that they all do.

a. **High reproductive cost.** During the reproductive season, reproductive females at Beza Mahafaly regularly double their body mass, and thus have much higher caloric requirements than do males. This is the only time of the year during which females are more active (as reflected in higher capture rates) than males.

b. **High adult mortality**. I have documented extremely high population turnover in mouse lemurs at Beza Mahafaly, and low probability of recapture of individuals from one year to the next (see Chapter 2, Table 2.3). Taking averages for the three forests at Beza, only 11.1% of all individuals captured in any one year is known to be alive the following year; these percentages decrease rapidly if one considers the following year (2.3%). Only 0.8% of individuals are known to be alive in four consecutive years, and the individual with the longest life span was less than 4.5 years old at last capture. Extremely high predation pressure has been recorded at Beza Mahafaly (Goodman et al., 1993a, b). Goodman et al. (1993a) estimated that *M. griseorufus* comprised 21.2 % of the total biomass of prey items in *Asio madagascariensis* owl pellets at Beza Mahafaly. Goodman et al. (1993b) estimated that the biomass of mouse lemurs in *Tyto* owl pellets at the nearby village of Ambinda reached an incredible ~ 65.8%. Infants and adults were both represented in the owl pellets.

c. **Scarcity of resources.** The strong differences in the activity patterns, choice of nest type, and feeding behavior of males and females, combined with the selectivity of resources that I demonstrated above, suggest that resource scarcity is indeed a problem for *M. griseorufus* at Beza Mahafaly.

d. **Climate unpredictability at Beza.** Madagascar is known for its unpredictable climate. The most severe seasonal changes are found in the southwestern part of the island, which suffers high temperature seasonality, high rainfall seasonality, low average rainfall, and rainfall usually concentrated into a few months each year, between October and March (Fenn, 2003; Ratsirarson, 2003; Kamilar and Muldoon, 2010). The average annual rainfall is less than 350 mm per year. Severe droughts generally occur every decade (Richard et al., 2002). The last extreme drought occurred in 1990 and 1991 (Sauther, 1998; Gould et al., 1999, 2003), but there were additional droughts in 1997 and 2005. Southern Madagascar is also regularly hit by cyclones (e.g., Gretelle in 2003, Gafilo in 2004, and Ernest in 2005). Cyclones and droughts are very destructive, and they are known to have impacted lemur populations.

To demonstrate a link between canine height dimorphism and the reproductive success of females, it would be nice to have direct data on agonistic conflicts between males and females – particularly those centering on coveted resources. Such data are extremely difficult to obtain in the wild, especially because body size differences between males and females are so weak, rendering sexes of uncollared individuals impossible to identify at a distance. Unsurprisingly, much of the research that has been conducted on mouse lemur agonism, therefore, has been carried out in captivity. Unfortunately, also, that research has focused not on *M. griseorufus*, but on other species. Probably the best study was one carried out on *M. murinus* by Radespiel and Zimmermann (2001) at the German Primate Center in Göttingen, Germany. These authors placed males and females that had never previously been housed together, two at a time, into experimental cages. The cages were equipped with wooden branches, platforms and tubes, as well as four sleeping boxes. The male-female dyads would then be offered some coveted item and the researchers would record their interactions. Of 792 conflicts, 99.9% (all but one) were won by the female. In all of the literature on female dominance in lemurs (e.g., Kubzdela et al., 1992; Pereira et al., 1990; Pereira, 1995; Pereira and McGlynn, 1997; Pereira and Kappeler, 1997; Waeber and Hemelrijk, 2003; Pochron et al., 2003; Overdorff et al., 2005; Marolf et al., 2007; Charrier et al., 2007; Dunham, 2008; Kappeler and Schaeffler, 2008; Rasoloharijaona et al., 2008), this is the strongest confirmation. In fact, some field workers studying female dominance in other lemur species have questioned its efficacy (see Pereira et al., 1990; Freed, 2007), but nobody can question the efficacy of female dominance in a species in which virtually 100% of conflicts are won by females.

Whereas I did no experimental work and could not collect direct evidence of female dominance over males for this dissertation, I did collect indirect evidence of such dominance. That evidence comes primarily in the form of documentation of selectivity for certain resources that are differentially accessed by males and females. Thus, for example, I demonstrated selectivity for certain gum producing trees that were disproportionally targeted by both males and females given their representation in the botanical plots, and I showed that these were accessed more by females than by males. Tree holes were accessed more by females than by males, and once again, certain species of trees were used selectively for nesting in tree holes. The question is, how are these particular resources critical to adult female survival or reproduction?

It is becoming increasingly evident that, rather than being fallback foods that are accessed only when other foods (e.g., insects) are unavailable, gums can be preferred over those other foods because they facilitate weight gain. The central importance of gums to many species belonging to the family Cheirogaleidae has only recently been recognized; gums are staple foods for many cheirogaleid species. Their sugar content may be a key to understanding their importance to small-bodied species with relatively high metabolic rates. Gums are like fruit in that they can contain very high concentrations of soluble sugar (Nash, 1986). Fietz and Ganzhorn (1999) noted that the frugivorous dwarf lemur, *Cheirogaleus medius*, consumes only fruit with high proportions of sugar, especially at the beginning of dry season (and just prior to the beginning of prolonged seasonal torpor for both males and females). It is the high soluble sugar content of these fruits that is critical to the ability of *C. medius* to increase its body fat within a period of only a few weeks before entering seasonal torpor (Fietz and Ganzhorn, 1999). In turn, such seasonal torpor or hibernation may provide individuals with a fitness advantage in terms of increased reproductive success (Michener, 1992; Kunz et al., 1998). If this is true, it is not surprising that the females' need for large amounts of soluble sugar would exceed that of males, and that they would exercise their dominance over males to obtain those soluble sugars. Indeed, the differential access of females and males to foods with high concentrations of soluble sugars may help to explain the rapid weight gain of pregnant and lactating females, while male weight remains roughly stable. It may also help to explain female weight gain at the beginning of the dry season (i.e., May and June, just prior to entering episodes of torpor and reduced activity) as well as in September, at the end of the dry season and the beginning of the reproductive season.

At Beza Mahafaly, foods providing large amounts of soluble sugar may be very limited, given the limited fruiting schedule of trees. Gums appear to serve the same function as fruits in such highly seasonal habitats. Phenological data at Beza demonstrate the limited availability of fruits in all months (even in November, only 10% of trees in botanical plots in the gallery forest were fruiting, and this value was less than 4% at the spiny forest and Ihazoara; that figure of 4% or less is maintained throughout the rest of the year at all forests; see Chapter 3). Fruits drop precipitously as food resources for mouse lemurs in May, and are not consumed until the commencement of the rainy season

(Chapter 3)] Gums provide an alternative resource with high soluble sugar year-round. It is significant that *Terminalia fatraea*, the tree most favored for exudate consumption at Beza by both males and females, is closely related to a tree that has been shown to have very high soluble sugar content (up to 88%) at Kirindy (see Dammhahn and Kappeler, 2008, on *Terminalia diversipilosa*). The soluble sugar content of *Terminalia fatraea* and other gum-producing trees at Beza Mahafaly should be examined. Exudates can be rich in protein as well, and are rapidly renewable (and thus available throughout the year; see Hladik et al., 1980; Nash, 1986). *Terminalia fatraea* exists in very low frequencies in the gallery forest (where the most important gum trees are *Acacia bellula* and *Rhopalocarpus lucidus*), but is more common in dry and spiny forests, which are the natural habitats of *M. griseorufus* (see Chapter 3).

Génin (2003) reported female dominance in Kirindy mouse lemurs in competition with males for access to gum trees. Female *M. murinus* that were captured close to gum trees were heavier than females captured further away. According to Génin (2003), females prevent males from gaining access to gum trees; the latter gain access to gum trees mostly when females are not in the vicinity. Génin (2003) argued that female priority of access to gum trees explains the tendency of females to cluster in social groups, as well as their tendency to remain anchored to a particular place within the forest, and the tendency for males to disperse farther than females. Each of these tendencies also characterizes mouse lemurs at Beza Mahafaly. I would add that differential access by females and males to gum-producing trees may also explain the sexual differences in male and female hibernation patterns (females enter torpor more than males at Beza Mahafaly) and activity patterns (females are less active than males).

Such differences were not recorded for *M. murinus* by Génin (2003) at Kirindy, but were documented by my earlier study of these animals at this site (Rasoazanabary, 2006). Sexual differences in activity patterns in both *M. murinus* and *M. griseorufus* are also reflected in the differences in relative frequency of capture (males more than females) and the time interval from first to last capture in males and females (females longer than males). A lack of access to those resources that could promote better "anchoring" or fidelity to a particular location (as is observed in females) would instead encourage more "risky" behavior (including wider ranging) in males.

With regard to sexual differences in the selection of sites for nesting, my data demonstrate a preference for tree holes by pregnant females, even during the hot wet season (November and December) when open nests are generally preferred for thermoregulatory reasons. A preference by pregnant females for tree holes over open nests at this time of year can be explained by the imminence of parturition. Mouse lemurs regularly have more than one offspring, and each is born in a relatively helpless state. As has been documented for *M. murinus* in captivity (Martin, 1972; Glatston, 1979), neonates have minimal hair, their abdomens are naked, and their eyes are shut for up to four days after birth. They don't begin to play until they are around 10-13 days old, and don't leave the security of their nest, even for brief periods, until they are 3 weeks old. While they are capable of clinging, they must be transported by the mother in her mouth. Infants are left in their nests while the mother forages at night; to protect their infants against predators, mothers may move their infants (one at a time) from one to another nest. Particularly for very young infants, nests must have with a secure base. Well-built leaf nests may suffice, but the open nests used by mouse lemurs in the sparse forests of

Beza are rarely leaf nests (I saw only one being built), and rarely do open nests have secure bases. The contrast with rain-forest nests is striking here, as mouse lemurs living in rain-forest habitats regularly build secure leaf nests for their neonates. Finding the materials or the locations at which to build a secure but cryptic leaf nest, well hidden from predators, may be more difficult in very dry forests. On the other hand, tree holes may fit the bill.

Pregnant females may prefer tree holes to secure an optimal platform on which to give birth or to hide their helpless young. Young *M. griseorufus* do grow rapidly, and soon may be able to thrive in open nests, according themselves (and their mothers) a thermoregulatory advantage. It would appear that the shift to open nests occurs rapidly during the wet season, as it is only pregnant females that show a statistical preference for tree holes at this time of year. Indeed, I did observe older infants who were less likely to fall, and their lactating mothers, in open nests.

Establishing networks of friendly females may be another reason for pregnant females to aggregate around spacious tree holes. Whereas I could not confirm allomothering for wild *M. griseorufus*, allomothering (females grooming and nursing infants that are not their own) has been documented in captive *M. murinus* (Eberle and Kappeler, 2004, 2006).

In their study of *Microcebus murinus* at Kirindy, Kraus et al. (2008) documented higher male mortality than female mortality during the reproductive season (when males need to roam further to gain access to more anchored females). Kraus et al. (2008) interpreted differences in adult male and female mortality as an indication of better access by females to safer sleeping sites (see also Radespiel et al., 1998). It is not clear to me that tree holes are safer than open nests; however, it is clear that they are preferred by females for restricted periods of time during the reproductive season, likely because they accord a safe platform for parturition and for the nurturing of very young infants.

4.4.2 Interpreting differences in activity patterns for males and females: Why do females of some species enter seasonal torpor, while others do not?

Variation in patterns of hibernation among male and female mouse lemurs has been well documented, but interpreting this variation has been difficult. In some species, both males and females enter seasonal torpor, although often to different degrees, with females tending to enter torpor more often and for longer periods than males. In others, neither sex does. This variation does not correspond to the seasonality of the habitats; indeed, sympatric species (species living in the same forests) may show opposite patterns, and populations of the same species may show opposite patterns in different forests. Sexual variation in torpor is sometimes documented not through direct evidence of different physiological states, but through the study of sexual differences in activity patterns (as inferred through capture-recapture studies, or focal individual sampling).

Mouse lemurs are able to maintain a stable energy balance in any season, either through torpor (and concomitant reduction in energy intake) or through seasonally-appropriate weight loss (involving both fat and fat-free tissues; Giroud et al., 2010). Because mouse lemurs need to attain a minimum body mass before entering hibernation (Schmid, 1997), immature individuals along with underweight adults must remain active until they do so (Fietz, 1998; Schmid, 1997). Individuals that remain active during the season of scarce resources (i.e., the austral dry winter) must compete for those resources, and they may simply lose weight. Entering periods of prolonged torpor is advantageous, as there may be a correlation between seasonal torpor and reproductive success (see Michener, 1992, on ground squirrels; see also Schmid and Kappeler, 1998 on mouse lemurs). Mouse lemurs may enter bouts of torpor lasting only a few weeks or lasting several months (i.e., throughout the dry season) with periodic arousals. Giroud et al. (2010) discuss the physiological advantages of torpor in adult male *M. murinus* using data collected in captivity.

My study found seasonal fluctuation in sex ratios of captured individual *M. griseorufus* at Beza Mahafaly, with female bias in October, November, January, February, and April, roughly equal sex ratios in May and September, and male-bias during the dry season, from June to August. (Samples were insufficient to test capture sex ratios in December and March.) Individual male *M. griseorufus* at Beza Mahafaly were more likely to be captured during the dry season (non-reproductive season), whereas females were more likely to be captured during the rainy season (reproductive season). The same condition was also found in *M. griseorufus* at Berenty in southern Madagascar (Génin, 2008), *M. murinus* at Kirindy in western Madagascar (Fietz, 1998; Rasoazanabary, 2006), and *M. rufus* at Ranomafana in eastern Madagascar (Harcourt, 1987; Atsalis, 1999b) as well as Mantadia, also in eastern Madagascar (Randrianambinina et al., 2003). At each of these sites, the capture sex ratio was highly male-biased during the months of June, July, and August, suggesting greater torpor in females than in males. More direct physiological research and/or focal individual sampling confirmed this pattern for *M. murinus* at Kirindy (Schmid and Kappeler, 1998; Ganzhorn and Schmid, 1998; Schmid, 1999; Schmid et al., 2000; Rasoazanabary, 2006), and for *M. griseorufus* at Beza Mahafaly (this study).

In sharp contrast, capture data confirmed a balanced sex ratio during the dry season in both *M. ravelobensis* and *M. murinus* at Ampijoroa, NW Madagascar (Radespiel et al., 1998; Schmelting, 2000; Schmelting et al., 2000; Lutermann, 2001; Randrianambinina, 2001; Reimann and Zimmermann, 2002; Randrianambinina et al., 2003; Lutermann et al., 2010). Indeed, there were more females captured than males during the 1998 dry season, but there was no indication of hibernation for either males or females, both of which remained active throughout the dry season. A similar pattern was observed for *M. berthae* at Kirindy (Ortmann et al., 1996, 1997; Schmid et al., 2000; Dammhahn and Kappeler, 2008a).

Interpretations have been varied. Schmid and Kappeler (1998) offered a behavioral explanation for the observed greater male than female activity in *M. murinus* at Kirindy during the dry season – i.e., that males (presumably the larger-bodied individuals with greater competitive advantage for access to females) need more "active" time to position themselves near the best females for the upcoming reproductive season. The implication is that more active males will have the higher reproductive success. I took issue with this explanation (Rasoazanabary, 2006), as I found no relationship between male body mass or activity levels and the ability of males at Kirindy to position themselves near nests with desirable adult females. Other explanations for the sexual differences in activity levels and for differences among species or populations must be sought. The pattern of variation does not appear to reflect seasonality, as mouse lemurs in the wettest and driest sites in Madagascar can exhibit similar tendencies for females to enter prolonged torpor, and mouse lemur species at the same site may exhibit different patterns. Instead, differential seasonal torpor in males and females, as well as differences in the existence of seasonal torpor in different species or populations of mouse lemurs, may reflect differences in their ability to attain the fat reserves needed to sustain torpor.

Table 4.11 summarizes the available data, and strongly suggests that the pattern reflects variation in diet, and not seasonality or variation in the intensity of male reproductive competition for females. Mouse lemurs whose primary dietary resource is rich in soluble sugars (fruit or gums) are able to enter seasonal torpor, while those relying primarily on insects or insect secretions (foods that are high in protein but not soluble sugars) cannot.

Table 4.11: Relationship between food items and seasonal torpor in female mouse lemurs.

Species	Site	Seasonal torpor for females?	Primary dietary resource	Rainfall seasonality
M. griseorufus	Beza Mahafaly	Yes[16]	Gums[16]	Very strong[25, 26]
M. rufus	Ranomafana	Yes[1]	Fruit[1]	Weak[25, 26]
M. murinus	Kirindy	Yes[5, 15, 21, 22, 23]	Fruit[2, 3, 4]	Strong[25, 26]
M. murinus	Mandena	Yes[24]	Fruit[6]	Weak[25, 26]
M. murinus	Ampijoroa	No[7, 8, 11, 13, 14, 17, 18, 19]	Insect secretions[12, 17, 19]	Moderate[25, 26]
M. ravelobensis	Ampijoroa	No[7, 8,11, 13, 14, 17, 18, 19]	Insect secretions[12, 17, 19]	Moderate[25, 26]
M. berthae	Kirindy	No[2, 9, 10, 20]	Insect secretions[2, 3, 4]	Strong[25, 26]

[1] Atsalis (1999)
[2] Dammhahn and Kappeler (2008a)
[3] Dammhahn and Kappeler (2008b)
[4] Dammhahn and Kappeler, (2009)
[5] Ganzhorn and Schmid (1998)
[6] Lahann (2007)
[7] Lutermann (2001)
[8] Lutermann et al. (2010)
[9] Ortmann et al. (1996)
[10] Ortmann et al. (1997)
[11] Radespiel et al. (1998)
[12] Radespiel et al. (2006)
[13] Randrianambinina (2001)
[14] Randrianambinina et al. (2003)
[15] Rasoazanabary (2006)
[16] Rasoazanabary (this study)
[17] Reimann and Zimmermann (2002)
[18] Schmelting (2000)
[19] Schmelting et al. (2000)
[20] Schmid (1996)
[21] Schmid and Kappeler (1998)
[22] Schmid (1999)
[23] Schmid et al. (2000)
[24] Schmid and Ganzhorn (2009)
[25] Muldoon and Goodman (2010)
[26] Kamilar and Muldoon (2010)

4.4.3 Interpreting sexual differences in body mass.

The literature paints a somewhat confusing picture of body size dimorphism in cheirogaleids. Reverse skull length dimorphism has been reported in several species. Jenkins and Albrecht (1991) found reverse dimorphism in skull length for male and female *M. griseorufus* (called *M. murinus*) at Amboasary (southern Madagascar). For a sample of 97 females and 96 males, females averaged 0.6 mm (or 1.9%) larger (t test 4.91, $p < 0.001$). This result matched mine; I did find significant differences between skull lengths of adult male and female *M. griseorufus* at Beza Mahafaly, although the differences were not consistent across all forests, and they were not as strong as the differences in canine height.

In his study of captive *M. murinus* at Duke University, Kappeler (1991) found significant reverse dimorphism in body mass (33 adult males and 27 non-pregnant adult females; $p < 0.001$). The problem here is that captive individuals tend to gain weight in a manner different from that of their wild counterparts, and the mean weights for both males (90 g) and females (109 g) are high. Kappeler did succeed in showing that the body mass dimorphism pattern in lemurs is distinctly different from that of lorisids and galagids, which tend to have males larger than females.

Other researchers have concluded that neither regular nor reverse body size dimorphism characterizes cheirogaleids. Fietz (1998) reported a lack of sexual dimorphism in body mass, head length, and other body measurements in *M. murinus* at Kirindy. Schmid and Kappeler (1998) attempted to resolve conflicting signals when they reported what they dubbed "fluctuating dimorphism" in the same population of mouse lemurs from Kirindy. In effect, they said, females are heavier than males at the end of the rainy season, just before hibernation, while males are heavier than females at the end of the dry season – i.e., just before the mating season. Wrogemann et al. (2001) reported a different pattern for captive *M. rufus* and *M. murinus*. Females were heavier than males during the breeding season, but there were no significant differences between adult males and non-pregnant adult females at other times of year.

My study found no differences in body mass between adult males and non-pregnant adult females at Beza Mahafaly, in a year-long comparison. Nor did we find a convincing pattern of "fluctuating" dimorphism, despite significant differences in the activity patterns of males and females. Specifically, during the months of September and October, males were not statistically significantly heavier than females. We did observe a small seasonal shift, with males being slightly (but statistically significantly) heavier than *non-pregnant or lactating females* when the comparison is made across the entire rainy season, when most females are indeed pregnant or lactating. There was no body mass difference between males and females captured (and thus active) during the dry season. Those non-pregnant and non-lactating females that were captured during the rainy season were actually captured at the beginning of the rainy season, and thus just after the season of scarce resources; thus, in this comparison, males captured during the entire rainy season are being compared to females captured at the beginning of the rainy season. Most females gain weight rapidly during the rainy season and become pregnant. Data on the reproductive success of individual males are needed to ascertain whether body size confers any reproductive advantage, but it is clear that females remain dominant over males at all times of the year.

How can these data be interpreted? In a comparative study of dental and cranial dimensions in strepsirrhine species, Kappeler (1996) attempted to interpret variation in the degree of dimorphism within the framework of sexual selection. He concluded that such models do not apply. He found no correlation between the degree of canine dimorphism and female body mass, and no correlation between canine dimorphism and mating system. Strepsirrhines fail to fit the predictive models of sexual selection theory with regard to intrasexual competition among males.

However, in interpreting the pattern of body mass dimorphism in wild *M. murinus*, Schmid and Kappeler (1998) did resort to sexual selection theory. Whereas females might need to be bigger than males prior to hibernation, the real test of sexual selection theory, they claimed, comes at the beginning of the mating season, when males are heavier than females. Presumably large-bodied males would gain a reproductive advantage in male-male competition for mates (Schmid and Kappeler, 1998). Unfortunately, when, in working at Kirindy, I examined male body mass fluctuation using paired t-tests for the same males weighed in different seasons, I found no weight gain at the beginning of the mating season (Rasoazanabary, 2006). I also failed to find any indication that large or active males could position themselves favorably with respect to nesting females.

In adult males at Beza Mahafaly, I found no significant correlation between body mass and canine height ($r = 0.15$, NS, $n = 117$). It would be necessary to run paternity tests to determine whether either large bodies or tall canines accord reproductive success in male mouse lemurs, but I stress that there is no evidence that they do. Among adult females, body mass increases markedly during pregnancy and lactation. If females with large canines have greater reproductive success than females with smaller canines, then we might expect a correlation between canine height and body mass in adult females. In fact, there is a significant correlation between log body mass and log (left) canine height in adult females at Beza Mahafaly ($r = 0.56$, $p < 0.001$, $n = 83$). This correlation may simply reflect a tendency for first-year cohort females (whose canines may not be fully erupted) to have a higher abortion rate or a higher rate of conception failure than older females. It is that body mass by itself accords any advantage to non-pregnant females in contests with males over food or nesting sites, as non-pregnant adult females are not heavier than adult males.

4.5 Conclusions

My results suggest that strong canine dimorphism in *M. griseorufus* is correlated with priority of access by females to preferred resources. “Preferred” resources can be flexible; tree holes may be preferred for different reasons at different times of the year, but access by adult females to the “right” gum trees, or the “right” tree holes at particular times of year may impact reproductive success. The fact that reverse canine dimorphism of the strength documented here has never before been reported for mouse lemurs may reflect real differences between *M. griseorufus* and other mouse lemurs, or a failure to test canine dimorphism on wild populations with proper controls for age and geographic variation. I hypothesize that, among lemurs in general, reverse canine dimorphism will have the greatest selective advantage in small-bodied species with the shortest life spans – i.e., those living in the most seasonal habitats with the highest predation pressure and adult mortality. This is a pattern that is very different from that observed in species with strong “regular” canine dimorphism, and that is not correlated with body mass dimorphism.

A broad comparison of patterns of seasonal torpor in mouse lemurs reveals a fascinating correlation between torpor and diet. It appears that sexual differences in access to soluble sugar-rich foods may explain the sexual differences in seasonal torpor frequency and activity levels of male and female mouse lemurs across the island of Madagascar. Female dominance and priority of access to sugar-rich foods may play an important role, but only mouse lemurs (species or populations) that target such foods and only individuals that succeed in obtaining sufficient quantities to build up fat reserves will enter seasonal torpor at all.

CHAPTER 5

BEHAVIORAL RESPONSES OF *M. GRISEORUFUS* TO HUMAN DISTURBANCE, HUMAN RESPONSES TO TOP-DOWN CONSERVATION POLICIES, AND CONSERVATION IMPLICATIONS FOR BEZA MAHAFALY, SW MADAGASCAR

5.1. Introduction

The title of this dissertation is “The human factor in mouse lemur conservation: resource utilization and habitat disturbance at Beza Mahafaly, southwest Madagascar,” which is the subject of this chapter. Thus far, we have examined the reproductive profiles and population dynamics of mouse lemurs of Beza Mahafaly in comparison to mouse lemurs elsewhere (Chapter 2), differences among mouse lemurs in three forests at Beza Mahafaly, with a focus on how those differences reflect basic differences in habitat characteristics, plant species representation and phenology (Chapter 3), and differences in the behavior of males and females, with a focus on the consequences of female dominance (Chapter 4). In this chapter, I draw from and expand upon earlier observations to examine mouse lemurs again within the context of differences across habitats, but now with a special focus on habitat differences in signs of human disturbance. I also examine temporal shifts in mouse lemur population dynamics, again within the context of human disturbance, specifically to address the question of the long term health of the mouse lemur populations. Finally I examine the humans themselves – their beliefs, behavior, and specifically their responses to conservation policies.

We know that the three forests have different vegetation and that mouse lemurs in the three forests have different behavioral and population profiles. Two of the forests, the spiny forest and Ihazoara, were shown in Chapter 3 to have similar plant species and phenological patterns, while the third forest, the gallery forest, was quite distinct. Of the three, the gallery forest is most protected, Ihazoara is unprotected, and the spiny forest is protected in name but not nearly as much in practice as the gallery forest. In order to determine whether the differences in mouse lemur behavior and population dynamics are influenced by human disturbance, we need to quantify the degree to which each forest suffers from human disturbance. On the basis of this information, we can examine the relationship between population and behavioral profiles on the one hand, and disturbance levels on the other. We can also examine temporal changes in mouse lemur population dynamics from 2003 to 2007, to determine whether there is a secular trend indicative of increased disturbance, or whether one forest appears to be changing more than the others. *This, then, is the first major goal of this chapter.* First I document forest disturbance levels, using transect walks, and scoring evidence of human activities (including the presence of domesticated animals). Then I ask: Are the differences in mouse lemur population dynamics and behavior across forests best explained by habitat similarities and differences, or by differences in the degree of habitat disturbance? In particular, I identify those differences in mouse lemur behavior that are best explained by variation in habitat disturbance levels. Finally I ask: Is there evidence that mouse lemur populations at Beza have been suffering increased threats over time? Here I examine changes in mouse lemur capture success rates over the period of my extended study, from 2003 to 2007.

The second component of this chapter focuses on human attitudes toward conservation. My purpose here was to explore not merely how human behavior impacts lemurs, but how conservation practices impact people. I examined the dynamics of interactions between villagers and conservationists. To document the attitudes of local villagers, I used a combination of participant observation and informal interviews. I interviewed people living in six villages both near to and far from protected areas. I wanted to determine how literacy or education influences attitudes toward conservation, as well as how far people walk to use resources in protected forests. I also wanted to ascertain whether adults and children differ in their attitudes toward conservation, and to determine the influence of conservation education. Effectively, I wanted to document barriers to conservation success and to the longterm health and survival of the local people.

The three forest habitats at Beza Mahafaly exhibit different degrees of protection: the gallery forest (BMSR Parcel 1) is the most protected; the spiny forest (BMSR Parcel 2) is protected, but less regulated; and the dry deciduous forest of Ihazoara is unprotected (Rasoazanabary, 2004). The two parcels belonging to the reserve are connected by a dry deciduous transitional forest, and the protected forest parcels are separated by a distance of ~7 km. The gallery forest is well monitored because it is adjacent to the research camp, where foreign researchers and conservationists are likely to camp, and because it is small in area, and thus easy to monitor. The spiny forest is almost two hours from the research camp by foot. Futhermore, the spiny forest is much larger than the gallery forest, and thus less easily managed.

5.2 Methods

5.2.1 Human disturbance in forest habitats

To document human disturbance intensity, my assistants and I conducted surveys of human activities inside the three forest habitats during the 2006-07 intensive research period. Each week, we conducted one transect walk of 1 km length in each forest. We varied the time of day but no transect walks were made at night. Signs of human presence (sight or sound), of humans engaging in specific activities (collecting food resources, smoking out bees to collect honey, hunting, herding cattle, clear-cutting vegetation, cutting individual trees), and/or the presence of domesticated animals (e.g., cattle or zebu fecal matter or footprints) were recorded. Initially, we thought we might see rats or domesticated dogs, but these were never observed on our transect walks. "Disturbance" (presence/absence) was recorded as 0 (no disturbance for the entire kilometer-long transect walk) or 1 (any sort of disturbance occurring anywhere along the transect). Type of human activity was recorded, as was disturbance *intensity* for human activities. The latter was coded as follows: 1 = low, including humans observed but inactive, or hiding; 2 = moderately low, or collecting fruit or roots of individual plants; 3 = moderately high, including hunting or smoking out bees to collect honey; 4 = high, including herding cattle; and 5 = very high, including felling individual trees. In total, 150 human disturbance surveys were conducted (50 in each forest), 78 during the rainy season and 72 during the dry season.

During the earlier years (2003 – 2005), I did not conduct systematic surveys of human disturbance. However, I did record human activities opportunistically, and some of these observations have been published (Rasoazanabary, 2004).

5.2.2 Mouse lemur population dynamics and behavior

The data used here were described in Chapters 2, 3, and 4, and methodological details are presented in the relevant chapters. I use mouse lemur c*apture-recapture* data (Chapter 2) collected in 2003/04 and 2006-07 to measure monthly capture success rates and to estimate relative rates of population turnover. To make statistical comparisons of monthly capture success rates, I divided the time I spent at Beza into two research periods: “Period 1” (comprising a total of 9 months, from 2003 to 2004) and “Period 2” (comprising a total of 12 months, from 2006 to 2007). The data that were collected in 2005 were excluded here because they were too sparse (there were many fewer traps set in 2005 than in other years) and all forests were not equally sampled. In addition to analyzing variation in capture success rates, I examined individual capture intervals (from first to last capture) across sites to estimate longevity. Data for individuals from the spiny and gallery forests have already been presented (Chapters 2 and 4); here I add data from the unprotected forest, Ihazoara. To document variation in mouse lemur behavior that may be related to disturbance levels, I used focal individual sampling data collected in 2006-07 and described in Chapters 3 and 4. Specifically, here, I compare gum consumption (Chapter 3), the use of tree holes for nesting (Chapters 3 and 4), and activity patterns by mouse lemurs in the three forests (Chapter 4).

5.2.3 Human attitudes toward conservation

5.2.3.1 Participant observation

Local villager attitudes towards conservation (i.e., the restrictions placed on their access to forests as well as the presence of both Malagasy and foreign conservationists in the forests) were assessed in two ways. First, and most important, I was able to understand the attitudes of villagers as a direct observer, living over a period of 22 months (during the period from 2003 to 2007) in a tent at the research camp bordering the gallery forest. Because I am Malagasy, I had little difficulty understanding the local dialect. Also because I am Malagasy (but not a member of the local Mahafaly ethnic group), I was treated differently than foreigners (not always for the better). Over the years, I developed friendships with both children and adults who became my principal "informants" (Appendix H). By hiring some local people as research assistants, I could spend extra time with them, sharing experiences informally after the work-night or work-day was over. Some assistants were entrusted with collecting data for my project during a two-month period in 2005 when I couldn't be present; for some people, being a research assistant not merely provided income but also prestige. I was also a member of the research staff at the reserve, and thus could spend time with other researchers and reserve staff administrators. I was charged with organizing Earth Day celebrations in 2003 and 2007, and through this process, I developed special relationships with school teachers and local school children. I could observe interactions between the administrators (none of whom belonged to the Mahafaly ethnic group) and the local people, including the local hired helpers (e.g., the camp cook, the guides). A requirement that applies to any researcher in Madagascar (foreign or Malagasy) is that he or she hire and train at least one graduate student from the University of Antananarivo. Thus, I also had with me a Malagasy student belonging to an ethnic group other than Mahafaly. The Mahafaly people of the region of Beza Mahafaly would come into contact with many "foreigners" – both Malagasy and "vahaza" (usually = white foreigners), and it was thus possible to observe their reactions. In other words, I obtained important information through classic ethnographic participant observation. In this context, the following observations are methodologically important:

1. Whether working at the gallery forest, spiny forest, or Ihazoara, I was in close contact with two local assistants and my cooks. Each assistant lived in his or her own tent (provided by me), but we talked whenever possible. Sometimes the cooks did not require tents as they had other local accommodations, but even then, sometimes they would remain with the rest of the group during "down" time. It was not hard to notice that my assistants would not share information as readily when living at the gallery forest research camp vs. the other two forests. In other words, when we worked at the gallery forest, local assistants (especially newly-hired ones) did not feel free to express themselves (likely because the reserve administrators might be nearby). In contrast, when we worked at the spiny and Ihazoara forests, local assistants expressed their feelings and reported other people's feelings much more freely.
2. Annual Earth Day events, mandated and organized by ANGAP (Association Nationale pour la Géstion des Aires Protegées à Madagascar), are part of the plan for raising the conservation consciousness of local people and involving school children in conservation activities. My collaboration with the ANGAP staff

allowed me to contribute to the process of planning this event and in its realization at the research camp site. In 2003, only teachers from Mahazoarivo brought their school children to the camp for this event, but they brought all of the children at this school (~ 100). In 2007, teachers from the Ambinda, Mahazoarivo, and Analafaly schools selected their top five students (5 from each class from each school, totaling ~ 50) to participate in this event.

3. While I was at Beza, the ANGAP staff organized two events featuring reforestation, specifically to plant *Alluaudia* cuttings. Many local villagers were invited to these events, which involved dancing and feasting on rice and a sacrificed goat, as well as planting the trees. Most of the local people who participated were from two of the nearest villages – Mahazoarivo and Analafaly (about 30 minutes away from the camp, by foot). My assistants and I participated in this activity.
4. In December, 2006, I donated accessories to the local schools. On three occasions during the year 2006-2007, my assistants and I were invited to come to the schools to teach about conservation.
5. Some of my encounters with local villagers were on the road. A main road (for people walking and for zebu carts) connects the three forests in which I conducted my research. Whenever I met someone on the road, I would stop to talk.
6. I also had opportunities to talk with local people during my half dozen trips (during the year 2006-2007) by zebu taxi to Betioky or Beavoha (for market days). During these trips I would often meet people I hadn't met during my interview visits to villages.

7. A few families invited me to their homes for family ceremony events (e.g., celebrating a new birth).
8. I also talked with local villagers who came to the camp as vendors to sell some food, such as chickens, eggs, milk, tomatoes, etc. Occasionally, local villagers came to the camp bringing foods such as corn or sweet potatoes as gifts.

These interactions enabled me to obtain information regarding how local people felt about conservation policies, their own disempowerment, their livelihoods, and their welfare, entirely independently of (and likely more openly and honestly than) information that I gleaned more formally through interviews, described below. In reporting conversations with reserve personnel and with villagers, I assigned people false names to maintain their anonymity. A list (with pseudonyms, sex, village affiliation, and relationship with me) is provided in Appendix I.

5.2.3.2. Human attitude questionnaires

I also obtained systematic information regarding local villagers' attitudes toward conservation from informal interviews. Once every month, I visited three villages. Thus, each of the six villages in my study was visited 5 or 6 times during the year. Two local assistants, either from the village being visited or from a friendly neighboring village, accompanied me. All respondents were volunteers, many of whom simply came to see us when we arrived at their village out of curiosity. Respondents were never paid directly; however, the village elders were rewarded with sugar and coffee. The purpose of my study was explained to each respondent, and their anonymity was guaranteed. Nobody was asked to complete a written questionnaire (this would have been impossible given the high rate of illiteracy); rather we sat and talked and my assistants and I asked questions informally, using a questionnaire that we had constructed to generate questions (posed in any order). A copy of the questionnaire is provided in Appendix H. The three of us recorded answers to targeted questions, and compared notes after each interview. Generally, we spent over an hour with each person, and we were able to interview around 6 people per visit to any village.

We selected the following six villages located in the vicinity of BMSR: Ambinda, Ampitanabo, Analafaly, Antaolambiby, Ihazoara, and Mahazoarivo (see Figure 1.3 for locations). Interviews were conducted either early in the morning (before the beginning of the regular work day) or at the end of the day when they returned from their work. The number of people interviewed in each village was not constant. While we tried to interview as many people as possible, we couldn't control the exact numbers. We did try to interview children as well as adults. The total numbers of adults and children interviewed at each village were as follows: Adults – Ambinda, 22; Ampitanabo, 26; Analafaly, 20; Antaolambiby, 12; Ihazoara, 12; and Mahazoarivo, 19; Children – Ambinda, 20; Ampitanabo, 24; Analafaly, 24; Antaolambiby, 1; Ihazoara, 13; and Mahazoarivo, 24. Approximately 25% of interviews were conducted entirely by my local assistants, to ensure that the local people would feel comfortable with the process.

5.2.4 Statistical analysis

I utilized the chi square (χ^2) test to analyze variation in the frequency of different types of human activity across sites (including the presence or absence of signs of human disturbance for any single transect). Disturbance intensity was coded from 0 to 5 as follows: 0 = no sign of human disturbance, 1 = low (people hiding), 2 = moderately low (collecting plant food or hunting animals), 3 = moderately high (smoking out bees to collect honey), 4 = high (herding cattle), and 5 = very high (felling trees for wood). Student t-tests were used to analyze the difference in disturbance intensity between protected and unprotected forests. Monthly mouse lemur capture success rates (number of individuals captured divided by number of traps set) were analyzed using ANOVA and Student t-tests to compare the three sites treated individually or as protected vs. unprotected forests. I also examined changes in capture success rates from 2003-2004 to 2006-2007. Captures made during the year 2005 were omitted from this analysis because the three sites were not sampled evenly and because the data for this year were sparse. Chi square was also used to investigate the stated attitudes of villagers towards local conservation practices, particularly to capture differences between adults and children with and without exposure to conservation education.

5.3 Results

5.3.1 Human disturbance in forest habitats

Of 100 transects within protected forests in the reserve itself, 72% showed signs of human disturbance (i.e., disturbance "present"). Of the 50 transects within the unprotected forest at Ihazoara, 100% showed signs of human disturbance. A chi square test of the difference in frequencies of disturbance in protected and unprotected forests was highly significant ($\chi^2 = 17.21$, df = 1, $p < 0.001$; Table 5.1), as was a test of the significance of differences across forest sites ($\chi^2 = 18.55$, df = 2, $p < 0.001$). The forests within the reserve showed similar percentages of transects with disturbance: 74 % in the gallery and 68% in the spiny forest, but both protected forests showed considerably less disturbance than did Ihazoara.

Table 5.1: Presence or absence of disturbance recorded during the entire 150 transects.

Protection	Presence of disturbance		Total
	Absence	Presence	
Unprotected	0	50	50
Protected	28	72	100
Total	28	122	150

Disturbance was always recorded at Ihazoara in part because zebu fecal matter and footprints were always present and observed on transect walks. Surprisingly, zebu fecal matter and footprints were also commonly observed in protected forests (Figure 5.1).

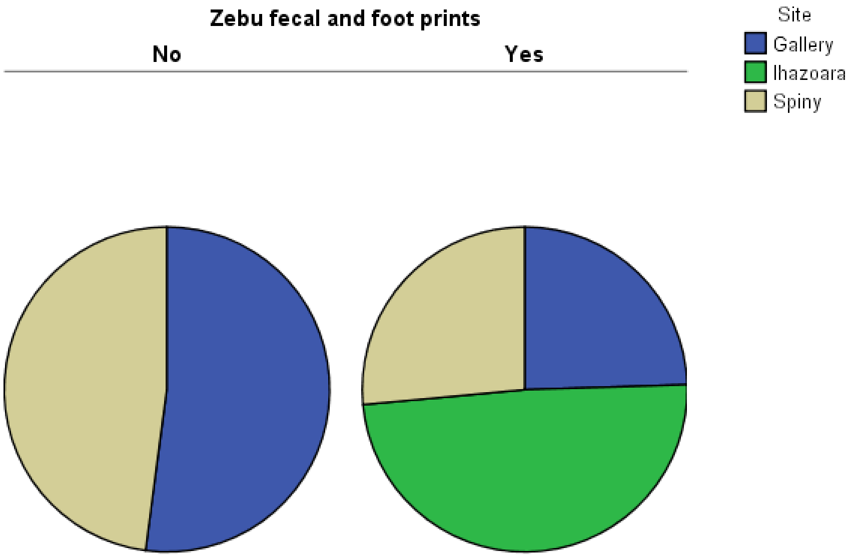


Figure 5.1: Presence or absence of zebu fecal matter or footprints recorded on transect walks in the three forests (% of total "no" and "yes" records for each forest). Note that at Ihazoara, zebu traces were always recorded.

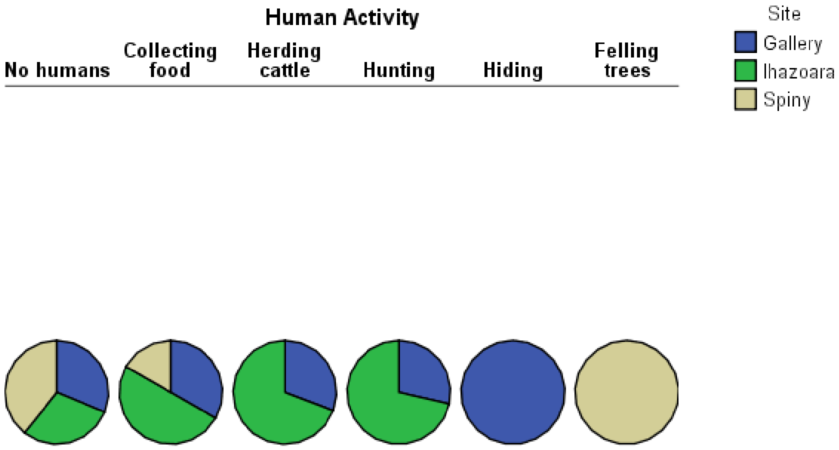


Figure 5.2: Pie chart showing observations of human activities (in % of each activity in each forest) during transect walks.

Specific human activities in the forests differed across sites ($\chi^2 = 41.65$, df = 10, $p < 0.001$; Figure 5.2). For example, all instances of humans hiding were observed in the gallery forest, where enforcement of forest access restrictions is greatest, and all instances of felling trees were observed in the spiny forest, where the preferred tree for market sale, *Alluaudia procera*, is most abundant.

Figure 5.3 shows mean disturbance intensity (scored on a 5-point scale as described in the Methods) across forests by month. Because we conducted one transect walk per week in every forest, monthly means were based on 4 samples. Disturbance intensity was greatest during the dry season, when resources were scarce, and the human need great. Mean disturbance intensity was significantly higher in the unprotected forest of Ihazoara (1.14 ± 1.67) than in the protected forests (0.53 ± 1.39) (t = 2.23, df = 84, $p <$

0.05), despite the fact that felling trees (the activity with the highest disturbance score) was only observed in one of the protected forests, the spiny forest. Ihazoara (and to a lesser extent, the gallery forest) was found to be disturbed throughout the year, while disturbance was much more seasonal (dry season only) in the spiny forest (Figure 5.3). Felling of large trees does occur during the wet season in the spiny forest, however, as long as reserve personnel are not present (I observed this during a brief return trip to Beza Mahafaly in January of 2009; Figure 5.4).

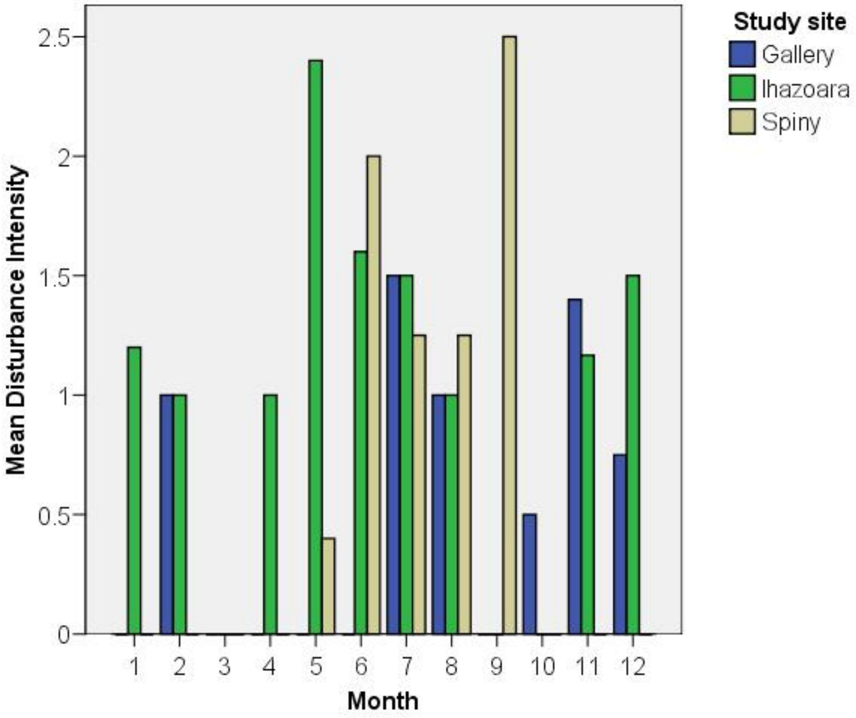


Figure 5.3: Mean disturbance intensity (each transect scored 0 to 5) at Beza Mahafaly by month (average of 4 transects each month) and by site.

Figure 5.4: Top) Remnants of a single *Alluaudia procera* tree in the spiny forest, felled by local people, wet season. Bottom) Boards of *Alluaudia procera* from the spiny forest being transported to the weekly market in Betioky during the dry season. Photo credits: Emilienne Rasoazanabary (top 2009, bottom 2007).

5.3.2 Mouse lemur population dynamics and behavior

5.3.2.1 Mouse lemur population dynamics

A total of 435 mouse lemur individuals were captured between the years 2003 and 2007, 164 in the gallery forest, 153 in the spiny forest, and 118 at Ihazoara. Capture success at all three sites was very low (an order of magnitude lower, for example, than capture success for *Microcebus rufus* at Ranomafana), but on average lower at Ihazoara than at either of the protected sites. Thus, the mean monthly capture success rate for mouse lemurs at Ranomafana was 0.23 ± 0.13 for 17 months, while the mean monthly capture success rate for mouse lemurs at Beza Mahafaly was 0.02 ± 0.02 for 70 months. Overall monthly capture success was 0.016 at Ihazoara and 0.02 at each of the other forests. These numbers change little when the data for 2005 are excluded; mean monthly capture success at Ihazoara drops to 0.015, while the means for the other two forests remain 0.02. Population turnover was inferred to be very high at all three forests. More than 88% (N = 386) of mouse lemur individuals were captured only once. The number of individuals captured more than once was 23 in the gallery forest and 20 in the spiny forest, but only 6 at Ihazora (see Chapter 2, Table 2.3).

I found that the mean intervals (in days) between the first and last capture date differed in protected and unprotected forests (t = 2.88; df = 367; *p* = 0.004). The populations of *M. griseorufus* in the protected (gallery and spiny) forests have the longest intervals (with the mean for the gallery forest being 95.0 days and that for the spiny forest 92.7 days) while that of the unprotected forest at Ihazoara is 51.5 days. Only three individuals, including one male (ID 0658-5DF4) and two females (ID 063B-EBF, ID 063B-37AA) have a maximum interval from first to last capture exceeding 500 days (see

Table 5.2). Comparative data for the spiny and gallery *M. griseorufus* populations are presented in Table 4.3.

Table 5.2: Individuals with intervals from first to last capture date exceeding 500 days at Ihazoara

ID	Body mass (g)	Sex	First capture date	Estimated age at first capture	Interval between first to last (days)	Minimum longevity in days	Minimum longevity in years
063B-E7AA	49	Female	5/5/2003	17 months	520	1030	2.82
063B-EBF2	39	Female	5/6/2003	5 months	522	673	1.84
0658-5DF4	36.5	Male	4/24/2005	4 months	546	669	1.83

My data document temporal changes in capture success over the years during which I conducted my research (2003-2007) (Table 5.3). Apparent demographic changes can be observed most clearly when the data are divided into two periods (2003-2004 vs. 2006-2007), as described in the Methods. Monthly mean capture success rate (mean number of successful captures per trap set) in the spiny forest differed significantly by period, being significantly higher in Period 1 (0.034) than Period 2 (0.010). Whereas capture success at Ihazoara did not change significantly from Period 1 (0.023) to Period 2 (0.010), the direction of change and the resulting capture success rate in Period 2 was as in the spiny forest. In contrast, capture success changed little in the gallery forest (0.021 in Period 1 and 0.019 in Period 2). This may mean that the population of *M. griseorufus* in the gallery forest was stable over this time, but more data need to be collected to corroborate this. Interestingly, during Period 1, capture success was highest in the spiny forest, while during Period 2, it was highest in the gallery forest.

Table 5.3: Mean monthly capture success rates for two periods at the three forest sites

Forest	Period	# Months	Mean ± SD	t-test
Spiny forest	1	9	0.034 ± 0.022	t = 2.96, df = 18; p < 0.01
BMSR	2	12	0.010 ± 0.013	
Ihazoara	1	9	0.023 ± 0.019	t = 2.02, df = 19; p = 0.057
Near BMSR	2	12	0.010 ± 0.012	
Gallery forest	1	9	0.021 ± 0.015	t = 0.11, df =19; NS
BMSR	2	12	0.019 ± 0.030	

5.3.2.2 Mouse lemur behavioral data (focal individual sampling)

M. griseorufus consume gums year round. They fed on 40 gum-producing tree species. I found a significant difference in the number of gum-producing tree species fed upon by mouse lemurs among the three forests ($\chi^2 = 1379.34$, df = 78, $p < 0.001$): 19 in the gallery forest, 24 in the spiny forest, and 14 at Ihazoara. Year-round gum consumption by focal individuals was lowest in the dry deciduous forest of Ihazoara; site differences in focal individual frequencies for feeding on gums were statistically significant ($\chi^2 = 33.93$, df = 2, $p < 0.001$). The same held for the part of the dry season (May, June, July, and August) when the build-up of fat reserves is critical for the onset of torpor ($\chi^2 = 14.18$, df =2, $p = 0.001$). During this season, gum consumption was 64.8% of focal feeding observations at Ihazoara, but 78.8% of focal feeding observations in the spiny forest, and 79.2% of focal feeding observations in the gallery forest. Insect consumption was 28.9% of the focal feeding observations at Ihazoara, 20.7% of the focal feeding observations in the spiny forest, and 20.1% in the gallery forest.

Tree hole nesting site use by focal individuals differed significantly by forest ($\chi^2 = 135.52$, df = 2, $p < 0.001$). Focal mouse lemurs in the spiny forest were found nesting in tree holes 61.9% of the time, while those in the gallery forests were in tree holes 48.0% of the time, and those at Ihazoara were found in tree holes 36.9% of the time. Tree holes tended to be located close to the ground at Ihazoara, where their residents are vulnerable to predators. Tree holes are favored by mouse lemurs during the dry season (see Chapter 3), but only at the spiny forest were more than 90% of focal individual nesting observations recorded in tree holes. The dry season percentage at Ihazoara is 72.4.

M. griseorufus at Beza Mahafaly are inactive during the dry season (see Chapter 4), but this inactivity differed significantly by site ($\chi^2 = 172.60$, df = 2, $p < 0.001$). During the dry season, focal individuals were found to be inactive in the gallery forest on 27.8% of focal-follow nights. This inactivity level was highest in the spiny forest (33.9% of focal-follow nights), while, at Ihazoara, inactivity was recorded for focal individuals on only 2.3% of focal-follow nights.

5.3.3 Human activities, attitudes and needs

5.3.3.1 General observations

The infrastructure of the BMSR is very simple. Between the years 2003 and 2007, there were three different heads of the reserve (these people generally remained at the reserve during weekends and weekdays, and they lived in the main building, which also provided space for communal dining, a public study room, and a place for social gatherings). They included Jeannicq Randrianarisoa, Ramanantsiory, and Andry William (these are their actual names). There were also five forest agents (two of whom shared a single position). Between 2003 and 2005, three of the five forest agents lived at the research camp, or at least stayed there overnight when on "guard" duty. Beginning in 2006, after a devastating cyclone destroyed some buildings at the camp site, three of the five forest agents moved to different villages (Oavy moved to Mahazoarivo, his actual village of origin; Reiv went with him, while Olev moved to "Antevamena," part of the village of Ambinda). Four of the five forest agents were from the Mahafaly ethnic group; the fifth was Antandroy (from southern Madagascar). Several of the others, while Mahafaly in ethnic origin, were not originally from the Beza Mahafaly region. Oavy and his family were unusually receptive and supportive of me, and they became family to me. Their house inside the camp was destroyed by cyclone Ernest (January 2005).

The heads of the reserve and the forest agents were hired by ANGAP to monitor the forest, enforcing the conservation regulations (entry prohibited), collecting fees from ecotourists and researchers visiting the reserve, and providing security for the tourists, researchers, and reserve staff (including the guides, research assistants, and cook). Inside the camp, there was a "center for training and research" and a "small museum" that were, from 2004 to 2007, headed by the "Director of Scientific Research," Ibrahim Antho Youssouf Jacky (this is his actual name). Jacky obtained his doctorate in 2010 from the University of Toliara for a research project that he conducted while at Beza. Five people from the surrounding villages were employed as permanent research assistants, and they were also responsible for the museum. Generally, these were local people who had special expertise with regard to the local plants or animals; one, for example, was an expert on insects and reptiles (Antsy), another on sifaka and plants (Fiana), another on ring-tailed lemurs (Afane), and another on birds (Sokola). These research assistants helped me to find, train and hire people from the surrounding villages as guides or assistants during my tenure at Beza. Some local people were happy to serve as guides or assistants, because this meant that they would receive a steady income. Indeed, there was sometimes jealousy regarding who got hired and who did not. Sometimes, two local people would share a single job; thus for example two women alternated every two weeks as camp cook. Occasionally, a local man would come to the research camp without seeking compensation, and that person might work for a few weeks in such a manner.

The person would simply "want" to be involved. Such volunteering might establish the helper as reliable, and eventually lead to his employment at the research camp.

The people who work at the reserve are well known to the local people, particularly those living in the villages that are closest to the research camp (Mahazoarivo, Analafaly, and Antenvamena which is a part of Ambinda). Most of the permanent local staff came from these villages. Back at those villages, adults and children alike are familiar with "Antanam-bazaha," which means the "village of the foreigners," and which is the name that local villagers use for the research camp bordering Parcel 1. They are familiar also with the conservation ethic spouted by camp personnel and may express approval when asked. All villagers (literate or not) have a profound knowledge of the plants and animals living in the forest. They all collect plants in the reserve for food or medicine, but they do not hunt lemurs because hunting lemurs is "*fady*" (culturally forbidden) among the Mahafaly. However, they do hunt wild birds and small wild mammals such as tenrecs (especially during the dry season) and they collect cicadas during the rainy season when these insects are plentiful. The economy of the Mahafaly people is dominated by cattle husbandry and by raising corn, cassava, beans, and sweet potatoes, supplemented by wild foods. The cattle comprise the wealth of the people; they are treasured and almost never sold at market. They are sacrificed only for ceremonies, at which time a single cow can feed large families and friends. Chickens are kept in the villages for local consumption. Stealing cattle is lucrative and many children aspire to be cattle thieves (called "dahalo"). At an early age, children who do not attend schools spend their time tending to the family cattle.

Spreading a conservation ethic was a primary goal of the conservation plan proposed for the Beza Mahafaly Special Reserve at its inauguration in 1986 (see Ratsirarson et al., 2001). The latter authors explain the main objective of the conservation program established at the reserve as follows:

> "L'objectif principal du projet n'est pas seulement de maintenir l'unique écosystème et biodiversité du Sud-Ouest de Madagascar en intégrant la conservation et le développement (PCDI) avec la collaboration et la participation des populations locales, mais aussi d'utiliser le site comme centre de formation et de recherché des étudiants et chercheurs nationaux et internationaux." [The main objective of the BMSR project is not merely to preserve the unique ecosystem and biodiversity of southwestern Madagascar under the umbrella of an Integrated Conservation and Development Project (ICDP) with the collaboration and participation of the local populations, but also to utilize the site as a center for education and research by national and international students and professors.]
>
> Ratsirarson et al. (2001: 7)

In principle, then, involvement by the local people was deemed paramount from the beginning, and the success of the BMSR project as a whole depended on that involvement. The goals of the project were to improve local education and development, and to establish a management plan for ecosystem conservation. A conservation ethic was communicated to the local people via radio programs (broadcasted from Betioky, using local villager voices) and to children by school teachers. That ethic was in fact "understood" and "accepted" by some local people, but never entirely supported. The people "understood" the conservation ethic because they knew the local people who were employed at the research camp and who communicated that ethic to them, and because the school children would repeat its basic tenets.

Local villagers might eagerly accept invitations to come to the research camp to participate in conservation events. But Sokola told me that the villagers were often motivated to do so because they believed the event would be fun, and not because they cared about conservation. Sokola stressed that “this includes us, as local assistants.”

In fact, the local people do not embrace the prohibitions that people from other parts of Madagascar and indeed from other countries had established in the name of conservation. Instead, they strongly believe that the forests are theirs – passed down to them by their own ancestors, and stolen by “foreigners” (including Malagasy who belong to other ethnic groups) who have violated their rights by restricting forest use and entry. They cannot accept the notion that they should no longer have free access to Mahafaly forests, particularly when they see foreigners appearing to do exactly that. One of my local assistants, Obad, an adult man from Ambinda, explained this to me, using strong language. *Foreigners are stealing the forests that belong to the people.* The people live with fear of punishment and anger at the audacity of those foreigners. Local people do enter the protected forests, but in the forests they feel uncomfortable, as if they are being forced to hide a bounty that is rightfully theirs in the first place. As Airitife (another assistant from Mahazoarivo) explained to me, *conservation is a luxury that the people cannot truly comprehend.* The concept does not fit within their world view. It “belongs” to the foreigners, while the forests truly “belong” to the people. He added that people cannot disavow their culture, because culture is what they have inherited from their ancestors.

Sometimes local people are driven to register their anger by destroying valuable plants inside or bordering the forests. Destroying plants is not sufficient; this must be done in such a manner that the destruction is obvious – a sign or warning directed at the "vahaza" (or foreigners) who should mind their own business and leave the forests alone. The people might deliberately pick strategic places where the destruction was sure to be noticed. For example, cutting a large tree such that it would block a main road might bring greater discomfort or punishment to foreigners than to the villagers themselves, as foreigners are the only people in the region who might have a vehicle. Local people can walk around the tree; even zebu carts can make a detour around a felled tree, but a vehicle might have to turn back.

Such an incident occurred in July 2005, when people from Antaolambiby felled a couple of big Famata trees (*Euphorbia tirucallii*) and placed them across the road leading to their village. It happened that at that time I was accompanying paleontologist Laurie Godfrey and a biodiversity film crew from the American Museum of Natural History in New York on a short excursion to Antaolambiby. The team wanted to make a film for public display at the museum in New York, featuring a Quaternary subfossil site located adjacent to the village. The site was of interest because the bones of many extinct giant lemurs (*Palaeopropithecus*, *Pachylemur*, *Archaeolemur*, *Megaladapis*, and *Mesopropithecus*) and other extinct mammals (*Cryptoprocta spelea*, *Hippopotamus*, *Plesiorycteropus*) had been found there alongside those of extant species, including sifakas, ring tails, *Lepilemur*, and tenrecs. The site had yielded the oldest evidence of human butchery of extinct lemurs, and the bones found there proved that this region of Madagascar was much richer in wildlife in the recent past than it is today. The film crew was forced to turn back, find a place to park their vehicle, and walk more than 30 minutes to the village. The people from Antaolambiby claimed that the famata trees had fallen in a storm, but it was obvious that they had been deliberately cut. There were rumors that some people from Antaolambiby were angry about conservation policy at the time. In general, the villagers from Antaolambiby were least inclined to abide by conservation restrictions compared to those from other villages, and they were least motivated to attend conservation ceremonies. This may have been because they enjoyed less benefit from the reserve than did people from nearer villages, as very few people from Antaolambiby had ever been employed at the research camp. Employment was a motivating factor, but one that reached few people. Several of my local research assistants (Artabam, Tine, and Soava) stated this directly, i.e., that the people from Antaolambiby might favor conservation policies if and only if they were hired to work at the camp. In the absence of such employment, the people from Antaolambiby actually benefitted more from ignoring the restrictions, as they could more easily hide resources taken from the protected forests in their distant village.

Sometimes "warning" messages would appear for no apparent purpose other than (probably) to register general discontent. For example, at Ihazoara, trees were destroyed near my study area, but not on a path (Figure 5.5). Alternatively, warnings might be placed exactly where resources valuable to people had been extracted, apparently to signal resource ownership. Figure 5.6 shows one such warning in the spiny forest. Here a trail used by researchers was blocked by vines strung across it at about human chest level, knotted at either end. This "barrier" was erected just in front of a place where a *Dolichos fangitse* root was dug out of the ground and traces of it deliberately left to indicate that it had been extracted. The tuberous root of *Dolichos fangitse* is eaten raw by local people. This vine barrier was situated adjacent to another tree that had been tagged by researchers with an identifying ribbon; thus the barrier was sure to be noticed by the foreigners in the forest. It was most likely erected by adults, judging from the dimensions of the vine (especially its diameter and height) and the complexity of the knots.

Figure 5.5: A tree destroyed by people at Ihazoara, located just northeast of my study area. The reason for the destruction was unclear. Photo credit: Emilienne Rasoazanabary, 2007.

Figure 5.6: Warning sign made from two plants in the spiny forest. Two vines were bent over a path and knotted together on either side of it, so that it would bridge the path at approximately chest level. Photo credit: Emilienne Rasoazanabary, 2007.

5.3.3.2 Local resource use within the reserve: The gallery forest

While it could be said that the gallery was the least disturbed of the three forests, it was clearly regularly used by local people. True, no "warnings" were constructed within Parcel 1 while I was at BMSR. However, the barbed-wire fence meant to keep cattle out was repeatedly damaged, particularly that section bordering the road to Mahazoarivo. Most commonly, people would sneak into the reserve during the day to gather food. They were always circumspect when they did so. Once I saw an old lady picking ripe tamarind fruit in the protected gallery forest and collecting it in a fold or pocket that she made using her blouse. When she spotted us, she ran away, catching her skirt on the barbed-wire fence and tearing it. We watched her running clumsily, disappearing down the road while holding the shreds of her skirt together as her bounty of tamarind fruit flew off behind her.

Sometimes the presence of a barbed-wire fence was appreciated by the local villagers. In October, November, and December 2006, the people from Mahazoarivo had received threats from dahalo that their cattle were to be targeted. (Traditionally in the Mahafaly culture, dahalo thieves warn their victims before they strike.) The villagers saw the gallery forest with its protective fence as a safe haven in which they could hide their cattle, day and night. They figured that the dahalo wouldn't dare enter a forest that was under foreign protection, and surrounded by barbed wire. Furthermore, the villagers knew where they might break the fence to allow cattle entrance, without themselves being observed by camp guards. Off and on, within this three-month period, the cattle would be marshaled into the reserve for their own protection. In doing my research on mouse lemurs at night during this period, I regularly encountered them.

Such incidents (with clear negative effects on mouse lemurs, as cattle may inadvertently bump into trees with foraging or nesting animals, or dislodge Sherman traps, causing them to fall) tended to be rare in the gallery forest, however. In general, researchers could flag trees, set live traps, set cameras, etc., without fear of having their research disrupted. The story was quite different even immediately outside the reserve. A researcher working on plant isotopes was able to find her tags in the gallery forest after a hiatus of over a year, but many tags located immediately outside the gallery forest had been destroyed.

5.3.3.3 Local resource use within the reserve: The spiny forest

Of the three forests, the spiny forest probably suffered the most human degradation during the period from 2003 to 2007. In 2003, the spiny forest was almost never guarded. Oavial (one of the four forest agents) alone was charged with guarding the spiny forest, but the task was impossible for a single person to assume, so he was reluctant to take this responsibility. The local people using the spiny forest were not afraid of him. It was then that the local people realized that the spiny forest, despite its protected status, would not be seriously monitored, and could be exploited safely. At the very least, the spiny forest could be exploited with less risk than could the gallery forest, particularly if resources removed from it could be carried to distant places. Here, the local people might hold the upper hand.

And indeed, the spiny forest became a place to grow hidden crops, herd cattle, collect plants for food, hunt, and collect marketable wood from *Alluaudia* trees. In 2003, shortly after I had first established my camp in the spiny forest, my team and I discovered a large area (considerably larger than my study area and just adjacent to my study site) that had been clear-cut and burned for corn cultivation. We discovered this because the people who had grown the corn blocked the trails that we had just cleaned with piles of wood (presumably to prevent us from finding or entering the cultivated cornfield).

The spiny forest is a rich source of *Alluaudia procera*, and selective harvesting of *Alluaudia* trees is rampant there. I witnessed such selective harvesting in 2003, when I came upon trees that had been felled but not used; perhaps the loggers had run away when they heard us in the forest. By 2007, loggers seemed not to fear the presence of researchers in the forest. Once, when I heard the sounds of large *Alluaudia* trees being felled in the spiny forest, my assistants advised me against confronting the people cutting the trees directly, as such an action might put us all in danger. It was common for local people to carry guns or knives into the forest.

Nevertheless, it is easiest for local people to exploit resources when no BMSR personnel or researchers are present in the vicinity. When I returned to Beza Mahafaly for a brief visit in January 2009, I came across dozens of cut stumps of huge *Alluaudia* trees inside my former study area in the spiny forest. The cuts were fresh; clearly, the trees had been felled while reserve personnel were out of town on holiday and the wood had been systematically hauled away. The local people did not know that we would be visiting; they did know that the head of the reserve and the scientific director were away. Effectively, this one incident may have made uninhabitable most of the forest in which I had studied mouse lemurs in the spiny forest from 2003 to 2007. The felled trees were important nesting sites for the population.

5.3.3.4 Human activity in unprotected forests: Ihazoara

Ihazoara is degraded throughout, more so than either of the protected forests. Of all the human activities that I recorded, only logging and hiding do not occur at Ihazoara, mainly because no trees appropriate for logging remain there, and because people have no need to hide in an unprotected forest. People were everywhere in the forest; cattle were everywhere. When I worked at Ihazoara, many of my Sherman live traps were stolen, and the flagging tape that I had secured to trees to identify them was sometimes removed.

The story of my establishing Ihazoara as one of my research sites well illustrates the conflicted views of the local people with regard to the conservation agenda and to the presence of foreigners in their vicinity. Of course, I needed to seek the permission of the people living in the village before I could work in the forest. I needed permission to erect my tent and those of my assistants, and I needed to be granted a place at which this might occur. I also needed to establish a main mouse lemur study site (225 x 275 m^2) within the forest.

In 2003, I approached Ihazoara accompanied by Afane (who was, at that time, living in the neighboring village of Ambinda). A few years earlier, Afane had worked with Rodin Rasoloarison (a Malagasy researcher who had shot mouse lemurs in the region of Ihazoara as part of his dissertation research on mouse lemur morphometrics and taxonomy), so Afane knew the villagers at Ihazoara well. There had been some tension between Rodin and the local villagers, but Afane was well liked, and the villagers greeted us with open arms. That didn't mean that they trusted me, however. In fact, some villagers were convinced that I had come with the intent to steal their forest for the foreigners. Afane had visited the village alone the week before (as is required by the villagers) to explain my purpose, but some villagers were skeptical. They did grant us permission to visit the village elders. I had no idea that they had also summoned a diviner ("ombiasy" or "mpisikidy") to determine my true intentions. The people who greeted us asked me and Afane to wait while they disappeared into the houses to discuss my request. While I waited outside, the older people gathered around the diviner who performed the "sikidy" ritual. The diviner would place beans on a mat and examine their configuration; that configuration would reveal whether the intentions of the visitor were good or evil. If evil intentions were discovered, the visitor could be punished – perhaps severely (see www.serenapowers.com/sikidy.html; see also Chemillier, 2007).

Happily, the diviner discovered no evil intentions on my part. When the ceremony was finished, the villagers reported to Afane their finding that I was a good person. They granted me permission to set up my tent as directed by the diviner. They also told Afane that, despite the fact that the diviner had determined my intentions to be honorable, they themselves were not fully convinced that I would not try to give their forest to foreigners.

One of the Ihazoara villagers, a man called Miahy, was particularly interested in my work on mouse lemurs. Whenever my assistants and I brought captured mouse lemurs to our Ihazoara campsite for marking and measuring, he would stand around, watching us work. In 2004, he told me that he wanted to work with me should I return to Ihazoara in the future. When I returned to Ihazoara in 2006, I did hire him as one of my research assistants. This was fortunate, as Afane informed me later; had I not hired Miahy, he was planning to kill me. Fortunately also, Miahy liked his job and he enjoyed working with me, primarily because of the income it provided. In 2007, he became one of the interviewees expressing the view that foreigners had no right to "protect" the Mahafaly forests. He, along with many other local people at Ihazoara and elsewhere, were emphatic in their opinion that conservationists were behaving immorally: "do not fence our forests; the forests belong to us."

In 2003, I discovered that I was not the only "foreign" Malagasy person to be subjected to the sikidy ritual in the region of the BMSR research camp. In fact, the head of the reserve at that time, Jeannicq, told me that his own wife had had a similar experience. She was a doctoral student at the Université d'Antananarivo medical school, studying the health of the people of southwestern Madagascar. Her ethnic affiliation was Merina, and she had visited Ihazoara to conduct some interviews. Like me, she discovered only later that she had been put on trial. Like me, she had escaped bodily harm, as her verdict was also good.

Working at Ihazoara was not easy. Although I could not see the village from my study site, I could always hear the villagers in the background, and I could hear children playing. In 2006, I selected four botanical plots to survey at Ihazoara (just as I had done at the two forests within the reserve). I measured and identified the trees, marking each with a flag so that I could track phenological changes throughout the year (see Chapter 3). I soon had to abandon one of the plots as I found that virtually all of the flags had been removed, likely by children. I found piles of flags on the ground, and some in children's hair.

5.3.4 Interviews

5.3.4.1 Stated activities

A total number of 217 people, including 84 females and 133 males (106 youngsters and 111 adults) were interviewed. I found significant differences in literacy between young people and adults ($\chi^2 = 20.75$, df = 1, $p < 0.001$). There were 154 people who were not educated, of which 56.6% were young and 80% adults. Literacy was significantly different between villages ($\chi^2 = 15.2$, df = 5, $p = 0.010$), with people in villages close to the research camp more literate than those living in more distant villages. In order of distance to the research camp, the percentages of interviewees claiming literacy were 46.5% at Mahazoarivo (20 out of 43) 38.6% at Analafaly (17 out of 44), 26.2% at Ambinda (11 out of 42), 20% at Ampitanabo (10 out of 50), 15.4% at Antaolambiby (2 out of 13), and 12% at Ihazoara (3 out of 25). These differences largely reflect the percentages of children attending school.

Table 5.4a-c show the observed frequencies of responses by all interviewees, and then by adults and children treated separately, to four questions regarding their activities within the reserve. I found significant differences in stated activities between illiterate and literate people. People who asserted an ability to read also claimed to: (1) visit forests outside the reserve more often than within; (2) enter protected forests very rarely (e.g., not more than twice a week); (3) avoid hunting animals within the reserve; (4) avoid felling trees in the reserve for construction; and (5) avoid herding cattle in the reserve. In contrast, people who said that they were not able to read also more readily acknowledged visiting the reserve, and hunting animals, herding cattle (e.g., Figure 5.7), and felling trees there. Indeed, they claimed to visit the reserve very often. Tables 5.4b and 5.4c show that the differences in alleged activities of literate and illiterate people are far more pronounced for children than for adults; differences between literate and illiterate people in general are likely driven by differences between literate children and all adults. There were no significant differences between illiterate and literate adults (see Table 5.4a).

Literate children and adults did not differ in their stated activities within and outside the reserve except that literate children claimed to fell trees inside the reserve significantly less than did literate adults ($\chi^2 = 10.07$, df = 1, $p < 0.001$; 15.2% for literate kids and 70.6% for literate adults). What is striking about the data are the high percentages even of literate people acknowledging illegal activities within the reserve. Approximately a third of educated people admitted to regularly entering protected forests to hunt (41.3%), fell trees (30.2%), or herd cattle (36.5%). More than a third (38.1%) professed to visit the reserve frequently. Of course, the percentages for illiterate people were considerably higher.

I found that educated young people were more likely to state that they *preferred* "visiting the reserve" rather than visiting other forests than illiterate youngsters ($\chi^2 = 10.35$, df = 1, $p = 0.001$). This was in part because most of the children going to school live close to the reserve, and when they visit a forest, it is likely to be the reserve. However, when asked whether they visit the reserve often or rarely, literate children were more likely to respond that they visited the forest rarely (Table 5.4c). Whereas this response may be heartening to conservationists, it may also reflect the fact that school children have less time to spend in any forest.

In terms of stated activities (Table 5.4c), illiterate children were more prone to acknowledge visiting protected forests frequently (34/60, or 57%) than literate children (15/46, or 33%). Of all children stating that they do visit protected forests frequently, 69% (i.e., 34/49) were illiterate. Two-thirds of those children claiming to hunt animals in the reserve were illiterate. Of all children who acknowledged felling trees in protected forests, 80% (i.e., 28/35) were illiterate. Finally, of all children who said they herd cattle in protected forests, 75% were illiterate.

Table 5.4a: Tests of significance of differences in stated activities of villagers by literacy (children and adults combined).

Literacy	Variable tested			Test of significance
	Frequency of visiting reserve			
	Rarely	Often	Total	
No	62	92	154	$\chi^2 = 8.42$, df = 1,
Yes	39	24	63	$p = 0.004$
	Hunting animals in reserve			
	No	Yes	Total	
No	66	88	154	$\chi^2 = 4.52$, df = 1,
Yes	37	26	63	$p = 0.034$
	Felling trees in reserve			
	No	Yes	Total	
No	71	83	154	$\chi^2 = 10.11$, df = 1,
Yes	44	19	63	$p = 0.001$
	Herding cattle in reserve			
	No	Yes	Total	
No	64	90	154	$\chi^2 = 8.62$, df = 1,
Yes	40	23	63	$p = 0.003$

Table 5.4b: Tests of significance of differences in stated activities of villagers by literacy (adults only).

Literacy	Variable tested			Test of significance
	Frequency of visiting reserve			
	Rarely	Often	Total	
No	36	58	94	$\chi^2 = 0.46$, df = 1, NS
Yes	8	9	17	
	Hunting animals in reserve			
	No	Yes	Total	
No	47	47	94	$\chi^2 = 1.25$, df = 1, NS
Yes	11	6	17	
	Felling trees in reserve			
	No	Yes	Total	
No	39	55	94	$\chi^2 = 0.88$, df = 1, NS
Yes	5	12	17	
	Herding cattle in reserve			
	No	Yes	Total	
No	45	49	94	$\chi^2 = 0.26$, df = 1, NS
Yes	7	10	17	

Table 5.4c: Tests of significance of differences in stated activities of villagers by literacy (children only).

Literacy	Variable tested			Test of significance
	Frequency of visiting reserve			
	Rarely	Often	Total	
No	26	34	60	$\chi^2 = 6.06$, df = 1, $p = 0.01$
Yes	31	15	46	
	Hunting animals in reserve			
	No	Yes	Total	
No	19	41	60	$\chi^2 = 6.58$, df = 1, $p = 0.01$
Yes	26	20	46	
	Felling trees in reserve			
	No	Yes	Total	
No	32	28	60	$\chi^2 = 11.64$, df = 1, $p = 0.001$
Yes	39	7	46	
	Herding cattle in reserve			
	No	Yes	Total	
No	19	41	60	$\chi^2 = 16.73$, df = 1, $p < 0.001$
Yes	33	13	46	

Figure 5.7: Cattle grazing during the day inside the gallery forest. Photo credit: Emilienne Rasoazanabary, 2007.

Figure 5.8: Interview at Antaolambiby village. Emilienne Rasoazanabary is seated in the foreground. As is common in the vicinity of Beza Mahafaly, the small house that is visible behind the people was constructed using wood from a small tree species, *Cedrelopsis grevei*, which is also used by people for medicine, and which is used by mouse lemurs for nesting. Photo credit: Atane, 2007.

There were differences in the stated activities of villagers that correlate roughly with village distance to the research camp. However, the direction of the differences may seem counterintuitive. Rather than showing that people living close to the reserve use the reserve more than people living far away, the opposite appears to be the case. In particular, people living in the isolated villages of Ihazoara and Antaolambiby (one to two hours from the camp by foot) claim to visit the reserve, hunt animals there, fell trees there, and herd cattle there far more often than do people from the “very close” villages of Mahazoarivo and Analafaly (less than a half hour by foot), as well as the ‘not too distant” villages of Ambinda and Ampitanabo (less than an hour by foot). In effect, the people living closer to the camp site are also more educated, and consequently more afraid of the sanctions or fines potentially levied against them for violating conservation regulations. Furthermore, people living far away from the camp can also bring the resources that they collect in the region of the camp to distant safe havens. They have a lower risk of being caught.

Table 5.5: Tests of significance of differences in stated activities of villagers by distance from the camp.

Distance from camp	Variable tested			Test of significance
	Frequency of visiting reserve			
	Rarely	Often	Total	
Very close	38	49	87	$\chi^2 = 36.0$, df = 2, $p < 0.001$
Not far	60	32	92	
Isolated	3	35	38	
	Hunting animals in reserve			
	No	Yes	Total	
Very close	45	42	87	$\chi^2 = 4.7$, df = 2, NS
Not far	46	46	92	
Isolated	12	26	38	
	Felling trees in reserve			
	No	Yes	Total	
Very close	61	26	87	$\chi^2 = 18.2$, df = 2, $p < 0.001$
Not far	41	51	92	
Isolated	13	25	38	
	Herding cattle in reserve			
	No	Yes	Total	
Very close	50	37	87	$\chi^2 = 6.5$, df = 2, $p = 0.04$
Not far	41	51	92	
Isolated	13	25	38	

The fact is that the protected forests are rich in resources that are both useful and well known to the local people. Table 5.6a-c lists the tree species that are targeted by villagers for their own use, for use by domesticated cattle, or for market. I show here the relative abundance of these trees in the three forests, as well as which of these species are used by mouse lemurs, and for what main purpose. For example, villagers collect honey for their own use from hives in *Salvadora anguistifolia* trees. To do so, individual *Salvadora* trees are smoked to chase the bees away, facilitating the process of retrieving the honey. The fruit of *S. anguistifolia* is also consumed by people. Mouse lemurs consume the same fruit and use these trees for nesting (tree holes). The latex produced by *Euphorbia tirucallii* is used to drug fish in small ponds so that they can be caught easily by hand. Mouse lemurs use this same plant for open nesting, and they lick exudates on the branches of these trees. Cattle in the forest eat leaves of certain trees such as *Albizzia*, sometimes destroying the entire plant. This species is very important to mouse lemurs at Ihazoara and the spiny forest for both food (gum consumption) and nesting (open). Finally, *Alluaudia procera*, which is most important to mouse lemurs in the spiny forest for nesting, is the tree species most often targeted by humans for its commercial value. Boards made from this tree are transported to Betioky and sold at the weekly market (see Figure 5.4). Smaller trees species are targeted for house construction; these trees are not sold at market, but are used to build the small family houses that are typical in this region (see Table 5.6c). *Alluaudia* trees are probably the most important trees for mouse lemurs in the spiny forest, as they present ideal nesting holes, particularly for use during the dry season, when human utilization of this resource also peaks. In total, of the 17 tree species targeted by humans, 11 (or 65%) are also important to mouse lemurs for either food or nesting. Several of the tree species that rank as extremely important to mouse lemurs (*Alluaudia procera*, *Terminalia fatrae*, and *Albizzia* sp. in the spiny forest, the latter two at Ihazoara, and *Euphorbia tirucallii*, *Tamarindus indica* and *Salvadora angustifolia* in the gallery forest) are also exploited by people.

Table 5.6a: Tree species collected for local use (food or medicine), with importance to mouse lemurs.

Scientific or common name	Frequency in all 11 botanical plots combined (number per 1.1 ha)	Frequency of usage by mouse lemurs (Feeding and nesting combined)			Usage by mouse lemurs
		Gallery	Ihazoara	Spiny	
Bridelia sp.	1	128	6	19	Food > Nest
Cedrelopsis grevei	88	---	6	66	Nest > Food
Salvadora angustifolia	18	125	---	---	Nest > Food
Tamarindus indica	53	149	---	---	Nest > Food
Euphorbia tirucallii	67	328	41	46	Nest > Food
Dolichos fangitse	---	---	---	---	none
Lamoty	---	---	---	---	none
Velahy	---	---	---	---	none

Table 5.6b: Tree species that provide food for cattle, with importance to mouse lemurs.

Scientific name	Frequency in all 11 botanical survey plots combined (number per 1.1 ha)	Frequency of focal individual usage by mouse lemurs (Feeding and nesting combined)			Usage by mouse lemurs
		Gallery	Ihazoara	Spiny	
Albizzia sp.	12	14	93	197	Food > Nest
Rhigozum madagascariensis	10	---	---	---	Nest > Food
Cedrelopsis grevei	88	---	6	66	Nest > Food
Tamarindus indica	53	149	---	---	Nest > Food
Grewia grevei	15	---	---	---	Nest > Food
Salvadora angustifolia	18	125	29	42	Nest > Food
Grewia franciscana	30	4	---	3	Food = Nest
Terminalia fatrae	40	26	289	538	Food > Nest
Pachypodium rutenbergianum	19				none
Kochneria madagascariensis	---	---	---	---	none
Opuntia dilleri	---	---	---	---	none

Table 5.6c: Tree species used by people for construction, with importance to mouse lemurs.

Scientific name	Frequency in all 11 botanical survey plots combined	Frequency of usage by mouse lemurs (Feeding and nesting combined)			Usage by mouse lemurs
		Gallery	Ihazoara	Spiny	
Alluaudia procera	127	---	---	383	Nest
Cedrelopsis grevei	88	---	4	60	Nest > Food
Grewia grevei	15	2	13	10	Nest > Food

5.3.4.2 Villagers' attitudes towards conservation

One cannot understand the attitudes of villagers toward conservation policy on the basis of interviews alone, because most people are reluctant to reveal in the context of a formal interview what they more readily reveal in unmonitored conversation – i.e., an aversion to conservation regulations (Table 5.7). On the basis of interview data, one would gather that most local people fully embrace conservation. Literate and illiterate people responded similarly to questions such as, "What do you think of conservation?" and "Do forests need protection?" To the former, they stated that they approve, and to the latter, they affirmed that forests do indeed need to be protected. When asked to whom the forests belong, however, they do not hide their strong belief that the forests belong to them; the forests do not belong to ANGAP.

There were some significant differences in the responses of literate and illiterate people to a few of the questions that my assistants and I asked. Educated people differed from illiterate people in more often expressing the opinion that fencing should be used to protect the forests ($\chi^2 = 11.12$, df = 1, $p = 0.004$). None of the educated people suggested that the job of protecting the forest should be left to village guards. A minority (13.7%), but much greater than zero, of illiterate people favored the village guard solution. Of course, village guards might be evaded easily; they might even become allies in allowing fellow villagers access to the forest. Barbed wire fencing is less friendly. Nobody suggested that "foreign" forest agents should guard the forests.

In addressing the question, "*Why* do forests need protection?" educated people were more likely than illiterate people to see the villagers themselves as the beneficiaries of sound conservation policies (the forests contain food, which benefits people; $\chi^2 = 23.37$, df = 2, $p < 0.001$). Illiterate people were more likely to see the animals and plants in the forests as the beneficiaries. Thus, in the context of the interview, illiterate people were more likely than literate people to express a "pure" conservation ethic (favoring conservation for conservation's sake), probably because this is what they heard, and this is what they believed we wanted them to say.

Table 5.7: Stated attitudes toward the forests and conservation policy (adults and children)

Literacy	Variable tested				Test of significance
	To whom does the forest belong?				
	Forest is ours	ANGAP	Total		
No	142	12	154		$\chi^2 = 0.62$, df = 1, NS
Yes	56	7	63		
	Do the forests need protection?				
	No	Yes	Total		
No	10	144	154		$\chi^2 = 0.15$, df = 1, NS
Yes	5	58	63		
	Why do forests need protection?				
	No	Yes	?	Total	
No	109	42	1	152	$\chi^2 = 23.37$, df = 2, $p < 0.001$
Yes	22	38	1	61	
	How should forests be protected?				
	No	Yes	?	Total	
No	131	21	1	153	$\chi^2 = 11.12$, df = 2, $p = 0.004$
Yes	59	0	2	61	
	Attitude toward conservation				
	Negative	Positive	Total		
No	16	138	154		$\chi^2 = 0.87$, df = 1, NS
Yes	4	59	63		

5. 4 Discussion

In this chapter, I present data on the use of protected and unprotected forests by humans, and how human activities impact the population dynamics and behavior of mouse lemurs. I document the responses of mouse lemurs to variation in habitat disturbance. I document the changes in monthly mouse lemur capture success rates in three forests over a five-year period. I document variation in the activities and attitudes of people living near those forests, focusing particularly on activities in and attitudes about the forests.

There are many factors that have been reported to influence attitudes of local people toward conservation. Local people may embrace conservation policies because they believe they improve ecosystem services such as the quantity and timing of rainfall (Uganda, Harter and Goldman, 2009; Harter, 2010), provide tourist revenues (for Indonesia, Walpole and Goodwin, 2001; for Trinidad, Waylen et al., 2009), or protect resources that may become invaluable at times of critical need (Ethiopia, Tessema et al., 2010). Education level influences attitudes of local people elsewhere in the world (for Myanmar, see Allendorf et al., 2006; for Tanzania, see Kideghesho et al., 2007; Ethiopia, see Tessema et al., 2010); age may (Tessema et al., 2010) or may not (Ferreira and Freire, 2009). My findings only weakly support a positive relationship between education (i.e., literacy) and the degree to which a conservation ethic is accepted. On the one hand, at Beza Mahafaly, both illiterate and educated people seem to embrace conservation. On the other hand, it is clear that their responses to questions may differ depending on whether or not someone associated with conservation officials is among the interviewers.

Under such circumstances, interviewees may be afraid to reveal their real attitudes. Nevertheless, it is probably true that illiterate people are less likely to understand the potential positive impacts of conservation policies. These small differences are also correlated with age and distance from the reserve at Beza Mahafaly; children are more likely to be educated than adults, and people living near the reserve are more likely to be educated than people living far from the reserve (simply because of the locations of the schools). Counterintuitively, therefore, it is adult people living far from the reserve that are most likely to violate conservation rules.

Given the difference between stated attitudes (as collected during interviews) and actions (as observed during disturbance transects), I do not believe that the local people at Beza have actually embraced a conservation ethic. Indeed they know, well in advance, how they are "expected" to respond to questions about conservation, regardless of education level.

Observed attitude or activity differences between educated and illiterate people may relate to factors other than their acceptance of a true conservation ethic. For example, educated people often have responsibilities (e.g., attending school, preparing children for school) that keep them outside the reserve; thus their lower levels of direct exploitation of forest products may not spring from a rejection of forest-product use. In contrast, illiterate people are more likely to be responsible for providing forest products to the villagers, and thus may engage more directly in exploitation of the reserve (see Table 5.4a).

In Madagascar as a whole, there is no doubt that people are aware of the existence of reserves in their area, but few people really understand conservation ethics or goals

(Ormsby and Kaplin, 2005; Klein et al., 2007). This is true at Beza Mahafaly; nobody was unaware of the existence of the BMSR, but few could articulate the rationale for its existence. If local people do not appreciate the long-term benefits of a reserve, they will have little desire to conform to conservation rules, particularly when they see those rules imposed by outsiders (see Gillingham and Lee, 1999, on Tanzania). At Beza Mahafaly, rule violations are common when reserve personnel are not present; villagers regularly monitor the activities of reserve staff, so that they can take advantage of every opportunity to enter the reserve to gather forest goods. Such violations are obvious after the fact, and they can create conflicts between reserve staff and forest-dependent people.

Another factor reported to affect attitudes of local people toward conservation, is the direct benefits accorded them, including jobs or tourist-based (Archabald and Naughton-Treves, 2001; Holmes, 2003; Gadd, 2005). Unfortunately, at Beza Mahafaly, local people benefit minimally from the existence of the reserve; fewer than ten people from the local communities are hired at any one time. Even these people may not embrace the conservation ethic, although they do appreciate the income generated by the reserve. Being hired is the main "benefit" of conservation as perceived by the local people. In fact, it is the negative impacts of the restrictive policies erected by conservationists (prohibitions against resource extraction) that are much better understood, and more important in the minds of local villagers (in Brazil, Ferreira and Freire, 2009). It is these impacts that often trigger conflict between reserve staff and local people (Walpole and Goodwin, 2001, on Indonesia). In Africa as a whole, such conflicts are occurring with increased frequency (Ormsby and Kaplin, 2005; Allendorf et al., 2006; Allendorf, 2007; Harter and Goldman, 2009).

At Beza Mahafaly, for example, conflicts between communities and reserve personnel were intense in 2003, ostensibly because very few people were hired by the reserve. A few people, known to reserve personnel, would be the first ones called as soon as jobs became available. Furthermore, when additional local assistants were hired, they were usually friends of the regular employees. Indeed, when I solicited local help, I had to consult with the regular employees. Similar problems have been reported elsewhere in Africa (Holmes, 2003; Tessema et al., 2010).

If habitat disturbance adversely affects mouse lemur population dynamics and behavior and if conservation policies adversely affect local people, then clearly there are conflicts that need to be addressed. How can such conflicts be reduced? What are the barriers to successful conservation? Can conservation policies actually work for and not against local people? How can negative impacts of conservation policy in the human realm be eliminated?

My data show that human disturbance is high in all three forests, protected and unprotected alike. The unprotected forest of Ihazoara is more disturbed than are the protected forests of the reserve. Unprotected forests also suffer from types of disturbance that are generally more harmful to mouse lemurs than that seen in protected forests; in effect, disturbance intensity is greater in unprotected habitats. Unprotected forests are disturbed all year round, but all forests suffer from human disturbance during the season of scarce resources – the dry season. The spiny forest, despite being “protected,” has suffered the greatest amount of destruction of trees that are very important to mouse lemurs. Beginning in 2003 and extending into 2009 (when I made a brief return trip to Beza Mahafaly), I witnessed systematic felling of *Alluaudia procera* trees in the spiny forest; they are cut into boards that have high market value at Betioky, to which they are transported. People who live in villages far from protected forests may be more successful in utilizing resources from those forests because they can more easily hide those resources from reserve personnel.

My data also suggest that mouse lemurs living in unprotected forests have shorter life spans than those living in protected forests. Monthly capture success rates are significantly lower in the unprotected than in protected forests. However, the forest that suffered the steepest decline in monthly capture success rates from 2003 to 2007 was one of the protected forests – the spiny forest. This was the forest that had the largest mouse lemur population in 2003. The spiny forest habitat is presumed to be ideal for *Microcebus griseorufus*; that of the gallery forest is not. For this reason, it is disturbing to witness the sharpest decline in mouse lemur populations in the spiny forest. It may be related to the systematic culling of *Alluaudia* trees there. In terms of large-scale destruction over a short period of time (i.e., the logging of large trees, the clearing of huge areas for crop cultivation), the spiny forest was hardest hit. Such large-scale destruction is not captured in the measures of human disturbance that I used to quantify differences in disturbance across forests.

Although humans do not hunt mouse lemurs, human activities certainly do impact mouse lemurs directly and indirectly. Many of the trees exploited by humans are also important to mouse lemurs for food and nesting. When mouse lemurs are disturbed, they tend to move, and this may put them at greater risk of predation particularly when they must move their dependent infants. Forests such as Ihazoara may have plant species similar to those in the spiny forest (see Chapter 3), but the trees that are missing or present in low numbers here are exactly those that provide the best nesting sites and the best foods for mouse lemurs. Their selective loss in this forest is likely due to prior human disturbance. Thus, it is interesting that mouse lemurs living in this unprotected forest have no access to *Alluaudia* trees (which provide the best tree holes), and few *Terminalia fatraea* and *Albizzia* sp. (which provide gums). As established in this chapter, these three trees are targeted by people for construction or for food for cattle. Mouse lemurs at Ihazoara do not enter torpor apparently because of the low numbers of gum-producing tree species in this forest. Available tree holes are low, and may provide poor protection from predators.

Even though local people express approval of conservation activities when asked their opinion by "foreigners," they strongly dislike being excluded from forests which they believe rightfully belong to them. Similar stories have been told for other places around the world (Anthony, 2007). Local people in the region of Beza Mahafaly harbor a lot of hostility that is not always recognized by reserve personnel. They may participate in conservation ceremonies organized by reserve staff. They may recite conservation rhetoric, but they do not embrace those policies in a meaningful manner. In fact they continue to exploit protected forests, sometimes defiantly, sometimes secretly. They cannot abandon the lands bestowed upon them by their ancestors, simply because "foreigners" have brought them small gifts, and promises about future benefits. Those foreigners have also brought barbed wire, and a suite of conservation rules and sanctions that make no sense to the villagers. What is most important to local villagers is that the forests continue to provide a sanctuary for their cattle. The Mahafaly people are first and foremost cattle herders (Kaufmann, 2006); zebu cattle represent social status, wealth, and power. They have practical value as well. Men without cattle may not be able to marry. During the most important social events (weddings or funerals), several zebu may be sacrificed to feed the extended family and friends. Less important, but still important, is the role zebu fill as vehicles of transportation. They pull carts that transport people to distant markets. It is inconceivable to the Mahafaly that zebu are excluded from protected forests.

Mouse lemurs are found everywhere on the island of Madagascar, at least everywhere where lemurs exist. *Microcebus griseorufus* is widespread in southern Madagascar. It occupies forests devoid of all other lemurs (such as Ihazoara); according to the IUCN Red List of endangered species (2010), it is not threatened. My study shows that these mouse lemurs may in fact be struggling in those very areas where they are assumed to be thriving. They are doing poorly in unprotected habitats, and they are doing little better in "protected" habitats in the southwest. At Beza Mahafaly, the populations of mouse lemurs may be declining in all forests; more genetic research is needed to confirm this. What is clear is that capture success in the forests of the southwest can be very, very low, and the secular trend is disturbing.

It is true that people are destructive to ecosystems (witness the effects that local people have on forests such as Ihazoara). The notion that local people will build conservation policies that will protect those ecosystems must be regarded as tenuous, and it may be, in the long run, that these ecosystems are doomed. But ecosystem destruction is inevitable if tensions between local people and conservation personnel persist, and if nothing is done to eliminate them. More direct involvement of local people in erecting conservation policies is desperately needed if in the long run conservation is to succeed. The policies must be "owned" by the people.

5.5 Conclusion

This is the first long-term study of behavioral responses of *Microcebus griseorufus* toward human activities. *M. griseorufus* is tolerant of a great deal of variation in habitat conditions, and it is able to survive in forests that are highly disturbed. This includes an unprotected forest in which no other lemur species currently survives. Clearly, the ability of *Microcebus griseorufus* to reproduce quickly, and repeatedly within a year, compensates for high mortality rates. In this chapter, however, I show that the continued survival of even this tolerant species may be in jeopardy in unprotected forests, and that human activities are taking a definite toll on the population there.

Finally, I examine the attitudes of the local people toward conservation policies, and consider the dynamics of their interactions with conservationists. I suggest that no conservation policy will work unless they are embraced by the local people. Conflicts between the cultures of (1) the people and (2) the "foreign" conservationists are destined to continue, unless they are directly acknowledged and addressed.

CHAPTER 6

CONCLUSIONS

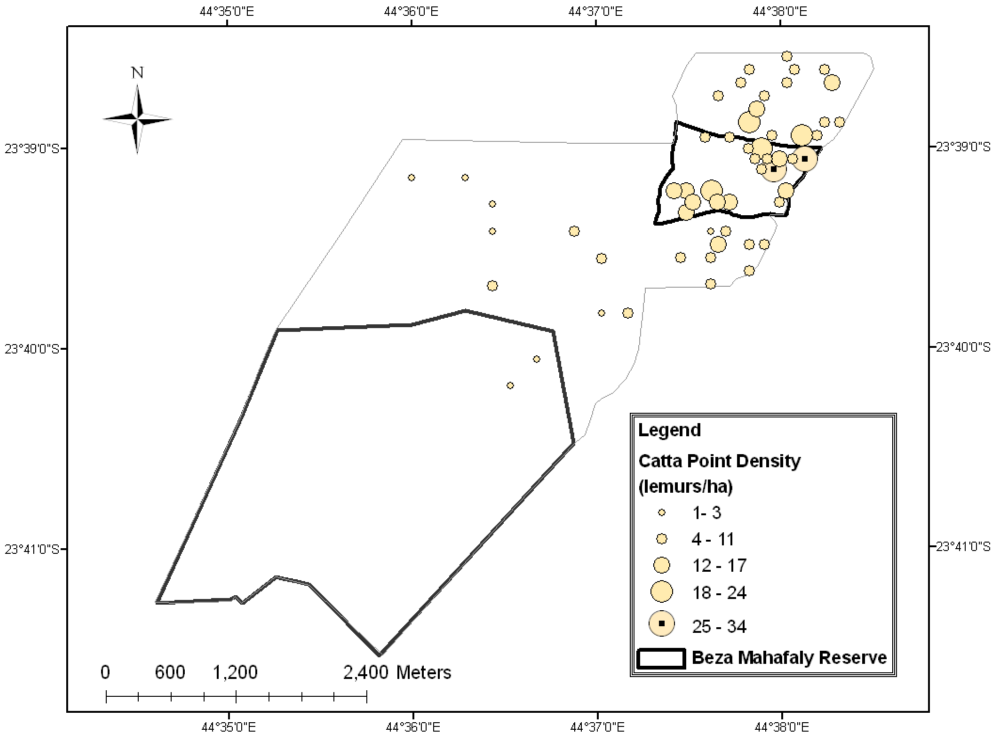
In this dissertation, I sought to understand the impacts of *human activities* and *natural habitat variation* on nocturnal mouse lemurs in the region of Beza Mahafaly, southwestern Madagascar.

At Beza Mahafaly, protected status for small patches of forest was requested in 1978, and, in 1986, a gallery forest bordering the Sakamena River, along with a portion of a spiny forest a bit closer to Betioky, became parts of a Special Government Reserve of Madagascar (Beza Mahafaly Special Reserve; see Richard et al, 1987). The forest of Ihazoara was not part of this Reserve. Concomitant with this, a program focusing on (1) lemur conservation research, (2) educating local people, and (3) local development was established. Conservation of the large-bodied diurnal species has been the first priority since 1986. Although studies of nocturnal lemurs (*Lepilemur petteri* and *M. griseorufus*) began a decade later (with Nash conducting fieldwork on sportive lemurs in the early 1990s, and Rasoloarison conducting a brief survey of mouse lemurs at Ihazoara in 1997; see Nash, 1998; Rasoloarison et al., 2000), nocturnal lemurs have never been incorporated into Beza Mahafaly's conservation plan. Behavioral and conservation studies of lemurs in southern Madagascar have focused on the two remaining largest-bodied diurnal lemur species, *Lemur catta* (the ringtailed lemur) and *Propithecus verreauxi* (Verreaux's sifaka). These include the following (and many others): at Berenty – Jolly, 1972; Jolly et al., 1982; Jolly and Pride, 1999; Norscia and Pelagi, 2008; and at Beza Mahafaly – Richard and Dewar, 1991; Sauther, 1991; Sussman, 1991; Richard et al., 1991, 2000; Gould, 1997a, b; Sauther, 1998; Brockman, 1999; Sauther et al., 1999; Lawler et al., 2003, 2007; and Lawler, 2009. The two largest-bodied diurnal species are very well known, and they are also currently classified as vulnerable (www.iucnredlist.org, 2010).

Six years after Rodin Rasoloarison conducted his survey, I began studying the behavioral patterns of small nocturnal mouse lemurs at Beza Mahafaly. I placed Sherman live traps in three forests (the gallery forest, spiny forest, and Ihazoara) and was surprised by exceedingly low capture success rates, particularly in the gallery and the dry deciduous forest of Ihazoara (Rasoazanabary, 2004). Low capture success rates were surprising because the people of the area do not eat mouse lemurs, and generally do not disturb forests at night when mouse lemurs are active.

Habitat disturbance, both natural and human, has influenced large-bodied diurnal lemur survival because it directly affects their feeding patterns and reproduction. The effects of drought and cyclones on *Lemur catta* in the southwestern dry forest of Beza Mahafaly were documented by Sauther (1998) and Gould et al. (1999; 2003). Researchers working at Beza Mahafaly have begun also to document the effects of human disturbance on the behavior of the larger-bodied, diurnal lemurs, focusing on fine-scale variation in disturbance levels in the vicinity of Parcel 1 itself (e.g., comparing the health of the "camp troop" of ringtails to the health of individuals belonging to troops living in more remote parts of the gallery forest, or comparing the behavior of ringtails in more and less disturbed parts of Parcel 1) (Loudon et al., 2005; Whitelaw et al., 2005; Sauther et al., 2006; Loudon and Sauther, 2007; Sauther and Cuozzo, 2009). Almost all of the published studies of *Propithecus verreauxi* and *L. catta* at Beza Mahafaly have been conducted in the gallery forest or its immediate vicinity.

Anne Axel did a survey of sifaka and ringtail presence in the spiny forest and gallery forest, as well as the transitional forest between them. She found few individuals of either species in the spiny forest (Axel and Maurer, 2011) and the greatest concentration of both ringtails and sifaka in the protected gallery forest (Figure 6.1, top and bottom). However, nobody has documented the density of these lemurs in forests close to villages, such as Ihazoara.



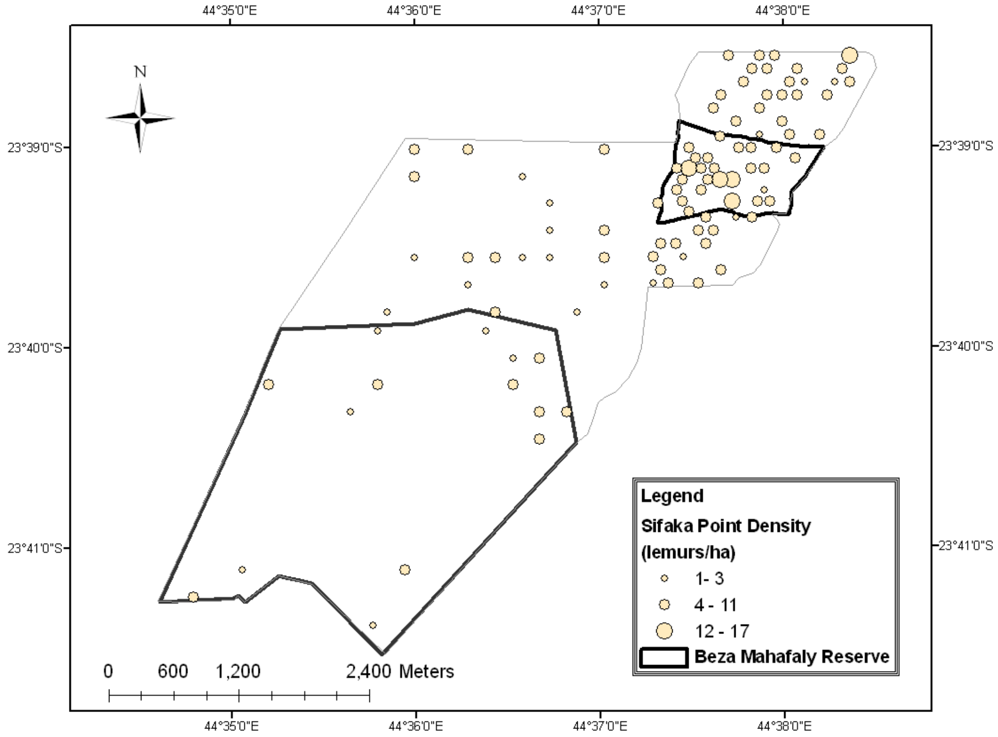


Figure 6.1: Top, group sizes of *Lemur catta* at sample points. Bottom, group sizes of *Propithecus verreauxi* at sample points. Parcels 1 (gallery) and 2 (spiny forest) are indicated in bold. Note that dot size is proportional to the number of individuals in each group. From Axel and Maurer, 2011, with permission.

During my five-year field study, I observed only two diurnal lemurs at Ihazoara. In 2003, I saw one individual *L. catta* with a collar (so from the gallery forest) at the entrance to the Ihazoara village, and in 2004 I saw one single *P. verreauxi* that had been injured by the village dogs, and was attempting to escape. The largest-bodied nocturnal species in the gallery forest at Beza Mahafaly is *Lepilemur petteri*, and even these were scarce or non-existent at Ihazoara. In 2004, I witnessed a *Lepilemur* that had been captured by villagers; it was “for sale” at somebody’s house. In all my years at Beza, I witnessed no wild *Lepilemur* within the Ihazoara forest. It appears that, of the lemurs living in the general vicinity and apparently thriving in the gallery forest, only the mouse lemurs can survive in disturbed forests near villages. This observation is disturbing, particularly in light of my observation that even mouse lemurs may be in trouble at Ihazoara.

Furthermore, prior to my own research, nobody had studied the resource needs and attitudes of the people living in the region of Beza Mahafaly in any depth. Aspects of the cultural practices of the Mahafaly people at Beza Mahafaly were reported by Ratsirarison et al. (2001), but there was no associated study of human activities inside the forests. At the inauguration of the Beza Mahafaly Special Reserve in 1986, people were told that they could no longer use the resources in the forests. This did not go down well with the local people, who continued to use the resources of the forest, either defiantly (in the open) or in secret. Attempts to build true conservation partnerships with the local people were meager and insufficient, as were attempts to monitor the actual behavior of the people. Of course, forests are very important to the daily lives of villagers. Unfortunately, human activities inside the forests may well impact the survival of lemurs.

Table 6.1 provides a long-term perspective. We know from research conducted at a subfossil site in the immediate vicinity of Beza Mahafaly and adjacent to a village (Antaolambiby), as well as other sites in the region, that 2000 years ago, there were many primate species living in the forests of southwestern Madagascar that are no longer alive. We now have a rich radiocarbon record of the demise of giant lemurs in the southwest (Crowley, 2010; Crowley and Godfrey, unpublished data), and we have direct evidence of human butchery of some of them (Perez et al., 2005). The table lists the lemur species that we know recently inhabited the region and their IUCN "conservation status." All species larger than 10 kg are extinct. The largest-bodied of the extant species are "threatened." Only the mouse lemurs are considered "unthreatened." This is a dismal picture of rapid disappearance of species in a region (and unfortunately one that was repeated in region after region across Madagascar). We know that some of the giant lemurs survived until around 500 years ago or more recently, but that the populations of the large-bodied lemurs were decimated by around 1000 years ago, at which time sifaka became the primary victims of human butchery (Godfrey et al., submitted). We also know from genetic data that the population of sifaka began to decline 2300 years ago (Lawler, in press) which is when we believe humans arrived in this region (Burney et al., 2004).

Table 6.1: Primates living today or in the recent past in the broad vicinity of the Beza Mahafaly Special Reserve (southwest Madagascar), with measured or estimated body mass and conservation status*. From Godfrey and Rasoazanabary, in press.

Species	Body Mass	Least concern	Threatened	Extinct
Microcebus griseorufus	60 g	x		
*Lepilemur petteri***	0.6 kg	Data deficient		
Lemur catta	2.2 kg		x	
Propithecus verreauxi	2.8 kg		x	
Mesopropithecus globiceps	11.3 kg			x
Pachylemur insignis	11.5 kg			x
Daubentonia robusta	14.2 kg			x
Archaeolemur majori	18.2 kg			x
Hadropithecus stenognathus	35.4 kg			x
Palaeopropithecus ingens	41.5 kg			x
Megaladapis madagascariensis	46.5 kg			x
Megaladapis edwardsi	85.1 kg			x

*For estimation of body mass of extinct lemurs, see Jungers et al. (2008).
**The populations of *Lepilemur* in southern Madagascar (including that at the Beza Mahafaly Special Reserve) have long been called *L. leucopus*. On the basis of genetic evidence, Louis et al. (2006) distinguished the populations living in eastern and western portions of this range, calling the latter (at BMSR) *L. petteri*. More research on these populations is warranted to verify their distinctiveness, and to assess their conservation status.

My dissertation project was initiated by a preliminary study that I conducted in 2003. In that study, I found that mouse lemurs existed in forests near villages as well as in different parts of the BMSR, and that there were signs of human disturbance even in the protected forests of the reserve. Analysis of ear tissue clips that I collected in 2003 established that the mouse lemurs in all of these forests belonged to a single species, *Microcebus griseorufus* (Heckman et al., 2006). Thus, it was clear that these animals were able to survive in very different habitats. But the question was, how well were they surviving? Are the populations declining? Are they doomed to failure? I wanted to understand how mouse lemurs cope with disturbance and survive in forest habitats that are under critical human pressure. I hoped to be able to disentangle behavioral variation that is linked to differences in "natural" habitats (forest structure, phenology, etc.) vs. human disturbance. My ultimate goal was to establish long-term monitoring program for mouse lemurs and to gather information sufficient to build a conservation plan based on a true understanding ecological requirements of mouse lemurs and needs of local people.

This dissertation presents the first long-term study of mouse lemur behavioral ecology in three different forest habitats. Included in this dissertation is an analysis of human activities and attitudes toward conservation. I provide detailed observations on habitat disturbance, responses of mouse lemurs to variation in their habitats, and the effects of conservation policies on the behavior of local people and their attitudes toward those policies.

Below I summarize the main goals and conclusions of Chapters 2-5. (Chapter 1 is introductory.)

In Chapter 2, I investigate the differences in the reproductive profiles and population dynamics of mouse lemurs living in different habitats across Madagascar. My goal was to test alternative explanations for variation in population turnover rates and longevity, one being Lahann et al.'s (2006) hypothesis that population turnover rates are higher in less seasonal habitats, and the other being Génin's (2008) hypothesis that population turnover rates should be higher in more seasonal habitats. I found that the population turnover rates in mouse lemurs do not conform to the predictions of either hypothesis, but rather appear to depend on factors other than seasonality (e.g., mortality rates). Effectively, population turnover rates can be exceedingly high in habitats that are highly seasonal and in habitats that have very low seasonality. I also explore how living in a strongly unpredictable environment affects mouse lemur life history parameters. Here, my focus is on testing a hypothesis put forth by Dewar and Richard (2007) that animals living in *unpredictable environments* tend to have unusual life history adaptations – i.e., either they are "bet hedgers" (reproducing slowly and dying at advanced ages) or they live their lives in the "fast lane" (reproducing rapidly and dying young). I demonstrate that at Beza Mahafaly, mouse lemurs can be described as living in the fast lane. Mortality rates are very high, few individuals are captured two years consecutively, and even fewer are captured three or four years in a row. I also show evidence of polyestry (multiple litters in single years). *M. griseorufus* are not "bet hedgers". The maximum longevity of mouse lemurs at Beza Mahfaly is less than five years. I also examine growth trajectories of infants and juveniles (when is adult body size attained, and how can immature individuals be recognized), age at weaning, and age at acquisition of sexual maturation.

In Chapter 3, I examine behavioral plasticity of mouse lemurs in three forests, as well as variation in morphological characteristics, to explore how members of a single species of mouse lemur are able to cope with the challenges of living in very different habitats. The goal here was to determine how mouse lemurs at Beza Mahafaly differ in feeding and nesting behavior in different habitats, and to investigate whether those differences correlate with morphology. I documented the differences in the plant species composition, species richness, species diversity, and tree characteristics of the three forest habitats, and demonstrated that two of them (the spiny forest and Ihazoara) are quite similar to each other and very different from the third (the gallery forest). I then showed that the mouse lemurs living in the gallery and spiny forests also differ the most in terms of morphology and certain aspects of their behavior. Those morphological differences do indeed appear to reflect differences in the way they use their habitats. In particular, I found that the hands and feet of gallery forest mouse lemurs are more hook-like (with relatively longer digits 3-5 and shorter thumbs and big toes) while those of spiny forest mouse lemurs are more clamp-like (with relatively larger thumbs and big toes). These differences can be explained by the amount of time they spend negotiating small branches in the high canopy, vs. large tree trunks and larger supports closer to the ground. Behavioral differences in both feeding and nesting are implicated. It does appear that habitat differences influence the biology of mouse lemurs in a non-trivial manner.

Finally, I showed that mouse lemurs are more selective with regard to feeding trees than they are with regard to trees selected for nesting. I reported evidence of seasonal shifts in food items, nest types, and nest height. I discovered that mouse lemurs in all three forests have no universal preference for tree holes over open nests, but rather that nest-type preference depends on season. I argue that the notion that higher tree holes are “safer” from predators is questionable, but that the differences are consistent with the hypothesis that the most important factor driving nesting site choice is thermoregulation.

The thermoregulatory hypothesis may also explain why the largest seasonal shift in nest height occurs in the spiny forest.

In Chapter 4, I explored sexual differences in the morphology and behavior of mouse lemurs. I tested Schmid and Kappeler's (1998) fluctuating sexual dimorphism hypothesis (i.e., that females are larger than males when preparing for seasonal torpor, while males are larger than females at the beginning of the reproductive season, when maneuvering for access to the best females), and found it lacking. There is no time of year when male *M. griseorufus* are consistently larger than females, and there is no reason to believe that large males have priority of access to females. Instead, I found that the mouse lemurs of Beza Mahafaly exhibit strong reverse sexual dimorphism in canine height. This appears to relate to female dominance, as I also documented significant differences in the behavior of male and female mouse lemurs, with females feeding significantly more on foods that are likely essential in building the fat reserves needed to enter seasonal torpor. I also argue that female dominance allows females to have priority of access to the "best" nesting sites at all times of year, but that the "best" nesting sites vary, depending on external temperature and rainfall, as well as reproductive needs (parturition). I hypothesize that, among lemurs in general, reverse canine dimorphism has greatest selective advantage in small-bodied species with the shortest life spans – i.e., those living in the most seasonal habitats with the highest predation pressure and adult mortality. This means that reverse sexual dimorphism may be expected to be greater in *M. griseorufus* than in mouse lemurs with longer life spans. In this chapter, I also examine the relationship between diet and seasonal torpor in mouse lemurs across Madagascar, and I suggest that sexual differences in access to soluble sugar-rich foods may explain the sexual differences in seasonal torpor frequency and activity levels of male and female mouse lemurs.

In Chapter 5, I examined the degree to which mouse lemurs living in the most disturbed habitats at Beza Mahafaly are truly thriving there. I demonstrate significant differences in the degree of human disturbance within the three forests, and show that no forest is free of such disturbance. Indeed, disturbance levels in the protected forests are surprisingly high. I also demonstrate that human activities do impact the behavior and population dynamics of mouse lemurs, despite the fact that mouse lemurs are not directly targeted by people for food. In particular, I show that the mouse lemurs living in the most disturbed habitat (Ihazoara) also have the shortest life spans and lowest capture success rates. This, and the failure of individual mouse lemurs at Ihazoara to fatten sufficiently to enter seasonal torpor, suggests that their long-term survival in this highly degraded forest may be in jeopardy. I also discuss a significant decline in the capture success rates of mouse lemurs in the spiny forest, and relate this to logging and clear-cutting practices. The spiny forest, despite being “protected,” has suffered the greatest amount of destruction of trees that are very important to mouse lemurs.

Most importantly, I document variation in the activities and attitudes of people living near those forests. I show that, whereas local people express approval of conservation activities when asked their opinion by “foreigners,” they strongly dislike being excluded from forests which they believe rightfully belong to them. Local people harbor a lot of hostility toward conservation practices. I relate that hostility to aspects of their culture and also to the way in which conservation regulations have been established. I show how that hostility is manifested in the behavior and activities of the local people.

I probe the apparent failure of conservation education to build a meaningful conservation ethic that is “owned” by the local communities, and I recommend greater involvement of the local people in building better conservation practices in the future – taking into account the needs and beliefs of the people as well as the needs of the lemurs.

APPENDICES

APPENDIX A

LIST OF TRAITS MEASURED FOR EACH INDIVIDUAL

Skull length	From the tip of the nose to opisthocranion (back of the skull)
Bizygomatic width	The width of the skull, across the zygomatic processes, perpendicular to skull length
Body length	From opisthocranion to the base of the tail
Tail length	From the base of the tail to the tip of the most distal vertebra, hair tufts excluded
Canine height	From the base to the tip of the crown
Ear length	From the top to the bottom of the pinna (maximum)
Arm length	From the greater tuberosity of the humerus to the olecranon process of the ulna (shoulder to elbow)
Forearm length	From the radial head to distal end the radius
Hand length	From the base of the palm to the distal end of the longest digit (digit 4), nail excluded
Palm length	From the base of the palm to the base of the proximal phalanx of digit 3
Palm width	From the medial to the lateral edge of the palm at the base of digit 1
Manus digit 1 length	From the base to the tip of digit 1, nail excluded (phalanges only)
Manus digit 2 length	From the base to the tip of digit 2, nail excluded (phalanges only)
Manus digit 3 length	From the base to the tip of digit 3, nail excluded (phalanges only)
Manus digit 4 length	From the base to the tip of digit 4, nail excluded (phalanges only)
Manus digit 5 length	From the base to the tip of digit 5, nail excluded (phalanges only)
Thigh length	From the greater trochanter of the femur (hip joint) to the knee
Leg length	From the proximal tibia (posterior face, below the knee) to the calcaneal tuberosity
Foot length	From the calcaneal tuberosity to the tip of the longest toe, nail excluded (digit 4)
Sole length	From the calcaneal tuberosity to the base of digit 3

Sole width	Perpendicular to sole length at the metatarsophalangeal joints
Pedis digit 1 length	From the base to the tip of digit 1, nail excluded (phalanges only)
Pedis digit 2 length	From the base to the tip of digit 2, claw excluded (phalanges only)
Pedis digit 3 length	From the base to the tip of digit 3, nail excluded (phalanges only)
Pedis digit 4 length	From the base to the tip of digit 4, nail excluded (phalanges only)
Pedis digit 5 length	From the base to the tip of digit 5, nail excluded (phalanges only)

APPENDIX B

LIST OF TREE SPECIES AND NUMBER OF INDIVIDUALS IN ALL BOTANICAL PLOTS RECORDED FOR PHENOLOGICAL SURVEYS

	Usage patterns*	Gallery 4 plots	Ihazoara 3 plots	Spiny 4 plots	Total
Acacia bellula	F, N	26	---	---	26
Acacia polyphylla	F, N	3	---	---	3
Albizzia sp.	F, N	---	10	2	12
Albizzia tulearensis	N	---	1	---	1
Alluaudia procera	N	---	---	127	127
Bridelia sp.	F	1	---	---	1
Calopikis sp.	F	---	3	---	3
Cedrelopsis grevei	F, N	2	8	78	88
Commiphora aprevalii	F, N	7	18	23	48
Commiphora brevicalyx	F, N	---	43	8	51
Commiphora marchandii	---	3	4	1	8
Commiphora rombe	N	1	36	50	87
Commiphora simplicifolia	---	---	1	2	3
Diospiros sakalavarum	---	1	---	---	1
Enterospermum pruinosum	N	---	3	---	3
Euphorbia decosei	N	---	---	9	9
Euphorbia stenoclada	N	---	3	5	8
Euphorbia tirucallii	F, N	54	---	13	67
Fernandoe madagascariensis	---	2	2	---	4
Gardenia sp 2	---	---	1	---	1
Gardenia sp.	---	---	1	---	1
Givotia madagascariensis	---	---	1	---	1
Grewia franciscana	F, N	25	1	4	30
Grewia grevei	F, N	1	13	1	15
Grewia leucophylla	F, N	19	---	---	19
Gyrocarpus americanus	F, N	1	118	140	259
Hymenodactyon decary	F, N	---	---	9	9
Macpersonia gracilis		---	---	5	5
Mahafanogne	F, N	---	15	4	19
Mimosa delicantuta	F, N	---	---	4	4

Operculicayarium decaryi	F, N	---	5	9	14
Pachypodium geayi	N	---	3	8	11
Pachypodium rutenbergianum	---	---	9	10	19
Phyllanthes decoryanus	F, N	---	5	39	44
Physena sessiliflora	F, N	1	---	---	1
Quivisianthe papionae	F, N	19	---	---	19
Rhigozum madagascariensis	F, N	4	---	6	10
Rhopalocarpus lucidus	F, N	36	1	---	37
Salvadora angustifolia	F, N	15	---	3	18
Salvadora sp.	N	16	---	---	16
Strychnos madagascariensis	F, N	4	3	---	7
Suregada chauvetiae	F, N	46	2	23	71
Tallinella grevei	F, N	4	2	---	6
Tamarindus indica	F, N	53	---	---	53
Terminalia fatraea	F, N	1	25	14	40
Terminalia seyrigii	F, N	17	3	6	26
Uncarina grandidieri	---	---	2	6	8
		362	342	609	1313

*F: food, N: nest

APPENDIX C

TREE SPECIES USED BY MOUSE LEMURS AS FOOD RESOURCES IN THE THREE FORESTS WITH TOTAL NUMBER OF FOCAL INDIVIDUAL FEEDING OBSERVATIONS ON EACH TREE SPECIES

	Gallery	Ihazoara	Spiny
Acacia bellula	169	---	---
Acacia minutifolia	7	---	---
Acacia polyphylla	1	---	---
Albizzia sp.	1	93	197
Bridelia sp.	128	6	19
Byttneria sp.	---	---	1
Calopikis sp.	---	---	2
Cedrelopsis grevei	---	2	6
Clerodendrum emirnense	---	---	1
Commiphora aprevalii	---	---	14
Commiphora brevicalyx	1	29	12
Cynanchum arenarium	---	---	4
Euphorbia tirucallii	3	---	2
Grewia franciscana	---	---	3
Grewia grevei	---	7	---
Grewia leucophylla	135	---	---
Grewia sp.	---	6	---
Grewia triflora	2	---	---
Grewia tuleariensis	2	---	1
Gyrocarpus americanus	---	5	1
Hippocratea anguistipetal	1	---	---
Hymenodactyon decaryi	---	---	4
Mahafanogne	---	5	---
Maragnatolake	---	---	13
Microsteira diotostigma	1	---	---
Mimosa delicantuta	---	---	44
Nato	---	1	---
Olax sp.	1	---	---
Operculicarya decaryi	---	7	44

Opuntia dilleri	---	---	17
Pentopetio sp.	---	2	---
Phyllanthus decoryanus	---	---	4
Physena sessiliflora	1	1	---
Quivisianthe papionae	4	---	---
Rhigozum madagascariensis	---	---	1
Rhopalocarpus lucidus	193	4	1
Roipitike	1	1	11
Salvadora angustifolia	20	---	---
Scutia myrtina	34	---	---
Strychnos madagascariensi	---	1	---
Suregada decidua	8	---	7
Talinella grevei	---	1	---
Tamarindus indica	10	---	---
Terminalia fatraea	26	90	353
Terminalia seyrigii	19	4	22
Terminalia tricristata	---	11	---
Tsivoanandro	---	2	---
Xerosicyos danguyi	---	2	

APPENDIX D

TREE SPECIES USED BY MOUSE LEMURS AS FOOD RESOURCES IN THE THREE FORESTS WITH THE TOTAL NUMBER OF FOCAL INDIVIDUAL FEEDING OBSERVATIONS ON DIFFERENT PLANT PARTS FOR EACH TREE SPECIES

	Season*	Leaves	Flowers	Fruit	Gums
Acacia bellula	R, D	---	2	1	166
Acacia minutifolia	D	---	---	---	7
Acacia polyphylla	R	---	---	---	1
Albizzia sp.	R, D	8	---	14	269
Bridelia sp.	R	1	5	146	1
Byttneria sp.	D	---	---	---	1
Calopikis sp.	D	---	---	---	2
Cedrelopsis grevei	R, D	1	---	---	7
Clerodendrum emirnense	D	---	---	---	1
Commiphora aprevalii	R, D	---	---	---	14
Commiphora brevicalyx	R, D	3	---	3	36
Cynanchum arenarium	R, D	---	---	---	4
Euphorbia tirucallii	R, D	2	---	1	2
Grewia franciscana	R, D	---	---	---	3
Grewia grevei	R	---	---	3	4
Grewia leucophylla	R	3	---	120	12
Grewia sp.	R	---	---	6	---
Grewia triflora	R	---	---	2	---
Grewia tuleariensis	R	---	---	1	2
Gyrocarpus americanus	R, D	2	---	2	2
Hippocratea anguistipetalia	D	---	---	---	1
Hymenodactyon decaryi	R	---	---	---	4
Mahafanogne	R	2	---	1	2
Maragnatolake	R, D	---	---	---	13
Microsteira diotostigma	R	---	---	1	---
Mimosa delicantuta	R, D	---	---	6	38
Nato	R	---	---	1	---
Olax sp.	R	---	---	---	1
Operculicarya decaryi	R, D	1	---	---	50
Opuntia dilleri	R, D	---	---	---	17
Pentopetio sp.	R	---	---	2	---
Phyllanthus decoryanus	R	---	---	---	4

Physena sessiliflora	R, D	---	---	1	1
Quivisianthe papionae	R, D	---	---	---	4
Rhigozum madagascariensis	R	---	---	---	1
Rhopalocarpus lucidus	R, D	---	---	3	195
*Roipitik*e	R, D	---	---	2	11
Salvadora angustifolia	R, D	7	---	---	13
Scutia myrtina	R	---	---	34	---
Strychnos madagascariensi	R	---	---	---	1
Suregada decidua	R, D	---	---	---	15
Talinella grevei	R	---	---	1	---
Tamarindus indica	R, D	---	---	---	10
Terminalia fatraea	R, D	3	1	160	305
Terminalia seyrigii	R, D	---	---	---	45
Terminalia tricristata	R	---	---	---	11
Tsivoanandro	R	---	---	---	2
Xerosicyos danguyi	R	---	---	2	---

*R: Rainy season; D: Dry season

APPENDIX E

TREE SPECIES USED BY MOUSE LEMURS FOR NESTING IN THE THREE FORESTS WITH TOTAL NUMBER OF FOCAL INDIVIDUAL NESTING OBSERVATIONS ON EACH TREE SPECIES

Tree species	Season*	Gallery	Ihazoara	Spiny
Acacia bellula	R, D	162	16	---
Acacia polyphylla	R	2	---	---
Albizzia sp.	R, D	13	---	50
Albizzia tulearensis	D	---	19	12
Alluaudia procera	R, D	---	---	383
Capparis chrysomae	D	---	22	---
Cedrelopsis grevei	R, D	---	4	60
Commiphora aprevalii	R, D	---	32	12
Commiphora brevicalyx	R, D	7	78	31
Commiphora rombe	R	---	17	11
Crateva excelsa	R	---	3	---
Cynanchum mahafalense	R, D	---	17	---
Dialium madagascariensis	R, D	13	---	---
Enterospermum pruinosum	R, D	1	30	---
Euphorbia decosei	R	---	---	28
Euphorbia sp.	R	---	3	---
Euphorbia stenoclada	R, D	---	---	96
Euphorbia tirucallii	R, D	325	41	44
Gonocripta grevei	R	5	---	---
Grewia franciscana	D	4	---	---
Grewia grevei	R, D	2	6	10
Grewia leucophylla	R, D	209	---	---
Grewia sp2.	R	---	---	5
Grewia tuleariensis	R	7	---	3
Greweia sp.	R	4	---	---
Gyrocarpus americanus	R, D	---	166	11
Hildergadia erythrosiphon	D	---	61	---
Hymenodactyon decaryi	R, D	---	---	18
Ipomae majungensis	R	---	---	1
Lafikosy	R	7	---	---
Leucosalpha poissonii	R, D	---	39	---
Mahafanogne	R, D	---	63	1

Metaporana parvifolia	D	8	---	---
Mimosa delicantuta	R	---	---	7
Nato	R, D	---	12	---
Operculicarya decaryi	R, D	---	53	---
Pachypodium geayi	D	---	28	---
Pentarhopalopilia sp.	R	3	---	---
Pentopetio sp.	R	1	---	---
Phyllanthus decoryanus	R, D		40	7
Physena sessiliflora	R, D	28	22	---
Quivisianthe papionae	R	5	---	---
Rhigozum madagascariensis	R, D	14	---	48
Rhopalocarpus lucidus	R, D	66	17	---
Rhoupellina boivini	R	4	---	---
Salvadora angustifolia	R, D	105	29	42
Salvadora sp.	R	3	---	---
Scutia myrtina	R, D	43	---	---
Seta	R	5	---	---
Strychnos madagascariensis	D	---	8	---
Suregada decidua	R, D	9	---	22
Tallinella grevei	R, D	25	1	3
Tamarindus indica	R, D	139	---	---
Terminalia fatraea	R, D	---	199	183
Terminalia seyrigii	R, D	6	1	20
Turrae sp.	R	---	3	---
Vanilla madagascariensis	D	---	---	7
Xerosicyos sp.	R, D	---	25	---

*R: Rainy season, D: Dry season

APPENDIX F

LIST OF ANIMALS RADIO-COLLARED DURING THE RAINY SEASON AND THEIR CHARACTERISTICS

Site	Collaring date	Transponder ID	Sex	Body mass (g)	Status*	Age	Names	Frequency
1	12/5/06	0659-DEF1	1	78	P	2	Rabekibo	150.293
1	12/2/06	0659-D0EF	1	89	P	2	Ravoatavo	150.103
1	1/6/07	0659-D356	1	60	L	2	Bozy	150.403
1	1/6/07	0659-2687	1	68	L	2	Rafotsy	150.262
1	1/1/07	065A-1C0D	1	64	L	2	Kala	150.152
1	1/6/07	065A-2C39	1	68	L	2	Madama	150.504
1	1/8/07	0659-6ECC	2	54		2	Rabogosy	150.303
1	1/13/07	0659-A7F1	2	45		1	Ranjoky	150.013
2	1/7/07	0659-D3A5	1	52	L	2	Kalabe	150.113
2	2/3/07	065A-2EF1	1	78	L	2	Madamabe	150.523
2	2/3/07	0658-57B6	1	80.5	P	2	Ravoatavo	150.324
2	2/11/07	0659-D170	1	70	P	2	Rabekibo	150.028
2	12/11/06	0659-5ED4	2	42		1	Ranjoky	150.421
2	2/6/07	065A-2F5D	2	56		2	Rabogosy	150.082
2	2/7/07	065A-27CC	2	52		2	Raplay	150.124
2	2/10/07	0658-60D3	2	57		2	Rabezesta	150.065
3	11/15/06	0659-BCC9	1	42		1	Jejo	150.134
3	11/18/06	0659-DC21	1	45		1	Kevoka	150.245
3	11/21/06	0659-B7F2	1	54.5	P	2	Rabekibo	150.044
3	11/21/06	065A-17A9	1	57	P	2	Ravoatavo	150.037
3	1/7/07	065A-0C04	1	57	L	2	Madama	150.202
3	1/19/07	065A-2927	1	55	L	2	Kala	150.484
3	11/17/06	065A-2E28	2	45		1	Ranjoky	150.15
3	12/13/06	0658-566B	2	63		2	Dadabe	150.363

Site (1 = gallery forest, 2 = forest of Ihazoara, 3 = Spiny forest); Status (P = pregnant, L = lactating); Sex (1 = WoMale, 2 = Male); Age (1 = subadult, 2 = adult)

APPENDIX G

LIST OF ANIMALS RADIO-COLLARED DURING THE DRY SEASON AND THEIR CHARACTERISTICS*

Site	Collaring date	Transponder ID	Sex	Body mass	Age	Name	Frequency
1	5/13/07	065A-157C	2	52	2	Edabo	150.785
1	5/15/07	064C-A8AB	2	45	1	Eniavo	150.564
1	5/17/07	0659-DA1E	2	58	2	Elaha	150.524
1	5/14/07	0659-9FC3	2	55	2	Efitiria	150.885
1	5/19/07	0659-D129	2	39	1	Edada	150.283
1	5/17/07	064C-B8A4	1	69	2	Delapra	150.665
1	5/13/07	0659-D356	1	65	2	Meltine	150.763
1	5/15/07	064C-C80D	1	58	2	Vavy	150.685
1	5/8/07	0658-6E81	1	50	2	Filaoke	150.625
2	5/24/07	065A-3A44	1	41	1	Kely	150.223
2	5/23/08	064C-D3A5	1	47	1	Aotsara	150.823
2	5/24/07	065A-0E6B	1	64	2	Bodary	150.003
2	6/2/07	0659-8B38	1	65	2	Bota	150.461
2	6/2/07	0659-D3A5	1	58	2	Katavy	150.721
2	5/1/07	0659-2A40	2	44	1	Bogosy	150.445
2	6/10/07	065A-38D4	2	45	1	Boroka	150.094
2	6/10/07	0659-C35D	2	53	2	Raglady	150.073
2	6/10/07	065A-101D	2	31	1	Zandry	150.344
2	6/10/07	0659-EB18	2	41	1	Pitsana	150.163
3	5/13/07	0638-F118	1	58	2	Berta	150.544
3	5/08/07	0659-A046	1	69	2	Botabe	150.580
3	5/07/07	0627-92C8	1	57	2	Bako	150.843
3	5/13/07	0659-FE7B	1	58	2	Bakoly	150.806
3	5/07/07	0659-BA7D	1	46	1	Bella	150.604
3	5/05/07	065A-2229	2	44	1	Kozatra	150.863
3	5/19/07	0659-C38D	2	53	2	Konan	150.052
3	5/20/07	064C-CFA1	2	37	1	Ballii	150.54F
3	5/20/07	0658-670D	2	45	1	Koto	150.382
3	5/13/07	0659-DD74	2	52	2	Kotity	150.745
3	7/18/07	065A-0B86	2	45	1	Kondry	150.624

*Site (1 = gallery forest, 2 = forest of Ihazoara, 3 = Spiny forest); Sex (1 = Female, 2 = Male); Age (1 = subadult, 2 = adult)

APPENDIX H

QUESTIONNAIRES FOR ADULTS AND CHILDREN (AGES 13-20 YEARS)

Village name: _ _ _ _ _ _ _ _ _ _ _ _ _ _ _ _	Interview date: _ _ _ _ _ _ _ _ _ _ _ _ _ _ _
Visit number: _ _ _ _ _ _ _ _ _ _ _ _ _ _ _	Interview location: _ _ _ _ _ _ _ _ _ _ _ _ _
Consent: _	Actual name:
Fake name: _ _ _ _ _ _ _ _ _ _ _ _ _ _ _ _ _	Marriage status: _ _ _ _ _ _ _ _ _ _ _ _ _
Age: _	Starting time: _ _ _ _ _ _ _ _ _ _ _ _ _ _ _ _ _
Sex: _	Ending time: _ _ _ _ _ _ _ _ _ _ _ _ _ _ _ _ _

Family history

	YES/NO	Number of ♀	Number of ♂
Number of Children			
Number of Great children			
Going to school			
Herding the animals			

Forest use

Most used forest				
Distance to village				
Frequency of use				
Most frequent time of use				
Activity in forest	YES/NO	Time spent	Species names	Goals
Hunting				
Felling trees				
Smoking out bees				
Collecting plants				
Herding				
Collecting fire wood				

Conservation issues

	YES/NO	Notes
To whom do the forests belong?		
Do the forests need to be protected?		
Why or why not?		
If so, how should they be protected?		
Is there a conservation plan?		
If yes, what do you think of it?		

Research concerns

Pertaining to most used forest	YES/NO	Notes
Are there researchers or foreigners inside your forest?		
What do you think about their activities in the forest?		
Would you like to work with researchers/scientists?		
What do you need from researchers?		

APPENDIX I

LIST OF INFORMANTS

Pseudonym	Sex	Age	Village	Role
Olobe	Male	Adult	Antaolambiby	Research assistant
Obade	Male	Adult	Ambinda	Research assistant
Adade	Male	Adult	Ampitanabo	Research assistant
Airitife	Male	Adult	Mahazoarivo	Research assistant
Antsy	Male	Adult	Analafaly	Research assistant
Fiaina	Male	Adult	Analafaly	Research assistant
Afane	Male	Adult	Mahazoarivo	Research assistant
Atane	Male	Young	Ambinda	Friend
Soava	Male	Adult	Ambinda	Research assistant
Miahy	Male	Adult	Ihazoara	Research assistant
Cire*	Male	Adult	Beza	Research assistant
Niry	Male	Adult	Antaolambiby	Research assistant
Laoka	Female	Adult	Ihazoara	Research assistant
Yrdan	Male	Adult	Ampitanabo	Research assisatnt
Tine	Female	Adult	Ampitanabo	Cook
Latare	Male	Adult	Ampitanabo	Research assistant
Oavial	Male	Adult	Mahazoarivo	Forest Agent
Sokola	Male	Adult	Analafaly	Research assistant
Artabam	Male	Adult	Ambinda	Research assistant
Jacky*	Male	Adult	Toliara	Scientific director
Hardos	Male	Adult	Betioky	Research assistant
Jeannicq*	Male	Adult	Antananarivo	Head of BMSR
Yrios	Male	Adult	Toliara	Head of BMSR
Diry	Male	Adult	Betioky	Head of BMSR
Liva	Male	Adult	Betioky	Forest agent
Olev	Male	Adult	Androy	Forest agent

*Non Mahafaly

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