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FEEDING ECOLOGY AND ASPECTS OF LIFE HISTORY IN *MICROCEBUS RUFUS*

(FAMILY CHEIROGALEIDAE, ORDER PRIMATES)

by

SYLVIA ATSALIS

A dissertation submitted to the Graduate Faculty in Anthropology in partial fulfillment of the requirements for the degree of Doctor of Philosophy,
The City University of New York

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Abstract

FEEDING ECOLOGY AND ASPECTS OF LIFE HISTORY IN *MICROCEBUS RUFUS* (FAMILY CHEIROGALEIDAE)

by

Sylvia Atsalis

Advisor: Professor Eric Delson

Annual fluctuations in body fat and activity levels, and feeding behavior in relationship to environmental seasonality were investigated in *Microcebus rufus* for 17 months in Ranomafana National Park, Madagascar.

Cyclical changes in thermoregulatory behavior occur in some small mammals during periods of environmental stress. It is common to associate the seasonal fattening and torpor characteristic of some Cheirogaleidae with the markedly seasonal climate and resource availability in west coast dry forests where most studies on cheirogaleids have taken place. Furthermore, primates of small body size are expected to include a high proportion of insects in their diet to meet protein and other nutritional requirements.

I monitored body fat and activity levels of known live-trapped individuals. Feeding behavior was determined primarily through analysis of fecal samples. Feeding data were compared to data collected on monthly fruit and insect availability.

A mixed diet of fruit and insects was consumed all year round. Mouse lemurs relied on a wide variety of fruit with consumption increasing in quantity and diversity during part of the rainy season, a time when fruit production peaked. During this period some individuals increased their body fat in preparation for the dry season when lower temperatures, precipitation and resource availability occur. These individuals

decreased activity during part of the dry season as suggested by their absence from traps. They resumed activity with reduction in body fat. Other individuals retained relatively constant body fat and activity levels.

The ratio of males to females trapped fluctuated, dramatically increasing in favor of males between June and September when other mouse lemurs were in torpor. This bias may be due to young males who are dispersing from their natal range.

The semi-parasitic epiphyte *Bakerella* was consumed year-round during periods of high and low resource availability. Along with its high lipid content this suggests that it serves as both a staple and a keystone resource. Coleoptera were consumed regularly year round. Insect consumption did not increase during the rainy season when insect abundance was at its highest.

Both east coast and west coast mouse lemurs have similar behaviors to cope with seasonal environmental stresses.

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CHAPTER ONE

INTRODUCTION

Microcebus belongs to the Family Cheirogaleidae, a group of small, nocturnal Malagasy strepsirhines which includes four other genera, *Allocebus , Cheirogaleus, Mirza* and *Phaner.* Small, solitary and nocturnal animals are difficult to observe and pursue. Thus, in contrast to the other Malagasy primates, the members of the family Cheirogaleidae are infrequently chosen as subjects of field research. The recent rediscoveries of *Allocebus trichotis,* which was thought to be extinct (Meier and Albignac, 1990), and of *Microcebus myoxinus* (Schmid and Kappeler, 1994; Atsalis et al., 1996) which was described in the last century and forgotten, are, perhaps, indicative of a recent increased interest in nocturnal lemurs. Yet several taxa of Cheirogaleidae (*Allocebus trichotis*; 3 of 4 subspecies of *Phaner furcifer: P. f .pallescens, P. f. parienti, P. f. electromontis*) have never been the subject of any study (Mittermeier et al., 1994) and all suffer from a lack of long-term systematic observation in the wild, including *Microcebus*, the most abundant and widespread Malagasy strepsirhine taxon (Richard et al., 1985; Harcourt and Thornback, 1990).

Microcebus, found in a diverse array of forest habitats, has primarily been the subject of brief studies in the highly seasonal dry deciduous forests of the west coast. My seventeen month field study in the east coast rainforest habitat of Ranomafana National Park, was the first long-term continuous study of one of the three known species of *Microcebus*, *M. rufus*, the brown mouse lemur. With a reported weight of 40-50 g (Harcourt, 1987; Wright and Martin, 1995; Atsalis et al., 1996) *Microcebus rufus* is among the smallest of the living primates, second only to *Microcebus myoxinus* whose average weight is 30 g (Schmid and Kappeler, 1994; Atsalis et al., 1996).

The research focused on feeding ecology and associated annual fluctuations in body fat and activity patterns. Due to the relatively long duration of this study compared to others, I was able to determine the variety of foods eaten, to document dietary patterns and how they change seasonally, to register rare feeding behaviors and to determine specific food sources that served as mainstays to the population. I found that this species consumed both fruit and insects, included a wide variety of fruit species in its diet and relied heavily on the fruit of one high-lipid semi-epiphytic plant. In addition, I found that seasonal increases in body fat and subsequent reduction in activity occurred, but did not characterize all members of the population. The results of my analyses help to understand how a small primate adapts to seasonally-based environmental stresses, and ultimately, provide a basis for comparing adaptations between east and west coast mouse lemur populations which are subject to differing intensities of seasonal environmental fluctuation.

Background Information on the Cheirogaleidae

The relationship of the Cheirogaleidae to the other strepsirhines

Madagascar is located 400 km east of the southern coast of Africa. Some researchers date its current position, isolated from the continent, at approximately 120 million years ago (Rabinowitz, et. al., 1983; Krause et al., 1997). Thus, the Malagasy strepsirhines have evolved in isolation from their haplorhine and strepsirhine relatives in Africa. Despite this separate radiation, there is no clear consensus as to the evolutionary relationship of the Cheirogaleidae to the other Malagasy primates. Based on certain aspects of behavior, ecology, and morphology, some taxonomists propose that the Cheirogaleidae are more closely related to the African galagos and lorises than to the other Malagasy (Szalay and Katz, 1973; Tattersall, 1982; Schwartz and

Tattersall, 1985). More recently, studies of molecular data point to a single ancestry for all extant Malagasy strepsirhines (e.g. Yoder et al., 1996). Whether the similarities that exist between the galagos, lorises and cheirogaleids are due to primitive retentions, convergent evolution or phylogenetic affinities does not directly bear on the present research. However, the issue should be taken into consideration when making comparisons between these groups.

Distinctive features of the Cheirogaleidae

The Cheirogaleidae are known to display features which are relatively uncommon in the Order Primates. Like many other nocturnal primates, they are solitary, nocturnal foragers who sleep in the daytime, either in leaf nests or in tree holes. Part of the way these nocturnal species socialize is through their daytime sleeping associations. Production of litters consisting of 2-3 offspring is common. Diets are diverse but some cheirogaleids have anatomical specializations for specific resources (tree gum in the case of *Phaner furcifer* and nectar for *Allocebus trichotis*).

Cheirogaleus, Microcebus and *Allocebus* are the only primates which are known to enter torpor or extended periods of hibernation following seasonal accumulation of body fat. Torpor signifies a substantial drop in normal body temperature, although not below 15° C, whereas, with hibernation, body temperature can drop to as low as 5° C, a temperature which can be sustained for up to several weeks (Lyman, 1982).

Ultimately, what influences all aspects of cheirogaleid ecology and behavior is the triad of small body size, nongregarious sociality and strictly nocturnal activity, factors which set them apart from their diurnal, large-bodied, group-living lemur relatives. The interacting influence of these features on various aspects of behavior remains largely unexplored. These traits are, in fact, shared with the majority of non-

primate mammalian species but their influence on behavior may be different within the nocturnal strepsirhines. To illustrate, although accepted theory states that small body size imposes, relative to large body size, high metabolic rates (e.g. Schmidt-Nielsen, 1984) it has been found that some nocturnal strepsirhines are hypometabolic (Kurland and Pearson, 1986; Ross, 1992). In addition, there is no clear consensus as to the extent of influence of small body size on life-history traits. The accepted theory is that small body size and resultant high metabolic rates act to shorten life-span and increase the rate of reproduction (Bourlière, 1975; Schmidt-Nielsen, 1984) but data from the nocturnal strepsirhines do not consistently support this idea. One analysis found body size to be a primary factor influencing life history (Rasmussen and Izard, 1988). Another analysis asserts that body size is acting on life history traits through differential mortality (Kappeler, 1995). Corroborating the latter view is the fact that small bodied mammals, including *Microcebus*, are particularly vulnerable to predation (Bourlière, 1975; Clutton-Brock and Harvey, 1977a; Wright, 1985; Goodman et al., 1993). Moreover, predation influences their ranging and nesting behavior promoting cryptic behavior. Therefore, non-gregarious types of social organizations characteristic of some taxa of small-bodied mammals can be considered extreme versions of cryptic type behavior. However, within the nocturnal strepsirhines, non-gregarious nocturnal sociality is not uniform, as previously thought (Charles-Dominique, 1975, 1978), but instead, is characterized by complexity and variety in the degree of home-range overlap, direct contact between individuals and nesting associations (Bearder, 1987; Barre et al., 1988; Clark, 1985; Harcourt and Nash, 1986a; Nash and Harcourt, 1986; Pagès, 1980; Pagès-Feuillade, 1988; Sterling, 1995). Some scientists consider that nocturnal solitary living among the strepsirhines is not necessarily different from diurnal

gregarious living in the degree of sociality, but in how sociality is mediated between individuals; nocturnal sociality relies primarily on olfaction, an indirect form of communication which persists in space and time (e.g. Clark, 1985).

Besides nocturnality, solitary habits and small body size, other traits which characterize *Microcebus*, such as litter production, nestbuilding and the ability to enter torpor, are widespread among non-primate mammals (Fleming, 1979). Possession of these traits has been used to support the idea that *Microcebus* is primitive and consequently a model for the earliest primate (Charles-Dominique and Martin, 1970). However, a growing body of ecological and behavioral evidence is shifting our perceptions of the nocturnal strepsirhines, which may be very much like diurnal primates in the diversity of their behaviors (Tattersall and Sussman, 1989; Richard and Dewar, 1991; Kappeler, 1995). Although received wisdom has been that small nocturnal primates are solitary, insectivorous and sexually monomorphic in behavior (Martin, 1972; Charles-Dominique, 1975), for *Microcebus rufus* some of these claims can now be tested using a substantial database based on data collected over a relatively long-term study period.

Background Information on *Microcebus*

Distinction among Microcebus *species*

Of the eight species of Cheirogaleidae, three belong to the genus *Microcebus*, the mouse lemurs, which are the world's smallest primates. Their average weights are approximately 60 g for *M. murinus*, 42 g for *M. rufus* and 30 g for the recently rediscovered *M. myoxinus* (Schmid and Kappeler, 1994; Wright and Martin, 1995; Atsalis et al., 1996). Besides body weight, the three species differ significantly in other

body measurements (Martin, 1973; Schmid and Kappeler, 1994; Atsalis et al., 1996) and in their DNA profiles (Schmid et al., 1995; Leipoldt et al., 1997).

Specifically concerning body size measurements, *Microcebus myoxinus* were found to have significantly shorter and narrower heads and ears, shorter hindfeet and longer tails than *Microcebus rufus* and were smaller than *M.murinus* in all dimensions (Schmid and Kappeler, 1994; Atsalis et al., 1996). *M. rufus* was found to be smaller than *M. murinus* for all variables except hindfoot length (Atsalis et al., 1996). With regard to body proportions, *M. myoxinus* had relatively shorter and narrower heads and longer tails than *M. rufus* and differed from *M. murinus* only in relative ear length and width (Atsalis et al., 1996; but see Schmid and Kappeler, 1994 concerning ear proportions). *M. rufus* had shorter and narrower ears and shorter bodies and tails than *M. murinus* (Martin, 1973, 1995).

Distribution of* Microcebus *species

Microcebus is geographically widespread (Figure 1.1). *M. murinus* occurs in southern and western Madagascar from Tolanaro to the Sambirano region in the northwest (Tattersall, 1982). *M. rufus* occurs in the eastern rainforests from Tolanaro to Montagne d' Ambre and in the Sambirano region where it seems to replace *M. murinus* (Tattersall, 1982; Harcourt and Thornback, 1990; Mittermeier et al., 1994). The known region for *M. myoxinus* extends from the Baie de Bombatoka (near Mahajanga) in the northwest to the Baie de St. Augustin (near Toliara) in the southeast, which is also the type locality (Peters, 1852). However, the continuity of this range has not been confirmed (but see Thalmann and Rakotoarison, 1994), nor have there been recent sightings to reconfirm the type locality.

M. murinus is found in proximity to *M. rufus* in the Fort Dauphin area (Tolanaro) (Martin, 1972) and in sympatry with *M. myoxinus* at the Kirindy Field Station near Morondava in western Madagascar (Schmid and Kappeler, 1994).

Previous studies on* Microcebus *species

Few field studies have been conducted on any species of *Microcebus*. The first systematic collections of data on *M. murinus* provided basic information on its natural history and established this species as an omnivore (Martin, 1972, 1973; Hladik et al., 1980) with seasonal shifts in the diet observed in the field (Martin, 1972, 1973; Hladik et al., 1980; Pagès-Feuillade, 1988) and confirmed in captivity (Petter-Rousseaux, 1974, 1980; Petter-Rousseaux and Hladik, 1980). Seasonal patterns in activity level, body weight and temperature were observed in the field (Martin, 1972, 1973; Hladik et al., 1980) and linked to changes in photoperiod affecting the pituitary gland (Perret, 1972). Initial observations on social organization based on location of animals at night and on daytime nest associations revealed a predominantly solitary species (Martin, 1972). It was furthermore suggested that *Microcebus* lives in "population nuclei" characterized by more females than males, with excess males pushed to the periphery (Martin, 1972, 1973). These observations were not confirmed by recent studies based on radiotracking which, conversely, revealed more overlap of the home-ranges of both sexes than previously thought for a solitary and territorial species (Barre et al., 1988; Pagès-Feuillade, 1988).

Previous studies on *M. rufus* in Ranomafana revealed a greatly biased sex ratio in favor of males (Harcourt, 1987; Wright and Martin, 1995) and indicated a preference for insects over fruit (Harste, 1993; Harste et al., 1997).

At the Kirindy Field Station, researchers have completed projects on the physiology of torpor of *M. murinus* and *M.myoxinus* (Ortmann et al., 1996, 1997; Schmid, 1996) and on activity (Fietz, 1997) and feeding patterns in *M. murinus* (Fietz, J. pers. comm.).

Past laboratory studies, almost exclusively on *M. murinus*, have examined reproductive physiology (e.g. Petter-Rousseaux, 1964, 1974; Andriantsiferana et al., 1974; Perret, 1974; Glatston, 1979) and certain aspects of social behavior in captivity (Glatston, 1979). More recent laboratory studies have focused on the inter-relationships between social factors, chemocommunication and physiology (e.g. Perret, 1992, 1995) as well as the role of vocalizations in communication (e.g. Zimmermann and Lerch, 1993).

Issues Examined in this Study

Feeding ecology

How small primates satisfy their protein and energy requirements is an important issue when discussing primate feeding ecology. It is frequently stated that the diet of small primates should include a large quantity of insects, or even be predominantly insectivorous, because insects are relatively high quality sources of protein and other nutrients (Hladik, 1979; Clutton-Brock and Harvey, 1983; Coe, 1984; Kay, 1984; Richard, 1985). Thus, there is the question of how insectivorous *Microcebus* really is, given that field observations (Martin, 1972; Martin, 1973; Hladik et al., 1980) hint that fruit may be the dietary staple. Previous studies on *Microcebus* did not provide sufficient information to determine the full complement of fruit and insects eaten, to monitor seasonal feeding behavior or to evaluate the importance of fruit and insects in the diet.

Due to the possibility that the behavior of *M. rufus* is cyclical in nature, my study, which was long-term, continuous and encompassed at least one complete annual cycle of seasonal changes in climate and resource availability, was suitable for a more accurate description of feeding ecology.

In chapter two I present a comprehensive discussion of the methods used to conduct the present research. I include a detailed description of the methods used to evaluate fruit and insect presence in the diet through analysis of the feces collected from live-trapped individuals. During my survey of the literature preparatory to undertaking this work, I found cases where potential shortcomings in methods and results were not explicitly stated. I have made a conscious effort to outline possible drawbacks or weaknesses in the methods I have used and in the results I obtained in an attempt to help future researchers avoid difficulties in the repeatability of this research.

In chapter three, I present the results of monitoring plant and insect abundance. These data are used to compare *M. rufus* feeding patterns to the availability of resources in the forest. Then, in chapter four, I initially examined *Microcebus rufus* feeding behavior by applying a simple model that compared monthly fruit and insect abundance to the relative proportions of fruit and insects in the diet. Results from this analysis indicated that mouse lemurs did not feed on fruit and insects based on available abundance. This led me to formulate hypotheses which tested the possibility that fruit and insect diversity in the diet of *M.rufus* does not follow generally available resource diversity and that specific fruits and insects were incorporated in the diet irrespective of general availability of resources.

To test the hypotheses, I collected dietary data primarily through weekly fecal analysis. These data were then compared to data on plant and insect resource availability. Phenological data collected monthly from plots which I established within the field site were used as indicators of the former, while the number and total fresh weight of phototropic flying insects trapped monthly were used to measure the latter. To identify preferred dietary items I determined the frequencies with which different items were eaten and evaluated the regularity of their presence in the fecal samples.

The advantages as well as the drawbacks of examining feeding patterns through fecal analysis are outlined in detail in chapter two ("Fecal analysis as a method for studying diet"). Here, I emphasize that for animals where direct visual observation of feeding episodes is difficult due to their small body size, nocturnal habits and the dense vegetation in which they are active, analysis of fecal matter is a valuable way of continuously and systematically monitoring food habits over a long period of time. In some cases , such as when attempting to determine the insect portion of a diet, fecal analysis can be more valuable than direct observation because the actual act of ingesting insects is sometimes difficult to verify when observing animals in the forest. Lastly, fecal analysis of samples collected from live-trapped individuals has the further advantage of allowing one to know the identity of the depositor.

Body weight fluctuations and annual activity patterns

The majority of research conducted to date on the Cheirogaleidae has taken place in the dry, deciduous forests of Madagascar's west coast where the problem that confronts individual lemurs is survival during the dry season. Dietary specializations and seasonal patterns in food intake (*Cheirogaleus medius*, *Mirza coquereli*, *Phaner furcifer*), anatomical specializations (*P. furcifer*), the ability to hibernate (*C. medius*) and

to enter torpor (*M. murinus*, *M. myoxinus*) and seasonal body fat accumulation (*C. medius* and *M. murinus*) are considered adaptive strategies to the highly seasonal conditions of food availability in the forests of the west coast (Hladik et al., 1980; Petter-Rousseaux, 1980; Petter-Rousseaux and Hladik, 1980; Schmid, 1996).

During the wet season *Microcebus murinus* and *Microcebus myoxinus* accumulate body fat which is metabolized during the dry season, a period when animals can reduce body temperatures and activity, resting in their nests for days at a time (torpor) (Hladik et al.,1980; Petter-Rousseaux, 1980; Petter-Rousseaux and Hladik, 1980; Ortmann et al., 1996, 1997; Schmid, 1996).

Past observations sometimes questioned the ability of *Microcebus* to enter torpor because animals were sighted in the forest year-round (Martin 1972). However, field studies on *Microcebus* physiology have confirmed this behavior for west coast species (Ortmann et al., 1996, 1997; Schmid, 1996) although the duration of the period of inactivity and the degree to which it characterizes all individuals requires further study.

It remained to be documented whether *M. rufus* underwent the distinct seasonal variations in body weight and activity levels characteristic of its west coast congeners. It has been stated that the climate in the eastern regions is not as highly seasonal as in the west (Donque, 1972) and yet seasonal periods of food scarcity do occur in Ranomafana (Overdorff, 1991; Hemingway, 1995). Prior to the present study, there were some indications, though no firm evidence, that body weight and annual activity do not fluctuate in *M. rufus* to the same degree as in *M. murinus* (Martin, 1972; Ganzhorn, 1988).

Other data suggested that in *Microcebus*, there may be behavioral differences between the sexes. Specifically, field observations on *M. murinus* suggest that body weight in some females can increase dramatically (Pagès-Feuillade, 1988) and that females may be generally heavier than males (Martin, 1973).

In order to investigate the behavior of *M. rufus,* in chapter five, I hypothesized that seasonal increase in body fat values, followed by reduction in activity during some part of the dry season, occur in some male and female individuals. To test the hypothesis I conducted a long-term trap-retrap study encompassing a full annual cycle. Through weekly mark-recapture sessions, I monitored body weight and tail circumference values (as indicators of body fat) of known individuals. Reduction in activity levels was inferred through individual absence in the traps for part of the dry season. I predicted that these mouse lemurs would metabolize their body fat during this period of lower activity or torpor and would thus return to the trappable population with reduced body weight and tail circumference values.

As in the case of feeding behavior, the fact that my observations covered more than one complete annual cycle, permitted an evaluation of seasonal changes in mouse lemur behavior.

In chapter six, I present an overall summary of the results from chapters four and five, discuss the annual cycle of *Microcebus* compared to seasonal environmental fluctuations and compare life-history traits of mouse lemurs to those of other small mammals. Lastly, prompted by the results and discussion of the present research, I suggest areas of future research that would further enhance our understanding of *Microcebus rufus* behavior and ecology.

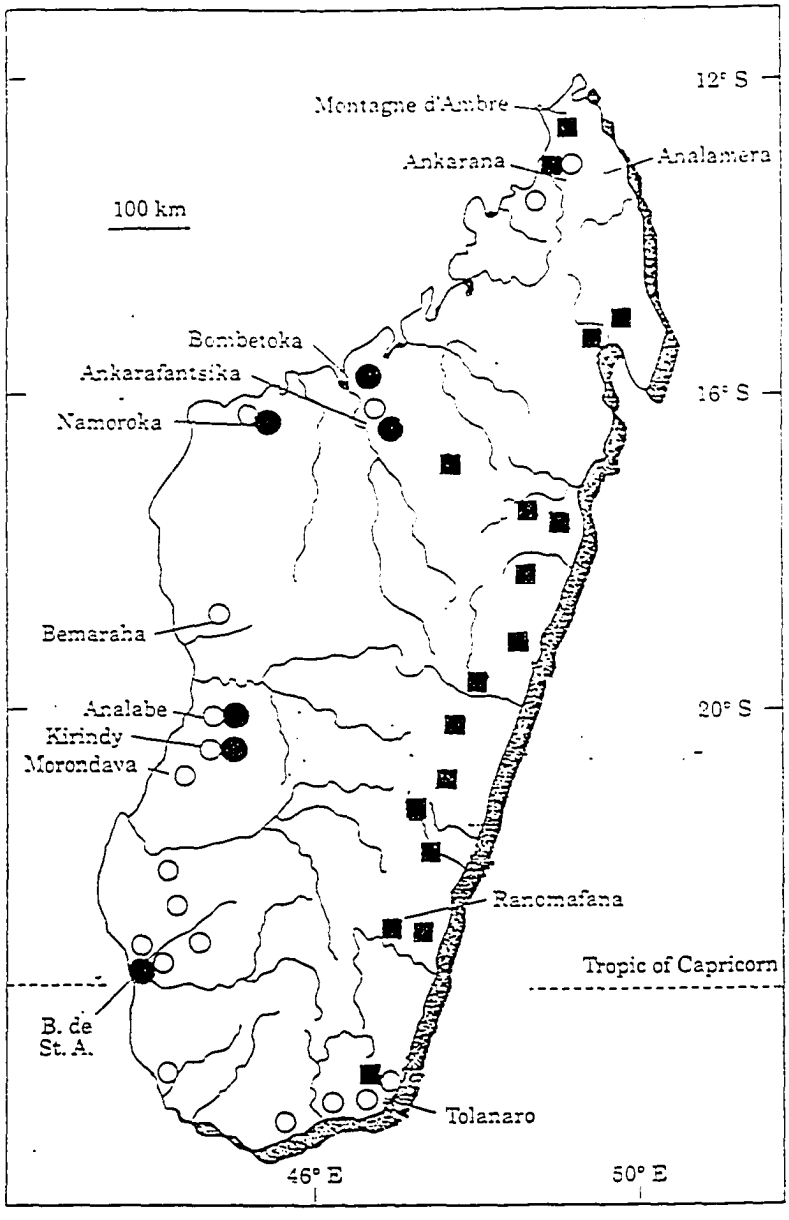


Figure 1.1 Distribution map of *Microcebus murinus* (○), *Microcebus rufus* (■), and *Microcebus myoxinus* (●). From Atsalis et al., 1996.

CHAPTER TWO

DESCRIPTION OF RESEARCH SITE, METHODS AND MATERIALS

This chapter presents a description of the study site and the methods and materials used to conduct the research including trapping methods, fecal analysis, radiotracking, nocturnal censusing, phenological sampling, insect sampling, collection of climatic data, and phytochemical analysis of fruits eaten.

Description of Research Site

My study of *Microcebus rufus* was conducted from January 1993 to June 1994 in the Ranomafana National Park (RNP) located in southeastern Madagascar in the province of Fianarantsoa (21°16'S and 47°20'E) (see Figure 1.1). The park, home to an integrated conservation and development project, was inaugurated in 1991 (Wright, 1997). It encompasses 43,500 hectares of lowland to montane rainforest, ranging from 500 to 1500 m. RNP belongs to that part of the eastern biogeographic region of Madagascar characterized by the highest species diversity and endemism in the country and among the highest in the world (Mittermeier et al., 1986). Characteristic of this richness are the twelve taxa of primates known to be found within Ranomafana National Park: *Avahi laniger* (Family Indriidae), *Cheirogaleus major, Microcebus rufus* (Family Cheirogaleidae), *Daubentonia madagascariensis* (Family Daubentoniidae), *Eulemur fulvus rufus, Eulemur rubriventer, Hapalemur aureus, Hapalemur griseus griseus, Hapalemur simus, Varecia variegata variegata* (Family Lemuridae), *Lepilemur* sp. (Family Lepilemuridae), and *Propithecus diadema edwardsi* (Family Indriidae). Of RNP's lemur species, five are nocturnal: *A. laniger, C. major, M. rufus,*

D. madagascariensis, and *Lepilemur* sp. (The classification followed here is that of Delson, et al., in press.)

Most studies of the primate population have been conducted on the diurnal species (e.g. Dagosto, 1989; Glander et al., 1992; Wright, 1992, 1995; Wright et al., 1997; Merenlender, 1993; Overdorff, 1993, 1996; Hemingway, 1995; Yamashita, 1996; Balko, 1997) but a few have focused on the nocturnal species (Harcourt, 1987, 1991; Wright and Martin, 1995; Roth, 1996; Atsalis et al., 1996).

I conducted my study at the Talatakely Research Station which encompasses a 5 km^2 mapped trail system within disturbed rain forest on steep terrain found at 1100m elevation. Talatakely was selectively logged in 1986 and 1987 (Wright, 1995), so there exists an understory of lower stature trees below the 20-25 m canopy, which makes *Microcebus* activity and nest sites sometimes easier to detect and observe. This understory is characterized by many shrubs belonging to the Rubiaceae and the Myrsinaceae, bamboo, epiphytes and epiphytic semi-parasites, particularly mistletoes, in the genus *Bakerella* (Turk, 1995).

Several viverrid carnivores, possible predators of *Microcebus* and other lemurs, exist in Ranomafana. Nocturnal viverrids include *Cryptoprocta ferox, Fossa fossana, Galidictis fasciata* and *Eupleres* sp. Predation has been documented for *Propithecus diadema edwardsi* by *Cryptoprocta* (Wright et al, 1997). The diurnal viverrid *Galidia elegans* and the boa *Sanzinia madagascariensis* have been observed to prey on *Cheirogaleus* (Wright and Martin, 1995). The Malagasy long-eared owl, *Asio madagascariensis*, has been demonstrated to be a significant predator on *Microcebus murinus* (Goodman et al., 1991). Other avian predators of *Microcebus* are the Malagasy serpent eagle, *Eutriorchis astur*, the Madagascar harrier-hawk,

Polyboroides radiatus (seen to prey on *Microcebus* while in their daytime sleeping nests) (Emile Rajeriarison, pers. comm.), Henst's goshawk, *Accipiter henstii*, and the Malagasy scops owl, *Otus rutilus*.

Methods and Materials

Trapping

Trapping methods

Fifty-four Sherman live traps (22.2 x 6.6 x 6.6 cm) were set along 7 trap lines which comprised the main trap area. Due to the steep terrain, only an approximation of a true grid could be established. The main trap area encompassed roughly 27ha and incorporated both forest ridge tops and valleys. In choosing the main trap area I selected an area of comparatively undisturbed, natural forest avoiding high traffic tourist trails, the more degraded areas of Talatakely, such as those near the research cabin, and bamboo patches. Six traps were also set near the cabin to capture individuals for radiotracking.

Traps were set at 50 m intervals following the fixed distance markers of the established trail system. This was done, in part, because a 50 m diameter may approximate the home-range diameter of *Microcebus* (Martin, 1972). Traps were placed 1.5-3 m above ground, in trees that were located 1-2 m into the forest from the trail. The traps were baited with banana on average 9 nights per month for 16 months (range between 4-15 nights/month) and checked at dawn. All traps with *Microcebus* were brought to the research cabin, the rest were cleaned of the uneaten banana and closed. Other small mammals which entered into the trap, usually *Eliurus* (a small endemic rodent), were recorded but released immediately into the forest. All traps with

captured animals were washed prior to their return to the forest and all traps were washed weekly.

Body measurements

When an individual was trapped for the first time, it was sexed and marked with ear notches that provided each animal with a distinct identity. In addition to its ear notch number, an individual was identified as M1,M2 etc if male, and F1, F2, etc if female. Skin from the ear notches was preserved for DNA analysis.

Body weights and measurements were taken using a 100 g Pesola spring scale, a flexible tape measure and a vernier caliper. Following measurement, all individuals were placed in socks which were tied to prevent escape and left undisturbed until they were released at dusk at the site of their capture.

Below I list the measurements and observations which were recorded for each individual. Body weight and tail circumference were taken each time an individual was caught. Other measurements were taken until successive measurements yielded the same results.

- Body weight to the nearest gram.
- Body/tail length: distance from foramen magnum to tip of tail.
- Length of head: greatest distance from back of head to tip of nose.
- Width of head: widest bizygomatic distance perpendicular to the previous measurement.
- Ear length: distance between basal end of tragus and tip of pinna.
- Ear width: maximum width perpendicular to the previous dimension.
- Length of tail taken on ventral side from base (junction with the peri-anal area) to tip.

- Circumference of tail taken at its widest point near base.
- Hindfoot length: distance between tarsus and tip of longest digit, excluding the nail.
- The animal's general state of activity (active or lethargic).
- Pelage color and condition.
- Distinguishing features, traumas or significant changes in an individual's appearance from a previous capture.
- The presence of external parasites was noted and ticks were collected for future identification at the American Museum of Natural History of New York.

Reproductive condition

In females the vagina is usually imperforate except during periods of estrus and parturition. For several days prior to opening, the vulval area becomes red and swollen. For each female, I noted whether the vulval area was imperforate, red and swollen, or open. I also noted whether or not she was lactating by gently squeezing her nipples to check for milk production.

In males scrotal size is small during the non-breeding season. During that period it was difficult to obtain a useful measurement of testicular size. In early August the testicles began to enlarge and remained so until November. I used vernier calipers to measure length and width of the scrotal sac.

Longitudinal data on individual mouse lemurs

Body weights and tail circumferences and associated capture dates were plotted for all individuals whose trap history, in 1993, covered the time period of February to September. The months April through July fall in the initial phase of the dry

season when seasonal fattening was expected to occur, and August through October coincided with the onset of the breeding season when all mouse lemurs were expected to be active. For those individuals whose trap history shows a complete interruption for at least one month during the dry season, I tested to see if the difference in body weight and tail circumference between the "last capture" prior to absence from the traps and "first capture" following this period was statistically significant (see section on statistical methods below). In this study, I inferred that absence from the traps for part of the dry season implied reduction in activity level for that period.

Monthly average population values

1. For all individuals I determined monthly average body weights and placed them in one of four weight classes: 20-30 g, 30-40 g, 40-50 g and 50+ g. I plotted the data as monthly histograms to graphically demonstrate shifts in population size classes over time.
2. For the period between June 1993 and May 1994, I determined monthly male and female averages and an annual average for body weight and tail circumference. I then determined the percent deviation of each monthly average from the annual average in order to identify periods of greatest magnitude in monthly body changes (Petter-Rousseaux, 1980).
3. I compared annual body weight averages between males and females to determine if statistically significant differences could be demonstrated at the population level.
4. I calculated monthly sex ratios (the number of individual males trapped to the number of individual females trapped) for information on differences in activity levels between males and females.

Constraints on the Interpretation of Trap Data

Several factors could influence the patterns I have reported. The sex ratio that results from trapping represents only the trappable fraction of the population. Therefore, the method of capture can influence the sex ratio. Capture in live traps may create a bias in favor of male

M. rufus if they are more active than females as has been shown to be the case in *M. murinus* (Martine Perret, pers. comm.), while capture in nests may favor females who tend to sleep together. Although for the purposes of this project, only results from trapping are considered (and not for example radiotracking data), the male bias in the sex ratio of the total number of animals trapped may be the result of more active males having larger home ranges (see below). In addition, potential bias in the results of trapping can be introduced depending on the intensity of moonlight luminosity. It has been demonstrated that small mammals, including prosimians, react to the presence of the full moon by reducing movement (Nash, 1982; O' Farrell et al., 1994). In this study moonlight levels were not taken into account when determining trap session nights. However, trap sessions took place randomly and frequently, thereby minimizing the effects of skewing in one direction or the other. Nevertheless, since biased trap success may result in erroneous information concerning the age structure, sex ratio, size etc. of the population, these data taken alone may not reflect true population composition. Their value lies predominantly in monitoring relative changes throughout the year rather than describing overall population structure. Finally, repeated captures can lead to loss of body mass due to stress and/or duration within the trap without food. Potential influences of trapping on body weight have been examined in non-primate small mammals (e.g. Kaufman and Kaufman,1994). The extent of loss is dependent on

a number of factors such as age, sex, reproductive condition, season, precipitation and temperature. In this study, many individuals were trapped repeatedly which meant that data could be averaged, therefore minimizing, but not necessarily eliminating, the effect of chance fluctuations in the values measured for each individual.

Collection of Dietary Data

Fecal analysis as a method for studying diet

Direct observation of feeding behavior was hindered by the low light levels in the understory at night, the study animal's small size, the thickness of the vegetation and the frequently rainy conditions during nocturnal observation. Instead, fecal analysis proved to be the most consistent method for gathering feeding data on *M. rufus*, although supplementary data were collected during nocturnal censusing and radiotracking.

Many studies on non-primate mammals rely on fecal samples from live-trapped animals to monitor individual and populational seasonal dietary patterns (e.g. Fenton et al., 1981). In primates, fecal analysis has been used to study diet in difficult to observe small nocturnal species of *Galago* (e.g. Harcourt and Nash, 1986b) as well as the large but elusive apes (e.g. Tutin and Fernandez, 1993; Yamagiwa et al., 1993).

One advantage of collecting fecal samples from live-trapped individuals, as in the case of small nocturnal primates, is the ability to verify the identity of the depositor (Moreno-Black, 1978). By knowing the identity of the individual it is possible to select samples from a large number of individuals thereby avoiding inadvertently biasing results toward the preferences of a few individuals only. Comparisons can then be made between different groups of individuals, e.g. between males and females.

Fecal analysis is useful in compiling lists of fruits, when seeds are swallowed, and insects, when chitin is present, and constitutes an important method of determining seasonal changes in diet in species that are difficult to follow (Tutin and Fernandez, 1993).

The main problem encountered with fecal analysis is the identification and quantification of the fecal food remains. Identification requires practice but the technique, used also in this study, of creating a reference library of whole insects and fruit found in the forest, to which masticated bits of insect and seeds found in the feces are compared, is an efficient and widely-used field method (Korschgen, 1966; Whitaker, 1988). However, not all seeds can be identified and seeds from species of the same genus cannot always be distinguished from one another (Tutin and Fernandez, 1993; pers. obs.). In addition, when soft plant parts such as pith and skins are found, they are frequently impossible to identify unless reference material (microscope slides) has been previously prepared as a way of comparison. Chitin can be so finely masticated that it becomes unidentifiable. Moreover there is the problem of differential digestibility of different kinds of chitin which makes certain hard-bodied insects more easily recognizable than others (Allen, 1989). SEM analysis has been used to identify small insect remains in bat fecal pellets but this is costly, time-consuming, and cannot be conducted under most field conditions (Coutts et al., 1973).

Another limitation of fecal analysis is that it may not reflect everything that has been eaten (Harding, 1981). Due to differential digestion, fecal analysis favors hard items such as seeds and chitin and underestimates soft plant parts (Williamson et al., 1990; Tutin and Fernandez, 1993) as well as soft-bodied insects such as flies, caterpillars or larvae (Whitaker, 1988). Easily digestible carbohydrates such as gums and sap are not detected through macroanalysis. Furthermore, there is the underlying

assumption that fruit will be represented in the feces by seed presence. Yet there may always be those fruits that are eaten but whose seeds are not ingested. On the other hand, fecal analysis may be a more accurate indicator of insectivory than is direct observation due to the difficulties of actually observing ingestion of insects (Moreno-Black, 1978; pers. obs.).

Quantification, too, poses problems when attempting to compare quantities of different categories of food. In the case of *Microcebus*, the question is how to reasonably quantify and compare the relative consumption of insects and fruit. In this study, I followed the example set by researchers conducting fecal analysis on apes and did not attempt a direct comparison of quantities of differing food categories. Instead, I presented the fluctuations that each undergoes separately. Other methods can be used. By applying a subjective volumetric score of 1-4, Harcourt and Nash (1986a) compared relative fruit and insect consumption in galagos by assuming that one volumetric unit of fruit is equivalent to one volumetric unit of insect. This assumption has no true justification, though the method provides a crude way of comparing the relative consumption of "apples and oranges". The comparison is more meaningful, but not necessarily more justifiable, if true volumes or weights of individual foods eaten are known so that they can be calculated as percentages of total food volume or weight (Korschgen, 1966; Whitaker, 1988). Ultimately, the importance of particular foods, such as fruit versus insects in the diet of *Microcebus rufus*, or any other animal species, goes beyond the question of volume or weight ingested. It is a matter of the interaction between the nutrient (energy, protein, minerals, etc.) content of the food item, the nutritional requirements of the individual, and the energy allotted to extract the contents of the food, i.e. digestibility of the food. As has been done for one other nocturnal

primate, *Daubentonia madagascariensis* (Sterling et al., 1994), these factors can be assessed using a combination of captive and wild populations. This is especially convenient for *Microcebus* because many populations of *M. murinus* already exist and do well in captivity. To date, most of the research on *Microcebus* in captivity centers on the physiological changes associated with its seasonal life-history cycle. Parallel studies on some of the above questions may enhance our understanding of *Microcebus* life history strategy.

Collection of fecal samples and identification of remains

Fecal samples were collected once weekly (the same day each week) from known individuals caught in the live traps which were set throughout a 16-month period. Additionally, due to time limitations, approximately five samples per week were collected randomly from available trapped animals. This number varied depending on the number of animals trapped during the collection night.

Feces were scraped from the trap and preserved in 70% alcohol to be analyzed usually within a few days. The mixture was poured onto a coffee filter to remove the alcohol and then transfered to a slide. The contents were teased apart and examined using a dissecting microscope and natural light or a flashlight. All material within the fecal sample was described even if it eventually remained unidentifiable. Special attention was given to fruit and arthropod remains. Seeds, skins, green vegetal matter, and arthropod remains were relatively easy to discern. Fruit pith was more difficult to distinguish.

The presence of fruit was recorded as either seeds, skin or pith. Seeds within each sample were grouped according to similarity, counted and measured (length and width). When only skins and pith were present, a brief description and a subjective

volumetric score of 1-3 (1=very few, 3=many) was noted. Methods of fruit quantification based on seed presence are described below in "*Analysis of fecal remains. Problems and constraints*".

Fruits eaten by *Microcebus* were identified by matching seeds in the feces to those of fruiting trees in the forest. When a match occurred, a local Malagasy name was provisionally applied with the help of the local field guides with whom I worked, Pierre Raliva and George Rakotonirina, as well as Dan Turk who worked for the Missouri Botanical Gardens. To find the taxonomic name of the plant, I used a master list which provided names (at least to family level) of the local plants. This list was compiled through the joint efforts of the Missouri Botanical Garden and Ranomafana field guides. More information on the fruits eaten was found in Turk (1995).

Seeds that could not be identified immediately were preserved for possible future identification. Other seeds found in the forest were also preserved to be used as reference material for seeds found in future fecal samples. The length and width of seeds were measured using vernier calipers.

Seeds of similar species could not usually be distinguished from one another. For example, there were several species of the semi-parasitic epiphyte, *Bakerella*, which produced fruit at the same time and whose seeds were almost identical in appearance. I could rarely distinguish, based on seed presence in the feces, if more than one species of *Bakerella* had been eaten. Therefore they were counted as one fruit type.

Seeds that remained unidentified were given an "Unidentified Fruit" designation accompanied by a number, e.g. Unidentified Fruit 1. In cases where seeds were similar enough to possibly belong to the same fruit they were all placed in a single group

designated as an "Unidentified Fruit Category" and given a number sequential to the "Unidentified Fruit" groups previously mentioned (see Tables 4.7 and 4.8).

Following a match with seeds found in the forest, fruits could be collected from the forest to determine color of ripe and unripe fruit, average weight of fruit, average size of fruit (length and width using vernier calipers), number of seeds per fruit, location of fruit on the tree (trunk or branch) and characteristics of fruit growth (singly, in clusters).

For each sample, a brief description of insect and spider remains (antennae, legs, wings, head capsules, tarsi, etc.) and a 1-3 volumetric score were recorded. Volumetric determination was based on amount of slide covered, though the material was usually so finely masticated that it occupied only a small part of the slide.

I was able to identify some insect and spider parts from the tarsi, legs and antennae by using Peterson's Field Guide to Insects (1970) and by comparing fecal remains to whole insects found in the forest. However, since identification requires expertise and practice, chitin remains from a subsample (115) of fecal samples, collected between April 1993 and May 1994, were brought back to the U.S. and identified by taxonomic expert Julian Stark (Department of Entomology, the American Museum of Natural History in New York). Identification of insect remains was usually to order and whenever possible to family level. The minimum number of prey items in each fecal sample and the length of the prey were estimated by reconstructing the remains. Insects were grouped into three length categories, <5 mm, 5-15 mm, and, >15 mm, the same subcategories used to classify insects captured during biweekly collections to measure prey abundance in the forest.

Number of fecal samples

Climatic conditions and seasonal changes in the activity patterns of the study species affected the number of fecal samples collected during each month of the study. The average number of fecal samples collected per month was approximately 20 but ranged from 9 to 34. Korschgen (1969) has argued that when attempting to determine the components of diet, span of sampling time is more important than actual number of samples . In the present study, there were samples from each month and across seasons. Nevertheless, since my intention was to look at seasonal fluctuations in the diet, the number of fecal samples collected monthly could affect results. However, the correlation between the number of samples collected each month and the total number of fruit genera found monthly in the feces was not statistically significant (Spearman correlation, rs=0.131, n=16), suggesting that the addition of more fecal samples did not necessarily result in finding more fruits in the feces.

Possible biases can also arise due to over-representation of frequently trapped individuals in the total pool of fecal samples. Only 22% of known males and 16% of known females contributed more than three samples each. Nevertheless, as a precaution against individual-specific dietary biases, selected tests were conducted in which multiple samples from the same individual were averaged.

Analysis of fecal remains

As a first approximation to understanding the dietary habits of *M. rufus*, fecal samples were placed in one of three gross dietary categories depending on whether the sample contained fruit remains only, insect remains only, or both fruit and insect remains (Harcourt and Nash, 1986b). A loglinear model (likelihood ratio chi square) was applied directly to the frequency counts of the three categories to test for

interaction between time period and dietary category. To obtain expected cell frequencies large enough to make use of this model, data from consecutive two month intervals were pooled. Multiple samples from the same individual were treated as independent observations.

To test the dietary hypotheses outlined in Chapter Four and to determine how frugivory and insectivory fluctuate over time, methods of quantifying the two variables were required. A single method of quantification is considered insufficient to provide meaningful results (Korschgen, 1969). One reason for this is the difficulty of directly comparing quantities of fruits and insects. For the present analyses, several values, some of which have been used to analyze ape fecal samples, were used to gain a measure of the fluctuations in quantity and diversity of fruits and insects eaten.

1) To quantify the amount of fruit found in each fecal sample, I initially calculated two values, the "Minimum Number of Individuals" for fruit (MNI-F) and the "Number of Identified Fruit Individuals" (NI-F). Both values are based on the number of seeds in a fecal sample. If I could identify the fruit species from which the seeds came I could determine the number of fruits eaten by that particular *Microcebus* individual from the number of seeds contained in a typical fruit. If a known fruit species contained a variable number of seeds, e.g. one or two, I always assumed that the minimum number of fruits had been eaten (one fruit and not two) if two seeds were found in the feces. If a fruit species contained many seeds I would count its presence as a single fruit in the feces irrespective of the number of seeds found. The NI-F was determined only on the basis of seeds that corresponded to known fruit species (i.e. when the number of seeds per fruit was known precisely). Skins were not included in the NI-F. In contrast, the MNI-F includes all seeds and skins even when the fruit species is

unknown. When a fruit species was unknown, the actual number of individual fruits to which the unknown seeds in the feces corresponded could not be determined and was reported as a single fruit. When only skins were found, I counted them as belonging to one individual fruit. Skins were not counted as an extra fruit if seeds were present. The same applied to other fruit parts that may have been present except for what may have been fruit flesh, which was discounted; in reality I was rarely able to distinguish what may have been fruit pulp from something else.

The two values did not differ significantly in the results they gave, either when compared as monthly averages or as individual fecal samples (for monthly averages: $r_s=0.815$, $p<0.01$, $n=16$; for individual samples: $r_s=0.865$, $p<0.01$, $n=331$). Thus, all analyses were conducted using the MNI-F.

The MNI-F is a conservative way of estimating fruit quantity in the feces. If the fruit from which the seeds are derived has been identified then the true number of fruits consumed by the individual mouse lemur can be determined. If however the fruit from which the seeds are derived has not been identified, I assume that they belong to one individual fruit even though more fruits may have been consumed. Since close to 44% of all fecal samples containing fruit seeds had at least one type of seed which remained unidentifed, the MNI-F underestimates the number of individual fruits eaten by *Microcebus rufus*.

2) The mean monthly number of fruit species found per fecal sample has been used as a measure for quantifying seasonal fluctuations in fruit versus other plant parts eaten, in analyses of ape diets (e.g. Tutin et al., 1991; Tutin and Fernandez, 1993; Yamagiwa et al., 1993; Remis, 1994). In this analysis, a similar measure, "Number of Fruit Types" (NFT), is applied to each fecal sample. This measure differs from the MNI-

F in that it pertains to diversity and not quantity. Seeds were grouped together according to similarity and are counted as one vernacular species. When skins but no seeds are present, they are counted as one vernacular species. The NFT is still a "minimum" measure because seeds from similar plants cannot always be distinguished from one another and are counted as one vernacular species. For example, several kinds of *Bakerella* are counted as one vernacular species even though it is obvious that there are several different species or subspecies fruiting at the same time. Another example comes from the fruit whose local name is "Voanananala" (*Psychotria*, family Rubiaceae). We found nine different kinds of "Voanananala" in the forest, four of which were known to be eaten by mouse lemurs. Because we could not distinguish the seeds of the various kinds of "Voanananala" from one another, they were counted as one vernacular species.

The advantage of the NFT is its more objective nature as compared to the MNI-F because it does not require as many assumptions. As long as seeds can be grouped together according to similarity, they can be included in this measure whether or not their identity is known. However, the NFT also has limitations and is not sufficient to describe the diversity of fruits eaten for the following reasons:

Although *Microcebus* may be able to eat a large variety of fruits per night, gut passage is fairly rapid (average 4.05 hours, Harste, 1993) so that the following morning's fruit remains may represent only a fraction of the night's feeding activity. In addition, due to its small size, the amount of fruit that an individual *Microcebus* is capable of ingesting during a nightly feeding bout is lower than that for an ape for a value similar to the NFT was originally formulated. Therefore, individual fecal samples cannot adequately represent the possible diversity of fruit eaten. On the other hand,

small size may limit *Microcebus* nightly ranging patterns so that fewer types of fruiting trees are visited per night. For these reasons a measure of diversity based on multiple fecal samples, such as the TFT described below, is useful.

3) An additional measure of diversity of fruits eaten, also used with chimpanzees and gorillas, is the total number of different fruit types found in the monthly collection of fecal samples (e.g. Tutin and Fernandez, 1993; Yamagiwa et al., 1993). In the present analysis, this measure will be termed "Total Fruit Types" (TFT) found per month. It is based on the findings for the NFT. As previously indicated, there is no statistically significant correlation between the TFT and the number of fecal samples collected per month making it a good measure for quantitying diversity of fruit eaten.

4) A 0-3 volumetric score (VS) was used to quantify the amount of invertebrate material (chitin and spider parts) found in the feces. A similar type of subjective scoring system has been used by other researchers conducting fecal analysis on apes (e.g.Tutin and Fernandez, 1993; Yamagiwa et al., 1993) and galagos (Harcourt and Nash, 1986b). A volumetric score was necessary since, with the exception of the fecal samples brought to the U.S. for inspection, I was not able to determine the number of individual arthropods to which the remains corresponded.

5) A "Minimum Number of Individuals" for insects, designated as the MNI-I, was ascribed to each sample of arthropod remains examined in the U.S. as a way to quantify prey items. The MNI-I for insects was determined by reconstructing the number of prey items from the remains of body parts present.

6) The diversity of insects eaten was measured for the subsample brought to the U.S. by determining the monthly average number of insect orders contained in fecal

samples. This measure of diversity is less fine-tuned than the NFT value used for fruit because an order is a broader grouping than a vernacular taxon. The reason for not using a finer distinction is that identification to lower taxonomic levels was frequently not possible.

For the purposes of analysis, the following information was determined for each month:

1. The percent of fecal samples containing fruit only, insects only, or fruit plus insects.
2. The total number of fruit types (genera or species) found in the month's fecal samples (TFT).
3. The average number of different fruit species or genera per fecal sample (NFT).
4. The percent of fecal samples containing each identified fruit type.
5. The average minimum number of fruit individuals per fecal sample (MNI-F).
6. The average volumetric score per fecal sample for arthropod remains (VS).
7. For those fecal samples returned to the U.S., the average minimum number of insects per fecal sample, MNI-I, average length of insect per fecal sample and average number of insect orders per fecal sample.
8. For those fecal samples returned to the U.S., the percent of fecal samples containing each insect order and the average number of insects per fecal sample belonging to each insect order.

Radiotracking

Materials and procedures

Four individuals were radiotracked at different times during the course of this project. I used a Telonics TR-4 receiver and a two-element RA 14 flexible antennna. Two Telonics (SIN 1226 and SIN 1225) and two Wildlife Materials SOM 2038 transmitters were fitted around the necks of individuals using cable-ties. The Telonics radiocollars had a peak current of 1.3, a pulse rate of 35, a pulse width of 19 milliseconds and an estimated battery life of 89 days. The Wildlife Materials collars had a peak current of 1.3, a pulse rate of 30, a pulse width of 15 ms and an estimated battery life was 98 days. Each transmitter with cable tie weighed between 4-5 g. The Telonics transmitters were polymerically sealed while the Wildlife Materials transmitters were coated in epoxy which supposedly rendered them 100% waterproof.

A team of at least two observers participated in each follow. One observer held the antenna and receiver and attempted to determine the location of the animal while another recorded data. Leica binoculars (7X42), headlamps and Maglites were used to locate and observe the individual.

Radiotracking took place between dusk and 2 am. Duration of radiotracking depended on weather conditions and our ability to locate the radiocollared individual. Reflective tape which made the radiotracked individual more visible was attached to each radio. When in view, data on the mouse lemur's behavior and location were taken continuously. When the individual was not visible but radiotransmission was still being received, data on location based on a system of triangulation were recorded by

taking compass bearings at two different known trail markers. This information was subsequently used, in conjunction with nest site locations, to determine home ranges.

The number of hours spent radiotracking were calculated from the time we detected the first radiosignal to the time we last heard the signal prior to terminating the radiotracking session. The time between these points included periods when the animal was out of sight and when the radio signal was lost.

"Sighting" of a radiotracked mouse lemur was recorded as a single event at the instant of the observation irrespective of how long the individual remained within view.

Problems and constraints

Radiotracking proved less helpful than expected as an aid to obtaining behavioral information on *Microcebus rufus* for the following reasons:

1) Both the radiotransmitters and the receiver suffered from water damage and functioned improperly. The receiver functioned moderately well when weather conditions were dry or if allowed to dry sufficiently following exposure to moisture, but it never achieved the 100 m distance in reception specified by the manufacturer.

The animal's tendency to chew on the antenna of the transmitter may have sometimes hindered transmission. We were able to reduce this tendency by threading the antenna through the cable tie around the animal' s neck so that only a small portion protruded in the back.

2) The lifespan of a radiotransmitter was expected to be about 90 days. However, when we were unable to get a signal, we could not be sure if this was due to malfunction or if the individual had moved out of his range. Male 22 was never recaptured so it remains unclear why his radiosignal was lost after 21 days.

The radiotransmitter of Female 22 was functioning, when it was removed, 30 days after she was fitted. We lost Female 2's radiotransmission after 8 days. When she was captured 42 days later, the radio was non-functional. Lastly, the radio of Female 19 functioned for 12 days. A record of its working condition when she was captured 22 days later was lost.

3) Direct observation of the radiocollared individual was hindered by its small size, the thickness of the vegetation and the heights which *Microcebus* frequented. On the rare occasions when feeding behavior was observed, it was difficult to discern what exactly was being eaten. We sometimes guessed what the animal might be eating based on its general behavior rather than our ability to visually distinguish food items. Since feeding and other behavioral observations of radiocollared individuals are rare and constitute a small proportion of total radiotracking time, they are reported as anecdotal observations.

4) Due to the above problems and constraints my initial plan of radiotracking 10 individuals for a month each was modified. Although my plan was to give equal emphasis to radiotracking and trapping, the latter became by far the more important method.

Nocturnal Censusing

Nocturnal censusing took place along one of three predesignated routes. All three routes followed the trail system already established at Talatakely. Route BF was 1790 m in length, route C was 1943 m and route BF/F was 1060 m. For variation, on several occasions we conducted "freelance" observations, where we walked along any path.

Censusing took place ad libitum. Censusing began either at dusk or around midnight. It continued until we reached the end of the predesignated route or until rain forced us to stop. Maximum time of a nocturnal census was approximately five hours but a typical walk was between 2 to 3 hours. Given the length of the three predesignated routes and the average time of a typical walk, the average pace of each census was 700-800 meters per hour.

Two observers always participated in the census. Observers would walk slowly along the trail shining light from headlamps and flashlights in a 180° arc in front of them. Red light filters and night vision scopes were not used. Each time a nocturnal primate was sighted the following data were recorded: Time sighted, species, observers' location on the trail, distance of animal from observers, perpendicular distance of animal from trail, height of animal, activity (feeding, traveling, moving, resting, etc.), vernacular name of the plant in which the animal was located, position of animal on plant (trunk, liane, branch, vine, etc.), and a brief description of the surrounding forest type (bamboo, guava patch, tall forest, short forest).

If the animal was *Microcebus*, instead of continuing the census following initial data entry, we would attempt to observe it from the trail as long as it was visible. Data were taken continuously as long as the animal was in view.

For each month, I determined the number of feeding observations recorded during the total number of hours spent walking. A feeding observation records the act of feeding on a plant part or insect by one individual.

Resource Availability

This section describes the methods used to estimate plant and animal food availability and abundance in the forest. Phenological monitoring focuses on overall

forest production, through four botanical plots, and on the production of particular species that serve as food sources for *Microcebus rufus*.

Description of composition of botanical plots

Within each plot we recorded the circumference (later converted to diameter) of all individual plants greater than or equal to 9.0 cm (or ≈ 3.0 cm diameter) at 1.2 m height. This yielded DBH, the standard diameter at breast height of ecologists. A small circumference was chosen to include understory and midstory trees in addition to those of the upper canopy. Height was estimated by eye to the nearest meter and reliability of estimate were tested among three observers. Plants were flagged, numbered and given a provisional local name by guides who had previous botanical training. A master list (the same used to determine *Microcebus* plant resources, which was compiled by local guides and the Missouri Botanical Garden) was consulted to designate family, genus and, whenever available, species names.

Relative dominance was estimated as the percent of basal area calculated at the vernacular species, genus and family levels by using the following equations:

$$\text{Relative Dominance} = \frac{\text{Basal area of species, genus or family}}{\text{Total basal area in the sample}} \times 100$$

Basal area is the sum of the cross-sectional area ($\pi \times R^2$, where R is the radius of a cross-section of the plant), at breast height, of all individuals of a vernacular species, genus or family.

Phenological samples in botanical plots

To obtain a general assessment of fruit and flower availability and abundance as potential food resources, trees and shrubs within four botanical plots were chosen

for systematic phenological monitoring. Plots were designated as X, E, D and SL and placed along trails located either within the designated trap site area or along my censusing route. Each plot measured approximately 50 by 10 m in area except for Plot D which was 43 by 10 m. Specific location of each plot depended on ease of accessibility (steep slopes were avoided) and the desire to incorporate a variety of habitats. Thus, two plots were situated in damp low areas while two were placed on drier hill ridges.

At the beginning of the study period 201 trees were being sampled in plot "X", 211 in plot "D", 275 in plot "E" and 234 in plot "SL", totaling 921 individual plants. Changes occurred during the duration of the project as plants died and were excluded from further monitoring.

Phenological data on the presence of unripe fruit, ripe fruit, buds and flowers were recorded on a scale of 0-5, using 0.5 intervals, following Oates (1977). Thus, a score of 2.5 was given when we judged that the plant crown had 50% of the maximum possible quantity of the phenophase in question. Reliability of the scores was tested among 2-3 observers. Local guides having previous familiarity with the forest flora proved indispensable in recognizing the typical fruiting and flowering patterns of the various plant types and in distinguishing the various phenophases of the plants monitored.

Phenological data were recorded during the first week of each month, from February 1993 to December 1994 for a total of 23 sampling periods. Data for the period following my departure, from July to December 1994, were collected by Ranomafana National Park guides. Monthly data from the four plots were plotted separately and then consolidated. Although data were recorded for all phenophases, in the analyses I concentrated on fruit production because fruit was the major plant

dietary item for *Microcebus*. Since determining ripeness of fruit through observation of seeds in the feces is not possible, it was unclear which stage of fruit ripeness for any species, *Microcebus* preferred. Therefore, I conducted analyses based on the presence of three fruit categories: ripe fruit only, unripe fruit only and all fruit (either ripe or unripe). Phenological data were compared to rainfall and temperature data to determine seasonal patterns in phenophase production.

Description of community-level phenological patterns:

I determined the monthly proportion of all individual trees and shrubs that contained any quantity of buds, flowers or fruit. In addition, I determined the monthly number and percentage of trees and shrubs within each particular phenophase.

I also determined monthly diversity of trees and shrubs within each phenophase by determining the proportion of different vernacular taxa which contained any quantity of buds, flowers or fruit.

I conducted these analyses counting all plants with phenophase abundance scores of 0.5 to 5.0. Since the lower scores of 0.5-1.5 were frequent but represented only a small amount of fruit, it was often difficult to clearly discern phenological patterns. Therefore, I repeated these analyses using only plants having a score of 2 or greater.

Description of the phenological patterns of particular families dominant in the understory:

The majority of the angiosperm plants which made up the composition of my botanical plots were 10 m in height or under, and the average height of all plants was 7 m. Therefore, I separately investigated the phenological patterns of two common families, dominant in the understory, the Myrsinaceae and the Rubiaceae, by

determining the monthly number and percentage of any plants within these families bearing any quantity of buds, flowers or fruit. Previous reports on the phenological patterns of the Ranomafana forest have not specifically investigated the phenophases of understory plants. Some of the shrubs in the two families I selected, such as *Gaertnera* and *Psychotria*, are known food sources for *Microcebus rufus* and other lemurs.

Phenological samples of* Microcebus rufus *plant resources

Fecal analysis and direct observation yielded information about the plants that constituted dietary items for *Microcebus*. I set up phenological monitoring for each plant eaten by *Microcebus* as it was discovered throughout the study period. Plant resources represented various plant types: trees, shrubs, epiphytes and lianas. Five to ten mature members of the plant in question were located along the established trail system and tagged. Individual plants were chosen for ease of visibility and proximity to the trail. For each plant, the following information was recorded: DBH, total height and height from the base of the tree to where the foliage of the crown begins. If the plant was a liane or vine I recorded the distance from the ground to wherever it had taken root. A vernacular name was used until formal identification was possible.

This phenological monitoring took place biweekly. The same scoring system was used as described for the botanical plots.

Apart from plants known to be *Microcebus* fruit sources, phenological monitoring also included *Micronychia* which had not been found in the feces but whose fruit, buds or flowers were seen being eaten by *Microcebus*. I also monitored two species of *Ficus* because they were presumably food sources for *Microcebus* based on the similarity of many of the unknown seeds in the fecal samples to *Ficus*, though this was not verified

through my direct observation. "Vahihafa", which was identified as a scrambling *Ficus* after the termination of the study, was not included in the phenological monitoring.

This phenology was used to compare the fruiting patterns of plants which are known to occur in *Microcebus* diet, with general plant resource availability, as shown by botanical plot data. For this purpose, only data from the first week of each month were used. The comparison was chosen to reveal how closely *Microcebus* fruit sources follow general fruiting patterns of the forest. Specifically, the following comparisons were performed:

1) I compared the monthly percentage of trees with any fruit in the *Microcebus* fruit source phenological sample with the number of individual trees and shrubs with fruit from the botanical plots.

2) I compared the number of individuals belonging to specific genera and families in the *Microcebus* fruit source phenological sample which were in fruit to the number of individual trees and shrubs with fruit from the botanical plots.

Phenological sampling: problems and constraints

1) A small stem circumference was chosen for plants in the botanical plots in order to include shrubs which might be potential food sources for *Microcebus*. However, small circumference leads to the inclusion of immature plants which do not produce fruit. Thus total fruit availability appears low when compared to total number of plants sampled.

2) Epiphytes and lianas (and herbs) were excluded from the botanical plot monitoring. Later it was found that they constituted important elements of *Microcebus* diet. On the other hand, all plant types included in the diet of *Microcebus* are part of the *Microcebus* fruit source phenological sample.

3) Ripe fruit did not remain on the tree for more than a few days either because it was eaten or because following a short ripening time, it dropped off. A biweekly census of fruit crops would have provided a more accurate picture of general ripe fruit availability in the botanical plots.

4) When adverse climatic conditions sometimes prevented data collection at the prescheduled period, data were taken as soon as feasible within the biweekly interval. The normal schedule would begin the following month irrespective of the intervening time. Exceptions occurred several times. Thus in July 1993, data were taken between the 22nd and the 26th and again only during the first week of September. No data were taken in August. In January 1994, data were taken between the 12th and the 17th. Sampling is incomplete for this month for the SL plot but data were taken normally in February. An intervening cyclone prevented data collection on the other plots until the end of that month. Data collection was resumed for all plots in mid-March 1994.

5) During the course of the study, careful observation of the leaf and fruiting patterns indicated that some plants that had been given a single vernacular name were, in fact, different species or, possibly, subspecies. This affected our *Microcebus* fruit source phenology. Thus, when it was detected that an initial sample actually contained different species, more plants were added to increase the sample of each separate species or subspecies to at least five individuals. Species that were discovered not to be part of *Microcebus* diet were not included in the analysis.

Sampling of insect abundance

To evaluate whether *M. rufus* selects its prey or eats whatever is available, it was necessary to compare diet with insect abundance in the forest. I investigated

fluctuations in insect assemblages primarily at the order level over a period of ten months to obtain a crude measure of their availability as potential food resources for *Microcebus*. This is the first time insect abundance and monthly fluctuations have been measured in Ranomafana. I conducted comparisons based on monthly variation in insect orders captured, number of insects captured and fresh weight and length categories.

Considering the arboreal habits of *M. rufus*, a method appropriate to collecting flying insects was used (modified from Smythe, 1982).

Collection took place in the middle and at the end of each month at the same two collection sites. Therefore, four "collection sessions" took place each month (two collection sessions per night, two nights per month) unless otherwise indicated.

One collection site was set up outside the Talatakely research cabin and the other outside my tent. Both sites were located underneath tarps to afford collectors and equipment protection from the rain. Although both sites were located within the forest they were surrounded by small clearcut areas. To check whether this would affect collection results, early in the project I conducted an additional collection at a location in the forest far from the cabin and tent area. Results from all three sites were so similar that only the initial two sites were maintained.

With the help of RNP research guides, insects were captured, at both sites simultaneously, for four hours following nightfall, which occurred between 18:00 and 18:30. A white sheet was suspended vertically facing the forest. At the tent site, a black light was tied just above the sheet while two lamps fueled with petrol were placed at the foot of the sheet. At the cabin site, two night lights powered by solar energy were used as sources of light. Since a second black light was unavailable, a blue filter

placed over one of the night lights approximated the black light used at the tent site. As insects landed on the sheets, they were captured using killing jars with ether. The various sources of light were used to attract different varieties of insects.

At the end of each collecting session the following data were recorded:

- Rainfall accumulation and temperature during the collection session.
- Total fresh weight of insects captured weighed separately for each site using a 10 g Pesola balance.
- Total number of insects captured at each site.
- Number of insects within each identified order, and whenever possible, number of insects within identified families.

In addition, to obtain an idea of size diversity within and between insect orders, all insects were classified according to three length categories, <5 mm, 5-15 mm and >15 mm.

Insect abundance can vary considerably within the same month. For example, in the middle of November 1993, 322 insects were captured compared with 1612 at the end of the month. In the middle of May 1994, 361 insects were captured compared with 55 at the end of the month. A single monthly average of insect abundance was computed for comparison with monthly phenological data and monthly averages from fecal analysis. This monthly figure was determined by calculating an average over both collection times and collection sites. There was only one collection session in July 1993. During both collection sessions in December 1993 and during the first session in March 1994, only one site was sampled.

Insects were identified initially by Emile Rajeriarison, a local guide with previous training in insect identification and later by myself. Peterson's Field Guide to Insects

(Borror and White, 1970) was the main reference source used. Warren Steiner (Smithsonian Institution) later corrected misidentifications.

Peterson's field guide uses an older classification with two orders, the Heteroptera and the Homoptera. Later classifications (such as the one presented in Borror et al., 1981 and used by Julian Stark to identify the chitin remains in the feces which I brought back to the U.S.) rank the Heteroptera (bugs) and the Homoptera (cicadas, leafhoppers etc.) as suborders of a single order of Heteroptera. The latter taxa are used throughout the thesis.

Additionally, the designation Orthopteroid used by Julian Stark is a superordinal taxon that represents the old concept of Orthoptera, containing crickets, mantises, grasshoppers, cockroaches and walking sticks.

Sampling of insect abundance: observations and constraints

1) Smythe (1982) states that light traps measure general seasonal abundance of insects but that the sampling method is biased in favor of the flying phototropic insects that are attracted to the particular light source being used. As an example, he mentions orthopterans which were never captured using his technique. Contrary to his experience, we captured most major orders of insects, including orthopterans. However, not all orders were represented equally and this could reflect either seasonal abundance, or the capture method, or both. For example, Lepidoptera were present every month but their abundance fluctuated while Dermoptera were captured only twice. In the latter case it remains undetermined whether the two instances of capture represent chance events or true seasonal fluctuations in abundance.

2) The method used does not sample terrestrial or rarely-flying spieces nor those that frequent the upper heights of the forest, both potential resources for *Microcebus*.

3) Collections did not begin until August 1993 and continued only until the end of May 1994. Data to test whether June and July are months of lowest insect abundance are not available from this study. However, previous observations have shown that insect abundance is extremely low at RNP in July (Patricia Wright, pers.comm.).

4) Data collection continued on two occasions when I was away from the research site but insects were not counted and identified immediately according to usual routine. Collections in December 1993 and the second session of February 1994 were preserved until my return. Therefore, disintegration resulted in underestimation of the abundance of some of the smaller insects, such as Diptera.

5) Although the black lights were maintained for the entire duration of the four hours, I was later informed that the number of insects attracted to black light decreases dramatically after the first two hours following dusk and that continued use of the lights probably had little effect on the resulting yield (Warren Steiner, pers. comm.).

Climatic Data

Weather data were recorded between February 1993 and November 1994. Rainfall was collected in a rain gauge placed in an open area near the Talatakely research station. It was emptied every morning or, in case of extreme rainfall, whenever full. Maximum and minimum temperatures were recorded every morning from a thermometer placed in the shade.

Rainfall in March 1994 may be underestimated since a cyclone rendered the research site inaccessible and data were not collected for 11 days. On the other hand, rainfall for April 1994 is probably overestimated since it includes rainfall accumulation from the last days of March when the container was not emptied.

Phytochemical Analysis

Biochemical analysis was performed on a selection of fruits commonly eaten by *Microcebus rufus*. This part of the study should be considered preliminary. Results are presented as supplemental information to that gleaned from fecal analysis.

Fruits were collected, the seeds removed (except in the case of figs) and the flesh with skin cut into fine pieces. Attempts at sun-drying were not successful as fungus grew on the fruit over the several days required for drying. Most specimens were prepared through a combination of sun and oven-drying (60 °). Phytochemical analyses were performed by Jörg Ganzhorn at the University of Tübingen. He determined total nitrogen, fat, fiber (Acid Detergent Fiber), extractable protein , condensed tannin, and sugar.

Protein concentrations were calculated using two methods:

1. By multiplying total nitrogen from the Kjeldahl by the factor of 6.25. This is a standard but crude estimate of protein content based on the average nitrogen content of protein.

2. By directly extracting protein from the powdered plant material using NaOH and then measuring the protein concentrations in the extract as equivalents to bovin serum albumin.

Condensed tannins were measured as equivalents to Quebracho tannin and are relative units (Ganzhorn, pers.comm.). Ganzhorn warns that his values are usually higher than those of other laboratories.

Besides fruits eaten by the mouse lemurs, two other species were chosen for analysis as an independent basis for comparison. *Pittosporum* and *Dypsis* were chosen because at the time of their collection they were found in abundance in the forest and yet their seeds, which were easily distinguishable from others, were never found in the feces.

Statistical Methods

Data were stored in Microsoft Excel and analyzed using SYSTAT (1992) for Windows. After testing several distributions for normality and finding many variables not normally distributed, non-parametric statistics were selected for use in most of the analyses reported in chapters three, four and five. Contrary to the commonly held view, some non-parametric tests are as powerful as their parametric counterparts and are free of many of the restraining assumptions which characterize the parametric tests (Siegel and Castellan, 1988). For example, Spearman rank correlation was used to examine relationships among indicators of diet and resource abundance. This test is 91% as powerful as a Pearson correlation (Siegel and Castellan, 1988). In addition, the samples involved the analyses conducted were frequently large, thereby increasing the power of the non-parametric tests (Martin and Bateson, 1995). To check for non-linear associations that would not be indicated by the correlation tests, I plotted data on scatterplots prior to analysis. Parametric tests were used to test some of the hypotheses in Chapter Five after establishing that the data were normally distributed. For all tests the level of significance was set at 0.05. Tests were two-tailed, unless

otherwise indicated. The Bonferroni criterion was applied when several tests were carried out sequentially (Rice, 1988).

Materials Used

An adequate supply of batteries is the most critical material needed when conducting nocturnal research. The monetary expense and cost to the local environment from the use of non-rechargeable batteries is high. Therefore, non-rechargeable batteries were used only when solar radiation was insufficient to power solar panels. Otherwise our needs were adequately met by using two solar panels, a gel-cell battery and several Ni-Cad battery chargers (Seelye Equipment Specialists).

CHAPTER THREE

CLIMATE, AND PLANT AND INSECT AVAILABILITY

Introduction

This chapter describes basic features of the physical environment of the Talatakely Research Station. These features include seasonality of climate, and temporal fluctuations through sampling of abundance and diversity of available fruits, flowers and insects. Phenological data were collected from February 1993 through December 1994. Fluctuations in insect abundance were monitored from July 1993 through May 1994. Phenological patterns have been previously examined in long-term studies in various regions of Ranomafana National Park (Overdorff, 1991, 1993; Meyers and Wright, 1993; Hemingway, 1995; Balko, 1997) but data on insect abundance and availability have not been previously reported. Additionally, this is the first study where the phenological patterns of certain plant families dominant in the understory were specifically investigated.

The underlying goal of this part of the study was to sample and describe seasonal floristic and insect availability as potential food resources for mouse lemurs.

Results

Climatic Patterns

Rainfall

Rainfall over one annual cycle encompassing one complete dry season and one complete wet season was an average of 4485 mm (Figure 3.1). Total rainfall from February 1993 (the first month of data collection) to January 1994 was 4262 mm. In 1994, data were collected from January to November for a total of 3847 mm.

Following Hemingway (1995), who also collected climatic data in Ranomafana, I designated the dry season as the period from the first month with less than 200 mm of rainfall following the wet season, to the last month with less than 200 mm, with no more than one intervening month in which >200 mm of rain fell. I designated the wet season to be the period from the first month with greater than 200 mm of precipitation following the dry season, to the last month with greater than 200 mm, with no more than one month intervening with <200 mm rainfall. These criteria suited my data because there was an evident gap between rainfall from December to March (rainfall ranging from 482 mm to 1170 mm) and rainfall from April to November (rainfall ranging from 55 mm to 513 mm). Therefore, I refer to the period between April and November as the dry season and the period between December and March as the wet season. Nevertheless, there was one exception to the criteria used. In 1993, there was over 200 mm of rainfall in two consecutive months. Since this was not repeated in 1994, I decided that the above criteria were adequate for my data.

Based on the above, the rainfall data which I collected encompassed one partial wet season, February and March 1993 (1471 mm), one complete wet season, December 1993 to March 1994 (3150 mm) and two complete dry seasons, April to November 1993 (1490 mm) and April to November 1994 (1179 mm) (Table 3.1).

Cyclones took place in March 1993, February 1994 and March 1994. The cyclone in February 1994 accounts for the 27% increase in rainfall when comparing February 1993 to February 1994. Data were not taken for 11 days in March 1994 when the study site was evacuated due to the cyclone, therefore underestimating total rainfall for this month. This explains, in part, why rainfall accumulation in March 1994 when a cyclone took place, was not much increased compared to March 1993, and why April 1994, which included rainfall accumulation from the end of March, was 41% increased

compared to April 1993. Despite this increase in 1994, April's precipitation remained under 200 mm.

Temperature

Temperatures were highest during the wet season, peaking in December 1993 and in November 1994 (Figure 3.2). Temperatures were lower during the dry season with the lowest temperatures occurring in August 1993 and in September 1994. Average minimal temperatures were significantly correlated with monthly rainfall, though this was not the case for maximal temperatures (Spearman correlation for minimal temperatures, $r_s=0.54$, $p<0.05$; for maximal temperatures, $r_s=0.21$; $n=22$).

Monthly average minimum temperatures ranged from 9.1-16.7 °C (mean=13.1, SD=2.5) and the mean of monthly maximum temperatures ranged from 15.8-26.9 °C (mean=22.5, SD=2.8).

Average temperatures can fluctuated from year to year; between the dry seasons of 1993 and 1994 there was little variation in the low temperatures but 1993 had a lower average high temperature than 1994 (Table 3.2).

Availability of Plant Resources

To understand the food choices of an animal species one needs to investigate the relative abundance of different components of standing crop as well as the cycles of plant part production in order to determine the patterns of resource availability and the factors which influence these patterns.

In tropical latitudes, diversity in phenological patterns varies depending on water availability and plant species diversity (Bullock and Magallanes, 1990). Below I examine phenological patterns in terms of general resource availability and diversity, and compare them to the rainfall patterns discussed earlier.

Botanical Plots

The total area of the four botanical plots covered 1.93 ha (Table 3.3). At the beginning of the two-year census 888 trees and shrubs (excluding the tree ferns, *Cyathea* because they were not angiosperms) with a DBH of 2.9 cm or more were marked and censused monthly. Combining data from all plots, individual trees and shrubs sampled belonged to 92 vernacular species (when subdivisions such as "madinidravina" or "vaventiravina" were not included), 54 known genera and 35 families. Total basal area for 831 stems (exluding trees and shrubs with multiple trunks) was 76,148 cm^2. In terms of standing biomass, the vernacular species with the highest basal area was "maka" (*Weinmannia*) (15,977 cm^2) (Appendix 1). This species also had the highest relative dominance (21%). "Maka" was the only species which belonged to the genus *Weinmannia*. This genus had the highest basal area (22,027 cm^2) and the highest relative dominance of all the genera (28.9%) (Appendix 2). However, the most abundant genus in terms of number of stems (99 of 831) was *Psychotria*. The family Cunoniaceae, to which *Weinmannia* belongs, had the highest basal area (22,027 cm^2) and the highest relative dominance (28.9%) (Appendix 3). However, the family Rubiaceae, to which *Psychotria* belongs, was the most abundant in terms of number of stems (149 of 831).

I did not collect abundance data for epiphytic plants, e.g. *Bakerella*, which later proved to be important in the diet of mouse lemurs.

Trees and shrubs sampled from all four plots combined ranged in DBH from 2.9 to 73.8 cm with an average of 8.2 cm (SD: 7.1cm) (Figure 3.3). Approximately 76% had a DBH between 4.5 and 9.6 cm. Heights ranged from 2 to 24 m with an average of 7 m (SD: 3.3 m) (Figure 3.4). Approximately, 86% were under 10 m in height.

Community-level phenological patterns

The monthly percentage of individual trees and shrubs that had buds, flowers or fruit was usually low, remaining under 20% for any given month possibly due to many immature plants included in the monitoring (Figures 3.5, 3.6 and 3.7).

Flower production peaked in the rainy season although the exact timing differed from year to year, and there was no significant correlation between flower production and monthly rainfall (r_s=0.133, n=21). During the first rainy season that data were collected, the monthly percentage of tree and shrub individuals in flower peaked in February 1993 (82 individuals, 9%) and, during the second rainy season, in December 1993 (90 individuals, 10%) (Figure 3.5). However, December 1994, the last month data were collected, flower production had not yet peaked, though the third rainy season had begun.

Flower production decreased substantially following the two peak months mentioned above and remained relatively low from March 1993 through September 1993 and from February 1994 to August 1994. During both years there was a small peak during the dry season, in July, a month of relatively higher rainfall.

The percentage of individual plants with unripe fruit is greater than the percentage of individual plants bearing ripe fruit (Figure 3.6). This may indicate that ripe fruit remains less time on the tree either because it is eaten by animals or because it becomes fully ripe quickly and falls from the tree. It is also likely that a large number of trees produce only a few fruit over a long period of time so that unripe fruit is present longer.

Precipitation levels and fruit production were not significantly correlated (r_s=-0.062, n=21). For both annual cycles covered, fruiting activity was relatively high (14-

19% of individual plants) from March (the last month of the wet season), April and May (the first months of the dry season). In 1993, fruiting activity was relatively low (8-10%) from October through January encompassing part of the dry season and part of the wet season. In 1994, fruiting activity was relatively low (10-12%) from June through December including once again part of the dry season and part of the wet season.

In general, individual plants contained only a small abundance of fruit (unripe or ripe) at any given time. For instance, my data indicate that approximately 70% of trees and shrubs that contained unripe fruit over the course of the study had a phenological score in the range of 0.5 to 2.0. Therefore, the fruiting peaks and troughs described above become clearer when plants having fruit phenological values of less than two are removed from the sample (Figure 3.7); peaks in March 1993 and May 1994 become more prominent even though only 6.0% and 6.6% of individuals carry fruit.

Diversity in bud production was highest during months of high precipitation, in February 1993 and December 1993 (14% and 19% of individuals respectively) (Figure 3. 8). These months were followed by peaks of smaller amplitude in diversity of flower production in April 1993 (7%) and February 1994 (11%).

In terms of diversity of fruit production, when accounting for all phenological scores, the monthly percentage of vernacular species with any fruit, ripe or unripe, remained within relatively close limits from approximately 15% to less than 25% (Figure 3.9). Some, but not all, of the high peaks in available fruit diversity coincide with periods of high rainfall: March 1993 (22%), July 1993 (21%), December 1993 (23%), February 1994 (21%), and December 1994 (24%). However, there was no statistically significant correlation between precipitation and diversity (r_s=0.189, n=21). Peaks in the pattern of fruit diversity are clearly exhibited when only trees with a phenological score of two or more are taken into account (Figure 3.10).

Phenological patterns of particular families dominant in the understory, Myrsinaceae and Rubiaceae

Due primarily to the difficulties of distinguishing among the forest strata and categorizing plants into canopy, subcanopy and understory species, I conducted separate analyses only on two families for which I had information on understory members.

Within the botanical plots the Myrsinaceae were represented by 98 individual shrubs belonging to 3-4 vernacular species of "kalafambakaka". "Kalafambakaka" plants belong to the genus *Oncostemum* which is endemic to Madagascar, the Comores islands and Mauritius (Turk, 1995).

The Rubiaceae were represented by 153 individual shrubs and small trees. The botanical plots included a variety of endemic vernacular species belonging to this family including 3 to 4 varieties of "bararata" (*Gaertnera*), 3 to 4 variations of "fatora" (*Mussaenda erectiloba*), "fatsikiahitra" (possibly *Alberta*), "hazotoho" (*Gaertnera* or *Psychotria*), "tongely" (of unknown taxonomic name), and 3 to 4 variations of "voanananala" (*Psychotria*). *Gaertnera* and *Psychotria* are known food sources for *Microcebus rufus* and other lemurs.

The two families had similar phenological patterns which centered primarily around the months of the rainy season. Bud production within the Myrsinaceae peaked at the beginning of or just before the rainy season (11-25% of individual plants) and was followed by flower production which peaked in mid rainy season (12-14% of individuals) extending into the early months of the dry season (Figure 3.11).

Fruit production for the Myrsinaceae began during the rainy season and peaked at the beginning of the dry season (1993: 53% of individual plants; 1994: 34% of

individual plants) (Figure 3.12). A peak in ripe fruit production also occurred later in the dry season, in July 1993 (44% of plants).

Bud and flower production within the Rubiaceae followed an even tighter pattern with very little production throughout most of the dry season months (Figure 3.13). Peak bud production, followed, with a short lag, by peak flower production was highest during the rainy season (24-32% of individuals in bud, and 11-15% of individuals in flower).

Fruit production, of fruit with any ripeness, for the Rubiaceae was high (56-65% of plants) from March through May for both years of data collection (Figure 3.14). This period represents the end of the rainy season and the beginning of the dry season. Ripe fruit was available during some portion of the dry season peaking both years in mid-season, in September (31% of plants in 1993, and 35% of plants in 1994).

In order to investigate how closely the specific phenological patterns of these understory families tracked the phenological patterns of all the trees and shrubs within the botanical plots combined, I compared the percentage of all individuals with flowers and fruit in the botanical plots (Figures 3.5 and 3.6) to the percentage of individual plants in the same phenophase for the understory families examined (Figures 3.11-3.14).

Flower availability of the Rubiaceae and the Myrsinaceae followed the pattern of availability for the plots as a whole, although there was no statistically significant correlation between general monthly flower production and flower production in either subgroup (for the Rubiaceae, $r_s=0.052$; for the Myrsinaceae, $r_s=-0.181$; $n=21$). Fruit availability in the Rubiaceae and the Myrsinaceae is highly correlated with fruit availability in the botanical plots as a whole, with peak production at the end of the

rainy season and the beginning of the dry season (for the Rubiaceae, rs=0.887, $p<0.05$; for the Myrsinaceae, rs=0.923, $p<0.05$; n=21).

Microcebus rufus Plant Resources

Nature of sample

I determined the plant resources which were part of the mouse lemur diet through fecal analysis and direct observation of animals feeding in the forest, and I began to collect phenological data on each plant source as soon as it was identified. A total of 176 trees, shrubs, lianas and epiphytic plants were included the phenological sampling which took place at two-week intervals. These plants belonged to 28 vernacular species, 18 known genera (two remained unknown) and 15 families. Although my intention was to monitor only verified sources of food for *Microcebus*, I eventually included plants for which I had only indications that they may be food sources. For instance, even though I could not establish a positive identification of seeds in the fecal samples, figs (*Ficus*) were frequently mentioned by local people, including the guides I worked with, as being a food source for *Microcebus*. Their seeds were similar to certain seeds found in fecal samples which remained without a positive identification. Captured individuals were also known to consume some species of *Ficus* (Harste, 1993). Therefore, various *Ficus* species were included in the phenological sampling. Verified food sources are listed in Table 3.4.

To calculate average DBH and height for the present analysis, I included only those plants which were known to be food sources and for which I had sufficient data on these values (Table 3.4).

The average height of the trees and shrubs included in this analysis was 5.4 m, i.e. slightly lower than that found for the botanical plots (SD: 3.0; Range: 1.0-15.0 m),

and the average DBH was 8.4 cm, i.e. similar to that found for the botanical plots (SD: 9.0; Range: 1.1-75.8 cm). The average height from the base of the tree to where crown foliage begins was 4.0 m (SD: 2.2; Range: 0.75-12.0 m).

Many resources upon which *Microcebus* relied were epiphytic or vines and, therefore, data were collected for the plants upon which they grew as well as for the resource itself. However, since individual plants included in the sample were selected to facilitate data collection, data are biased toward the shorter end of the spectrum. The average height for the plant resource itself was 6.9 m (SD: 4.0; Range: 1.0-16.0 m). The average height, DBH and height from base to foliage of the tree or shrub upon which the resource was found was 9.6 m (SD: 3.2; Range: 1.0-16.5 cm), 15.2 cm (SD:12.3; Range: 3.4-69.0 cm) and 7.9 m (SD: 2.8; Range: 2.5-15 m) respectively.

Data were collected on several species of *Ficus* (*Ficus brachyclada* or *Ficus politora*, [Famakilela madinidravina and vaventiravina]; *Ficus botryoides*, [Voararano]; *Ficus sp.*, [Voara special]). For these species the average height was 7.7 m (SD: 2.8; Range: 3.0-14.0 m), DBH was 31.3 cm (SD: 31.5; Range: 2.9-101.0 cm) and height from base to foliage was 4 m (SD: 1.2; Range: 2.0-5.5 m). For "Voararano" and "Voara special", fruit could be found on the trunk from 0.25 to 10 m off the ground.

In the phenological analysis described here, I included *Medinilla*, *Rhipsalis*, *Bakerella*, *Viscum*, and, *Psychotria,* which are fruit sources whose seeds were found in fecal samples for a period of five months or more. In addition to these genera, I also include the family Moraceae (figs) because of its potential importance in the diet of *Microcebus*.

Phenological samples of the genera *Medinilla*, *Rhipsalis* and *Viscum* included only one vernacular species each. The *Psychotria* sample included three vernacular

species, two of which have been identified as *Microcebus* fruit sources. The *Bakerella* sample included two subspecies of *Bakerella clavata*, the species *Bakerella grisea,* and one other unknown species of *Bakerella*. With the exception of one of the *Bakerella clavata* subspecies, all of the other taxa are verified food sources for mouse lemurs. I also included four different vernacular species of *Ficus*, "Voararano", "Famakilela madinidravina" , "Famakilela vaventiravina" and "Voara special".

Phenological patterns

The various *Ficus* species taken together produced fruit throughout the year, peaking in availability both during part of the dry season (April through August) and throughout the wet season (December through February) (Figure 3.15).

For both *Psychotria* (Figure 3.16) and *Bakerella* (Figure 3.17 a&b), the pattern of fruit availability was similar during both years of data collection with high availability from the end of the wet season through most, but not all, months of the dry season. Specifically, high availability, as reflected by the presence of unripe fruit, occurred during the months of February through August with the exception of a substantial decline in *Bakerella* fruit availability at the end of April and throughout May 1994.

Bakerella is an important food resource for *Microcebus*. For this plant I have included the phenological cycles for all phenophases (Figures 3.17 a&b). Bud and/or flower production is protracted and takes place throughout most of the annual cycle with substantial fluctuations, but with only a short gap between June and August. With regard to fruiting activity, the only months when both ripe and unripe fruit were substantially decreased (to zero), were October and November of 1993, the last months of the dry season. However, since there was no indication of a decrease in the

following year, the observed pattern may be indicative of variability on an individual plant level rather than on a generic or family level.

Viscum, Medinilla and *Rhipsalis* showed a similar pattern of fruit availability in being more seasonally restricted, though this may be because each phenology encompassed what we concluded was a single vernacular species. *Viscum* was available for part of the dry season and all of the wet season in 1993 (Figure 3.18). As with *Bakerella,* availability of *Viscum* fruit, at least on an individual plant level, may be relatively irregular or inconsistent, since in 1994 no fruit was available by October when we stopped recording data.

Rhipsalis was available throughout the dry season (Figure 3.19). *Medinilla* shows a consistent pattern of peaking in fruit availability during periods of high rainfall (Figure 3.20).

Insect Resources: Abundance, Seasonal Activity and Size Patterns

Insects were captured all 21 nights that collections took place. During the majority of these nights insects were trapped at two different locations for a total of 39 collection sessions. The total number of insects captured was 9975 with a fresh weight of 271 g.

Fourteen different orders were identified. Overall, Lepidoptera was the most frequently captured order (Table 3.5). The large number of insect species and the taxonomic problems associated with insect identification make it difficult to collect and analyze data on tropical species as compared with those in the temperate zone (Claridge, 1986). Few data sets for tropical insects exist to help identification beyond the ordinal level. Therefore, only a limited subsample of insects could be identified to a finer taxonomic level beyond the order level (Table 3.6). In general, identification to

family level needs to be considered as tentative since it was not conducted by an expert entomologist and since the reference guide which we relied upon in the field, the "Peterson Field Guide to Insects" (Borror and White 1970), may be less authoritative for tropical insects. In some cases, marked by "?", family identification was even more tentative. Within the order Coleoptera, identification sometimes could be made only at the superfamily level of Curculionoidea and Elateroidea. Many of the Homoptera identified were plant and leaf hoppers, and aquatic insects were detected within the Coleoptera, the Diptera and the Hemiptera (family Corixidae).

Figure 3.21(a&b) shows the bimonthly fluctuations in number and fresh weight of insects. The maximum number of insects was captured during the second of the two November trap nights and is attributed to the presence of large numbers of ants (Hymenoptera). During the first night in November almost no ants were captured; the second night may have been part of their seasonal mating flight. The contrast in the number of insects captured in December might have been less dramatic if collection had occurred as usual, at two sites per collection night instead of only one and if the insects had been counted immediately. For the first night in December the disintegrated insects appeared to be Diptera; only one hymenopteran was captured. On the other hand, during the second night the majority of insects captured were ants once again (348 of 441 total insects captured), indicating another seasonal mating flight. Maximum fresh weights of insects occurred during both nights of capture in January. During the second night, a large number of these insects (498 of 1258) were Hemiptera (bugs), which are generally larger and heavier in weight than Hymenoptera or Diptera. Some of the Hemiptera were tentatively identified as Nabidae (440 individuals) while others were identified as Pentatomidae (58 individuals). Nabidae, or damsel bugs, are common predaceous insects which occur in low vegetation

(Borror and White, 1970). In the second night in March, the number and fresh weight of insects captured also shows a peak in abundance. As in January, the peak is due to large numbers of Nabidae (259 of a total of 885 insects captured). The difference between the two nights in March is due partly to the fact that collection took place at one site only during the first night, and partly to the large number of ants, which are light in weight, captured (197 of 394 insects). The number of insects (abundance) and fresh weight were significantly correlated (r_s=0.827, $p<0.05$, n=11).

Neither of these two values were significantly correlated with rainfall (number of insects and rainfall, r_s=0.297; fresh weight and rainfall, r_s=0.636. N=10, excluding July 1993 for which I had only partial data). Both values maximized in January, a month of relatively high rainfall accumulation (Table 3.7). On the other hand, in February, the month of highest rainfall, insect abundance and fresh weight, although still relatively high did not reach the levels of the previous month. Some of the months (October to January) with a high number and fresh weight of insects captured were also associated with a high count in the number of trees in flower (Table 3.7). However there were no significant correlations between number of insects or fresh weight of insects and number of trees and shrubs in flower (for number, r_s=0.298; for fresh weight, r_s=0.055; n=10). However, February through April remained relatively high in insect production without correspondingly high flower productivity.

The number of different orders captured per month did not fluctuate greatly (Table 3.8) although peaks in productivity varied among orders (Table 3.9). For some groups the variation was more dramatic than for others. In general, peaks in abundance took place during or near the rainy season. Maximum peaks in abundance for Hymenoptera occurred in November, the last month of the dry season, and to a lesser extent, in March, the last month of the rainy season. Maximum peaks in

abundance for Hemiptera occurred during the rainy season, in January and March. Orthoptera peaked, once, in January. Diptera, on the other hand, were relatively abundant during the dry season, in August and September, and peaked again in March, at the end of the rainy season.

Distribution of length classes for seven orders are depicted in Figure 3.22. Among all 14 orders (not all shown in the figure), Lepidoptera, Hemiptera, Orthoptera, Trichoptera, Dermaptera and Isoptera exhibted a similar pattern, with the 5-15 mm size class contributing the most to total abundance. Homoptera, Hymenoptera and Diptera were represented in their majority by the "<5 mm" size class. Coleoptera were distributed between the "<5 mm" (51.9%) and the "5-15 mm" size class (38.6%).

Discussion and Conclusions

Phenology

Ranomafana shows seasonal variation in flower and fruit availability and abundance. I found that fluctuations in the percent of individual trees and shrubs in flower had a more defined peak and trough pattern than was the case for fluctuations in fruit production. The time of maximal availability of the former occurred during the rainy season. Peak fruit production immediately followed peak flower production. Fruit production (ripe and/or unripe) occurred all year round, ranging from 6% to approximately 19% of trees and shrubs but peak fruit time coincided with the period at the end of the rainy season and the beginning of the dry season. The exact months of highest fruit and flower production varied yearly.

Fruit production did not appear to be affected by the cyclones that took place during both years of the study except for the lowered incidence of ripe fruit in March 1994 as compared to March 1993, which may have been the result of rain and wind

damage. Otherwise, the patterns in amplitude for the two years were similar. The percent of trees and shrubs in fruit was always relatively low, under 20%, but this may be due in part to the inclusion of juvenile as well as adult plants in the phenological monitoring. Meyers and Wright (1993), whose phenological study also took place at Talatakely, found two peaks of fruit production, in the mid-rainy season during January, and mid-dry season during July. Hemingway (1995), who conducted phenology at Vato, a site in Ranomafana five kilometers away from Talatakely, found that the greatest number of individuals produced flowers and fruited during the wet season. Overdorff (1991), also at Vato, found high levels of fruit production at the end of the rainy season, in March, and in the middle of the dry season, in August. As in my study, neither Hemingway nor Overdorff found correlations between fruiting patterns and rainfall or temperature patterns. Additionally, all three studies found that the time of highest phenophase production, i.e. flower and fruit production, varied from one annual cycle to another. This may be related to the fact that, in tropical forests, individual plants within the same species do not necessarily flower every year (Frankie et al., 1974). In terms of yearly flowering peaks, a strong correlation has been found between tropical plant phenologies and rainfall but the correlation is weaker for less the seasonal rainforests than for dry forest due to rainfall differences (e.g. van Schaik et al., 1993). Comparison with other phenological studies in Madagascar confirms this statement. For one rainforest, Sterling (1993) found that peaks in phenological patterns differed from annual cycle to the next. On the other hand, studies conducted in the dry forests of Madagascar have demonstrated that phenological patterns were closely correlated to rainfall patterns (Hladik, 1980; Sauther, 1992; Meyers, 1993; Sörg and Rohner, 1996).

The peak timing in the number of vernacular species producing buds, flowers and fruit occurred mainly, but not exclusively, in the rainy season. Timing of peak diversity differed from one annual cycle to the other. Hemingway (1995), too, found highest diversity in flower and fruit production during the wet season.

Comparing the percentage of individual trees and shrubs in fruit, i.e. abundance, with the percentage of vernacular species in fruit, i.e. diversity, I found that the two were strongly coincident only in March 1993. On the other hand, in 1994, the number of vernacular species in fruit rose at the height of the rainy season while the number of individual trees and shrubs in fruit was high at the beginning of the dry season.

These observations suggest that whether diversity and abundance peak at the same time depends on the relative density of the vernacular species in fruit; if a few common species are in fruit then abundance, but not diversity, may peak.

Data from the phenologies of two important, common understory families in Ranomafana, the Myrsinaceae and the Rubiaceae, as well as from the *Microcebus* fruit sources, indicate that the rainy season is the time when many different groups of trees and shrubs produce fruit. For the Myrsinaceae and the Rubiaceae phenophase activity occurred primarily during and just following the rainy season. However, ripe fruit was available later in the dry season. This was particularly true of the Rubiaceae, several species of which are food sources for *Microcebus*. With the exception of the Moraceae, the phenological cycles of the other *Microcebus* fruit sources examined were more restricted to the time prior to, during, or just after the wet season. Although *Medinilla*, *Rhipsalis*, *Viscum*, and *Bakerella* are all epiphytic and may be more dependent on water availability, their phenologies were similar to general patterns.

Bakerella is of special interest since feeding data indicate that it is an important resource for mouse lemurs. Phenological data demonstrate that in November 1993, no fruit was present on the individuals being monitored, and yet *Microcebus* feces contained seeds of this plant. This may be indicative of how phenological data do not always accurately depict the phenophases of those species which are either less seasonal or where there is a lot of variation among individuals within a species.

Hemingway (1995) found that canopy and understory species differed in the time and amplitude of their peak flowering and fruiting activities, with a higher proportion of individuals and species active in the understory. When I compared overall bud, flower and fruit production (percent of individual plants) in the botanical plots to that for the Rubiaceae and the Myrsinaceae, I found that buds and flowers were in highest abundance during the rainy season although peak production did not always occur during the same monthin the three groups. The amplitude of flower production was generally low, under 15%, for all three groups. In terms of amplitude of fruit availability, the percentage of plants with any fruit in the Rubiaceae usually exceeded that of the general phenology. The percentage of plants with fruit in the general phenological sample was over 18% for only three months, while within the Rubiaceae, this percentage was exceeded in 18 of the 23 months of data collection and was over 50% for six of those months. Similarly, the amplitude of fruit production within the Myrsinaceae was generally higher than that demonstrated in the general phenological sample. To illustrate, peak monthly fruit production for the Myrsinaceae was over 50%, for the Rubiaceae, over 60%, but for the plots as a whole just under 20%.

Insect Availability

The goal of this part of the study was to examine fluctuations in insect availability and diversity in relation to seasonal climatic changes. Ranomafana does show seasonal variation in insect availability and abundance. No single method measures the total number of insects present, but black lights can help to measure seasonal abundance as food for vertebrates (Smythe, 1982), which was the purpose of this study.

The light-traps I used to attract the insects clearly do not sample the entire insect community, but only the subcommunity of flying phototactic insects found in the specific habitat at the height sampled. Other methods, such as the use of an air suction trap, may introduce less bias by not relying on a phototactic response from insects (Buchler, 1976). Black (1974) concedes that although black lights are biased toward positively phototactic insects, he agrees that they are the most effective way to sample insect diversity. Indeed, this was confirmed during my study; contrary to Smythe (1982), who found a total absence of orthopterans which he attributed to the sampling method of using a black light, I captured a wide range of insect orders including Orthoptera.

Flying phototactic insects undergo seasonal changes in abundance (Smythe, 1982). However, even within a season, the abundance, size and taxonomic composition of insects can vary depending on a variety of factors such as the relative moisture of the habitat (Janzen and Schoener, 1968; Schoener and Janzen, 1968), the height sampled (Johnson, 1957), or even the dominance of native versus introduced tree species (Southwood, 1961). These observations indicate that results from this

study can only be considered as describing a very local picture of insect abundance and composition.

The relationship between the number of insects caught per month and their fresh weight depends upon the specific order of insects prevalent at the time of capture. The November peak in number of insects but not in fresh weight is due to an increase in the order Hymenoptera (ants), which are relatively light in weight. January's peak in both number and fresh weight can be attributed to an increase in the heavier Hemiptera (=Heteroptera) and Orthopteroids.

Moister habitats can support a greater abundance of insects particularly smaller ones which may have less difficulty maintaining water balance (Janzen and Schoener, 1968). However, it is not necessarily true that in the tropics the number of species and individuals is always low during the dry season. When the dry season is mild, the number and diversity of insects can rise (Janzen, 1973). However, at Talatakely, abundance and fresh weight of insects was generally lower during the dry season than during the rainy season. Specifically, with the exception of November, the period of highest abundance in terms of numbers of insects captured occurred during the months of the rainy season, while lowest abundance was always observed during the dry season. In terms of both fresh weight and number of insects captured, there was a sharp peak relatively early in the rainy season, in January. Smythe (1982), too, found a sharp peak early in the rainy season, at least with regard to the total weight of insects. Fresh weight numbers of insects captured in Ranomafana remained generally high throughout most of the remaining wet season.

Few insects in the >15 mm length class were captured. The <5 mm length category was common in November and March when ants were prevalent. Most insects captured were 5-15 mm in length. The 5-15 mm range is considered medium to large

when compared to the size of insects in general since 2-4 mm has been mentioned as a small-to-intermediate size range characteristic of most individuals in the most common insect species (Schoener and Janzen, 1968). Insect species are generally believed to be significantly larger in tropical samples than in temperate ones (Schoener and Janzen, 1968) and the results of this study corroborate this observation. The prevalence of the 5-15 mm size class has been suggested to be generally important to vertebrates (Smythe, 1982). Data concerning the size range of insects ingested by *M. rufus* await future analysis, and, therefore, it remains to be confirmed concering whether the most prevalent size class of insects is also the one most often consumed by mouse lemurs. It should be noted, however, that fecal analysis has demonstrated that Coleoptera, whose numbers were shown to be highest in the small (<5 mm) size range, is the preferred insect resource for this species (Chapter Four).

Table 3.1. Monthly rainfall during two dry and two wet seasons at Talatakely, RNP from Feb-93 to Nov-94.

Partial wet season		Complete wet season	
Month	Rainfall (mm)	Month	Rainfall (mm)
		Dec-93	482
		Jan-94	819
Feb-93	853	Feb-94	1170
Mar-93	618	Mar-94	679
Total Rainfall	1471		3150

Complete dry season		Complete dry season	
Month	Rainfall (mm)	Month	Rainfall (mm)
Apr-93	110	Apr-94	186
May-93	55	May-94	184
Jun-93	325	Jun-94	66
Jul-93	513	Jul-94	234
Aug-93	130	Aug-94	185
Sep-93	66	Sep-94	90
Oct-93	144	Oct-94	125
Nov-93	147	Nov-94	109
Total Rainfall	1490		1179

Table 3.2. Temperature variations in degrees Celsius during the dry and wet seasons at Talatakely, RNP from Feb-93 to Nov-94.

	Minimal temperatures		
Season	Mean	Standard deviation	Range
Dry (April-November 1993)	12.0	2.2	9.1-15.0
Dry (April-November 1994)	11.7	1.3	10.4-14.5
Wet (December-March 1994)	16.2	0.26	15.5-16.7

	Maximal temperatures		
Season	Mean	Standard deviation	Range
Dry (April-November 1993)	20.1	2.9	15.8-23.8
Dry (April-November 1994)	23.5	2.0	20.8-26.9
Wet (December-March 1994)	24.3	0.5	23.3-25.8

Table 3.3. Description of four botanical plots at Talatakely, RNP

Plot name	Area hectares	Initial no. of trees and shrubs*	No. of vernacular species	No. of known genera	No. of known families	Max. no. of unidentified genera	Max. no. of unidentified families
SL	0.5	234	63	32	26	10	5
D	0.43	211	83	35	28	15	3
X	0.5	201	48	25	21	9	2
E	0.5	275	65	32	28	11	3

*all trees and shrubs with a DBH of at least 2.0 cm including the tree fern Cyathea and ones that eventually died.

Table 3.4. Plants used to determine DBH and height of *Microcebus rufus* plant resources at Talatakely, RNP.

Vernacular name	Taxonomic name	Family	Plant type	Verified food source*
Fatsikiahitra madinidravina	*Alberta humblotii*	Rubiaceae	Shrub	Yes
Dendemivavy	*Anthocleista amplexicaulis*	Loganiaceae	Tree	Yes
Fandramanana lavaravina	*Aphloia theaeformis*	Flacourtiaceae	Tree	Yes
Tongolahy madinidravina longue feuille	*Bakerella clavata* subsp.1	Loranthaceae	Epiphytic semi-parasite	Yes
Tongolahy madinidravina ronde feuille # 1	*Bakerella clavata* subsp.2	Loranthaceae	Epiphytic semi-parasite	Yes
Tongolahy vaventiravina longue feuille	*Bakerella grisea*	Loranthaceae	Epiphytic semi-parasite	Yes
Tongolahy fotsy	*Bakerella* sp.	Loranthaceae	Epiphytic semi-parasite	Yes
Vahirano madinidravina	*Cissus* sp.	Vitaceae	Liane	Yes
Famakilela madinidravina	*Ficus.brachyclada* subsp.1	Moraceae	Small tree	No
Famakilela vaventiravina	*Ficus.brachyclada* subsp. 2	Moraceae	Small tree	No
Voararano	*Ficus botryoides*	Moraceae	Tree	No
Voara special	*Ficus* sp.	Moraceae	Tree	No
Bararata vaventiravina	*Gaertnera* sp.	Rubiaceae	Tree	Yes
Harongana	*Harungana madagascariensis*	Clusiaceae	Shrub to medium-sized tree	Yes
Hazondrano	*Ilex mitis*	Aquifoliaceae	Tree	Yes
Voarafy	*Maesa lanceolata*	Myrsinaceae	Shrub to small tree	Yes
Kalamasombarika	*Medinilla* sp.	Melastomataceae	Epiphyte	Yes
Sehana	*Micronychia madagascariensis*	Anacardiaceae	Scrambling shrub	Yes
Lambinanala	*Nuxia* sp.	Loganiaceae	Tree	Yes
Kalafana madinidravina	*Oncostemum botryoides*	Myrsinaceae	Tree	Yes
Goavy gasy	*Psidium cattleianum*	Myrtaceae	Shrub	Yes
Voanananala madinidravina longue feuille	*Psychotria* sp.	Rubiaceae	Shrub	Yes
Voanananala madinidravina ronde feuille #	*Psychotria* sp.	Rubiaceae	Shrub	Yes
Voatsilelolelo	*Rhipsalis baccifera*	Cactaceae	Epiphyte	Yes
Voananamboa	Unidentified	Rubiaceae	Shrub	Yes
Tongolahy maitso	*Viscum* sp.	Loranthaceae	Epiphytic semi-parasite	Yes

*see text for explanation

Table 3.5. Data on the collection of 14 insect orders and suborders at Talatakely, RNP from Jul-93 to May-94.

Insect (sub) order	Total no. of collection sessions*	No. of nights captured*	Total no.of insects captured
Lepidoptera	39	21	2275
Hymenoptera	26	20	1854
Diptera	36	21	1567
Heteroptera	26	16	1010
Orthoptera	32	19	933
Coleoptera	36	21	770
Homoptera	34	20	556
Trichoptera	35	20	241
Isoptera	7	6	28
Ephemeroptera	6	5	26
Collembola	3	2	21
Neuroptera	8	6	8
Dermaptera	2	2	2
Zoroptera**	1	1	1

Insect (sub) order	Percent of total insects captured
Lepidoptera	22.90
Hymenoptera	18.67
Diptera	15.78
Heteroptera	10.17
Orthoptera	9.40
Coleoptera	7.75
Homoptera	5.60
Trichoptera	2.43
Isoptera	0.28
Ephemeroptera	0.26
Collembola	0.21
Neuroptera	0.08
Dermaptera	0.02
Zoroptera**	0.01

The category of "Unidentified" appeared 14 times.
*Based on a total of 21 nights and 39 collection sessions.
**Identification remains tentative.

Table 3.6. List of families identified within certain insect orders captured at Talatakely, RNP.

Insect order	Family
Coleoptera	Blattidae
Coleoptera	Canthoridae
Coleoptera	Cerambycidae
Coleoptera	Chrysomelidae
Coleoptera	Coccinelidae
Coleoptera	Curculionidae
Coleoptera	Elateridae
Coleoptera	Eucnemidae
Coleoptera	Lampyridae
Coleoptera	Loinchaidae
Coleoptera	Meloidae?
Coleoptera	Elateridae
Coleoptera	Scarabidae
Coleoptera	Staphylinidae
Coleoptera	Throscidae?
Diptera	Cecidomyiidae
Diptera	Chironomidae
Diptera	Chyroncuidae
Diptera	Culicidae
Diptera	Dolichopodidae
Diptera	Drosophilidae
Diptera	Muscidae
Diptera	Mycetophilidae
Diptera	Psychodidae
Diptera	Sciaridae
Diptera	Sphaeroceridae
Diptera	Tupilidae
Heteroptera	Alydidae=Coricidae
Heteroptera	Corixidae (aquatic)
Heteroptera	Lygaeidae
Heteroptera	Mesoreliidae?
Heteroptera	Nabidae
Heteroptera	Pentatomidae
Heteroptera	Pyrrhocoridae?
Heteroptera	Tingidae
Homoptera	Achilidae
Homoptera	Cicadallidae
Homoptera	Cicadidae
Homoptera	Cixiidae
Homoptera	Flatidae
Hymenoptera	Formicidae
Hymenoptera	Ichneumonidae
Hymenoptera	Proctotrupidae
Neuroptera	Chrysopidae
Neuroptera	Mantispidae
Orthoptera	Blattidae
Orthoptera	Gryllacrididae
Orthoptera	Gryllidae
Orthoptera	Mantidae
Orthoptera	Tettigoniidae

Table 3.7. Monthly (4 collection sessions) number and fresh weight of insects captured compared to rainfall accumulation and flower availability at Talatakely, RNP.

Month	No. of insects	Fresh weight (g)	Rainfall (mm)	Counts of individual trees & shrubs with flowers
Jul-93*	46	0.75	513	30
Aug-93	648	12.75	130	
Sep-93	752	9.15	66	17
Oct-93	642	10.20	144	42
Nov-93	1934	22.70	147	67
Dec-93*	766	19.70	482	90
Jan-94	1905	95.40	819	49
Feb-94	870	32.50	1170	17
Mar-94**	1279	34.00	679	5
Apr-94	717	18.25	186	15
May-94	416	16.00	184	11
Totals	9975	271.40	4519	343

*based on two collection sessions.
**based on three collection sessions.

Table 3.8. Number of different insect orders captured monthly at Talatakely, RNP.

Month	Number of insect orders
Jul-93*	7
Aug-93	9
Sep-93	11
Oct-93	10
Nov-93	11
Dec-93*	10
Jan-94	9
Feb-94	8
Mar-94**	11
Apr-94	12
May-94	9

*based on two collection sessions.
**based on three collection sessions.

Table 3. 9. Variation in the number of insect orders and suborders captured monthly at Talatakely, RNP.

Insect (sub) order	Total no. captured Jul-93-May-94	Percent captured in: Jul-1993*	Aug-93	Sep-93	Oct-93	Nov-93	Dec-93*	Jan-94	Feb-94	Mar-94**	Apr-94	May-94
Lepidoptera	2275	0.75	13.02	9.10	11.57	8.36	5.58	14.73	8.44	8.22	10.16	10.11
Hymenoptera	1854	0.05	0.38	1.46	0.16	56.04	18.82	7.71	1.67	11.70	1.73	0.22
Diptera	1567	1.34	17.23	20.36	11.61	9.25	1.47	5.62	9.64	11.42	7.34	6.25
Heteroptera	1010	0.00	3.27	1.29	0.69	1.39	0.30	52.57	11.09	25.84	1.58	1.98
Orthoptera	933	0.11	0.21	1.61	3.64	10.40	14.26	42.66	20.36	4.39	4.82	0.64
Coleoptera	770	0.26	0.65	11.56	15.06	9.22	7.27	18.57	9.09	10.13	16.49	1.95
Homoptera	556	0.36	0.72	5.76	5.04	13.67	2.52	22.84	13.49	21.40	10.07	4.14
Trichoptera	241	0.37	10.82	14.18	8.96	17.91	3.73	5.97	3.73	16.04	11.19	7.09

Only most frequent orders captured are shown.

Average no. captured is the average number of an order captured per night per session.

*based on two collection sessions.

**based on three collection sessions.

Fig.3.1. Monthly rainfall at Talatakely, RNP from Feb-93 to Nov-94.

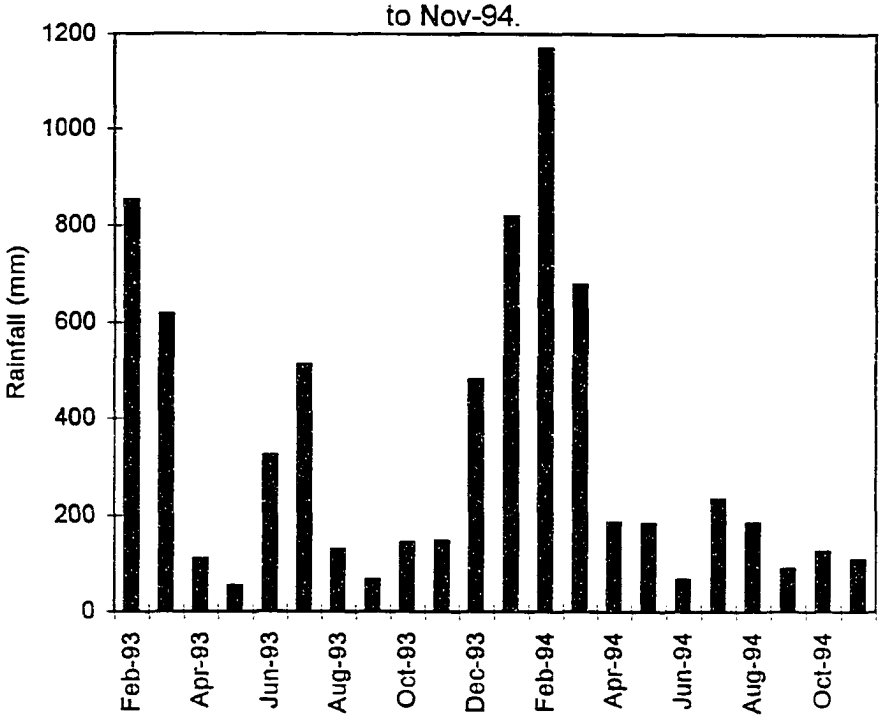


Fig. 3.2. Monthly average maximal and minimal temperatures at Talatakely, RNP from Feb-93 to Nov-94.

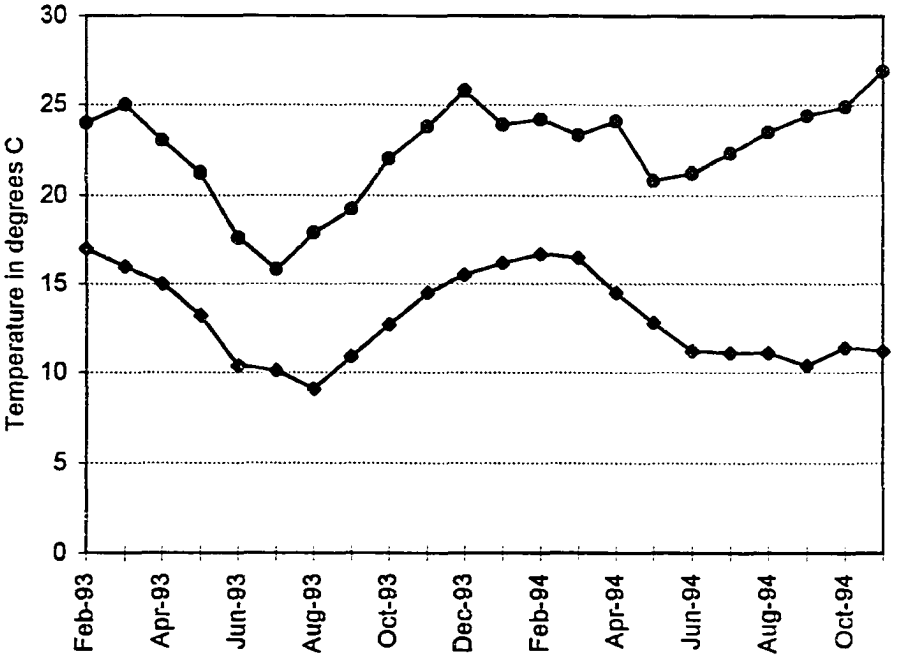


Fig. 3.3. Frequency distribution of DBH of trees and shrubs at Talatakely, RNP.

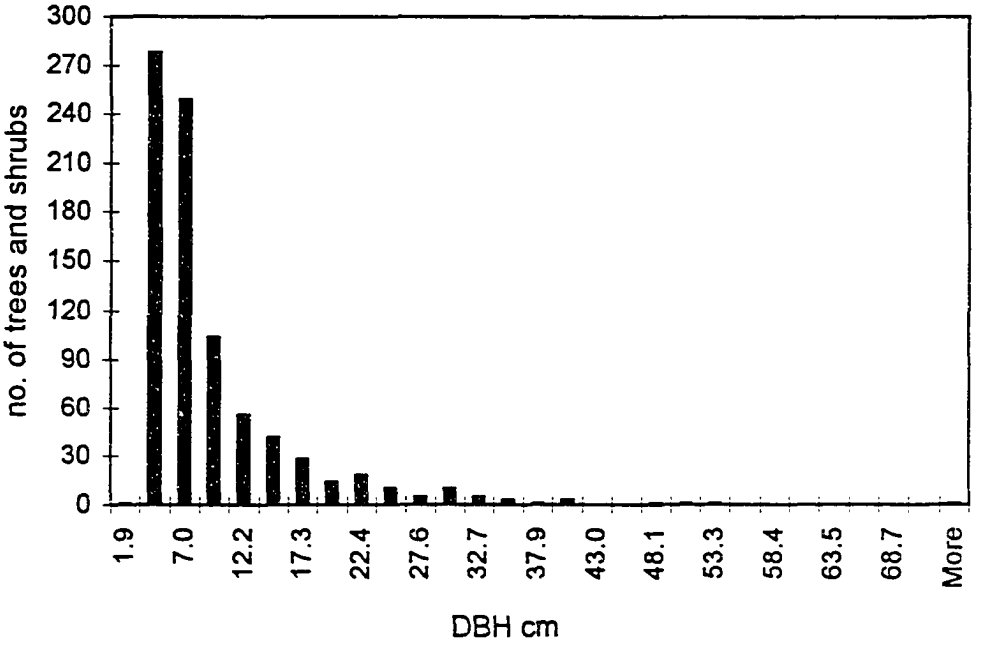


Fig.3.4. Frequency distribution of heights of trees and shrubs at Talatakely, RNP.

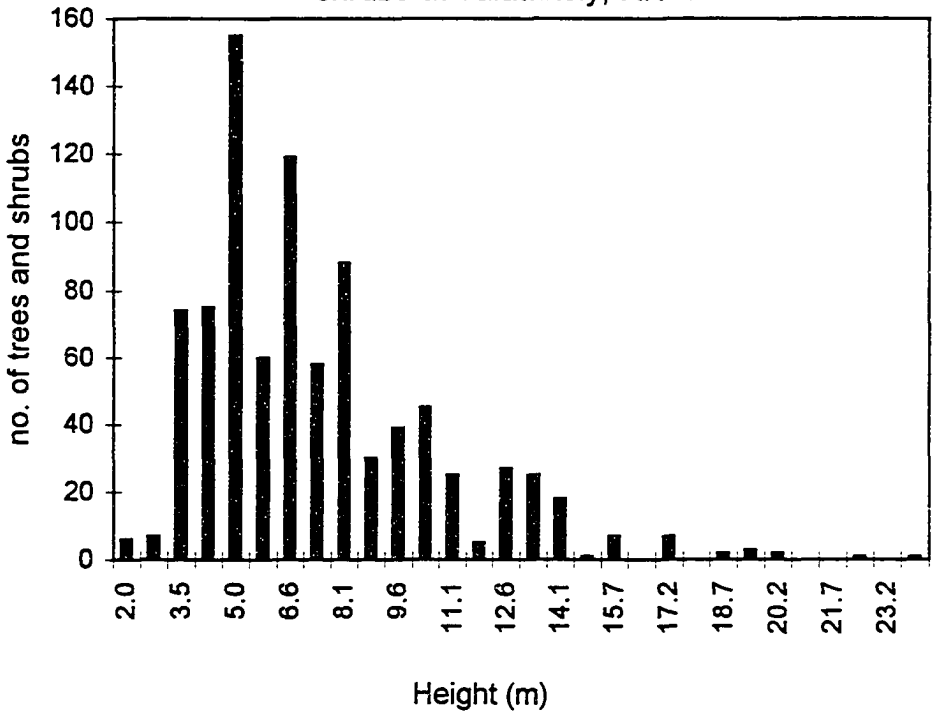


Fig. 3.5. Monthly percentages of individual trees and shrubs with buds and flowers from 888 sampled at Talatakely, RNP.

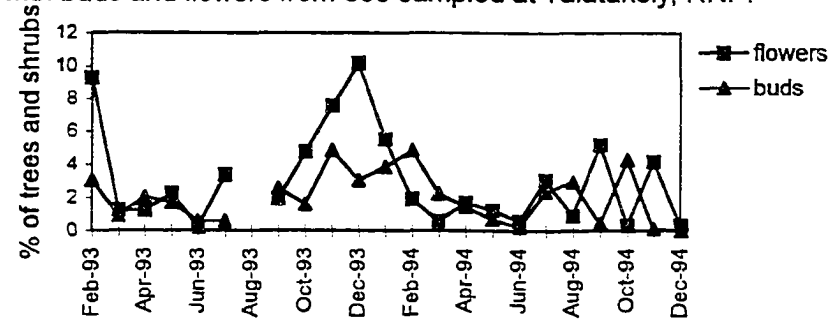


Fig. 3.6. Monthly percentages of individual trees and shrubs in fruit from 888 sampled at Talatakely, RNP.

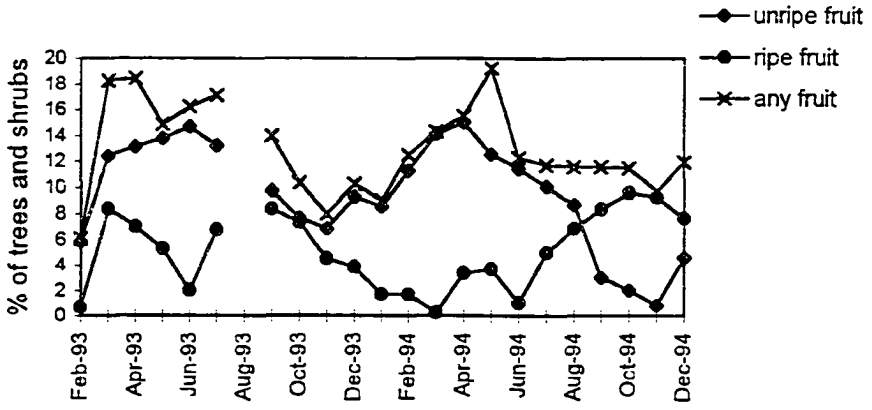


Fig.3.7. Monthly percentages of individual trees and shrubs with unripe or ripe fruit having a phenological score of 2 or more sampled at Talatakely, RNP.

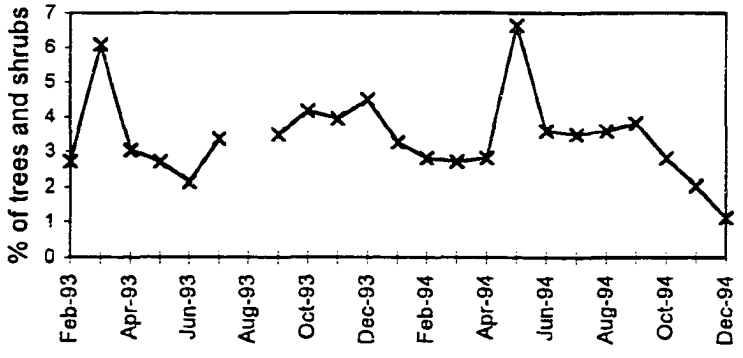


Fig. 3.8. Monthly percentages of 161 vernacular species with buds or flowers sampled at Talatakely, RNP.

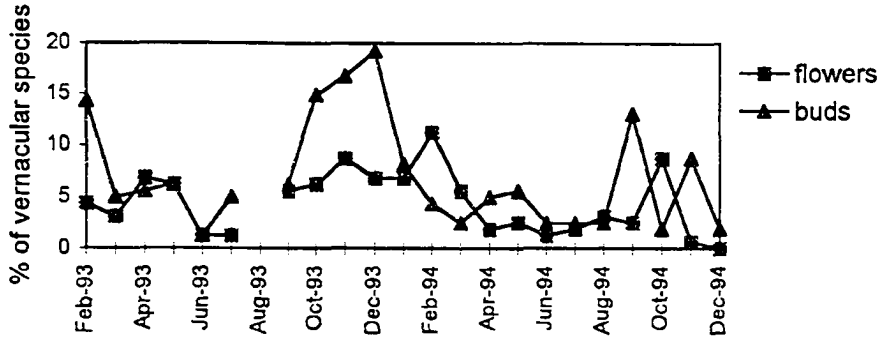


Fig. 3.9. Monthly percentages of 161 vernacular species in fruit sampled at Talatakely, RNP.

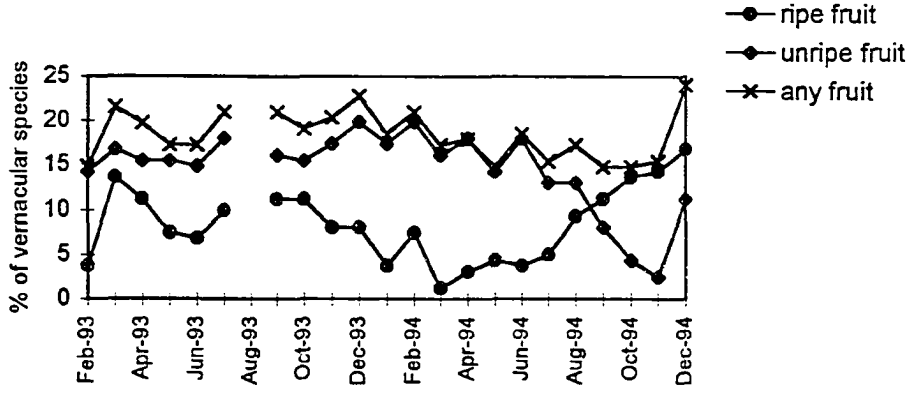


Fig. 3.10. Monthly percentages of 161 vernacular species with unripe or ripe fruit having a phenological score of 2 or more sampled at Talatakely, RNP.

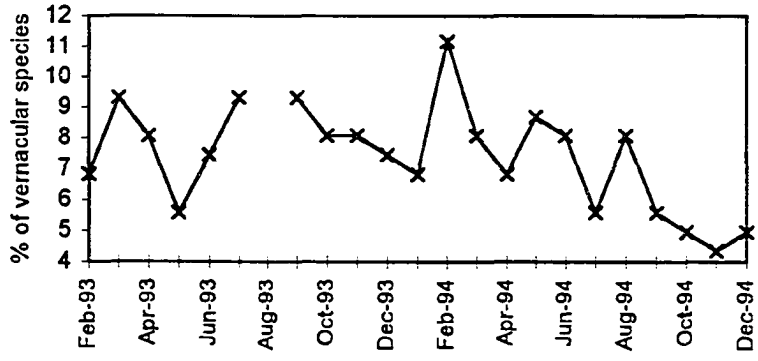


Fig. 3.11. Monthly percentages of 98 Myrsinaceae shrubs with buds and flowers sampled at Talatakely, RNP.

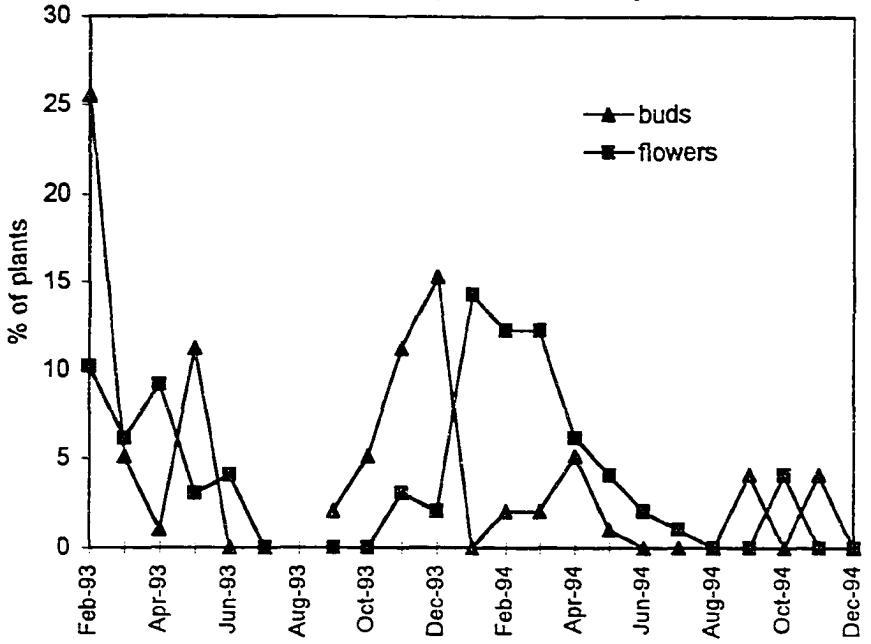


Fig.3.12. Monthly percentages of 98 Myrsinaceae shrubs in fruit sampled at Talatakely, RNP.

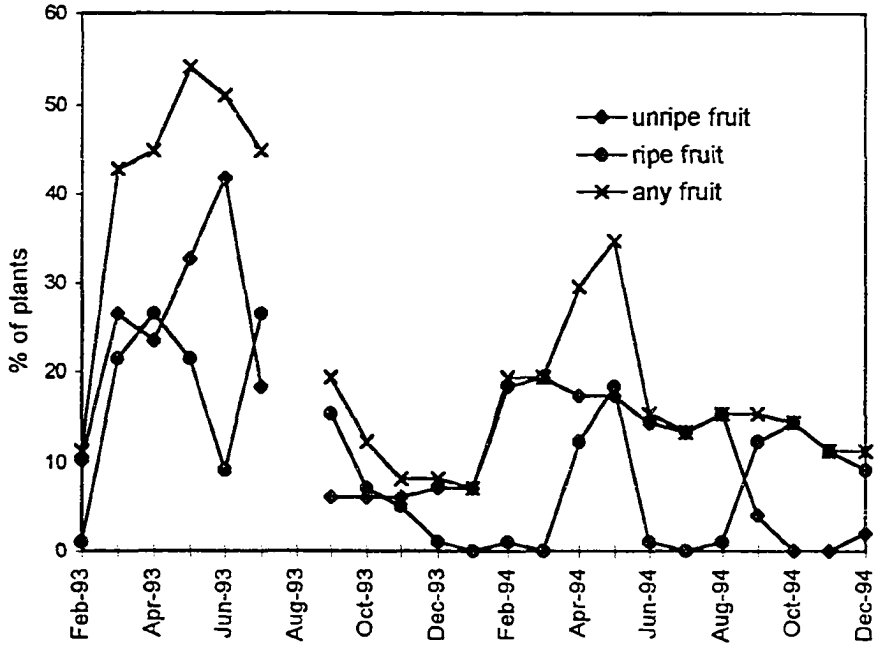


Fig. 3.13. Monthly percentages of 153 Rubiaceae shrubs with buds and flower sampled at Talatakely, RNP.

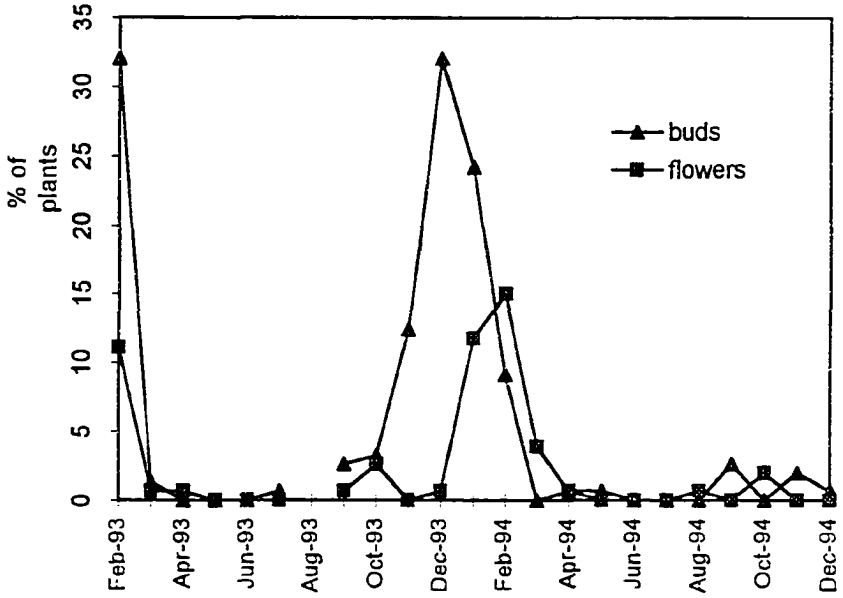


Fig. 3.14. Monthly percentages of 153 Rubiaceae shrubs in fruit sampled at Talatakely, RNP.

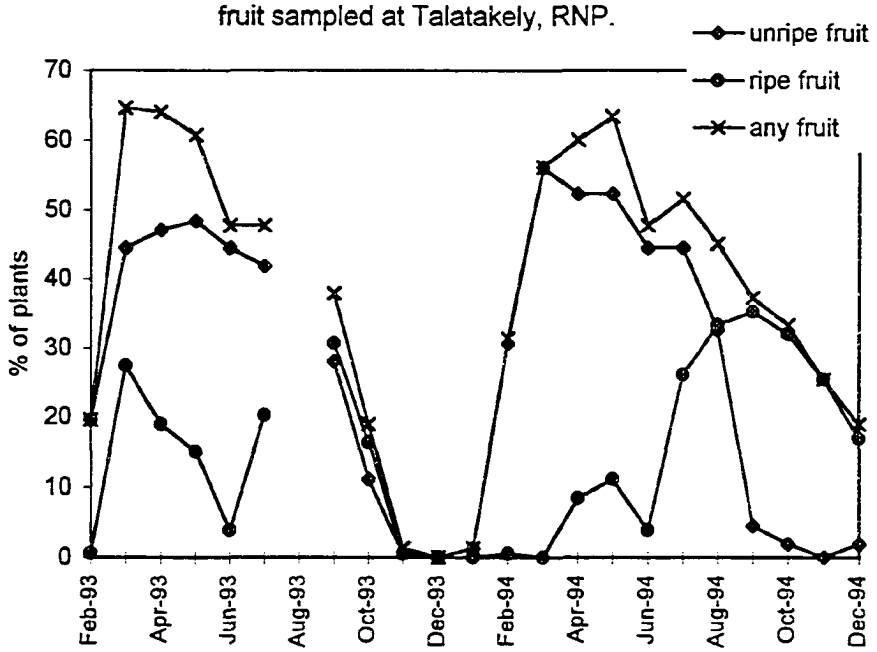


Fig. 3.15. Percent of *Ficus* (Moraceae) plants in fruit sampled biweekly at Talatakely, RNP.

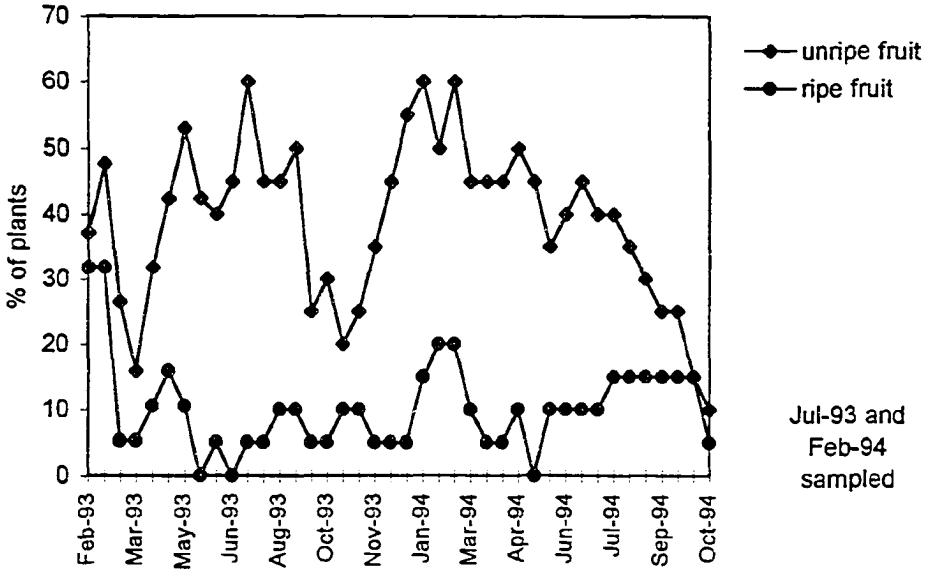


Fig. 3.16. Percent of *Psychotria* (Rubiaceae) plants in fruit sampled biweekly at Talatakely, RNP.

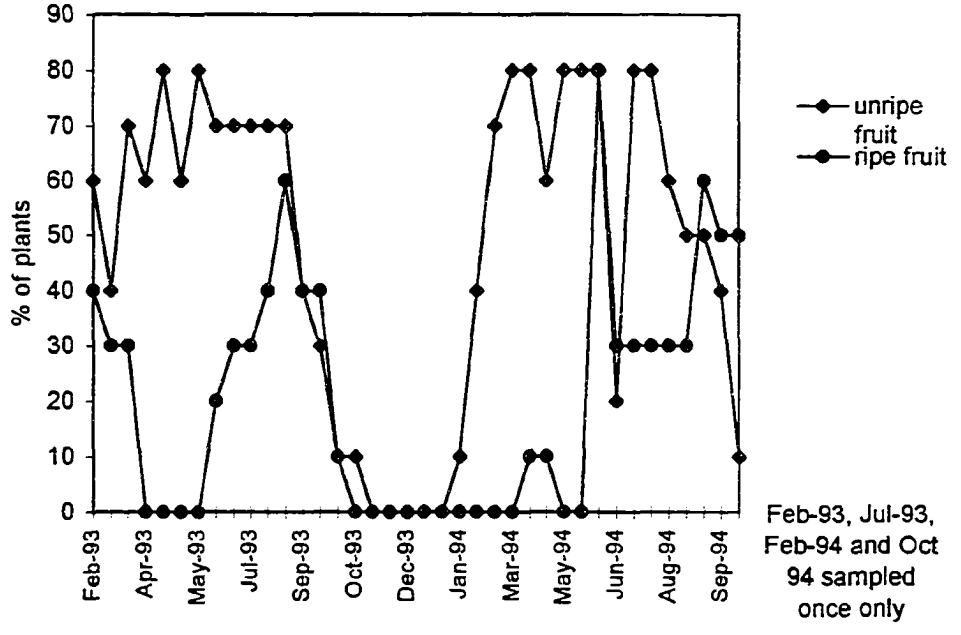


Fig. 3.17a. Percent of *Bakerella* (Loranthaceae) plants with buds and flowers sampled biweekly at Talatakely, RNP.

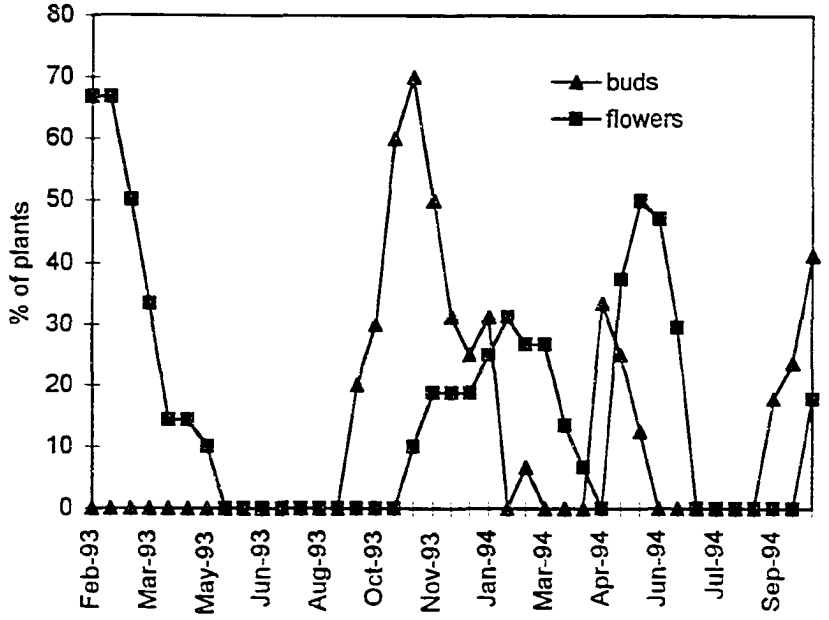
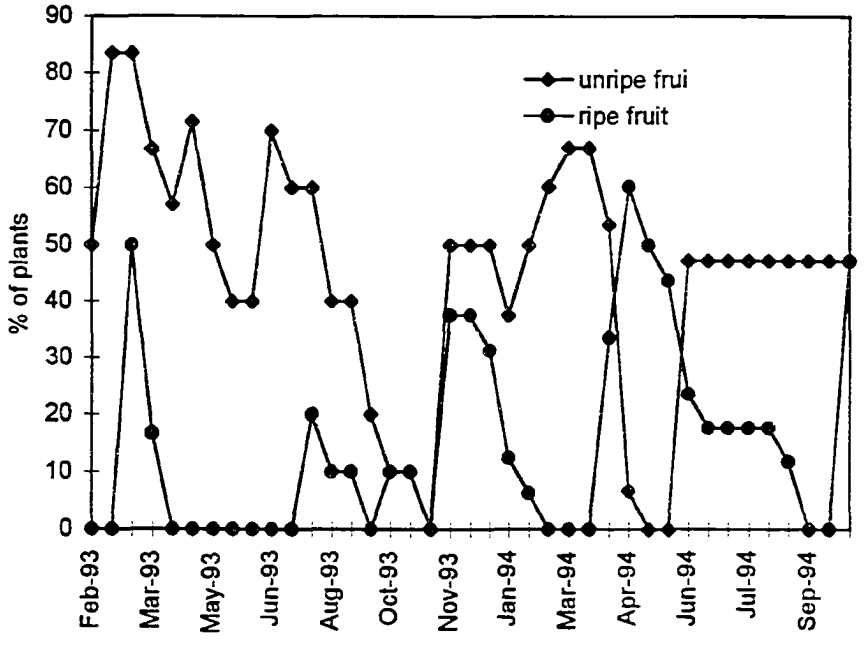


Fig. 3.17b. Percent of *Bakerella* (Loranthaceae) plants in fruit sampled biweekly at Talatakely, RNP.



Jul-93, Feb-94 and Oct-94 sampled only once

Fig. 3.18. Percent of *Viscum* (Viscaceae) plants in fruit sampled biweekly at Talatakely, RNP.

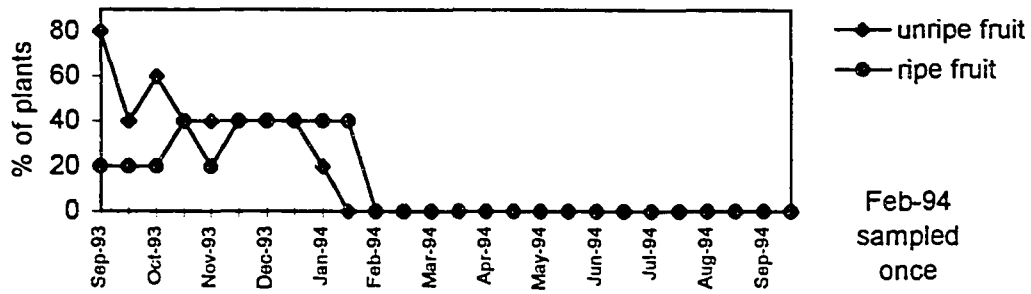


Fig. 3.19. Percent of *Rhipsalis* (Cactaceae) plants in fruit sampled biweekly at Talatakely, RNP.

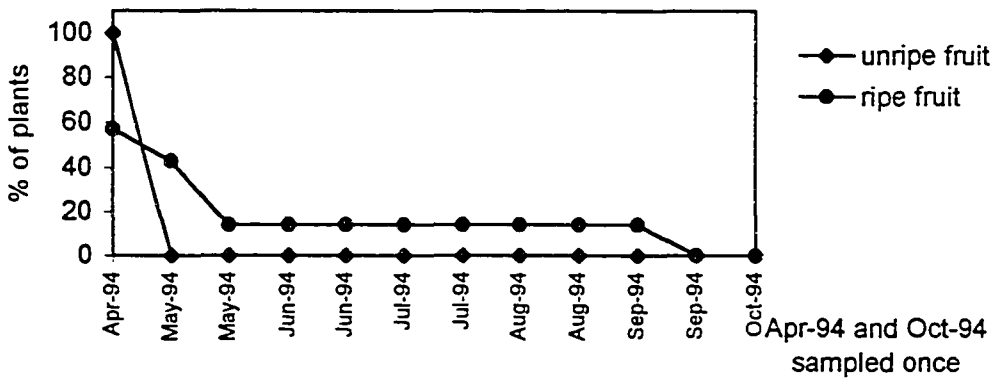


Fig. 3.20. Percent of *Medinilla* (Melastomataceae) plants in fruit sampled biweekly at Talatakely, RNP.

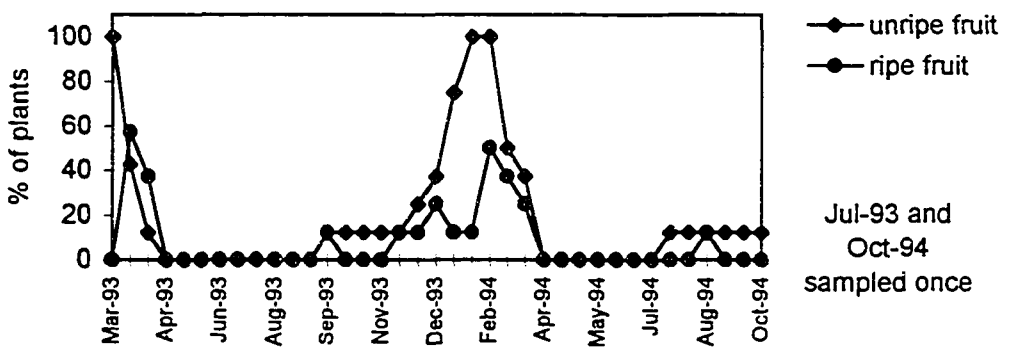


Fig. 3.21a. Fresh weight (g) of insects captured biweekly at Talatakely, RNP.

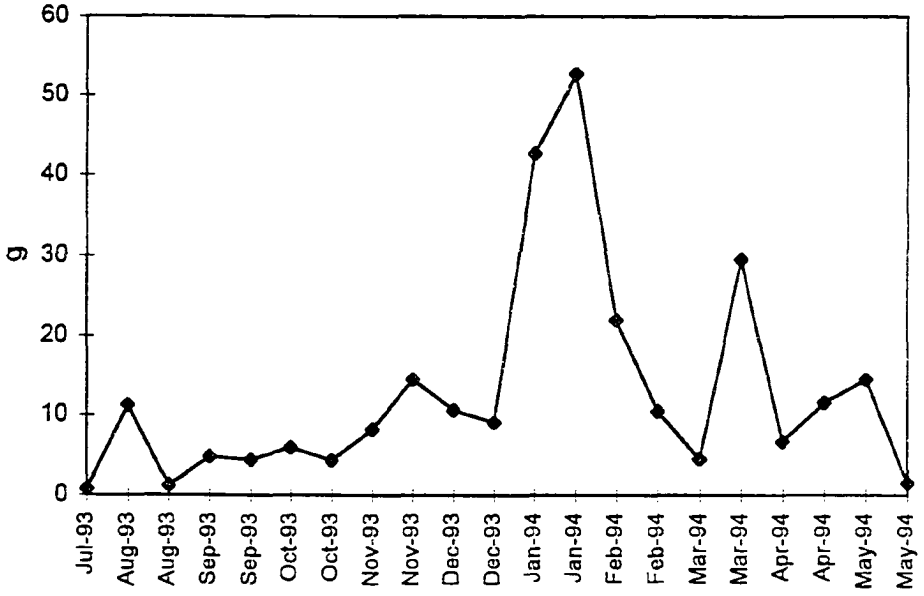


Fig. 3.21b. Number of insects captured biweekly at Talatakely, RNP.

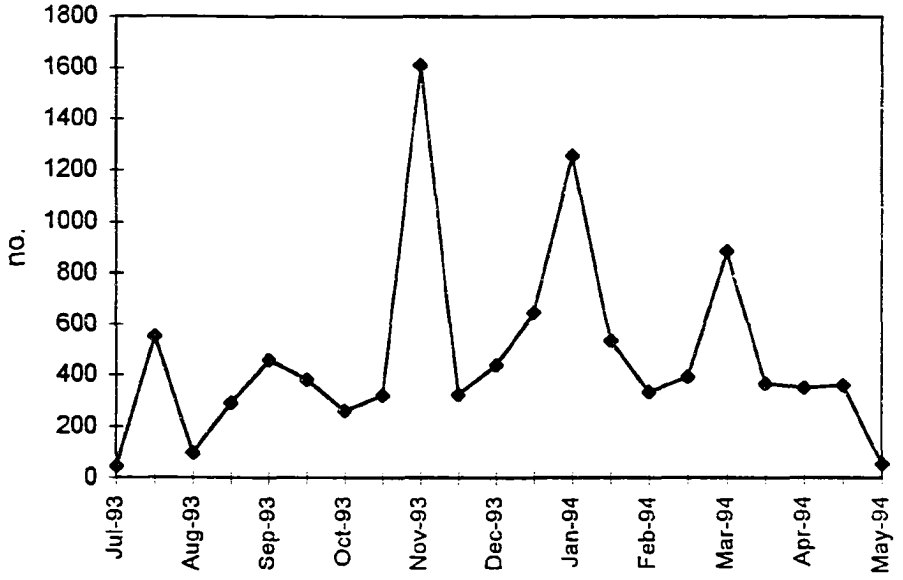
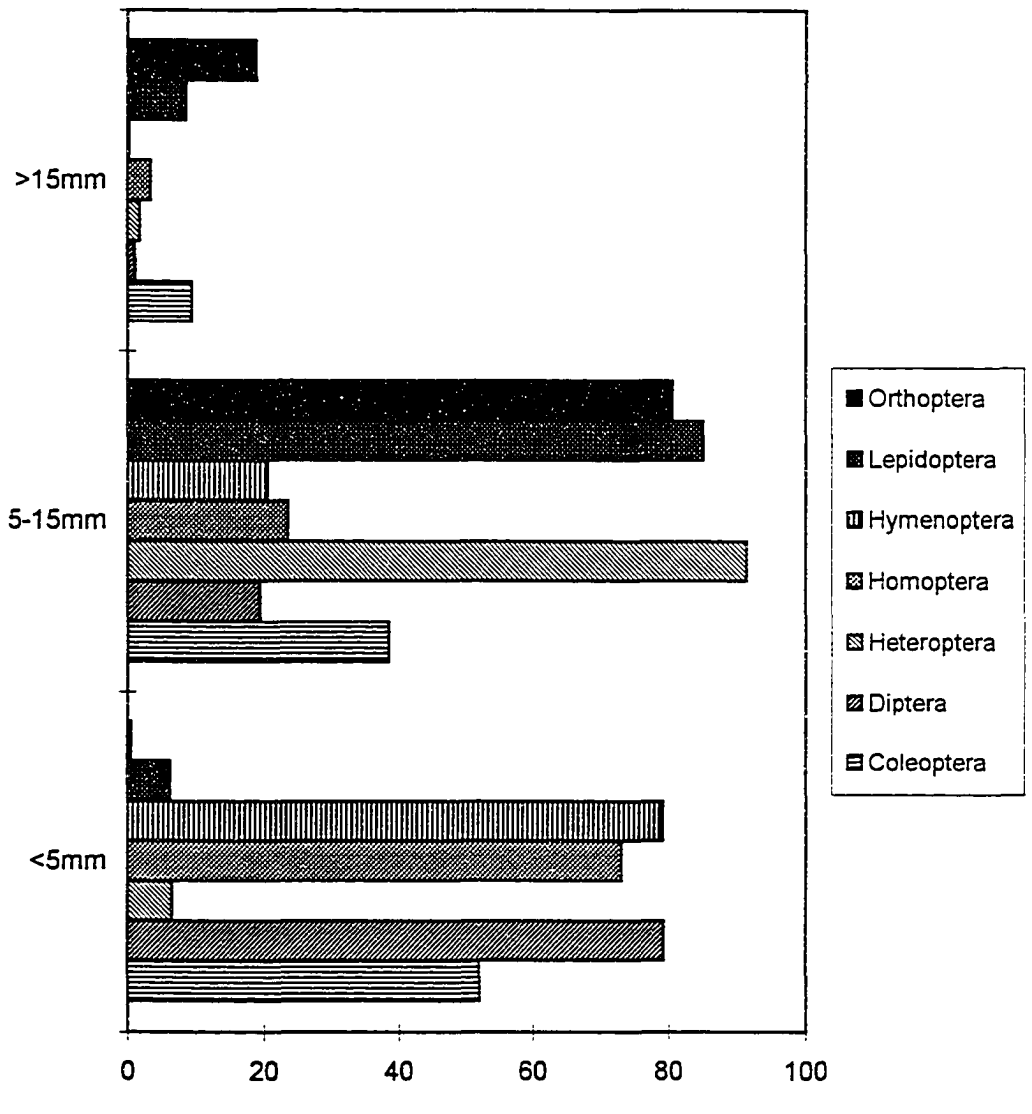


Fig. 3.22. Distribution of length classes for 7 insect orders captured from Jul-93 to May-94 at Talatakely, RNP.



CHAPTER FOUR

FEEDING ECOLOGY OF *MICROCEBUS RUFUS*

Introduction

In the Introduction to this chapter, I discuss what is known about the feeding habits of *Microcebus* and how they may be influenced by body size. Results concerning the feeding ecology of *M. rufus* are presented in several sections which include determining the components of the diet and patterns of feeding behavior through fecal analysis, testing dietary hypotheses by comparing diet to resource availability, feeding observations from radiotracking and nocturnal censusing, and results of biochemical analysis of certain *Microcebus* food sources. In the Discussion I comment on how results from this research compare with previous observations on *Microcebus'* diet and how they affect accepted assumptions concerning the dietary behavior of mouse lemurs.

The Effect of Body Size on Diet in Small Primate Species

The study of a primate's natural diet is important to understanding its behavioral, morphological and physiological evolution and adaptation. How members of a species acquire nutrients and accumulate energy in a specific environment affects all factors of life, such as reproduction, ranging patterns and interactions with other species. A significant factor influencing the diet of a species is its body size (Begon and Mortimer, 1986; Boyce, 1988) because size affects the kinds of food an animal requires and is able to utilize (Temerin et al., 1984).

Microcebus has the distinction of being the smallest living primate genus (Atsalis et al., 1996). Empirical evidence has demonstrated that small mammals have high metabolic rates relative to their body size (Kleiber, 1961; Schmidt-Nielson, 1970) and,

therefore, require a high quality diet to accomodate their greater per-unit-weight energy requirements (Geist, 1974; Gaulin, 1979). For instance, small ungulates tend to feed on plants with a low fiber and a high protein content (Bell, 1971; Geist, 1974; Jarman, 1974).

In the case of primates, too, it has been argued that body size is a good predictor of how a species meets its dietary needs, specifically its protein requirements (Kay, 1975; Clutton-Brock and Harvey, 1977a, 1983; Gautier-Hion, 1978; Gaulin, 1979; Coe, 1984; Ripley, 1984; Garber, 1987; Martin, 1990). Insects are considered to be rich sources of protein, as well as of carbohydrates, fats and essential minerals (Gaulin, 1979; Hladik, 1981; Richard, 1985). However, because insects are rarely found in sufficient quantities to satisfy the protein and other nutritional needs of large primates, these species tend to concentrate on herbaceous matter which can be found in bulk but which would be indigestible to smaller primates (Hladik, 1978; Cork and Foley, 1991). On the other hand, it is generally accepted that small primate species, a 200-350 g threshold has been suggested by Kay (1984), include a high proportion of insects in their diet to satisfy their protein requirements and to sustain their increased nutritional needs due to high metabolism (Clutton-Brock and Harvey, 1977a; Hladik, 1979; Coe, 1984; Fleagle, 1984; Kay, 1984; Ripley, 1984; Richard, 1985). Some researchers have argued that, based on body size/diet predictions, small primates should rely on animal matter as their major food type and should be be primarily insectivorous (Hladik, 1979, 1981; Gaulin, 1979; Clutton-Brock and Harvey, 1983; Kay, 1984).

By extension, *Microcebus*, being the smallest of the primates, should be the most insectivorous. This view has been reinforced by its comparison to the galagos

(Charles-Dominique and Martin, 1970; Szalay and Katz, 1973; Cartmill, 1975), where some data suggest a high incidence of insectivory (Charles-Dominique, 1972; Harcurt, 1986; Harcourt and Nash, 1986b; Harcourt and Bearder, 1989), and by the proposal that *Microcebus* and some species of *Galago* are similar to early primates which are thought to have been primarily predatory (Charles-Dominique and Martin, 1970).

The Diet of *Microcebus*

Several lines of evidence suggest that *Microcebus* may not necessarily follow the predictions from the widely accepted body size/diet relationship. For instance:

1. As has been noted elsewhere (Tattersall, 1982; Tattersall and Sussman, 1989), field data suggest that *Microcebus* is not highly insectivorous (Martin, 1972; 1973; Hladik et al., 1980). Field studies have shown that diets of west coast cheirogaleids, including *Microcebus*, are mixed and show seasonal shifts. Dietary elements include fruit, flower nectars, gums, insects and insect secretions, and small vertebrates for *Cheirogaleus medius* (Hladik et al., 1980), secretions of homopteran larvae, insects, spiders, fruit, flowers, gums, small vertebrates, and bird eggs for *Mirza coquereli* (Pagès, 1978; 1980; Hladik et al., 1980), and gums, bud exudates, sap, secretions of insect larvae, and insects for *Phaner furcifer* (Charles-Dominique and Petter, 1980; Hladik et al., 1980). The diet of *M. murinus*, the west coast relative of *M. rufus,* consists of fruit supplemented by insects, flowers, buds, gums, nectars, plant and insect secretions, small vertebrates and some leaves (Martin, 1972, 1973; Hladik et al., 1980; Barre et al., 1988). Furthermore, although existing data were insufficient to evaluate the importance of either fruit or insects in the natural diets of the two species of *Microcebus*, seasonal shifts in the dietary composition of *M. murinus* were found wherever studies included more than one season (Hladik, 1979; Hladik et al., 1980;

Barre et al., 1988; Pagès-Feuillade, 1988). Martin (1972) also pointed out that *Microcebus murinus* tended to specialize on local plant food sources, particularly berries, while insect food sources were selected more opportunistically based on peaks of availability.

2. Field studies hinted that some west coast Cheirogaleidae, including *Microcebus,* were able to cope with the varying conditions of food availability in the dry deciduous forests by accumulating body fat during the season of high resource availability and entering torpor during the season of low resource availability (Petter, 1978; Hladik et al., 1980; Petter-Rousseaux, 1980; Petter-Rousseaux and Hladik, 1980). Studies of thermoregulatory behavior have confirmed that both species of west coast mouse lemur, *M. murinus* and *M. myoxinus,* possess the ability to enter torpor (Ortmann et al., 1996; Schmid, 1996). By regulating energy requirements through metabolic depression (Ortmann et al., 1996), torpor may allow mouse lemurs to have less demanding dietary needs.

Whatever the specific metabolic requirements of *Microcebus*, the varied dietary behavior described above is not unusual. Most small mammals are characterized by diversity in their dietary patterns and consume a variety of plant and animal matter (Bourlière, 1975; Eisenberg, 1981; Cork, 1994). With few exceptions, the only overall trend that characterizes mammalian diets as body weight becomes smaller is a decrease in the consumption of high fiber foods (Cork, 1994). Furthermore, the adoption of a diet which changes according to temporal changes in the natural abundance of food sources has been recorded for many primate species (e.g. Oates, 1977; Richard, 1977; Overdorff, 1993). This tactic may be particularly important for

small mammals that are limited by climatic fluctuations which affect availability of insects, producing pressure to "escape" from faunivory to herbivory (Janzen, 1983).

Prior to this study, seasonal data on the feeding habits of the brown mouse lemur and other east coast rainforest cheirogaleids did not exist. In the eastern regions the dry season is less pronounced, though some areas experience a decrease in rainfall between April and October (Donque, 1972; Wright, 1997). In Ranomafana, this period is characterized by relative scarcity in fruit and insect abundance as well as cooler temperatures (Overdorff, 1991; Hemingway, 1995; Meyers and Wright, 1993; Wright, 1997). It remained to be documented whether *M. rufus*, adapted to the conditions of east coast rainforests, had similar dietary strategies accompanied by distinct physiological changes, as did *M. murinus* of the west coast. The few available data for *M. rufus* suggested a diet which included insects but also a high proportion of fruit (Martin,1972; Harcourt, 1987; Ganzhorn,1988; 1989; Wright and Martin, 1995).

Aims of Research

Due to the paucity of information on *Microcebus rufus,* my goal was to study year-round diet, and to monitor fluctuations in feeding behavior in relation to resource availability. Examination of the diet and quantification of resource abundance through a complete annual cycle were necessary to understand how this tiny primate survives in a fluctuating environment. Specifically, the aims of this part of the research project were:

1. To determine the components of the diet in the natural habitat, i.e. to identify the fruits, flowers, insects and other resources that make up the bulk of the diet of this population of *M. rufus.*

2. To determine the importance of fruit versus insects in the diet.

3. To determine choices in feeding behavior by comparing monthly resource availability with food preferences.

4. To determine which food items may be serving as keystone resources and/or dietary staples.

The Importance of Fruit and Insects in the Diet

Possible dietary strategies of* Microcebus rufus*: application of a model

Given that available data pointed toward a mixed diet in *M. rufus*, I proposed several feeding strategies for this species based on the relative frequencies of fruit and insects in the diet.

Feeding strategy one; the null hypothesis:

M. rufus eats both fruit and insects and has no dietary preference for either, but is a generalist that consumes these foods depending on their respective quantitative availability. This proposition effectively serves as the null hypothesis.

Alternative feeding strategies:

Two specialist strategies are that *M. rufus* eats both fruit and insects but prefers either one or the other.

To evaluate these alternatives, I applied a simple model comparing monthly fruit and insect abundance to the relative proportions of fruit and insects in the diet.

Predictions from feeding strategy one:

If the first and simplest feeding strategy was followed, I expected mouse lemurs to feed upon fruit during periods of general fruit abundance and upon insects during periods of general insect abundance. Mouse lemurs were expected to feed equally on fruit and insects when these resources were both either abundant or in low supply.

Predictions from alternative feeding strategies:

If fruit was preferred, I expected mouse lemurs to supplement their basically frugivorous diet with insects when fruit quantity was low. If insects were preferred, mouse lemurs were expected to supplement their basically insectivorous diet with fruit when insect quantity was low. In other words, I expected mouse lemurs to eat the primary food source almost exclusively when it was abundant, irrespective of the relative abundance of the secondary food source. Only when the secondary food source was relatively more abundant than the primary source were mouse lemurs expected to incorporate significant amounts of the secondary source in their diet.

Further hypotheses

As will be seen, results from testing the model demonstrated that these strategies did not adequately describe mouse lemur diets. These results were supported by additional analyses which examined the presence of insects and fruit as gross dietary categories within the fecal samples. Therefore, another option was to investigate the possibility that there existed specific fruit and/or insect species which predominated in the diet. For this purpose, I proposed two additional hypotheses.

Hypothesis on fruit presence:

Microcebus rufus incorporates specific preferred fruits in the diet irrespective of the general diversity of fruit resources available. I proposed that fruit diversity in the diet of *M. rufus* does not follow generally available fruit resource diversity.

To evaluate the hypothesis, I compared the monthly number of vernacular species of trees and shrubs with fruit within the combined botanical plots, to the monthly number of kinds of fruits present in the feces. This comparison estimated how

closely fruit diversity in the diet of mouse lemurs followed general fluctuations of fruit resource diversity.

To identify preferred dietary items I compared the frequencies with which various items were eaten by determining the percentage of the total number of fecal samples containing each specific type of fruit identified, and by evaluating the regularity of their presence in the fecal samples over the duration of the project.

Hypothesis on insect presence:

M. rufus incorporates specific insects in the diet which it prefers irrespective of the insect diversity which is generally available.

To evaluate this hypothesis I compared monthly diversity in insect availability (number of orders of insects present) to the number of orders of insects present monthly in the feces. This established how closely diversity in the diet of mouse lemurs follows the fluctuations of insect resource diversity. I then proposed that there are specific types of insects that are eaten regularly irrespective of the general diversity of insect resources available.

To identify preferred insect items I followed the same method outlined for fruit above.

The above hypotheses are supported if diversity in *Microcebus'* diet is not correlated with diversity in available resources.

Data Collected

To evaluate the dietary hypotheses, I collected year-round data on the abundance and diversity of foods consumed by *M. rufus* and compared these to general plant and insect resource availability. In order to determine whether fluctuations in these variables were related to seasonal changes in climate I also

checked standard data on weather conditions. (See Chapter Two for a more detailed description of methods).

Results

Components of the Diet

General information on fecal samples

A total of 334 fecal samples was examined from 111 known individuals, 66 males and 45 females. More samples were collected from males because of the male-biased trap ratio (102 males were trapped versus 72 females). In a small number of cases, the identity of the individual to whom the sample belonged, was unknown. Therefore, for some of the analyses, these fecal samples were excluded.

On average 1.3 samples per known individual were collected per month (Table 4.1). This implies that, at least on a monthly basis, the same individuals were not over-represented in the pool of fecal samples. The overall range in the number of fecal samples collected from mouse lemur individuals varied from 1 to 23, with an overall average of 3 samples per individual, and yet 51% of individuals from whom samples were collected provided only one each. Collecting samples from a wide range of individuals helps to avoid biases that can result from the dietary preferences of specific individuals.

Quantity and diversity of fruit within fecal samples

Of 334 samples, 266 contained some evidence of fruit, either seeds or skins, while 240 contained some type of fruit seed.

As explained in more detail in the Methods chapter, several values were used to describe quantity and diversity of fruit in the fecal samples. The MNI-F is the minimum number of individual fruits found per fecal sample. It is a minimum estimate of fruit

quantity in the feces and is based on the number of different kinds of fruit seeds and skins found. The NFT is the number of fruit types in each fecal sample. It is a minimum estimate of the diversity of fruits eaten based on grouping together similar seeds and skins. The TFT is the total number of fruit types found monthly in all the fecal samples. It is based on results from the NFT.

The MNI-F ranged from 0 to 36 with an average of 4.5, a median of 2 and a mode of 1. The range in NFT per fecal sample was 0 to 6, with an average of 1.3 and a median and mode of 1. Eighty-eight percent of fecal samples (235) contained only one or two types of fruit, while the remaining 12% contained from 3 to 6 fruit types. The TFTper month ranged from 3 to 15, with a monthly average of 7.6, a median of 7.5 and a mode of 5.

I identified 24 different kinds of fruit in the diet of *M. rufus*, either in the feces or through direct observation (Table 4.2). For those fruits for which data were collected, the average ripe fruit eaten by the mouse lemurs weighed 1300 mg, was 11.2 mm in length and 9.2 mm in width (Table 4.3).

I was able to distinguish 15 families (assuming "Kalamasombarika" is a correct identification of a specimen in the family Melastomataceae) among the fruits eaten. Within the 15 families, 16 fruits were identified to genus level (including three possible misidentifications of *Medinilla, Nuxia* and *Alberta*). Based on external morphology, an additional two genera may have been present (one represented by *Psychotria* and the other by "Voananamboa"). Eleven were identified to species (including the possibly misidentified *Alberta humblotii*). Seven of the fruits come from epiphytes or lianes. *Aphloia, Bakerella, Gaertnera, Psidium* and *Harungana* are known to be commonly eaten by other lemurs and birds.

There is wide disparity in the frequency with which various fruit seeds were present in the feces (Table 4.4). Close to 58% of the 240 fecal samples that contained any kind of fruit seed had *Bakerella* seeds, while *Medinilla* was second in seed presence with 9.6%. It is also interesting to note that the fruit of some of the trees with the highest basal area, e.g. *Weinmannia*, are not included in the diet (see Appendix 1).

Of the 240 fecal samples, 105 (43.8%) had at least one type of unknown fruit seed. Based on external appearance, I estimate the number of unidentified seeds in the feces to belong to a minimum of 40 and a maximum of 52 different fruits. As many as 19 of the unidentified fruits may belong to the genus *Ficus,* based on general similarity to other known fig seeds in terms of their very small size and large number within each fecal sample. However, although small seeds in large numbers appeared ratherregularly in the fecal samples, a positive identification could not be made when comparing them to any of the more common *Ficus* plants. "Voara" and "Famakilela madinidravina" were two common *Ficus* trees, the fruits of which *Microcebus rufus* is reputed to eat in Ranomafana and which captured individuals consumed in trial tests (Harste, 1993). Yet we were not able to make a positive match between seeds in the feces and the seeds of these fruits. Nonetheless, I discovered that there were many more species of *Ficus* than were readily apparent. For instance, "Vahihafa", a fig, was found to be a shrub with a liane-like "climbing habit" (Simon Malcomber, pers. com.) that had gone unnoticed by us when searching for the fruits of fig trees. Turk (1995) states that there are at least ten fig species in Ranomafana, ranging from small shrubs to large trees. Therefore, it is possible that many species of *Ficus*, some of which may have been eaten by *Microcebus*, remained undiscovered by me and my assistants.

Quantity and diversity of arthropods within fecal samples

Of 334 samples, 254 (76%) contained evidence of insects and, more rarely, spiders. As described in the Methods chapter, the MNI-I, is the value I used to quantify prey items within each fecal sample. It is based on reconstruction of the number of prey items from the chitin remains in the subsample of fecal samples examined by an expert entomologist. Of the 115 fecal samples thus examined, the MNI-I per fecal sample ranged from 1 to 12, with an average of 2.2, a median of 2 and a mode of 1.

Insects belonging to nine different orders were identified (Table 4.5). Caterpillars were placed in a separate category from adult Lepidoptera because of the different habitats that they may occupy. The "Unknown Invertebrate" category contains material that could not be identified to class. In 16 fecal samples, hymenopteran insect remains could not be distinguished from heteropteran remains and were placed in the "Unknown Insect" category. Therefore, either one or both of these categories may be underestimated.

Within the subsample of fecal samples examined 56% contained only one of the categories listed in Table 4.5, while close to 96% (110 samples) contained from one to three categories. The average number of categories found within a fecal sample was 1.7, while the maximum number was 5.

Other material found in the feces

Besides fruit and arthropod remains, other plant and animal matter appeared in the fecal samples. In the case of the plant matter, it was not possible to determine whether its presence was the result of accidental ingestion while consuming fruit, nectar or sap. Flower parts were especially common in August 1993, when filaments

and anthers of "Maka" (*Weinmannia bojeriana* Tul., family Cunoniaceae) were found in seven different fecal samples. An unidentified flower petal and an intact flower were also found on two other occasions. Woody filaments and tiny pieces of bark and twig (sometimes with leaf) were occasionally present and, on a few occasions, bits of moss. These latter items may have been ingested in the process of obtaining gum or sap. At least once a mouse lemur was seen licking exposed cambium, possibly lapping up gum or sap; the bark of that particular tree was covered with moss.

Animal matter was difficult to identify with certainty. Filaments that may have been moth scales were detected. The egg case of a praying mantis was found once. A sample thought to contain an intestinal parasite, which was brought back to the U.S. for identification, was found to be part of a soft invertebrate, possibly an earthworm. Similarly, ten other samples of soft invertebrates examined by Louis Sorkin at the Department of Entomology of the American Museum of Natural History were not parasites but insect eggs, larvae or pupae (one contained a hatched puparium, possibly a drosophilid), most likely ingested with fruit. Intact ants were also found, probably ingested when eating fruit.

The Importance of Fruit and Insects in the Diet

Fruit and insects as gross dietary categories within the fecal samples

A total of 207 out of 334 fecal samples (62%) contained the remains of both fruit and insects. Fecal samples containing both fruit and insects predominated in number for almost all months of the study period (Figure 4.1). Seventy-three fecal samples (21.9%) contained only fruit remains (skins, pulp or seeds) while 48 (14.4%) contained only arthropod remains (mostly chitin from insects; multiple samples from a single individual were not averaged in these analyses).

Loglinear analysis demonstrates that the proportion of fecal samples in each of the three dietary categories changes significantly during the study period ($\chi^2 = 49.89$, $p<0.001$). Of the three categories, the "insect only" category exhibits the greatest fluctuation, decreasing to zero in December 1993, January 1994, February 1994, March 1994 and May 1994 (Figure 4.1). The "fruit only" category does not show a similar pattern. In the analyses below, I concentrate on the percentage of fecal samples designated as "insect only" to reveal possible patterns in the fluctuations observed.

Comparison of the "insect only" category to resource abundance

I compared the "insect only" category with fruit and insect availability to test whether there is a correlation between resource availability and the number of fecal samples containing the "insect only" remains. No correlation was found.

With regard to fruit availability, there was no significant correlation between the "insect only" category in the fecal samples and the percentage of trees and shrubs in the botanical plots containing unripe or ripe fruit (for unripe fruit, rs=0.348; for ripe fruit, rs=-0.127; n=15), nor with the percentage of trees and shrubs containing unripe fruit within the *Microcebus* fruit source phenology sample (rs=-0.181, n=16). The correlation approaches statistical significance when comparing the "insect only" category to percentage of trees and shrubs in the botanical plots bearing ripe fruit (rs=0.504, $p<0.10$, n=16).

With regard to insect availability, I used only data from the capture of insects at the one collection site (tent site) where there were no gaps in the sequence of data collection. I added the data together as an indicator of the total quantity of insects available monthly. I found that the percentage of fecal samples with "insect only" remains is negatively correlated with the fresh weight of insects captured (rs=-0.808,

$p<0.01$, $n=10$) as well as with the number of Coleoptera captured ($rs=-0.653$, $p<0.01$, $n=10$). It is precisely during some of the months when the fresh weight of insects collected is highest that the number of fecal samples with "insect only" remains decreases to zero (Figure 4.2). Since, as will be discussed, Coleoptera are a preferred resource, the negative correlations are probably not due to a lack of available preferred insects. They may instead be due to increased consumption of alternative resources available, i.e. fruit. Therefore, I tested to see if there existed a negative correlation between the values which measure monthly fruit intake and the percentage of fecal samples with "insect only" remains. I found that there was a negative correlation between the percentage of samples in the "insect only" category and values of fruit intake, i.e., the monthly average MNI-F in a fecal sample ($rs=-0.630$, $p<0.05$, $n=16$) and the monthly average NFT in a fecal sample ($rs=-0.719$, $p<0.01$, $n=16$).

Quantity and variety of fruit in the average fecal sample is negatively correlated with the overall percentage of fecal samples containing "insect only" remains, suggesting that fruit intake is an influential factor in general feeding patterns. This suggests that patterns in fruit consumption can influence insect consumption, and that fruit intake is an influential factor in general feeding patterns.

Evaluation of feeding strategies: application of the model

As previously noted, three alternative feeding strategies were proposed for *Microcebus rufus*:

1. That mouse lemurs consume fruit and insects depending on their quantitative availability with no specific preference for either.
2. That mouse lemurs consume both fruit and insects but prefer fruit.
3. That mouse lemurs consume both fruit and insects but prefer insects.

In order to choose among these, I applied a simple model based on several variables described below.

Fruit resource abundance, "F": the monthly number of trees and shrubs in all four botanical plots that contained any quantity of ripe or unripe fruit.

Insect resource abundance, "I": the monthly number of insects collected from the tent collection site.

Fruit quantitiy in the diet, "Fo": the monthly average MNI-F.

Insect quantity in the diet, "Io": the monthly average MNI-I.

Relative observed fruit quantity in the diet: a measure of fruit quantity in the feces relative to total intake of fruit and insect. It is determined by the formula (Fo/(Fo+Io)) X 100.

Relative predicted fruit quantity in the diet: a measure of fruit quantity based on available fruit and insect resource abundance. It is determined by the formula (F/(F+I)) X 100.

Relative observed insect quantity in the diet: a measure of insect quantity in the feces relative to total intake of fruit and insect. It is calculated as (1-(Fo/Fo+Io)) X 100.

Relative predicted insect quantity in the diet: a measure of insect quantity based on available fruit and insect resource abundance. It is determined by the formula (I/(F+I)) X 100.

As is evident by the formulas used, the model requires that measures of fruit and insects are roughly equivalent. Yet, the raw numbers, MNI-F and MNI-I, and, the monthly number of insects collected and the monthly number of trees in fruit, measure very different aspects of the data. Therefore, for each of these four variables, over the course of the months that data were collected, I set the maximum monthly quantity to

100. The other monthly values were set to the percentage of that value. By setting the maximum to 100, I try to make the ranges of the data fairly equivalent so that when I combine Fo and Io, and, F and I, they are unitless numbers which at least approach similarity.

Note that application of the model is limited to the period from September 1993 to May 1994 because of missing data values; I do not have MNI-I prior to September 1993 and data collection for feeding ended in May 1994.

Assuming the no-preference feeding strategy, i.e. that mouse lemurs consume fruit and insects depending on their quantitative availability, I compared fruit resource abundance to both the observed fruit quantity in the diet and to the predicted fruit quantity in the diet (see Harcourt and Nash, 1986b for a similar application to galago diets) (Figures 4.3 and 4.4).

Between November 1993 and March 1994, the observed fruit quantity in the diet is close to the predicted fruit quantity in the diet (Figure 4.3). This means that actual fruit consumption follows general fruit resource abundance. However, this does not occur for the months just prior to and following this period, when observed fruit quantity in the diet falls far below predicted fruit quantity. The latter remains high because fruit resource abundance is high.

If fruit in general is the preferred food source, then during the months prior to November 1993 and after March 1994, when fruit abundance is at its highest, mouse lemurs would be expected to eat fruit almost exclusively, and yet it is during these periods that mouse lemur consumption of fruit is relatively low as compared to abundance.

If insects are the preferred food source, then they should be eaten almost exclusively when they are in abundance, irrespective of the quantity of the secondary

food source, i.e. fruit. Yet, observed insect quantity in the diet differs greatly from predicted insect quantity in the diet during the months of September, October, April and May, and to a lesser degree, in December, January and March (Figure 4.4). In fact, insects are eaten in large quantities during some of the months when their relative abundance is low, i.e. September 1993 and October 1993. The above findings suggest that mouse lemurs do not opportunistically feed on fruit and insects based on fluctuations in general abundance.

These findings are further supported by a comparison of the dietary values which measure quantity and diversity in the diet to measures of general resource availability (Table 4.6). Specifically, there was no statistically significant correlation between the monthly average MNI-F in the fecal samples and the monthly number of trees and shrubs in fruit in the botanical plots (r_s=0.411 for ripe and unripe fruit combined, n=15). Nor was there a statistically significant correlation between monthly average NFT and the monthly number of trees and shrubs in fruit in the botanical plots (r_s=0.336 for ripe and unripe fruit combined, n=15). Similarly, no statistically significant correlation was found between the monthly average volumetric score for insect remains in the feces and the monthly average fresh weight of insects collected (r_s=0.109, n=11), or between the monthly average MNI-I and the monthly number of insects collected (r_s=0.455, n=10).

Tests of additional hypotheses and determination of preferred resources

Hypothesis on Fruit Presence

The results from the application of the model indicate that *M. rufus* feeding patterns do not consistently follow the general availability of fruit and insects. Therefore, I also tested the hypothesis that fruit diversity in the diet of *M. rufus* does not

follow generally available fruit resource diversity. I compared the monthly number of vernacular species of trees and shrubs in the botanical plots which contained fruit to monthly values of fruit diversity in the diet, both as measured by NFT and by TFT. Because *Microcebus rufus* consumes both ripe and unripe fruit, comparisons were done separately for unripe fruit, ripe fruit, and any fruit (ripe or unripe). All correlations were non-significant. (NFT for unripe fruit, rs=0.357; for ripe fruit, rs=-0.144; for any fruit, rs=0.224, n=13. TFT for unripe fruit, rs=0.288; for ripe fruit, rs=-0.115; for any fruit, rs=0.339, n=13) (Figures 4.5 and 4.6). These results support the hypothesis that fruit diversity in the diet is not correlated with generally available fruit resource diversity.

Preferred Fruits

To identify preferred dietary items, I determined the percentage of the total number of fecal samples that contained each specific type of fruit identified. I found that the predominant fruit found in the feces of *M. rufus* is *Bakerella*. *Bakerella* is an epiphytic semi-parasite endemic to Madagascar which belongs to the family Loranthaceae, the mistletoes. *Bakerella* seeds appear in 139 of 334 fecal samples, which constitute close to 40% of all samples examined (or 58% of the 240 samples that contained any kind of fruit seed) (Table 4.4).

Although comparing the quantities of different fruit in the feces may not always reflect their true relative significance in the diet (see section headed "*Bakerella*" below), the importance of *Bakerella* to *Microcebus rufus* is indicated by the fact that it is the only fruit present in the fecal samples during every month of the study period (Figure 4.7; Tables 4.7 and 4.8). Over the course of the project's duration, six different varieties of *Bakerella* were discovered in the study area. Through direct observation and fecal analysis it was determined that *Microcebus* fed on at least three, though

judging by the regularity of presence in the fecal samples more species were probably exploited.

Hypothesis on insect presence

I also tested the hypothesis that insect diversity in the diet of *M. rufus* does not follow generally available insect resource diversity. I compared the monthly number of orders of insects captured during the sampling sessions to the monthly number of orders of insects present in the feces, and found no significant correlation between the two (r_s=0.492, n=11).

There was a greater diversity of insects represented in the monthly forest collections than in the collection of fecal samples each month. Eight of the 14 orders identified during the monthly capture sessions were regularly present over the course of this project. On the other hand, although nine orders were identified in the total assortment of fecal samples examined, the average number of orders identified per month in the fecal samples was 3.2 (with a mode of 2).

However, a caveat to the above finding is that the number of orders found in the fecal samples each month is positively correlated with the number of fecal samples collected for that month (r_s=0.794, $p<0.01$, n=12). This suggests that the variety of insect orders represented within the fecal samples is influenced by the number of samples collected each month. If more samples had been examined per month, a more diverse array of insects may have been detected in the diet.

Preferred insects

To identify preferred dietary items, I determined the percentage of the total number of fecal samples that contained each specific type of insect identified in order to evaluate their regular appearance in the fecal samples.

I found Coleoptera (beetles) to be the predominant insect order in the feces of *M. rufus* (Table 4.5). Close to 70% of the 115 samples examined contained specimens from this order of insects. More specifically, the importance of Coleoptera is indicated by its frequent multiple appearances within single fecal samples as compared with the other orders. Including these multiple appearances, Coleoptera were identified 121 times out of a total of 250 insect identifications made.

Like the plant resource *Bakerella*, Coleoptera is the only insect order to be present in the fecal samples for all months that chitin remains were collected. It appears in over 50% of the fecal samples for 9 out of 12 months sampled (Figure 4.8).

Feeding Patterns

Patterns in consumption of fruit

During the wet season, February 1994 is characterized by a distinct peak in monthly average MNI-F. This value also peaks in July 1993, in the mid-dry season. A similar pattern is seen in the monthly average number of *Bakerella* seeds found per fecal sample. Monthly average MNI-F and monthly average number of *Bakerella* seeds found per fecal sample are highly positively correlated ($r_s=0.915$, $p<0.01$, $n=16$). Thus, the peak in monthly average MNI-F in July 1993 may be explained by the corresponding increase in monthly average number of *Bakerella* seeds present in the feces. However, the increase in MNI-F in February 1994 cannot be explained solely by the increase in *Bakerella* consumption because NFT also peaks during this month. This signifies that in February 1994, individual mouse lemurs increased not only the amount of *Bakerella* they were consuming but also the variety of fruits they were consuming in general (Tables 4.6 and 4.8). In fact, in February and March 1994 there is increased diversity in available fruiting plants as well as increases in the values that

measure dietary diversity (both NFT and TFT) in the feces. This indicates that in February 1994 *M. rufus* was incorporating not only more *Bakerella* in the diet but also other fruit resources not included in July's diet. This may be due to preferred species of fruiting plants becoming available and/or to specific nutritional needs of mouse lemurs during this period. In February 1994, several new kinds of fruit seeds make an appearance in the feces of *M.rufus*, although only one of these was identified (*Gaertnera*). Among the fruits identified in February 1994, *Rhipsalis* and *Medinilla* are epiphytes. Given the heavy reliance of mouse lemurs on another epiphytic plant, *Bakerella*, it is possible that mouse lemurs have a preference for this group of plants.

Epiphytes are sensitive to drought and therefore February and March may have been beneficial for these plants due to increased rainfall from two sequential cyclones. March 1993, when another cyclone increased rainfall in Ranomafana, is also characterised by relatively high TFT and NFT. However, April 1994 has high values for dietary diversity despite low levels of rainfall, suggesting that the influence of rainfall on the vegetation is not the sole force driving *Microcebus* feeding patterns.

NFT is positively correlated with MNI-F both on an individual fecal sample basis ($r_s=0.680$, $p<0.05$, $n=334$) as well as on an average monthly basis ($r_s=0.768$, $p<0.01$, $n=16$) (Figure 4.9). This suggests that dietary fruit diversity increases as the number of seeds in a fecal sample increases, i.e. the more seeds found in a fecal sample (based on MNI-F) , the more likely they will belong to different kinds of fruit (NFT).

TFT has its highest peak in April 1994. Since no statistically significant correlation was found between TFT and number of fecal samples collected per month ($r_s=0.131$, $n=16$), it is reasonable to assume that this peak in TFT is not entirely due to

the large number of fecal samples collected in April (indicated in Table 4.1). Five new fruits, which remained unidentified, were added to the diet during this month.

In general, however, individual mouse lemurs seem to consume similar kinds of fruit each month. This is indicated by the lack of a significant correlation between the monthly TFT and the monthly average MNI-F (rs=0.422, n=16), suggesting that the total number of fruit types found in the feces per month does not necessarily increase with an increase in the quantity of fruit found per sample.

To summarize:

a. Fruit feeding during the end of the rainy season is influenced by variety in available fruit resources and possibly in the specific kinds of fruit resources available (i.e. epiphytes). These patterns in fruit feeding may be related to the specific needs of mouse lemurs at certain times in their annual life cycle (see Chapter Five).

b. When increased consumption of fruit occurs it always involves an increase in consumption of *Bakerella.*

The relationship between the* Microcebus *fruit source phenological sample and the botanical plot phenological sample

It has been shown that overall *Microcebus* fruit-eating patterns do not follow the general phenological patterns of fruit availability in the forest. This implies that the specific fruits eaten by mouse lemurs may not always follow the phenological patterns of general fruit availability, either. To investigate this possibility, I compared the monthly percentage of all plants containing unripe fruit in the *Microcebus* fruit source phenological sample with the monthly number of plants containing unripe fruit in the combined botanical plots and found that there was no statistically significant correlation between the two (rs=0.236, n=20) (Figure 4.10). (Unripe fruit was chosen because

values for ripe fruit in the *Microcebus* fruit source phenological sample were frequently very low or zero.)

To check the possibility that there were correlations obscured by combining the data from all the *Microcebus* fruit sources together, I conducted comparisons between specific categories (families or genera) within the *Microcebus* fruit source phenological sample for which there existed a fairly large data set (based on monthly percentage of plants in fruit) and the data from the combined botanical plots (based on monthly number of plants in fruit).

In only two cases did I find statistically significant correlations between data from the *Microcebus* fruit source phenological sample and data from the botanical plots: the percentage of unripe fruit from the family Viscaceae (which included only one genus) was negatively correlated with the total number of trees and shrubs in fruit in the four botanical plots ($r_s=-0.726$, $p<0.05$, $n=9$), and the percentage of unripe fruit representing *Psychotria* (family Rubiaceae) was positively correlated with the number of fruiting trees and shrubs in the botanical plots ($r_s=0.877$, $p<0.01$, $n=14$). These results further support the hypothesis that fruit consumption in mouse lemurs is not closely linked to general fruit abundance in the forest.

Patterns in consumption of insects

Like the correlation between NFT and MNI-F, the average number of insect orders per fecal sample (the diversity value for insects) is positively correlated with the MNI-I found in the fecal samples (per fecal sample, $r_s=0.856$, $p<0.05$, $n=109$; as monthly averages, $r_s=0.781$, $p<0.01$, $n=12$). This implies that the more insects a single mouse lemur consumes, the more likely they will be different kinds of insects.

On the other hand, unlike NFT, the average number of insect categories per fecal sample does not vary significantly among months (Kruskal-Wallis=11.19, n=111) and monthly variation in MNI-I is only borderline significant (Kruskal-Wallis=19.33, p=0.055, n=112). Yet the volumetric scores for arthropod remains in the feces fluctuated significantly among months (Kruskal-Wallis=94.43, $p<0.05$, n=334) (see Table 4. 6 for monthly averages).

One explanation for this is that although the average number and range of diversity of insects (as indicated by number of different orders of insects in the feces) that are eaten by individual mouse lemurs may not vary significantly over time, the specific kinds of insects eaten may vary, yielding different amounts of chitin remains.

Insects are eaten in relatively low quantities, based on MNI-I, during the months of November 1993, December 1993, January 1994 and March 1994 (see Table 4.6), which coincide with certain times of highest insect abundance (in terms of total numbers). November and December 1993 spanned the mating season of the Formicidae, so there was a preponderance of winged queen and male ants in the collections. Although non-intact ants are found in the fecal samples of mouse lemurs, the fact that their remains do not increase in accordance with the period of their greatest abundance in the forest suggests that ants may be consumed accidentally, perhaps in the course of ingesting figs or other fruit. The increase in insect abundance in January 1994 is due to the family Gryllidae in the order Orthoptera, a family identified only once in the fecal samples. The Gryllidae are a group of terrestrial insects which may explain why they are not consumed in large numbers by an arboreal species. The increase in March is accounted for by a preponderance of ants and two families of Hemiptera. One family identified is the Pentatomidae, commonly known as "stink bugs". Mouse lemurs may have avoided these toxic insects since their remains were

never found in mouse lemur feces. The second family of Hemiptera, identified as Nabidae, constituted a large number of the Hemiptera collected during this month (146 Nabidae out of 259 Hemiptera). These insects, although not terrestrial, occur in low vegetation (Borror and White, 1970) which may account for their lack of presence in the mouse lemur diet.

The increase in insect consumption in September 1993, October 1993 and February 1994 is due to an increase of Coleoptera in the diet (see Figure 4.8).

The above, once again, support previous findings that consumption of insects is not related to general insect abundance in the forest. There are groups of insects which increase in numbers, apparently without concomitant increase in consumption by mouse lemurs. On the other hand, an increase in the presence of Coleoptera in the forest resulted in increased consumption of members of this order (see below).

Important Dietary Items

Bakerella

Since *Bakerella* was so common in the feces of mouse lemurs, I compared *Bakerella*'s presence in the forest with its presence in the feces. Surprisingly, I found that there was no statistically significant correlation between the average number of *Bakerella* seeds in the fecal samples per month and the percentage of *Bakerella* plants in fruit (r_s=0.319 for unripe fruit, n=16), nor between the percentage of fecal samples with *Bakerella* seeds and the percentage of *Bakerella* plants in fruit (r_s=0.142 for unripe fruit, n=16) (Table 4.9). To illustrate, in November 1993 *Microcebus* was able to find *Bakerella* plants with fruit even though phenological data indicated that none of the plants being monitored were in fruit. *Bakerella's* constant presence in the diet even

when quantities of this fruit were seemingly low in the forest suggests that *Bakerella* may be a dietary staple.

There is however, significant monthly variation in the presence of *Bakerella* in the fecal samples (Kruskal-Wallace=74.75, $p<0.001$, n=334). *Bakerella* is found in 11% of the fecal samples in December 1993 but reaches as high as 70% in February 1994 (Table 4.9). Its presence in the fecal samples is relatively low for all months of the dry season except July 1993, which experienced more rainfall than the other winter months. This may have resulted in increased availability of this fruit. The appearance in the feces of *Viscum* (family Viscaceae), another epiphytic semi-parasite similar to *Bakerella,* overlaps some of the months of the dry season during which *Bakerella* seeds are found in least quantity in the feces (Figure 4.7). However, in July 1993 there was an increase in the number of varieties of fruit available in the forest (see Figure 3.9) and yet *Bakerella* was the only fruit whose consumption increased at this time.

Bakerella fruit are berries that do not contain a true seed but rather an embryo surrounded by a starchy endosperm (Balle, 1964; Mabberley, 1987). The "seed" lacks testa but is surrounded by viscous material which is covered by the outer pericarp. The viscous material covering the seed of this fruit renders it very sticky and difficult to detach from the pericarp. Since it may be difficult NOT to ingest the seed, seed presence in the feces may be closer to the amount of fruit actually consumed than for other fruits. Other factors, too, may influence fruit seed presence in the feces. For example, the seeds of *Psidium* appear in only 5 of 334 fecal samples examined (Table 4.4). *Psidium* has a juicy pulp with many large and heavy seeds in contrast to *Bakerella* seeds which are soft, so that swallowing *Psidium* may be actively avoided by mouse lemurs. On the other hand, it is possible that the difference in the presence of

Psidium in the feces compared to *Bakerella* may be due to its relatively low lipid content (see Table 4.10).

Coleoptera

The constant and high presence of Coleoptera in the diet suggests that, like *Bakerella*, this insect order is a dietary staple. In addition, the presence of Coleoptera in the feces is significantly correlated with the number of insect orders per fecal sample, although not very highly ($r_s=0.381$, $p<0.05$, $n=113$) (When compared as monthly averages, there was no significant correlation [$r_s=0.248$, $n=12$]). This suggests that the presence of Coleoptera in the fecal samples is not predicted well by the number of insects per fecal sample.

Since the order Coleoptera was predominant in the feces, I compared a measure of the order's presence in the forest to measures indicating its presence in the fecal samples. I found that the average number of Coleoptera caught during sampling each month is not significantly correlated with the monthly percentage of fecal samples containing Coleoptera ($r_s=0.274$, $n=11$), but is significantly correlated with the average number of Coleoptera found per fecal sample per month ($r_s=0.847$, $p<0.01$, $n=11$). In other words, it appears that although the number of *Microcebus* consuming Coleoptera does not increase or decrease as Coleopteran abundance fluctuates in the forest, the number of Coleoptera consumed per mouse lemur individual is correlated with this order's abundance.

Nocturnal Censuses

Approximately 224 hours were spent walking along the trails in order to conduct nocturnal censuses. Mouse lemurs were sighted 342 times. Forty-two sightings involved feeding episodes. Of these 43 feeding episodes, 19 were on fruit, 22 involved

insects, one was on sap or gum and one remained undetermined. Of the 19 fruit-eating observations, 13 were on three different species of *Bakerella*, three were on *Gaertnera* and one each involved *Psidium* (goava fruit) and *Micronychia madagascariensis* (a scrambling shrub in the family Anacardiaceae). (On separate occasion a mouse lemur had also been seen to feed on *Micronychia* flowers and/or buds).

Insect feeding episodes include cases in which individuals were seen actively searching for insects even though they were not feeding at the time of observation. Insect-searching behavior was easily recognizable; mouse lemurs darted rapidly back and forth, frequently in a thick tangle of lianes and vines. *Microcebus rufus* remained undaunted by size when pursuing insect prey. On several occasions, they were seen clutching what appeared to be large insects, with the insect protruding from each end of the hand. Once a mouse lemur was observed intensely investigating a millipede, later measured at 110 X 20 mm. To give an indication of the size of this insect compared to its predator, the average body length of a male mouse lemur is approximately 190 mm (from occiput to tip of tail, excluding the head) (Atsalis et al., 1996). The mouse lemur abandoned the millipede only after the latter reared up the front part of its body in defense. In test trials conducted at RNP one female spent four hours conquering and consuming a scarab beetle measuring 45 X 25 mm (Harste, 1993). *Microcebus murinus* is also known to prey upon large insects (Martin, 1972).

During nocturnal censusing, mouse lemurs were often seen to take an interest in insects that flew near them, following them with their heads, although they were rarely seen attempting to capture isolated flying prey. On the other hand, mouse lemurs were attracted to flying insects when they were found clustered in large

numbers around flowering trees. This difference in terms of how mouse lemurs feed on flying insects suggests that the energetic cost of pursuing a single flying insect may be too high. The alternative strategy is to go to areas where these insects are localized rather than dispersed. This is supported by one radiotracking experience described below.

Radiotracking

Four individuals (M22, F22, F2 and F19) were radiotracked for 181 hours. During these hours, the radiotracked *Microcebus* were sighted a total of 874 times. The majority of these sightings were of M22 (405 sightings) and F19 (437 sightings).

In terms of feeding behavior, radiotracking data for M22 were the most informative. The period from October 1993 through January 1994 was a time when plant flowering was at its greatest extent. On four of the seven nights spent radiotracking this individual in the early part of October 1993, the animal remained within the flowering crowns of two adjacent *Dombeya hilsenbergii* trees. This tree is characterized by a cyme type of flower where a cluster of many small flowers constitutes an inflorescence (Turk, 1995). Although the pendant inflorescence is said to facilitate pollination by bats (Dan Turk, pers. com.), it was not bats which surrounded the flowering crowns but a large number of flying insects representing the orders Diptera, Lepidoptera and Coleoptera. Numerous *Microcebus,* including the radiotracked individual, as well as *Cheirogaleus,* congregated on these trees during the flowering period. Since my assistants and I were situated at a distance of 16-18 m, it was sometimes difficult to discern precisely what the animals were doing. However, it was clear that individuals were feeding as well as engaging in competition. Competition was fierce and involved chases, cuffing, and direct full-body contact which

resulted in mouse lemur individuals losing their grip and falling as far as an estimated 18 meters to the ground level.

The problem was which food resource was the probable cause of this intense activity. I hypothesize that three non-mutually exclusive feeding behaviors may have been involved:

a) mouse lemurs were extracting flower pollen,

b) mouse lemurs were extracting nectar,

c) mouse lemurs were attracted to the array of insects which were, in turn, attracted to the flowers.

An additional explanation for the competition observed, at least between the mouse lemurs, is that these individuals were competing over breeding opportunities. For instance, male mouse lemurs may have been competing not only for food but for the females who were in the immediate vicinity as well. Since *Dombeya* trees are fairly abundant in the forest and flower synchronously, it may be more likely that the physical competition observed was the result of breeding competition rather than competition for the resources on the tree.

I suggest that mouse lemurs may be attracted to flowers in part for the large numbers of insects they attract for the following reasons:

Pollen is a complex carbohydrate which may be difficult for a small mammal to digest, although it has the benefit of being high in protein compared with other plant tissues (Harborne, 1972; Howell, 1974). Alternatively, nectar is a simple sugar which is easily broken down. Although neither of these resources can be excluded as possible sources of food, several of our observations included mouse lemurs "visiting" flowers and "tasting" something in the flower which could have been nectar. A "visit" is defined

here as a stay near or at a flower for a variable amount of time, and includes behaviors involving feeding such as up-and-down head motion at the flower ("tasting"), searching, and catching insects. Some visits to flowers lasted a minute or more and were accompanied by the up-and-down head motion over the flower.

If nectar feeding was the only behavior taking place, extraction must have been extremely inefficient because the same flowers were visited repeatedly and successively. During one radiotracking session, the same three flowers were visited by M22 at least eight times, not including visits from other individuals. During the course of radiotracking, M22 was sighted 405 times, of which 160 involved visits to flowers. The flowers themselves were full of insects which could be seen taking flight following the darting approach of a mouse or dwarf lemur. The frequent and brief visits to the same flower suggest that individuals were targeting insects as food sources, although this does not exclude the possibility that the flowers themselves were being exploited. Further evidence of insect-feeding is that individuals were frequently seen swiping the air with their hands and then directing the hand to the mouth.

The quantity of the *Dombeya* flowers, where the competition was occurring, decreased from 90% of crown cover to 20% in the course of one week, but the cheirogaleids continued to come to the trees. On the last day of radiotracking M22, we observed seven insect catches, compared to three the day before and zero on the two previous days. M22 may have been concentrating on capturing insects rather than on the diminishing returns from nectar or pollen in flowers.

I conclude that the crowns of large trees in flower are important attractors of mouse lemurs. The flowers may provide pollen and nectar as well as serving as

reservoirs of large numbers of flying insects. In addition the crowns of these trees can serve as arenas where breeding competition is played out.

Fruit Phytochemical Analysis

Table 4.10 shows the results from biochemical analyses conducted on several fruits included in the diet of *M. rufus* . Results from two fruit species not known to be eaten by mouse lemurs, *Pittosporum* and *Dypsis*, were used for comparative purposes.

Most notable is the relatively high fat content for almost all the *Bakerella* specimens examined, with the exception of the one called "Tongolahy". This specimen may have contained unripe fruit, in contrast to the other *Bakerella* specimens, though details on its collection were lost.

Not only do *Bakerella* species contain a high fat content, they also have among the highest fiber content. *Bakerella clavata* sp. 2, with exceptionally high levels of lipids, also has the highest fiber content and the lowest protein-to-fiber content. The high fat content may explain why this species is a food source in spite of its high fiber content.

As previously noted, two methods were used to measure protein content. Results from the two methods were not found to be correlated (J□rg Ganzhorn, pers. com.). Both methods demonstrated that the *Psychotria* species has high levels of protein. However, *Bakerella* sp. 2 was high only when measured using the BioRad technique.

The reasons why the two methods yielded different results remain unclear. One source of difference may be that the Kjeldahl technique uses a conversion factor of 6.25 which is based on the average nitrogen content of protein, and therefore assumes probably incorrectly, that all nitrogen is found in protein (Herbst, 1988). A more

accurate protein estimate requires conversion factors appropriate for the particular food types being examined (Milton and Dintzis, 1981). Conversely, the second method, which is based on extracting protein, is a more direct way of measuring protein content.

Only one of the *Bakerella* species has high sugar content. *Alberta, Psidium, Harungana* and *Psychotria* all have relatively higher sugar content and lower fat content than the staple *Bakerella*. They are all available and are eaten during more seasonally restricted periods.

Tannin levels varied among the specimens. Ganzhorn (pers. com.) warns that his tannin values are usually higher than those of other researchers and should not be used to compare with results from other laboratories. Among the samples analyzed, *Dypsis nodifera*, a fruit not eaten by *Microcebus*, has very high levels of tannin. Two of the *Bakerella* specimens are also relatively high in tannin, but still less than half the value of *Dypsis nodifera*.

Discussion

In contrast to previous field observations on the diet of *Microcebus*, the results from this research are based on a long-term continuous project that included analysis of a large number of fecal samples from a large number of individuals. Shorter-term sample sizes cannot as easily reveal the full complement of food items eaten, detect staple or keystone dietary items nor demonstrate seasonal changes in diet.

Analysis of the long-term feeding data collected during this study demonstrated that the semi-epiphytic plant *Bakerella,* and Coleoptera (beetles), are preferred dietary items appearing in 58% and 70% respectively of the samples examined, and were present in the fecal samples during each month of the study period. I also demonstrated the high-lipid content *Bakerella*. The importance of high-lipid food

sources for *Microcebus* are reported, here, for the first time. The regular consumption of *Bakerella*, during periods of both high and low resource availability, and the high fat content, suggests that this fruit is not only a dietary staple but a keystone resource (Terborgh, 1986) which sustains the population during periods of scarcity and is essential to their survival.

Frugivory

Earlier in this chapter I discussed the generally accepted statement that small primate species include a high proportion of insects in their diet to fulfill their protein requirements, and to meet elevated energy needs imposed upon them by their high metabolism.

Insectivory allows small primates to take in sufficient quantities of digestible protein. For these reasons, insectivory and small body size have been considered a circular metabolic and competitive trap (Eisenberg, 1981). The present research does not refute the importance of animal matter in the diet of *Microcebus rufus*. Fecal analysis showed that arthropods (basically insects) are consumed all year round. Although I could not directly compare frugivory to insectivory in terms of raw quantities consumed, I demonstrated a heavy dependence on fruit in terms of quantities eaten. Fruit was less frequently totally absent from fecal samples of individual mouse lemurs than insect matter. And, lastly, I found that mouse lemurs consume many different varieties of fruit on a regular basis and seasonally diversify their fruit repertoire.

I suggest that *M. rufus* is typical of most other tropical small mammals (Fleming, 1975) in being a highly frugivorous species. These findings are in keeping with certain other field observations on the diet of *Microcebus murinus* which hinted at a high dependence on plant matter, especially fruit (Martin, 1972; Hladik et al., 1980).

Fruit resources are not sought after in an opportunistic manner based on general availability in the forest. For instance, I demonstrated the importance of *Bakerella* in the diet which parallels the specialization on local plant food sources noted by Martin (1972) for *M. murinus*.

Other fruits found in the feces, which remained unidentified, may also play a significant role in the diet of *M. rufus*. Many of the unidentified seeds closely resemble those of *Ficus* spp. Various *Ficus* plants are part of the diets of the other lemur species studied in Ranomafana (Overdorff, 1993; Hemingway, 1995; White et al. , 1995), and there are at least ten fig species in the area ranging from small shrubs to large trees (Turk, 1995). Therefore, it is very likely that one or more *Ficus* species found in Ranomafana are important food items for mouse lemurs.

Seasonal Patterns in Frugivory

There was marked increase in fruit intake, both in quantity and diversity, in February and March 1994, two months which coincided with a relatively high diversity of trees in fruit. March 1993 was characterized by a similar pattern in *M. rufus* feeding habits, though not as pronounced as in 1994. The degree of difference in the feeding indices between the two years may be due to differences in the kinds of trees in fruit. Trees in Ranomafana show variability in their phenological patterns, producing fruit seasonally but not necessarily every year (Hemingway, 1995; Deborah Overdorff, pers.com.). Nevertheless, these findings suggest that fruit feeding patterns in mouse lemurs may be related to the diversity of fruit resources available during the latter part of the wet season in conjunction with the specific needs of mouse lemurs at that time in their annual life cycle. As was noted for *M. murinus* (Hladik et al., 1980), increased fruit intake in *M. rufus* coincides with the period of seasonal fattening in preparation for the

dry season (discussed in Chapter Five) and with the period when young mouse lemurs begin to feed independently.

Therefore, I suggest that both *M. murinus* and *M. rufus* may have similar seasonal feeding patterns despite the differences in the environments which they inhabit. Since a complete set of feeding data over an annual cycle is lacking in *M. murinus*, a more thorough comparison of these patterns remains to be conducted.

Insectivory

Like fruit resources, insect resources are not necessarily consumed based on generally available quantity and diversity. For example, insect consumption (as measured by the MNI-I) did not increase for *M. rufus* during the wet season (December 1993 to February 1994), as has been reported for *M. murinus* on the west coast (Hladik et al., 1980), even though this period included months when insect abundance was at its highest. In the case of *M. murinus*, insect food sources were presumably selected more opportunistically than fruit resources, based on peaks of availability (Martin, 1972; Hladik et al., 1980). I suggest that the data for both *M. murinus* and *M. rufus* demonstrate that individuals do exploit rapidly ephemeral insect food sources. Certainly the case of mouse lemurs congregating on the flowering crowns of *Dombeya* trees is an example of opportunistic exploitation of a briefly available resource. At the same time, they have insect resource preferences which are not necessarily related to general insect availability.

To illustrate, although Coleoptera are captured in fewer numbers than Lepidoptera, fecal analysis indicates that the former are more important in the diet of *Microcebus.* Moth consumption does not go undetected because of the many scales which are found in the feces (Whitaker, 1988), so that if *Microcebus* were feeding on

moths it would be readily apparent. There are at least two possible explanations for the pattern observed. The prevalence of Lepidoptera over Coleoptera among captured insects may simply be a bias produced by the sampling method, which favored flying insects over terrestrial ones. As adults, Lepidoptera are flying insects while Coleoptera can be found in a variety of habitats, many of which are on or in the ground and would not be sampled. However, if flying insects are selected at random by mouse lemurs, then one would expect the hanging sheets used to capture insects in this study to be randomly sampling the very same population of insects. This appears not to be the case. The alternative possibility is that *Microcebus* does not favor Lepidoptera in its diet and does, indeed, prefer Coleoptera to other insects. Since both my study on *M. rufus* and previous studies on *M. murinus* (Martin, 1972; Hladik et al., 1980) have demonstrated a high incidence of Coleoptera in the diet, I suggest that this is an order of insects which constitutes a regular part of mouse lemur diet while others are added as they become available and as they are nutritionally needed.

Since insect populations change rapidly, there may be several families of Coleoptera upon which *M. rufus* in Ranomafana particularly relies. Among the families of Coleoptera which were identified in the fecal samples, most are largely phytophagous and non-terrestrial (Tenebrionidae, Scarabidae, Cerembicidae, and Curculionidae) (Borror and White, 1970). The majority of other insects and spiders identified were also phytophagous and non-terrestrial (Julian Stark, pers.com.). However, the fact that a few fecal samples contained the remains of Scarabinae (dung beetles) and Gryllidae (crickets), both terrestrial species, attests that these arboreal primates may occasionally descend to the ground to search for insects.

Microcebus rufus, a Frugivore-Faunivore

Primate species are often placed in gross dietary categories as a basis for finding relationships between diet and other traits such as home range size and social organization (e.g. Rodman, 1973; Clutton-Brock and Harvey, 1977b), molar tooth design (Kay, 1975), and metabolic rate (e.g. McNab, 1986). However, the complexity of evolutionary adaptations that underlie the dietary habits of primates defy the use of simplistic categorizations. These categories are losing their value even as simple descriptive tools in the face of the diversity and variation being discovered in each primate species (e.g. Harding 1981; Garber, 1987; Rosenberger, 1992). This observation is regularly reinforced as the results from an increasing number of long-term field studies are becoming available. An obvious example of a species which has benefited from long-term studies is the gorilla which has traditionally been classified as a folivore based on studies of the mountain gorilla, *Gorilla gorilla beringei.* This description complied with accepted theoretical views on diet and body size. Yet, results from studies on a different subspecies, *Gorilla gorilla gorilla*, showed that 98% of fecal samples examined contained fruit (Williamson et al, 1990) and 30% contained insects (Tutin and Fernandez, 1992). Closer at hand, many studies are discovering wide dietary diversity in species of diurnal lemur (Overdorff, 1991, 1993; Sauther, 1992; Colquhoun, 1993; Meyers and Wright, 1993; Freed, 1995; Hemingway, 1995; White et al., 1995). In addition, although dietary studies on small nocturnal species are few, one recent long-term study on the aye-aye (*Daubentonia madagascariensis*) found that the morphological specializations of this species, such as the ever-growing anterior dentition and elongated middle finger, are used not only to gain access to larvae

hidden in wood and to coconuts (Petter, 1977) but also to harvest additional food sources, including seeds and fungi (Sterling, 1993).

My study on *M. rufus* suggests that fruit may not just be a complementary source of energy to insects as previously stated but may be a primary source of energy at least with regard to the high-lipid *Bakerella* fruit (Petter, 1978). Therefore, analysis of the data on *M. rufus* diet support the view of Richard and Dewar (1991) that the value of body size as broadly predictive of diet in primates is not easily applicable in lemurs. For instance, they note that *Varecia variegata*, the most frugivorous of all lemurs, weighs three times as much as *Lepilemur*, the most folivorous of all lemurs, while the Cheirogaleidae (the smallest of lemurs) are not strongly insectivorous but favor a mixed diet.

The variety within the mouse lemur diet seems to merit the description of "omnivorous" proposed by Martin (1972). Yet an omnivorous diet characterizes most primates to one degree or another, and diversity rather than specialization is typical of the order (Harding, 1981). Additionally, "omnivore" can be a catch-all category for those situations where there is insufficient dietary data available, and one which says little about the kinds of selective pressures that influence mouse lemur behavior. If a category is required, perhaps the best provided thus far is that of "frugivore-faunivore" (Chivers et al., 1984), with the stipulation that, given the seasonality in the dietary patterns of *Microcebus*, and the importance of at least one fruit staple in the diet, this category reflects diet only in the broadest sense.

The Characteristics of *Bakerella* and Other Mistletoes

Fruits vary in their adequacy as protein sources for frugivores (Hladik, 1978; Waterman, 1984; Stiles, 1993). Martinez del Rio (1994) argues that there are few data

to uphold the notion that fruits are poor protein sources, at least in the case of those eaten by birds and bats. To assess whether fruits are sufficient in protein or not, one needs to evaluate the relationship between the protein requirements of the particular species in question and the protein content of the fruit (Oftedal, 1991). For instance, frugivorous New World bats may not need to consume insects if they selectively choose their fruit (Herbst, 1986).

Some fruits can be unusually high both in protein and lipids as well as in carbohydrates (Foster and McDiarmid, 1983; Waterman, 1984; Ishaki and Safriel, 1989). Biochemical analysis conducted indicated that the fruit most commonly eaten by mouse lemurs, *Bakerella*, is one with unusually high lipid content. Other mistletoes in the family Loranthaceae have been reported to be especially high in lipids (see below) while those in the family Viscaceae (also eaten by *M. rufus*), are said to be carbohydrate-rich (Martinez del Rio, 1994, quoting Restrepo, 1987). Stiles (1993) states that lipid contents greater than 10% dry weight are found in only one-quarter of all fleshy fruits. Citing Snow and Snow (1988, Birds and Berries. Poyser, Calton), Stiles reports the lipid content of *Viscum album* (family Viscaceae) to be 8.61%. Walsberg (1975) reports 15% lipids for *Phaninopepla nitens*, a mistletoe favored by house finches. *Trichilia cuneata* (family Meliaceae) also has an exceptionally high lipid content, which at 59.7% renders this fruit very nutritious (Foster and McDiarmid, 1983). Although *Bakerella* is not as lipid-rich as *Trichilia,* it is as high or higher in lipids than the examples presented here for comparison. Since lipids are considered to have twice the energy content of carbohydrates, the regular consumption of *Bakerella* by mouse lemurs suggests that the high fat content may be essential to their survival.

Besides their valuable nutrient content, other factors, too, make mistletoes convenient food sources for mouse lemurs. *Bakerella* plants are found in small patches and therefore are proportional in size to the needs of a small species traveling singly. Like other fruit species, they are patchily, but regularly distributed in the forest. Selective logging, which has opened the canopy in Ranomafana, rather than inhibiting the growth of the highly photophyllic Loranthaceae, has probably increased their abundance. This has also been noted in the case of neotropical Loranthaceae (Bazzaz and Pickett, 1980). Tropical Loranthaceae occur on a broad range of hosts (Richards, 1952; Van Leeuwen, 1954), a fact confirmed in Ranomafana where, in addition, they were observed at all heights of the forest, making them widely available to mouse lemurs which also range at all heights. Lastly, unlike other epiphytes, the Loranthaceae are semiparasitic, obtaining water and nutrients through roots which penetrate their host. Thus, I suggest that, in contrast to other epiphytes, the Loranthaceae may be less sensitive to seasonal dry spells, a factor which may account for their year-round availability and contribute to making them a reliable food source.

Tropical mistletoes have long been known to be significant in the feeding ecology of many tropical New World and Old World birds (Richards, 1952; Van Leeuwen, 1954; Davidar, 1983; Stiles, 1993). A close interaction exists between birds and high-lipid mistletoes (Stiles, 1993). Birds act as specialized dispersers of mistletoe seeds (Van Leeuwen, 1954; Davidar, 1983), while mistletoe fruit are high energy packets of food for birds. However, the energy and nutrient value of a fruit depends in part on the digestive efficiency of the animal (Worthington, 1989). This may explain why some birds have physiological adaptations that permit differential access to the nutrients of the characteristic sticky mistletoe fruits (e.g. Waslberg, 1975; see Stiles,

1993 for short review) which may be difficult to digest (Van Leeuwen, 1954). It is not known if mouse lemurs have special physiological adaptations to digest mistletoes, yet their relationship is an example of endozoochorous dispersal. Seeds are ingested and voided intact and sticky. The characteristic viscid appearance of mouse lemur feces containing mistletoe seeds was frequently seen on forest substrates in Ranomafana.

The ability of *M. rufus* to exploit small patchily-dispersed fruit sources whose presence is unaffected or even enhanced by disturbance in the forest may contribute to its status as a widespread and abundant lemur species. In Ranomafana, *Bakerella* is also consumed by at least one bird species (Razafindratsita, 1995) as well as several other lemur species (*Eulemur fulvus and E. rubriventer*, Overdorff, 1993; *Propithecus diadema edwardsi*, Hemingway, 1995, 1996, and Patricia Wright, pers.com.; *Varecia variegata*, White et al., 1995; *Cheirogaleus major*, pers. obs.). Birds are known dispersers of Loranthaceae seeds (Richards, 1952) but it is not known whether other lemurs, besides mouse lemurs, pass the seeds or destroy them. Hemingway suggested that the leaves of *Bakerella clavata* constitute a staple dietary item for *Propithecus,* but the lack of *Bakerella* seeds in *Propithecus* fecal samples during ad-libitum field observations may indicate that seed dispersal is not involved though fruits are eaten (Nayuta Yamashita, pers. com.).

Apart from the present study, mistletoes have not been mentioned as features of the diet in other mouse lemur populations. The interaction between mistletoes and mouse lemur ecology has only begun to be investigated and further research is required to reveal other aspects of this relationship, such as the ways by which mouse lemurs are able to digest mistletoe fruit. Contrary to the view that the epiphytic flora plays a small role in the "economy" of the forest (Richards, 1952), they can constitute a

considerable component of some rainforest canopies particularly those of high tropical mountains (Nadkarni, 1984). Nadkarni (1981, 1983, 1984) has discovered and studied epiphytes as important attractors and circulators of minerals, leading me to suggest that the study of Ranomafana's epiphytic vegetation, in conjunction with its contribution to lemur and other animal diets, would be meaningful for a better understanding of the dynamics of this rainforest.

The Nutrient Content of Insects

As in the case of fruit, insects vary in the quantity of nutrients available to predators (Allen, 1989) and may not be uniformly high-quality dietary items for small primates. For instance, a wide variety of flying insects sampled were found to contain low levels of calcium and iron resulting in nutrient deficiencies in insectivorous bats (Studier and Sevick, 1992; Studier et al., 1994a,b), but were excellent sources of potassium, nitrogen and magnesium (Studier and Sevick, 1992; Studier et al., 1994a). On the other hand, Allen (1989) found that the assertion that most insects contain 50-65% protein is an overestimate, since, firstly, conventional methods of measuring organic nitrogen encompass non-protein nitrogen in their estimates, and, secondly, the protein found in close association with chitin in the insect cuticle may be indigestible to insectivores. Therefore, the true levels of protein in insects and their value to predators as protein sources remain unclear and require further research.

Other Possible Factors Affecting the Feeding Ecology of *Microcebus rufus*

Metabolic rates

Studies have shown that some prosimians maintain low metabolic rates for their size, not conforming to the expectations of the Kleiber relationship (Daniels, 1984; M□ller, 1975, 1985; M□ller et al., 1985; McNab, 1986), and, therefore, may have less

demanding dietary needs. A low metabolic rate has been proposed to be an energy-saving adaptation (M□ller, 1985; Kurland and Pearson, 1986) which can result in low maintenance nitrogen requirements (Stevens, 1995). The metabolic rate of *M. rufus* has not yet been the subject of investigation, but *Cheirogaleus medius*, which belongs to the same family as *Microcebus*, as well as certain galago species, have been found to be hypometabolic (McCormick, 1981; also see Kurland and Pearson, 1986 and Ross, 1992 for reviews).

In addition, the ability to periodically enter torpor further expands the range within which species can regulate their rate of energy expenditure (McNab, 1980). Many small mammals, particularly those living in seasonal environments, have the ability to reduce their metabolism as a response to decreased food availability, thus avoiding energy and nutrient deficiencies (Bourlière, 1975; Cork, 1994). Within the order Primates, only certain members of the Cheirogaleidae can hibernate or enter torpor. Therefore, this ability, whose physiological basis has been studied in the dry forest mouse lemur species *Microcebus murinus* and *M. myoxinus* (Petter, 1978; Andriantsiferana and Rahandraha, 1973; Russell, 1975; Hladik et al, 1980; Petter-Rousseaux, 1980; Ortmann et al. 1996; Schmid, 1996), may be an influential factor in mouse lemur feeding ecology.

Physical and chemical properties of food

Some studies on lemurs have investigated diet based on the physical properties of foods eaten (Sterling et al., 1994; Yamashita, 1996), while others have concentrated on chemical composition (Ganzhorn, 1988, 1989; Sauther, 1995). Differences in the physical and biochemical properties of plant and animal matter require different adaptive solutions for efficient foraging and digestion (Rosenberger, 1992). For

instance, differences have been found in molar tooth morphology between frugivores and faunivores (Strait, 1993a).

The basic components of the diet of *M. rufus* and *M. murinus,* including their preference for beetles, have now been established. Examination of dental casts of *M. rufus* molar teeth taken in Ranomafana, and of *M. murinus*, have indicated a difference in their dental morphology despite the dietary similarities suggested by this study. *M. murinus* falls out among primate frugivores (Strait, 1993a), but preliminary analysis shows *M. rufus* to be closer to the insectivorous prosimians (Suzanne Strait, pers. com.). These findings may support the hypothesis, at least in the case of *M. rufus*, that dental morphology is more closely related to foods that represent a "biomechanical challenge" (Rosenberger, 1992) than to foods which are more frequently eaten.

Strait (1993b) also found that among insectivores, dentitions differed between those that regularly fed on hard-bodied prey (e.g. beetles) and those that fed on soft-bodied prey (e.g. moths, caterpillars, worms). This supports suggestions by bat specialists (Strait quotes Freeman, 1981, 1984 and Warner, 1985) that "moth-strategist" species are more restricted in their diets than "beetle-strategists" which can take advantage of a greater variety of prey. If further analysis confirms an insectivorous dental morphology for *M. rufus*, then the next step is to see how closely their dentition approaches that of a beetle-strategist.

Competitive interactions with sympatric species

The distribution and abundance of resources, and competition with other species for access to them, also influence feeding behavior. My observations during radiotracking suggested that there may be fierce feeding competition between *Cheirogaleus major* and *M. rufus,* demonstrating that clear niche separation does not

always take place when a coveted resource appears within the range of members of sympatric species. On the other hand, Ganzhorn (1988, 1989) found that *M. rufus*, when compared to *Cheirogaleus major*, ate fruits with lower tannin concentrations and no alkaloids which suggested that food resources were partitioned based on differences in their biochemical makeups as a way of decreasing competition.

Table 4.1. Monthly number of *Microcebus rufus* fecal samples collected from Feb-93 to May-94 at Talatakely, RNP.

Month	No. of Individuals	No. of Samples	Ratio of samples to individuals*
Feb-93	8	10	1.3
Mar-93	22	34	1.5
Apr-93	12	13	1.1
May-93	10	12	1.2
Jun-93	16	20	1.3
Jul-93	17	30	1.8
Aug-93	21	25	1.2
Sep-93	26	32	1.2
Oct-93	18	23	1.3
Nov-93	19	27	1.4
Dec-93	8	9	1.1
Jan-94	9	10	1.1
Feb-94	10	10	1.0
Mar-94	16	21	1.3
Apr-94	19	27	1.4
May-94	10	18	1.8

*Average ratio of samples to individuals from Feb-93 to May-94: 1.3

Table 4.2. *Microcebus rufus* fruit sources identified between Feb-93 and May-94 at Talatakely, RNP.

Taxonomic Name	Family	Vernacular Name	Plant type	In fecal sample/ direct observation
*Alberta humblotii**	Rubiaceae	Fatsikiahitra madinidravina	Shrub	yes/no
Anthocleista amplexicaulis	Loganiaceae	Dendemivavy	Tree	y/y
Aphloia theaeformis	Flacourtiaceae	Fandramanana lavaravina	Tree	n/y
Bakerella sp.	Loranthaceae	Tongolahy Fotsy	Epiphytic semi-parasite	y/y
Bakerella clavata subsp. 1	Loranthaceae	Tongolahy Madinidravina L.F.**	Epiphytic semi-parasite	y/n
Bakerella grisea	Loranthaceae	Tongolahy Vaventiravina L.F.	Epiphytic semi-parasite	y/y
Cissus sp.	Vitaceae	Vahirano Madinidravina	Liane	y/n
Ficus sp.	Moraceae	Vahihafa	Scrambling Shrub	n/y
Gaertnera sp.	Rubiaceae	Bararata Vaventiravina	Tree	y/y
Harungana madagascariensis	Clusiaceae	Harongana	Shrub to medium-sized tree	y/n
Ilex mitis	Aquifoliaceae	Hazondrano	Tree	y/n
Maesa lanceolata	Myrsinaceae	Voarafy	Shrub to small tree	y/n
Medinilla sp.	Melastomataceae	Kalamasimbarika ***	Epiphyte	y/n
Nuxia sp.	Loganiaceae	Lambinanala****	Tree	y/n
Oncostemum botryoides	Myrsinaceae	Kalafana madinidravina	Tree	n/y
Psidium cattleianum	Myrtaceae	Goavy gasy	Shrub	y/y
Rhipsalis baccifera	Cactaeae	Voatsilelolelo	Epiphyte	y/n
Viscum sp.	Viscaceae	Tongolahy Maitso	Epiphytic semi-parasite	y/n
Unknown	Menispermaceae	Hazotana	Liane	y/n
Psychotria sp.	Rubiaceae	Voanananala Madinidravina L.F.	Shrub	y/n
Psychotria sp.	Rubiaceae	Voanananala Madinidravina R.F. #1	Shrub	y/n
Psychotria sp.	Rubiaceae	Voanananala Madinidravina R.F. #2	Shrub	y/n
Psychotria sp.	Rubiaceae	Voanananala Vaventiravina R.F.	Shrub	n/y
Unknown	Rubiaceae	Voanananamboa	Shrub	y/n

*or *Cavaco* (Dan Turk, pers. com.)

**L.F.: long-leafed; R.F.: round-leafed.

***May be a misidentification.

****May be a misidentification; fruit of "Nuxia" are small, dry and capsular, possibly not edible by mouse lemurs (Turk, pers.com.)

Table 4.3. Measurements (mm and mg) of *Microcebus rufus* fruit sources at Talatakely, RNP.

Vernacular Name	Av seed length	Av seed width	(Av) no. of seeds/fruit	Av weight of unripe frui	Av weight of ripe fruit	Av length of ripe fruit	Av width of ripe fruit
Fandramanana lavaravina	2.5 (50)*	2 (50)	7 (20)	170 (54)	320 (20)	9.3 (20)	11.5 (20)
Tongolahy Madinidravina L.F.	7.8 (20)	2.5 (20)	1 (20)	80 (75)	200 (40)	7.5 (35)	4.2 (35)
Tongolahy Vaventiravina L.F.	5.8 (27)	2 (27)	1 (27)	130 (75)			
Bararata Vaventiravina	5.9 (30)	4.5 (30)	2 (30)	160 (78)	290 (25)	8.3 (25)	7.4 (25)
Kalamasimbarika	1.5 (34)	0.5 (34)	70 (34)	310 (14)	470 (34)	8.9 (34)	8.5 (34)
Goavy gasy	4.5 (30)	0.3 (30)	25 (30)	6600 (30)	7600 (30)	22.9 (30)	23.1(30)
Voanananala Madinidravina R.F. #1	7.2 (20)	5.8 (20)	2 (20)		500 (20)	10.8 (20)	9.7 (20)
Voanananala Madinidravina R.F. #2	5.5 (20)	4.7 (20)	2 (20)	190 (100)	320 (51)	9.4 (51)	7.7
Voanananala Madinidravina L.F. #1	4.5 (6)	3.6 (6)	2 (16)	88 (50)	100 (16)	5.7 (16)	5.8 (16)
Voanananala Vaventiravina R.F. #1			2 (50)	1000 (50)			
Hazondrano	3.2 (10)	1.7 (10)	5 (2)	70 (67)			
Voarafy			1?				
Vahirano Madinidravina	7.1(70)	4.4 (70)	1(70)	190 (70)			
Harongana			5-10 (20)				
Tongolahy Maitso			1(20)				
Lambinanala	6 (5)	4.3 (5)	1 (5)			6.6 (5)	4.8 (5)
Voanananamboa			1 or 2 (80)	30 (80)			
Tongolahy Fotsy			1 (5)				
Fatsikiahitra madinidravina	8.3 (10)	4.5 (10)	1(10)			8.7 (10)	6 (10)
Kalafana madinidravina			1 (5)				
Voatsilelolelo	1.3 (50)	0.5 (50)	20 (50)		127 (26)	9.8 (50)	4.6 (50)
Dendemivavy	2.5 (8)	1.8 (8)	70 (8)	2700 (8)	4000 (20)	25.7 (25)	16.4 (25)
Vahihafa	2 (10)	2 (10)	40 (10)	450 (10)	870 (10)	12.3 (10)	10.1(10)
Hazotana			1 (10)				
AVG	4.70	2.80	11.1	870	1300	11.20	9.20
MAX	0	0	0	0	0	0	23.1
MIN	0	0	0	0	0	0	7.7

*Sample size is in parentheses.

Table 4.3.-*Continued*

Vernacular Name	Av length of unripe frui	Av width of unripe frui	Color of unripe fruit	Color of ripe fruit
Fandramanana lavaravina	7.8 (54)	8.1 (54)	green	white
Tongolahy Madinidravina L.F.			green	yellowish
Tongolahy Vaventiravina L.F.	7.4 (65)	5.7 (65)	green	yellowish
Bararata Vaventiravina	7.1 (78)	6.8 (78)	green	white
Kalamasimbarika	8.2 (14)	7.9 (14)	orange-green	deep red
Goavy gasy			green	red
Voanananala Madinidravina R.F. #1	5.3 (50)	4.3 (50)	yellow	red
Voanananala Madinidravina R.F. #2	7.8 (50)	6.9 (50)	green-yellow	red
Voanananala Madinidravina L.F. #1	5.7 (50)	5 (50)	green	deep purple
Voanananala Vaventiravina R.F. #1	14.4 (50)	12 (50)	green	
Hazondrano	4.5 (67)	4.9 (67)	green	red
Voarafy				white
Vahirano Madinidravina	8.4 (71)	6 (71)	green	
Harongana			yellow	
Tongolahy Maitso				green
Lambinanala	7.2 (1)	5.7 (1)		
Voanananamboa	4.6 (80)	3.4 (80)	green	white
Tongolahy Fotsy				
Fatsikiahitra madinidravina	8.7 (10)	6 (10)		
Kalafana madinidravina				
Voatsilelolelo			light green	light green
Dendemivavy	24.9 (8)	14.3 (8)	green	yellow-brown
Vahihafa				
Hazotana				
AVG	8.70	6.90		
MAX	0	0		
MIN	0	0		

*Sample size is in parentheses.

Table 4.4. Quantity of *Microcebus rufus* fecal samples that contained identified fruit based on seed presence at Talatakely, RNP.*

Name	No. of fecal sample with fruit seeds	Percent of total fecal samples collected	Percent of fecal samples containing any fruit seeds
Bakerella	139	41.6	57.9
Medinilla	23	6.9	9.6
Viscum	22	6.6	9.2
Rhipsalis	18	5.4	7.5
Psychotria	16	4.7	6.7
Gaertnera	9	2.7	3.8
Nuxia	7	2.1	2.9
Psidium	5	1.5	2.1
Cissus	4	1.2	1.7
Maesa	3	0.9	1.3
Fatsikiahitra	3	0.9	1.3
Anthocleista	2	0.6	0.8
Ilex	2	0.6	0.8
Hazotana	1	0.3	0.4
Harungana	1	0.3	0.4
Voananamboa	1	0.3	0.4

*A total of 334 fecal samples were collected of which 240 contained fruit seeds.

Table 4.5. Quantity of *Microcebus rufus* fecal samples that contained arthropod remains at Talatakely, RNP.*

Arthropod Category	No. of fecal samples with arthropod category	% of fecal samples to total number examined for arthropod remains	No. of times category was identified based on multiple presence in fecal samples
Coleoptera	77	67	121
Unknown Insect	31	27	33
Orthopteroids	26	23	25
Hymenoptera	22	19	30
Heteroptera	17	15	18
Aranea	9	8	9
Diptera	3	3	4
Lepidoptera	3	2.6	3
Homoptera	2	2	2
Caterpillars	2	2	2
Siphonoptera	1	0.9	1
Ephemeroptera	1	0.9	1
Unknown Invertebrates	1	0.9	1

*Based on 115 fecal samples containing spider, insect or unknown invertebrates.

Table 4.6. Dietary values determined monthly based on fruit and invertebrate remains in fecal samples of *Microcebus rufus* at Talatakely, RNP.

Month	Av. no. of insect orders	Av. "insect volumetric score" (VS)	Av. "minimum number of insects" (MNI-I)	"Number of fruit types" (NFT)	"Total fruit types" (TFT)	Av. "minimum number of individual fruit" (MNI-F)
Feb-93		1.3		0.77	3	2.31
Mar-93		0.83		1.37	10	6.66
Apr-93		1.27		1.31	7	4.38
May-93		0.85		1.54	8	5.31
Jun-93	2	1.22	3	0.87	8	1.22
Jul-93	2.38	0.93	2.5	1	5	5.87
Aug-93	1.6	0.92	1.6	0.65	6	2.81
Sep-93	1.93	1.32	3.6	1.09	9	2.06
Oct-93	1.67	1.82	2.67	1.08	5	2
Nov-93	1.55	0.88	1.58	0.96	4	2.56
Dec-93	1.25	0.75	1.25	1.22	6	3
Jan-94	1.5	1.23	1.67	1.3	9	4.8
Feb-94	2.25	0.95	2.75	3.2	10	11.5
Mar-94	1.53	1.43	1.8	2.23	12	7.18
Apr-94	1.53	1.60	1.87	1.52	15	5.7
May-94	1.75	0.44	2	1.33	5	7.33

Table 4.7. Overall frequency of specific fruits in fecal samples of *Microcebus rufus* at Talatakely, RNP. (Based on a total of 16 months of fecal sample collection.)

Fruit category	No. of months detected in fecal samples
Bakerella	16
Unidentified Fruit 2	9
Unidentified Fruit Category* 4	9
Viscum	7
Medinilla	6
Unidentified Fruit Category 11	6
Voanananala	6
Rhipsalis	5
Cissus	4
Psidium	4
Gaertnera	3
Unidentified Fruit 8	3
Unidentified Fruit 15	3
Unidentified Fruit 17	3
Dendemivavy	2
Fatsikiahitra Madinidravina	2
Lambinananala	2
Unidentified Fruit Category 1	2
Unidentified Fruit Category 18	2
Unidentified Fruit 12	2
Harongana	1
Hazondrano	1
Hazotana	1
Voanananamboa	1
Voarafy	1
Unidentified Fruit Category 9	1
Unidentified Fruit Category 27	1
Unidentified Fruit 3, 5-7, 10, 13-14, 16, 19-26, 28-30	1**
Voanananamboa	1
Voarafy	1

*A Fruit Category may include more than one type of fruit seed.
**Represents one month for each unidentified fruit.

Table 4.8. Monthly presence of specific fruits in fecal samples of *Microcebus rufus* at Talatakely, RNP.

No. of fruits present monthly	Feb-93	Mar-93	Apr-93	May-93
1	*Bakerella*	*Bakerella*	*Bakerella*	*Bakerella*
2	Hazotana	Hazondrano	*Medinilla*	*Cissus*
3	*Rhipsalis*	*Medinilla*	*Psidium*	Harongana
4		U. F. 2*	*Rhipsalis*	U. F. Category 1
5		U. F. 3	U. F. 2	U. F. 2
6		U. F. Category 4**	U. F. Category 4	U. F. Category 4
7		U. F. 5	Voanananala	*Viscum*
8		U. F. 6		Voanananala
9		Voanananala		
10		Voarafy		

	Jun-93	Jul-93	Aug-93	Sep-93
1	*Bakerella*	*Bakerella*	*Bakerella*	*Bakerella*
2	*Cissus*	U. F. 2	*Psidium*	Lambinanala
3	U. F. Category 1	U. F. Category 4	U. F. 2	U. F. 2
4	U. F. 2	U. F. 8	U. F. Category 4	U. F. 8
5	U. F. Category 4	*Viscum*	U. F. Category 9	U. F. 10
6	U. F. 7		*Viscum*	U. F. Category 1
7	*Viscum*			U. F. Category 4
8	Voanananala			*Viscum*
9				Voananamboa

	Oct-93	Nov-93	Dec-93	Jan-94
1	*Bakerella*	*Bakerella*	*Bakerella*	*Bakerella*
2	Lambinanala	Fatsikiahitra Madinidravina	Dendemivavy	Dendemivavy
3	U. F. 11	U. F. 11	Fatsikiahitra Madinidravina	U. F. 11
4	U. F. Category 4	*Viscum*	*Medinilla*	U. F. 12
5	*Viscum*		U. F. 11	U. F. 13
6			U. F. 12	U. F. 14
7				U. F. 15
8				U. F. 17

	Feb-94	Mar-94	Apr-94	May-94
1	*Bakerella*	*Bakerella*	*Bakerella*	*Bakerella*
2	*Gaertnera*	*Gaertnera*	*Cissus*	*Cissus*
3	*Medinilla*	*Medinilla*	*Gaertnera*	*Psidium*
4	*Rhipsalis*	*Rhipsalis*	*Medinilla*	U. F. Category 4
5	U. F. 15	U. F. 11	*Psidium*	Voanananala
6	U. F. 16	U. F. 15	*Rhipsalis*	
7	U. F. 17	U. F. 2	U. F. 17	
8	U. F. Category 1	U. F. 23	U. F. Category 18	
9	U. F. 19	U. F. 24	U. F. 2	
10	U. F. 20	U. F. 25	U. F. 22	
11	U. F. 21	U. F. 26	U. F. Category 27	
		U. F. 8	U. F. 28	
			U. F. 29	
			U. F. 30	
			Voanananala	

* Unidentified Fruit

**A "Fruit Category" may include more than one type of fruit seed.

Table 4.9. Monthly presence of *Bakerella* seeds in *M. rufus* fecal samples and as fruit in the forest at Talatakely, RNP.

Month	Percent of fecal samples with *Bakerella* seeds	Average no. of *Bakerella* seeds/fecal sample	Percent of *Bakerella* plants with fruit (unripe
Feb-93	18.8	1.6	83.5
Mar-93	67.7	6.1	83.5
Apr-93	29.5	4.1	57.2
May-93	55	2.5	50
Jun-93	31.3	0.5	40
Jul-93	42.4	4.9	60
Aug-93	16.7	1.4	60
Sep-93	15.4	0.3	40
Oct-93	27.8	0.6	10
Nov-93	35.3	0.9	0
Dec-93	11	0.4	50
Jan-94	22	2.5	37.5
Feb-94	70	8.7	60.3
Mar-94	50	4.8	67
Apr-94	63	4.4	53.6
May-94	68	6.6	0

Table 4.10. Phytochemical analysis of selected *Microcebus rufus* fruit sources

Species	Family	Ripe/ Unripe	Total % Nitrogen (Kjeldahl)	Percent Protein (Kjeldahl)	%Fat	%Fiber	Extractable Protein (BioRad)	Condensed Tannin
*Pittosporum verticillatum**	Pittosporaceae	ripe	1.9	12.38	0.52	28.75	4.49	1.81
*Dypsis nodifera**	Palmae	?	0.84	5.44	1.12	35.91	8.68	86.23
Alberta humblotii	Rubiaceae	ripe	0.55	3.6	0.65	28.47	5.55	0
Psidium cattleianum	Myrtaceae	ripe	0.47	3.03	1.68	25.03	1.14	2.95
Psidium cattleianum	Myrtaceae	unripe	0.5	3.23	0.91	37.41	2.72	7.41
Harungana madagascariensis	Clusiaceae	?	1.07	6.94	4.73		4.2	4.91
Bakerella sp. 1	Loranthaceae	unripe?	0.82	5.32	5.73	27.26	5.47	36.16
Bakerella sp. 2	Loranthaceae	?	0.64	4.18	9.57	61.13	8.22	20.34
Bakerella clavata sp. 1	Loranthaceae	ripe	0.98	6.36	14.72	27.42	3.31	4.71
Bakerella clavata sp. 2	Loranthaceae	ripe	1.13	7.34	26.57	53.3	2.92	0.59
Bakerella grisea	Loranthaceae	ripe	0.73	4.78	13.53	29.94	5.4	18.23
Psychotria sp.	Rubiaceae	unripe	1.67	10.86	1.06	34	10.54	33.53

Species	Percent Sugar	Protein to Fiber Ratio
*Pittosporum verticillatum**	40.7	0.16
*Dypsis nodifera**	32.4	0.24
Alberta humblotii	59.8	0.19
Psidium cattleianum	38.5	0.05
Psidium cattleianum	22.9	0.07
Harungana madagascariensis	4.4	
Bakerella sp. 1	22.1	0.20
Bakerella sp. 2	9.7	0.13
Bakerella clavata sp. 1	6.7	0.12
Bakerella clavata sp. 2	2.4	0.05
Bakerella grisea	8.5	0.18
Psychotria sp.	36.9	0.31

* These are not *Microcebus* fruit sources.

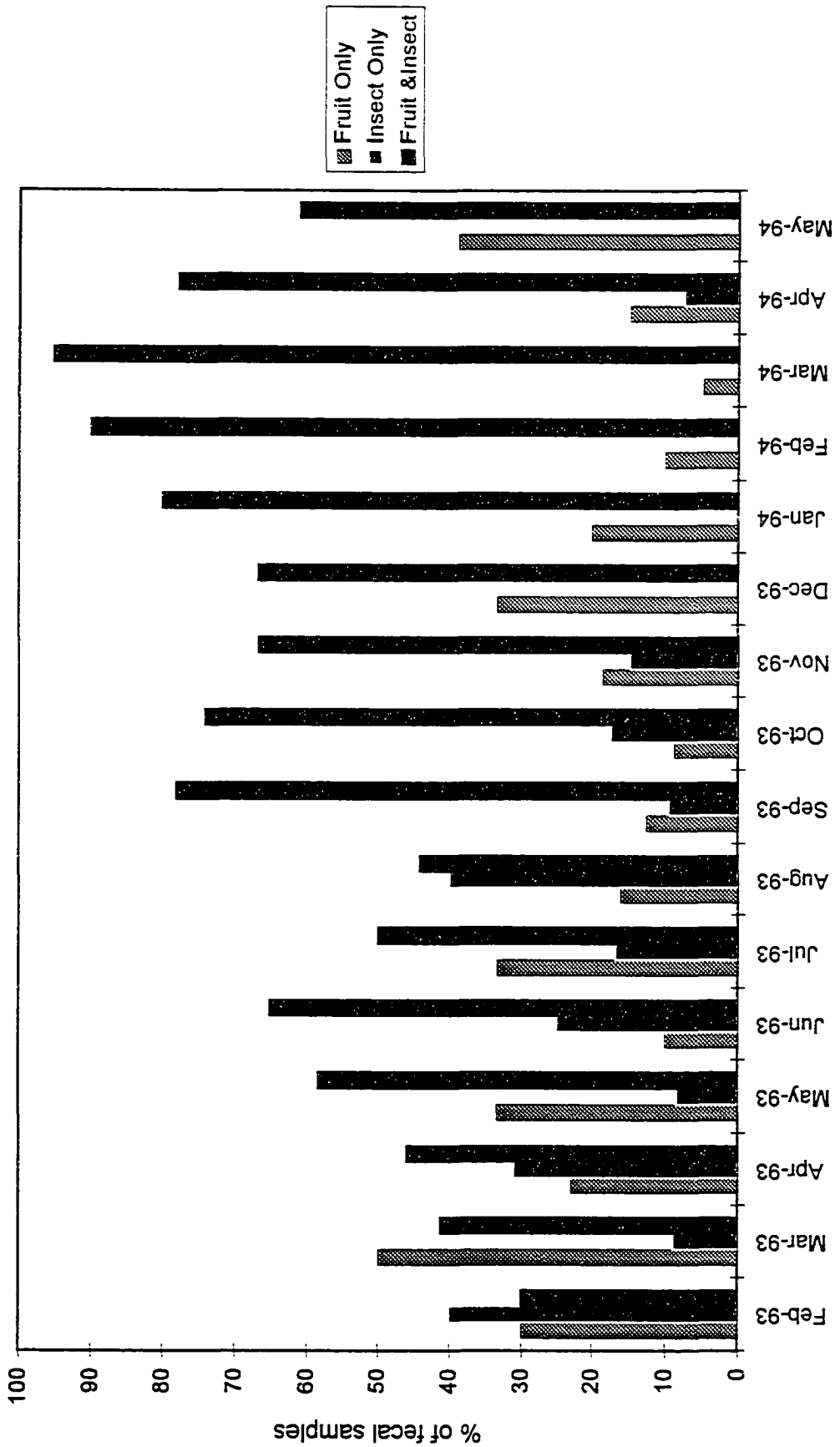


Figure 4.1. Monthly percentages of *Microcebus rufus* fecal samples in three gross dietary categories at Talatakely, RNP.

Figure 4.2. A comparison of the percentage of *Microcebus rufus* fecal samples containing insect remains only with insect abundance in the forest at Talatakely, RNP.

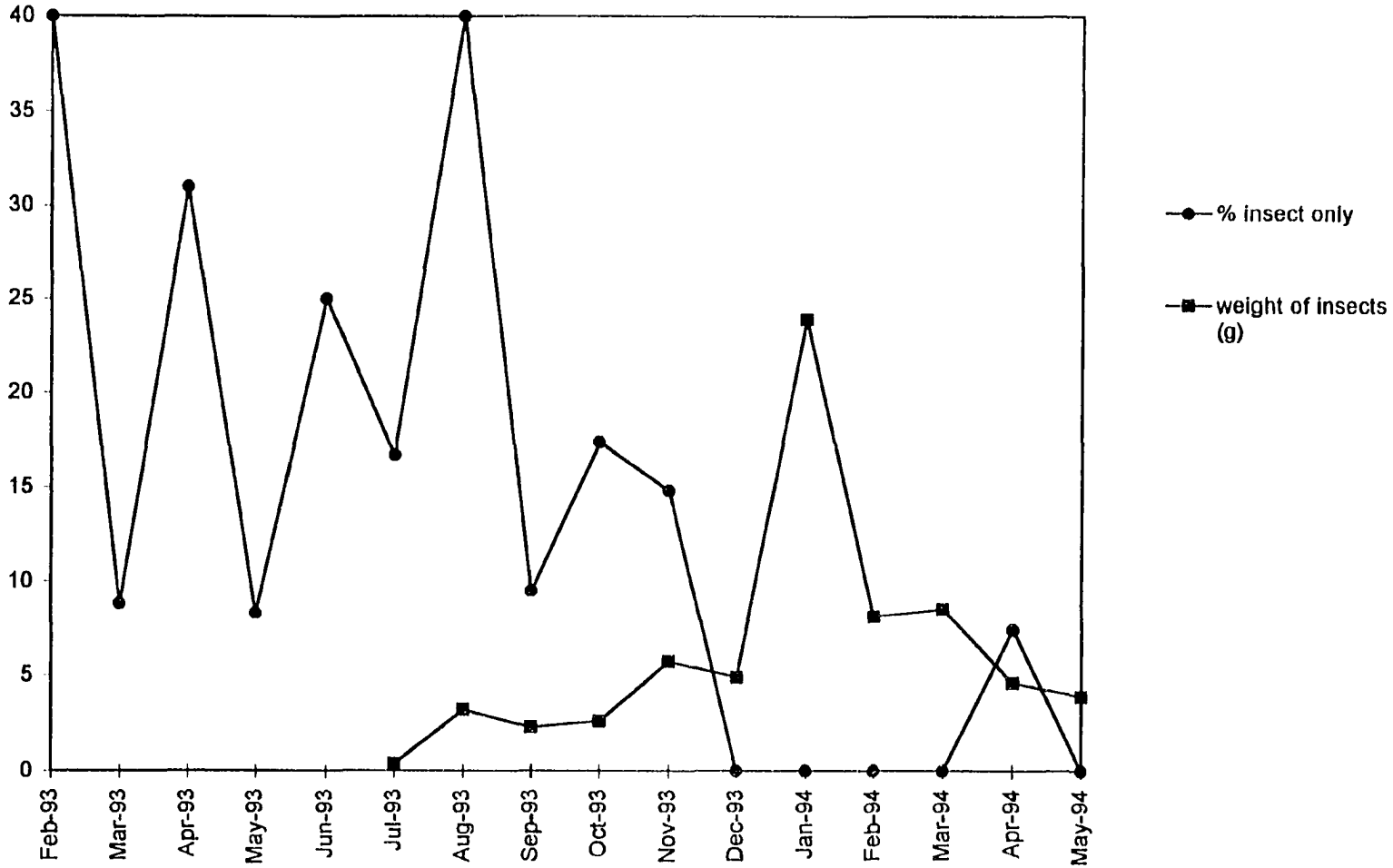


Figure 4.3. Evaluation of fruit feeding strategies of *Microcebus rufus*.

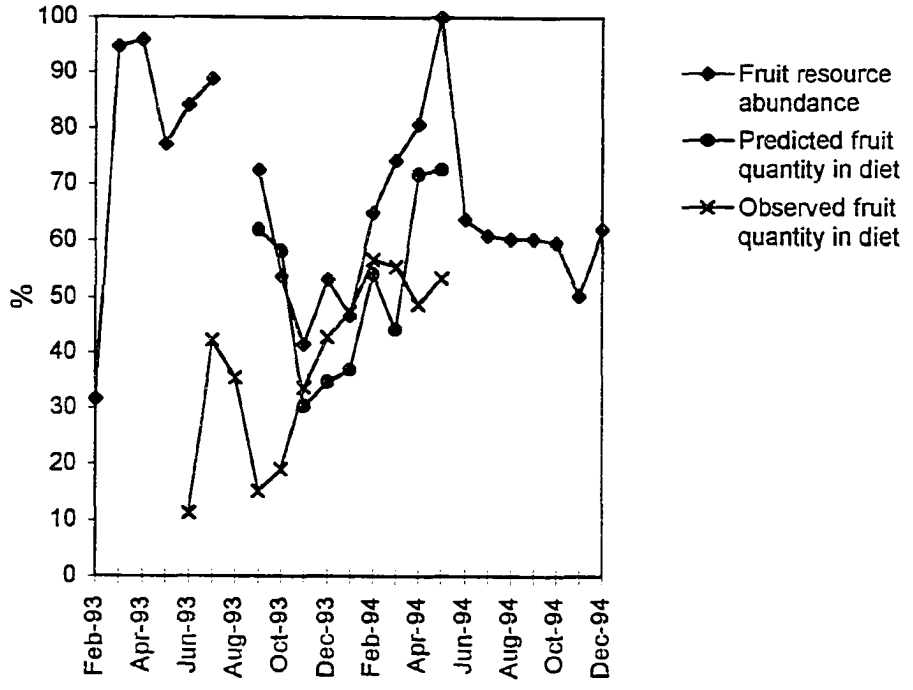


Figure 4.4. Evaluation of insect feeding strategies of *Microcebus rufus*.

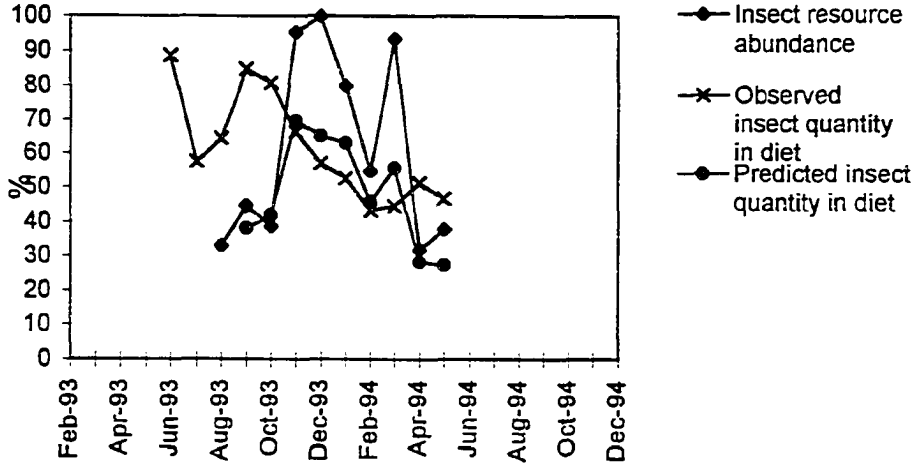


Figure 4.5. Scatterplot of the monthly number of vernacular species with any fruit and the monthly average "Number of Fruit Types" (NFT) in *M. rufus* fecal samples.

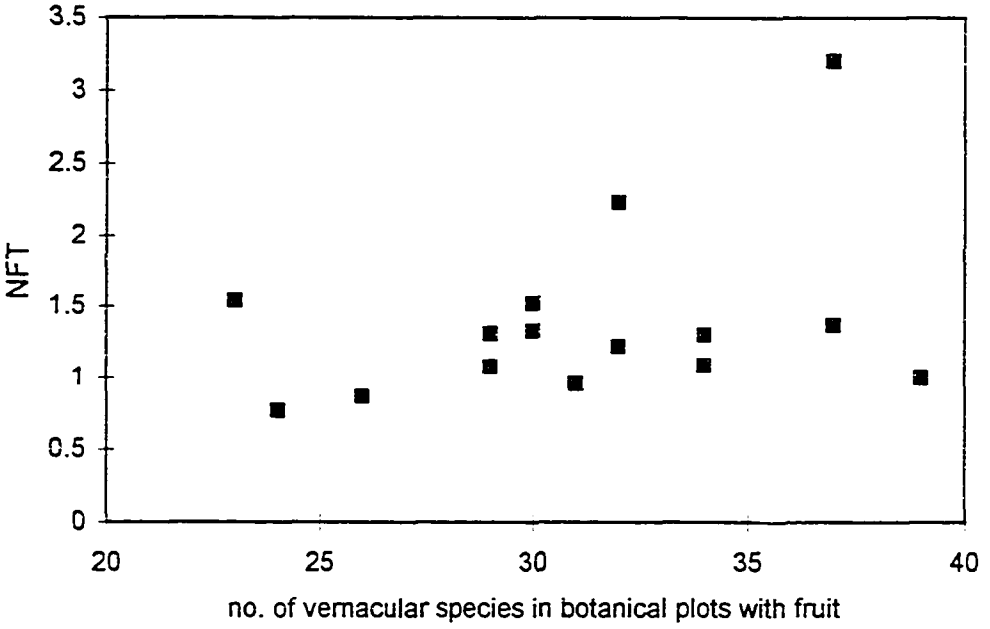
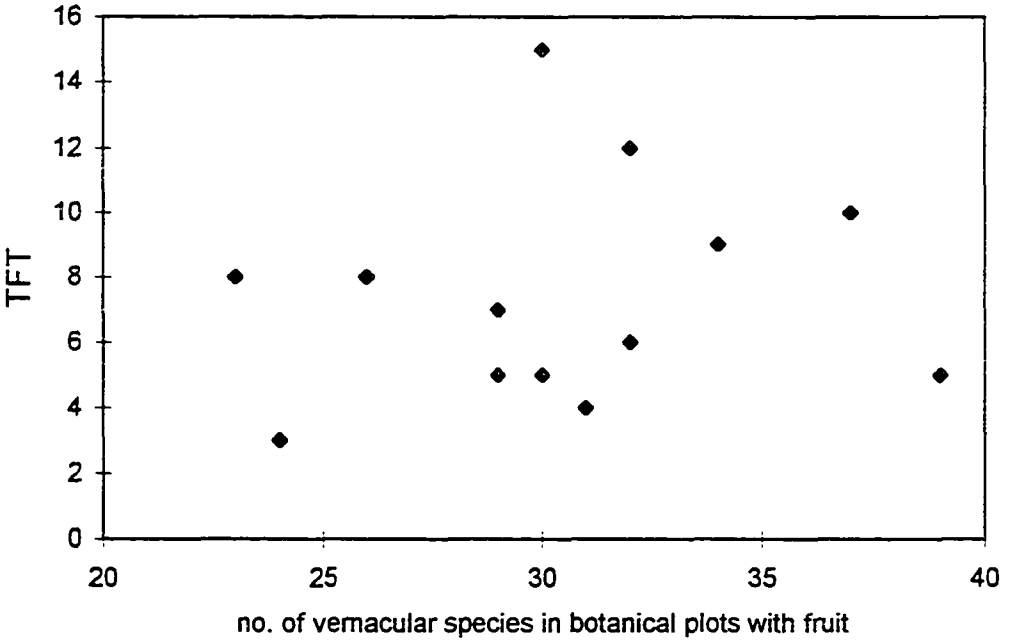


Figure 4.6. Scatterplot of the monthly number of vernacular species with any fruit and the monthly "Total Fruit Types" (TFT) in *M. rufus* fecal samples.



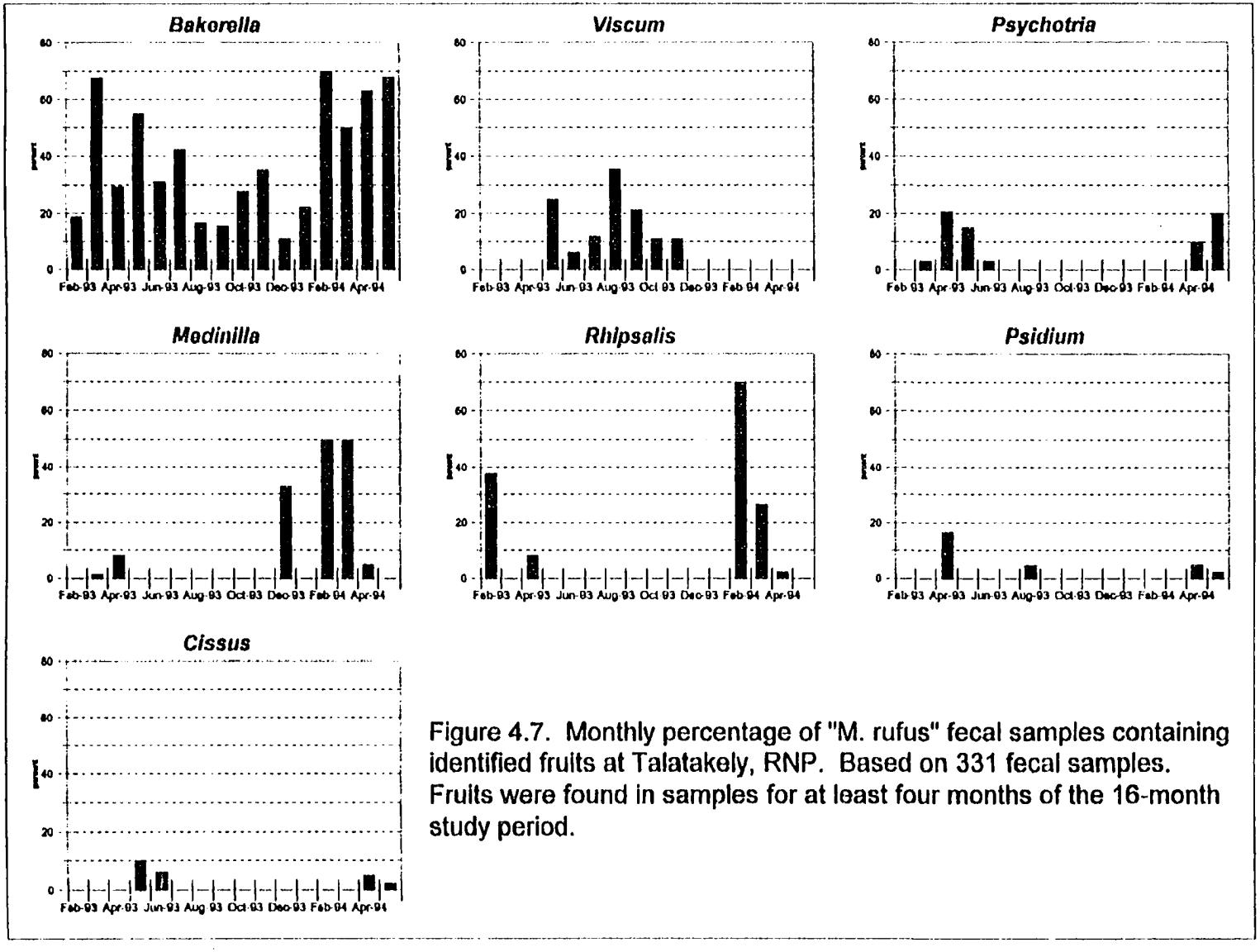


Figure 4.7. Monthly percentage of "M. rufus" fecal samples containing identified fruits at Talatakely, RNP. Based on 331 fecal samples. Fruits were found in samples for at least four months of the 16-month study period.

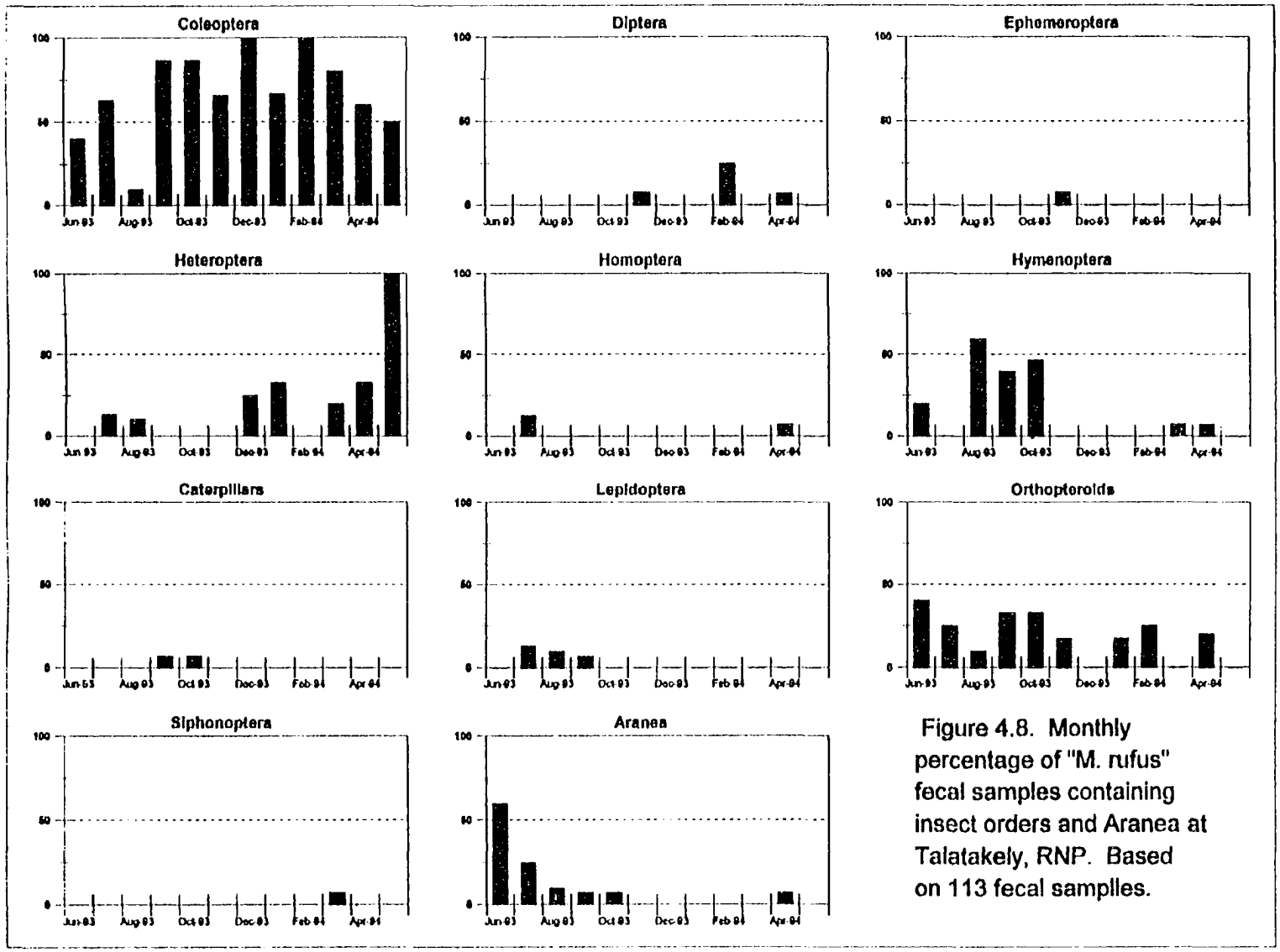


Figure 4.8. Monthly percentage of "M. rufus" fecal samples containing insect orders and Aranea at Talatakely, RNP. Based on 113 fecal samplles.

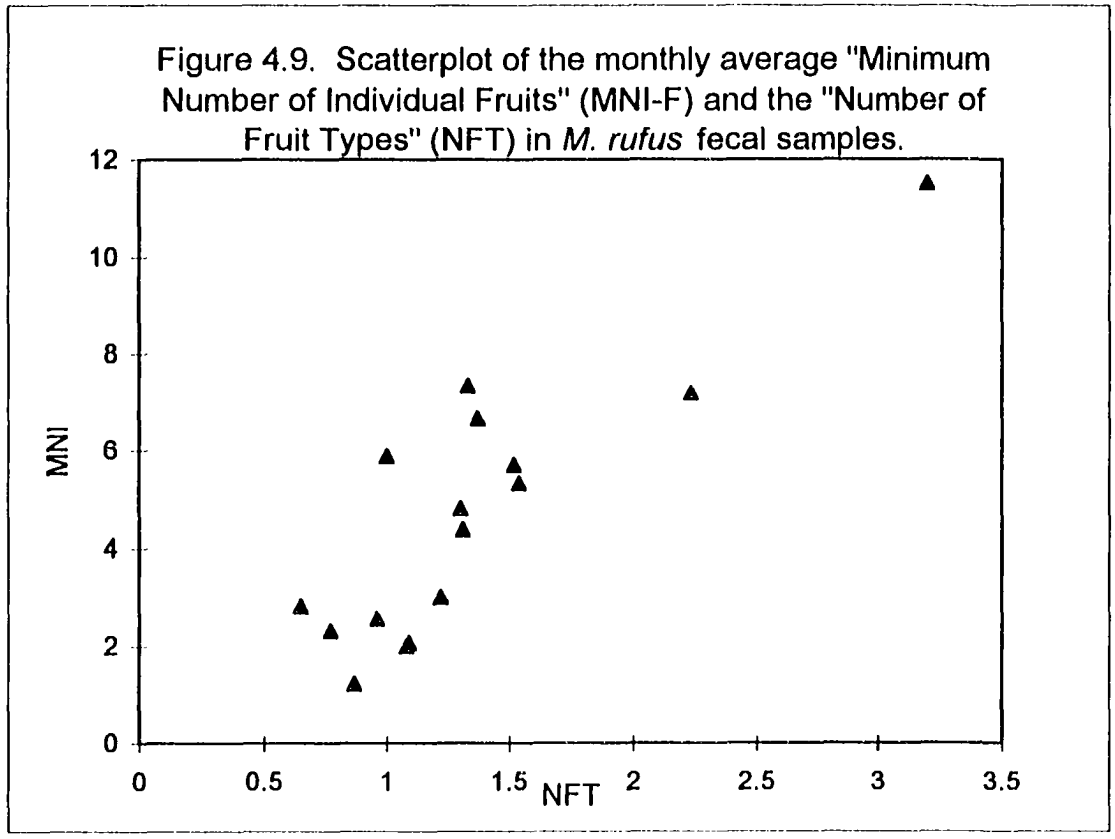
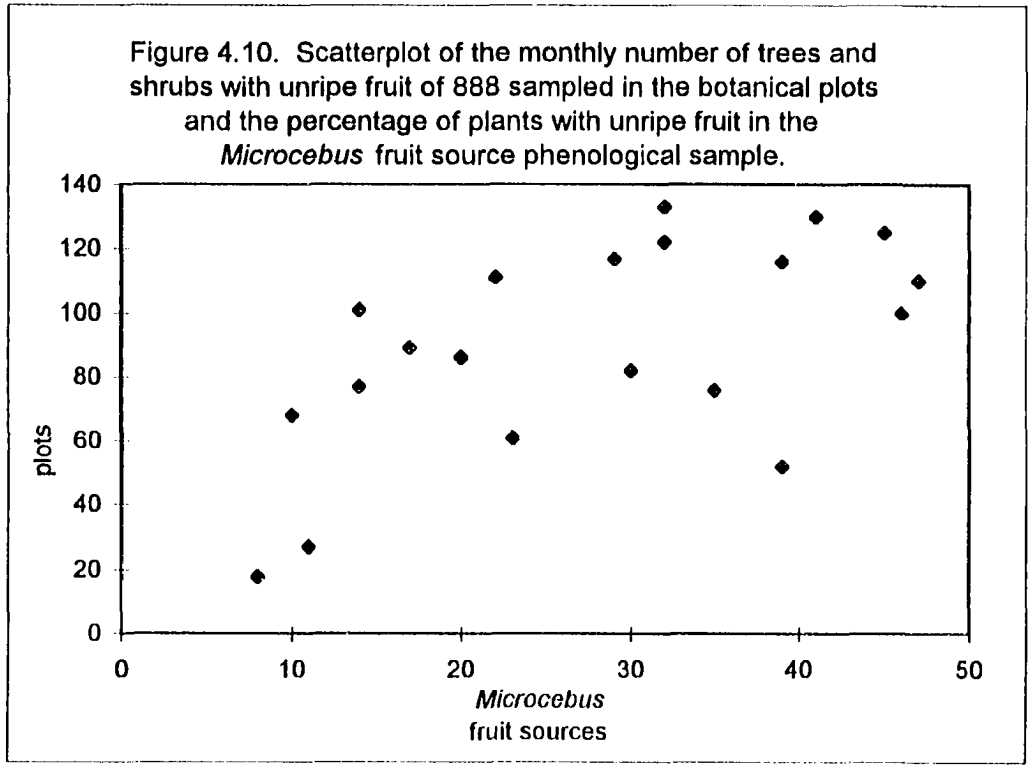


Figure 4.9. Scatterplot of the monthly average "Minimum Number of Individual Fruits" (MNI-F) and the "Number of Fruit Types" (NFT) in *M. rufus* fecal samples.



CHAPTER FIVE

ANNUAL CYCLES IN BODY FAT AND ACTIVITY LEVELS OF *MICROCEBUS RUFUS*

Introduction

I have previously shown that *M. rufus* consumes fruit and insects all year round with a strong reliance on the high-lipid fruits of the semi-parasitic epiphyte *Bakerella*. The amount and diversity of fruit in the diet increases in the months between February and March, coinciding with the period when there is relatively high diversity of trees in fruit, while March through May is the period of greatest fruit abundance. These events occurred within the wet season, which lasts from December through March and is associated with higher temperatures than the dry season.

This chapter discusses data on seasonal fluctuations in body fat and activity levels in the study population of *M. rufus*, fluctuations which occur concurrently with changes in diet and resource availability discussed in the previous chapters.

Seasonal Body Fat and Activity Level Fluctuations in Small Mammals

In small mammals, maintaining energy balance is especially important since their relatively high metabolism places on them an extra burden of increased energy requirements, particularly during the winter months. Cyclical changes in behavior related to maintaining energy balance during periods of seasonal climatic and resource stress are known to occur in small-bodied mammals (e.g. Bourlière, 1975; Fleming, 1979).

Photoperiod is a predictable environmental cue that can signal oncoming environmental changes (Hoffmann, 1981; Petterborg, 1978). Combined with the influence of resource availability and climate, it instigates changes in body fat and

activity levels in many small mammals which are manifested in a variety of ways (Rusak, 1981), a few examples of which are briefly presented below.

Daily or seasonal torpor, once considered a primitive form of thermoregulation in marsupials (Lyman, 1963), is now also known to occur in small eutherian mammals and is a way to reduce energy demands in environments which are physiologically stressful and/or where food supplies fluctuate daily or seasonally (e.g. Mrosovsky, 1977; Fleming, 1979). With torpor, an animal's body temperature drops markedly below its normal range but not below 15° C whereas a "true hibernator" can remain at 5° C for intervals ranging from a few days to weeks (Lyman, 1982). In constrast to a hibernator, a torporing individual can return to normothermia with the onset of the next active phase of the circadian period (Ortmann et al., 1996).

Small mammals vary in their physiological responses to seasonal stress. For instance, the ability to store fat has been considered a prerequisite to entering states of hypothermia (Fleming, 1979), but this is not always the case. In small insectivorous dasyurids (*Antechinomys laniger*, *Sminthopsis crassicaudata*, *Sminthopsis macroura*, and *Dasyuroides byrnei*) the frequency of seasonally-based torpor is influenced by the presence or lack of food but is not accompanied by fluctuations in body mass as in the case of placental rodents (Geiser, 1986; Geiser and Baudinette, 1987). Even within the rodents, some temperate North American species, such as the eastern chipmunk (*Tamias striatus*), enter periods for torpor of up to eight days without accumulating body fat (Godin, 1977). Others, such as the woodchuck (*Marmota monax*), the meadow jumping mouse (*Zapus hudsonius*), and the woodland jumping mouse (*Napaeozapus insignis*), accumulate fat prior to hibernation (Whitaker, 1963; Godin, 1977).

Furthermore, seasonal reduction in activity can be modified by fluctuations in food availability and controlled by winter's low ambient temperatures, as in the case of hedgehogs in Europe (*Erinaceus europaeus)* and South Africa (*Atelerix frontalis*), respectively (Fowler, 1988; Gillies et al., 1991), and North American heteromyid desert rodents (*Dipodomys microps, D. merriami* and *Perognathus longimembris*) (Kenagy, 1973). Another example comes from captive pygmy mice (*Baiomys taylori*) where the presence of food and water affected the length of their daily torpor (Hudson, 1965). On the other hand, fluctuations in activity levels and body weight in captive dormice (*Glis glis),* were part of a circannual cycle which persisted even under constant environmental conditions (Mrosovsky, 1977). Some members of the family Cricetidae (voles and hamsters) **reduce** body weight in response to seasonally shortened photoperiod in the autumn (Iverson and Turner, 1974; Ure, 1984, Petterborg, 1978) which results in less body tissue to sustain during the winter months (Iverson and Turner, 1974; Ure, 1984). A similar strategy is followed by a variety of shrews and rodents in the strongly seasonal environment of subtropical southern Africa (Korn, 1989). Temperate zone bats undergo deep hibernation while tropical or subtropical species utilize partial torpor (Lyman, 1982).

In Madagascar, certain tenrecs, endemic species of insectivores (*Microgale dobsoni, Setifer setosus*, *Echinops telfairi, Tenrec ecaudatus*, *Hemicentetes nigriceps*, *H. semispinosus*), are characterized by varying degrees of body weight and activity level fluctuations in response to the austral winter (Eisenberg and Gould, 1970). These species are geographically distributed across the climatological spectrum of Madagascar including the east coast rainforests.

The above examples demonstrate that small mammals inhabiting a variety of climatic environments, including tropical, utilize thermoregulatory and metabolic mechanisms to regulate energy balance when they are vulnerable to climatic and resource stress.

Seasonal Body Fat and Activity Level Fluctuations in the Cheirogaleidae

Fluctuations in behavior, such as reproduction, occur in primates (e.g. Rasmussen, 1985; van Schaik and van Noordwijk, 1985; Chick et al., 1992). In lemurs they are especially pronounced because of the existence of strict breeding seasons (Pereira, 1991). Apart from reproduction, other environmentally influenced behavioral fluctuations, such as changes in dietary choices due to temporal shifts in food availability (e.g. Overdorff, 1993; Nash, 1995), ranging patterns (e.g. Meyers, 1993; Overdorff, 1993) and activity levels (e.g. Morland, 1993) exist in the gregarious diurnal lemurs and are influenced by a variety of factors (Richard and Dewar, 1991; Morland, 1993).

Among lemur species, certain members of the family Cheirogaleidae are known to experience seasonal behavioral cycles which parallel those of the small non-primate mammals described above. Specifically, observations on *Microcebus* (outlined in more detail below) and *Cheirogaleus* have indicated the presence of distinct cycles associated with food intake (Petter-Rousseaux and Hladik, 1980), body weight changes (Petter, 1978; Hladik, 1979; Hladik et al., 1980), thermoregulation (Petter-Rousseaux, 1980; McCormick, 1981), activity levels (Petter, 1978; Petter-Rousseaux, 1980; Hladik, 1979; McCormick, 1981; Foerg and Hoffmann, 1982; Ortmann et al., 1996; Schmid, 1996), reproduction (Petter-Rousseaux, 1962; Perret, 1972, 1992; Andriantsiferana et al., 1974) and endocrine activity (Perret, 1972, 1985, 1995). *Cheirogaleus* shows the

most extreme behavioral cycles. Following a period of substantial weight gain, *Cheirogaleus medius* is said to be able to hibernate for up to eight months during the dry season (Petter, 1962; Hladik et al., 1980). Hibernation also characterizes *Cheirogaleus major* in Ranomafana, as inferred by the lack of sightings during certain months of the year (Wright and Martin, 1995). However, under experimental conditions *Cheirogaleus medius* does not always enter a hibernating phase (Russell, 1975; Petter-Rousseaux, 1980; Foerg and Hoffmann, 1982) but at least in the Russell study that may be due to a lack of photoperiodic cues (McCormick, 1981).

Researchers have usually associated the behavioral cycles of the Cheirogaleidae with variations in food availability correlated with rainfall patterns, since most studies have been conducted on west coast dry forest species where climate and resource availability are markedly seasonal. For instance, Martin (1972) states that east coast mouse lemurs are less likely to lay down fat stores since seasonal fluctuations in availability of resources are less pronounced in the east coast rainforests. And yet in Ranomafana various studies point to a relative scarcity of resources as well as low temperatures and rainfall during certain months of the dry season (Overdorff, 1993; Meyers and Wright, 1993; Hemingway, 1995). Therefore, although the climate in the east coast is characterized by relatively high humidity (Jenkins, 1987), the lack of a dry season exhibited as distinctly as in the deciduous forest of the west coast does not necessarily imply year-round abundance of food resources and equable climate.

Seasonal Fluctuations in Body Fat in Free-Ranging *Microcebus*

Due to the short duration of most field studies, cyclical fluctuations in body fat in free-ranging *Microcebus* have seldom been confirmed. Short duration field studies are

confined to providing information on the range of body weights that occur during a very specific period. For example, one study reported that the weights of adult *M. rufus* captured between August and December ranged from 36 to 55 g while the weights of *M. murinus* ranged from 39 to 98 g (Martin, 1972; Martin, 1973). Similarly, weights of brown mouse lemurs captured over the course of one month (June-July) in Ranomafana were reported to be 35-70 g for males and 42-64 g for females (Harcourt, 1987). Another study which also took place in Ranomafana, reports a range of weights from 34-54 g for both males and females captured during September (Wright and Martin, 1995).

Longer term trap-retrap studies which include more than one season are able to show changes in body weight for individual mouse lemurs over time and are more informative. In Marosalaza 72 *M. murinus* individuals recaptured between March and May had undergone an increase in overall body weight as well as in the volume of the tail where fat is differentially stored. Throughout the study period, variation in recorded body weight and tail volume ranged from 50 to 80 g and 2 to 9.5 cm^3 respectively (Hladik, 1979; Hladik et al., 1980).

Martin (1972, 1973) suggested the existence of individuals with different life-history strategies, suggesting that there are heavy and light males whose body weights reflect their social, and ultimately reproductive, status in the population. In fact, the wide range in mouse lemur body weights collected by Martin (1972, 1973) and Hladik (1979) may be indicative of differing life history cycles among segments of the population. In those studies, female body weights were generally greater than those of males, including those males measured during the period when seasonal fattening occurred. Martin (1972, 1973) established the average weight of brown mouse lemurs

to be 41 g for males (n=11) and 47.5 g for females (n=2), and for gray mouse lemurs, 59 g (n=37) and 63 g (n=126). Similarly, captive female gray mouse lemurs have been shown to be heavier than males by as much as 21% (Kappeler, 1990, 1991; Jenkins and Albrecht, 1991). Measurements taken on museum collections of both species demonstrated small but statistically significant differences in skull length favoring the female (Albrecht and Jenkins, 1988; Albrecht et al., 1990; Jenkins and Albrecht, 1991). Although these observations hint that sexual dimorphism is present in mouse lemurs, not all data confirm this. The sexes have been found to be monomorphic in body size values in wild gray mouse lemurs captured at Kirindy near Morondava (i.e. head length and width, ear length and width, tail length body length, hindfoot length and body weight) (Fietz, 1997) and, at least in body weight, in wild *M. rufus* captured in Ranomafana (Harcourt, 1987; Wright and Martin, 1995). These observations are insufficient to determine whether male and female size differences exist as part of overall sexual dimorphism and/or as a result of differences in specific phases of the life-history cycle.

Seasonal Fluctuations in Activity Levels in Free-Ranging *Microcebus*

To make inferences about seasonal activity levels of free-ranging mouse lemurs, previous studies have relied on sightings of animals in the forest. Martin (1972) stated that claims of "dormancy" in *Microcebus* were incorrect since there was no difference in the relative frequency of sightings when comparing dry season to wet season. In contrast, *Cheirogaleus* is said to be a true hibernant because no individuals are sighted in the forest during certain months of the dry season (Martin, 1972). Other researchers have noted that *M. murinus* undergoes periods of decreased activity during the dry season but no true hibernation (Petter, 1978; Hladik, 1979). Petter-Rousseaux

(1980) noticed that animals tended to stay in tree hollows for several consecutive days during this time. More recent studies, using implanted temperature-sensitive transmitters, have clearly demonstrated that the west coast mouse lemur species, *M. murinus* and *M. myoxinus*, do undergo torpor, every night, of varying degree and hourly duration, with a metabolic depression of close to 90% and a reduction in body temperature to close to ambient temperature (Schmid, 1996; Ortmann et al., 1996, 1997).

In addition, through trap-retrap studies (Harcourt, 1987; Atsalis et al., 1996; Fietz, 1997) it is suggested that a difference between the sexes may exist in the annual patterns of activity levels. In Ranomafana, Harcourt (1987) trapped 23 male and 5 female *Microcebus rufus* during the course of a one month study which took place between June and July. In the dry forest environment of Kirindy, Fietz (1997) discovered that from August to October (a period coinciding with the end of the dry season and the beginning of the breeding season) the number of individual females trapped increased while the number of males remained the same. Fietz suggests that previously inactive females were rejoining the population. An alternative explanation is that males also were inactive but emerged from winter lethargy earlier than females.

Annual Fluctuations in Body Fat and Activity Patterns in Captive *Microcebus*

Captive studies, mostly on *Microcebus murinus*, have shown that body weights increase to their maximum during the non-breeding period as daylength gets shorter (Russell, 1975; Glatston, 1979). In another captive study mouse lemurs visibly fattened each winter period with tail volume increasing from an average of 5 to 20 cm^3 (Petter-Rousseaux, 1980). In contrast, in both *M. murinus* and *M. rufus* minimal body weights

occurred during the breeding season (the period when daylength increases) (Bourlière and Petter-Rousseaux, 1966).

Other studies have indicated that storage of tail fat is most noticeable in older individuals, particularly in females (Glatston, 1979), and that maximum body weights are correlated with very low body temperatures in all individuals (i.e. young males who were under 18 months old as well as older males who were at least 30 months old), but that only older males are observed to enter states of lethargy (Russell, 1975). It has also been shown that body weight and tail fat fluctuations, as well as in other behaviors such as reproduction, are the result of endocrinological changes related to changes in thryoid activity which are instigated by changes in photoperiod (Perret, 1972), and which take place even under constant resource and environmental conditions in both *M. murinus* and *M. rufus* (Bourlière and Petter-Rousseaux, 1966; Petter-Rousseaux, 1970, 1974; Russell, 1975).

Summary of Results from Previous Work

Previous observations on mouse lemurs and their environment have indicated the following:

1. Mouse lemurs, particularly the west coast dry forest species *M. murinus*, are known to undergo fluctuations in body weight and tail volume, with the period of increase in these values coinciding with the onset of the austral winter or dry season.

2. Mouse lemurs are known to experience torpor of varying duration but there are no data to indicate that individuals hibernate for long periods of the dry season. Unlike *Cheirogaleus*, mouse lemurs are sighted in the forest all year round.

3. Mouse lemurs may exhibit sexual dimorphism in morphological traits and/or annual life- history cycles. It is also possible that the details of the annual life-history cycle may vary even within the same sex.

4. The dry season in Ranomafana, in comparison to the wet season, is characterized by less rainfall, cooler temperatures and relative scarcity of food resources.

Aims of Research

The above observations taken together indicated that data were needed:

a. To determine if annual cycles in body fat and activity level occurred in any members of the east coast rainforest species *Microcebus rufus*. Given what was known about the climate and food resources during part of Ranomafana's dry season, it was expected that during this season the east coast cheirogaleids would exhibit physiological changes similar to those exhibited by the west coast species.

b. To reveal which individuals of the population displayed these behaviors.

Data Analysis

Previous reports on body weight in *Microcebus rufus* (Martin, 1972; Harcourt, 1987; Wright and Martin, 1995) covered short periods so that seasonal comparisons based on monthly averages could not be made. Even for *Microcebus murinus,* the drawback of the majority of previous field studies was their short-term duration or the fact that analyses were based on cross-sectional (monthly or overall) averaging of the data. Each period's averages do not necessarily include the same individuals. Therefore, it is difficult to detect, for example, whether monthly averages reflect true seasonal changes in body weight, or demographic changes, such as the addition of new individuals of different sizes into the population. My study is unique within the

context of mouse lemur field research because I collected long-term, longitudinal data on body weight and tail circumference fluctuation covering more than one complete annual cycle. Longitudinal data on wild-ranging primate species are rare even for large diurnal species. By monitoring changes in known individuals I could detect groups of mouse lemurs that were characterized by differing annual cycles.

The generally descriptive nature of data based on population averages served as supporting evidence to make comparisons between months as well as between the sexes.

Hypothesis and Testing

Based on the foregoing observations, I hypothesized that seasonal increase in body weight and tail circumference, followed by reduction in activity during some part of the dry season or austral winter occurs in some, but not all, brown mouse lemurs. I further hypothesized that this response is not sex-specific. I predicted that there would be individuals who would not have a trap record for part of the dry season and that for these individuals body weight and tail circumference data taken at the "last capture" date, i.e. just prior to the period of no trap record, would differ significantly from data taken at the "first capture" date, just following the period of no trap record.

To test my hypothesis, I conducted a long-term trap-retrap study which encompassed one complete annual cycle and one partial one. During this period, I conducted weekly mark-recapture sessions to monitor changes in body weight and tail circumference of known individuals over the course of the study period (longitudinal data analysis). (Body weight is sometimes variable depending on recent food intake and it is in the tail where fat storage is readily visible). Fluctuations in activity levels were inferred by monitoring presence or absence in the traps.

Supporting data come from various analyses based on monthly population averages for body weight and tail circumference, as well as from monitoring the overall number and sex of mouse lemurs trapped monthly.

Results

My results are divided into three main sections. Initially I present the results from male and female longitudinal data which focus on changes in body fat and trap presence in a set of known individuals. Analysis of these data constitute the main test of the hypothesis. I then compare male and female body weight and tail circumference averages to investigate the existence of sexual dimorphism in these values. Lastly, I conduct several analyses based on monthly population averages and examine changes in the sex ratio over the course of the study period.

Analysis of Longitudinal Data

In order to test my hypothesis I relied on data from individual mouse lemurs who were trapped in the period from February to September 1993. These months include a period of high resource availability (February through May), when mouse lemurs would be expected to increase their body fat. This period also includes the main part of the dry season just prior to the start of the breeding season (in August), characterized by low resource availability, precipitation and temperatures, when mouse lemurs may be expected to enter torpor.

I captured 102 males and 72 females and sorted the members of each sex into three groups:

Group One consisted of individuals for whom data were insufficient to provide adequate information on body weight, tail circumference and activity level fluctuation.

Group Two individuals were those who fit the basic parameters of my hypothesis. My aim was then to test for the significance of the changes in body fat indicators spanning the period of absence from the traps. In order to be certain that a consistent criterion was used for inclusion in Group Two I selected individuals who either:

a. demonstrated a decrease in body weight and tail circumference between their last capture, which took place between April and June (the first months of the dry season) and recapture, which took place between August and November. These individuals had at least one month's absence from the traps between last capture and first recapture.

or

b. if recapture data were not available, demonstrated increasing values in body weight and tail circumference during the first few months of the dry season and ceased to be trapped by June. June was chosen as the cutoff month because for individuals following criterion "a" , this was the last month when they were trapped before recapture.

Empirical evidence has shown that a 2-3 g difference in body weight can be due to chance fluctuation as the result of prior food intake. Therefore, I included in Group Two only those individuals where body weight changes were associated with changes in tail circumference. Simultaneous changes in both values are consistent indicators of changes in fat storage. I chose a minimimum criterion of a 5 g difference in body weight and 0.3 cm difference in tail circumference which needed to be displayed by individuals fitting either "a" or "b" in order to be placed within Group Two.

Group Three individuals exhibited a variety of patterns in body weight, tail circumference and activity level fluctuation other than that demonstrated in Group Two.

Males

I grouped the 102 male mouse lemurs which I captured as follows:

- Group One consisted of 64 males who were not captured frequently enough or during the requisite time period to provide sufficient information to test the hypothesis in question.

- Group Two consisted of six males (M01, M02, M07, M11, M22 and M60; see Table 5.1). The body weight difference between last capture and first recapture in August ranged from 5 to 35 g, while the difference between last capture and the first September capture ranged from 9 to 39 g (Table 5.2). The difference in tail circumference between last capture and first recapture in August ranged from 0.4 to 0.8 cm, and between last capture and first September capture, the range was from 0.9 to 1.6 cm. Figure 5.1 depicts the body weight and tail circumference fluctuations of M02, a typical example of Group Two males.

I placed M01 in Group Two even though the change in this male between last capture and recapture in August (5 g in body weight and 0.4 cm in tail circumference) was not as dramatic as in the others. On the other hand, his body weight difference between last capture and first capture in September was 10 g which was similar to the difference exhibited by some of the other mouse lemurs in this group for August.

- Group Three consisted of the remaining 32 males for whom data existed for the period discussed for Group Two and/or for the first months of 1994, January through May, when data were collected (Table 5.3 shows select examples). Within this group, certain individuals (e.g. M40, shown in Figure 5.2, M63, M79) demonstrated an increase in body weight and tail circumference in 1994. Since data collection terminated in May what their behavior would have been for the period from June through August 1994 remains unknown. In 1993, they showed no apparent fluctuation

in body weight and tail circumference and thus were distinct from Group Two. Certain other individuals (e.g. M16, M32, M36, M44, M48), some of whom were absent from the traps during part of the dry season (e.g. M32, M44), also appeared to show little change in their body fat values over the course of the 1993 period in question. Still other individuals (e.g. M05, M09, M12, M19) actually appeared in August 1993 with increased weight and tail circumference. For others it is more difficult to definitively assess the situation. For example, in 1994 M14 demonstrates a dramatic increase in body fat with respect to data collected in 1993. However, unlike M40, M63 and M79, the progression of change in 1994 for M14 is not available. M70 also shows an increase in 1994 compared to 1993 especially in tail circumference. Although the increase does not approach that demonstrated by M40, it is difficult to assess what would eventually happen to M70 especially since fat can increase visibly within one month (for example, see changes in M40 from April to May 1994).

The statistical analyses which follow are restricted to males placed in Group Two. Firstly, body weight and tail circumference were positively correlated ($r_s=0.762$, $p<0.05$, $n=31$). This indicates that body weight, which can fluctuate depending on recent food intake, tracks changes in tail circumference, which is a more consistent indicator of fat storage. I then wanted to test if this group of males demonstrated significant seasonal differences in body weight and tail circumference.

For Group Two, the month of last capture varied from April to June, while August was the month of first recapture. Therefore, I compared last capture data to first recapture data in August. I also compared last capture data to first recapture data in September because firstly September data, but not August data, existed for all males in group two, and secondly, September values were even more decreased than the ones in August.

Because the sample size for the comparison between weight at the last capture to that of the first recapture in August was too small to use a Wilcoxon Sign Rank test (minimum sample size needed is six; Sokal and Rohlf, 1995), I tested comparisons using the Student t-test and, only where applicable, the Wilcoxon Sign Rank test (Table 5.4).

Because several t-tests are carried out simultaneously, it is necessary to modify the alpha level at which significance is determined. Following Rice (1989), the modified (sequential) Bonferroni criterion was applied sequentially: the p-values for all t-tests were ranked from lowest (most significant) to highest; the basic alpha level (0.05) was divided by N and the resulting Bonferroni alpha value was compared to the p-value for the highest-ranked test; if the p-value was larger than the alpha, the test was judged non-significant and no further values were checked; if the p-value was smaller than the alpha, the test was judged significant, and the next highest ranked test compared to alpha divided by N-1, etc. Using this approach, I found that the highest ranked test (which compared the difference in male tail circumference between last capture and September recapture) had a p-value of 0.000009. As there were 6 tests, the first alpha became 0.05/6 = 0.008. This is greater than 0.000009, and thus the highest rank test was judged significant. Using the Bonferroni criterion all the tests were significant. These results support the hypothesis that some male mouse lemurs underwent an increase in body weight and tail circumference at the onset of the dry season, reduced their activity during part of the dry season as manifested by their absence in the traps, and resumed activity with a reduction in body fat values.

Females

I grouped the 72 females which I captured as follows:

- Group One included 44 females who were not captured frequently enough or during the requisite time period to provide sufficient information to test the hypothesis in question.

- Group Two consisted of ten females (F08, F10, F13, F 19, F22, F29, F32, F38, F42 and F49; see Tables 5.5 and 5.6). The body weight difference between last capture and first recapture ranged from 5.5 to 23.0 g, while the difference in tail circumference ranged from 0.5 to 1.2 cm. For two females in this group, F13 and F29, I have no recapture data. I included them in Group Two due to the increase in body weight and tail circumference that they demonstrated over the course of a few months at the beginning of the dry season. Figure 5.3 depicts the body weight and tail circumference fluctuations of F08, an example typical of individuals in Group Two.

- Group Three consisted of the remaining 17 females for whom data existed for the period discussed for Group Two and/or for the first months of 1994 (Table 5.7 shows select examples). Certain individuals (e.g. F25, F37, F47) some of whom were absent from the traps during part of the dry season (F37), appeared to show little change in their body fat values over the course of the 1993 period in question (F47 is shown in figure 5.4). One other female (F27) was absent from the traps for part of the dry season and reappeared in September with slightly increased weight and tail circumference although the level of change is difficult to assess. Other individuals did not exhibit such a clear pattern in body weight and tail circumference fluctuation (e.g. F04, F20).

As indicated for males, the statistical analyses which follow are restricted to individuals in Group Two (but only for those females for whom recapture data existed). Body weight and tail circumference were highly positively correlated ($r_s=0.907$, $p<0.05$,

n=37). As with Group Two males this indicates that body weight fluctuations track tail fat storage.

In Group Two, females who underwent fattening were last trapped in April, May or June 1993 and retrapped in September, October or November. Because the sample size for the comparison involving tail circumference was too small to use a Wilcoxon Sign Rank test, I applied the Student t-test to both comparisons and the Wilcoxon test only to the comparison involving body weight. Last capture body weight and tail circumference data were both statistically significantly different from first capture data (Table 5.4). These results support the hypothesis that some female mouse lemurs underwent an increase in body weight and tail circumference at the onset of the dry season, reduced their activity during some part of the dry season as manifested by their absence in the traps, and resumed activity with a reduction in body fat values.

Descriptive Statistics on Body Weight and Tail Circumference

In the course of the trap-retrap sessions, 102 males and 72 females were captured. In this section, I present data on overall averages in body weight and tail circumference values in males and females (Table 5.8). These data are descriptive in their purpose. In general, they serve to make comparisons between the sexes and between different populations of *M. rufus*, as well as between various mouse lemur or other species.

As previously explained, I applied a modified Bonferroni criterion when interpreting the results of the statistical tests (Table 5.9). Using this approach, I found that the highest ranked test (which compared the body weights of 1994 juvenile males to 1994 juvenile females) had a p-value of 0.02. As there were 9 tests, the first alpha

became 0.05/9 = 0.055. This is less than 0.02, and thus the highest rank test was judged non-significant; therefore all the tests were non-significant.

Specifically results were as follows:

There was no statistically significant sexual dimorphism based on body weight and tail circumference, when comparing **all** the male capture data (category 1, Table 5.8) to **all** the female data, excluding pregnant and lactating individuals (category 2, Table 5.8).

In order to compare **only adult** male and female averages, two separate sets of data were analyzed. One set was based on the period between June 1993 and May 1994 while the other was based on the period from August 1993 to May 1994 excluding the dry season months of June and July. The rationale behind this depends on how one defines adulthood in mouse lemurs. It has been reported that captive gray mouse lemurs are weaned at seven weeks and are able to breed by the first reproductive season following their birth (Petter-Rousseaux, 1964; Glatston, 1979; Perret, 1992). My study demonstrated that brown mouse lemurs, also, are able to breed by the first reproductive season following their birth. However, at which point young mouse lemurs, albeit independent individuals, achieve full adult body size is not clear. Perret (1992) reports that captive gray mouse lemurs achieve adult body size and dental characteristics by three months. This would justify including June data in the analysis since most pregnant females were trapped in November and most new-to-the-population individuals were captured in February. Therefore, by June new-to-the-population individuals would be at least three months old. However, Glatston (1979) reports that captive juvenile mouse lemurs did not achieve adult-level body weight during the first short daylength period following their birth (i.e. what would be their first

dry season following birth) although, by the breeding season, their weights were indistinguishable from those of the other mouse lemurs. If this is true for brown mouse lemurs, it would mean that new-to-the-population individuals do not achieve adult body weights before August or September. Therefore, I conducted a second analysis which excluded June and July data. Although the average body weights for both males and females increased (Table 5.8, compare categories 3 to 5, and 4 to 6), in both sexes the difference was not statistically significant (Table 5.9). When comparing August 1993 to May 1994 adult-only male and female body weights and tail circumferences (categories to 5 to 6) I found that, as in the case of the first comparison (categories 1 to 2) there was no statistically significant dimorphism (Table 5.9).

To compare juvenile males to juvenile females (categories 8 to 9), I included only 1994 data because only for this year could I determine, based on their absence from the previous year's trap data, which individuals were new-to-the-population and therefore may have been born during the most recent breeding season. Taking all data into account, juvenile males have a higher average body weight than juvenile females. However, this may be explained by the fact that, although a similar number of male and female juvenile individuals had been captured by the middle of May when my project ended, new females made their appearance much earlier in the traps than males. Because young females were caught earlier, they may have biased the data toward smaller, lighter individuals. Indeed, the lower limit of the body weight range of animals trapped was smaller in females (20 g) than in males (30 g). I conducted two different comparisons in which all the data were included and the other where I used only data from April and May (see categories 8 to 10). These are the two months for which I had capture data for both sexes together. I excluded February and March when only

females were trapped. In both cases the differences between male and female juvenile body weight and tail circumference were not statistically significant (Table 5.9).

Analysis of Monthly Average Population Values

The following analyses based on population averages are presented as further support for the results of the longitudinal data analysis. I investigated changes in monthly population averages among the various size classes of mouse lemurs. I also compared male-female seasonal differences in body weight and tail circumference between males and females. Lastly, I examined fluctuations in the monthly sex ratios as indicative of male-female differences in activity levels.

Comparison of percent deviation of monthly average population values from overall averages

In order to assure that individuals for this analysis were adults, only data from August 1993 to May 1994 were used to determine monthly and overall averages.

Monthly average male body weights and tail circumferences deviate negatively from the annual average in October, November and December 1993 (Table 5.10, Figure 5.5). This period encompasses the main part of the breeding season. Except for tail circumference in January 1994, body weights and tail circumferences are above the annual mean at the start of the new year and continue into the period marking the onset of the dry season, when seasonal fattening begins.

In females, body weights and tail circumferences deviate negatively from the annual average between August and November 1993 (Table 5.10 and Figure 5. 6). Subsequently, body weight (but not tail circumference, except in December) deviates in a positive direction from the overall average during the months between December 1993 and February 1994.

The sample sizes are small (only one female each in December and January) because there was a dramatic decrease in the number of individuals trapped from December through February and because females that were trapped but had detectable pregnancies or that were visibly lactating were not included in the analysis. However, even the females included in these months may have been lactating (as indicated by the loss of fur around one or more of their nipples, though no milk was present) or have recently given birth without my having detected their condition, which may account for the high body weights which are not tracked by increased tail circumference. This may explain the difference demonstrated between the male and female patterns. Additionally, the breeding season may be energetically more costly for males, thus contributing to the pattern of decreased body weight and tail circumference between October and December.

From March 1994 to the end of the study period, a time which coincides with the period of hypothesized seasonal fattening at the onset of the dry season, both body weights and tail circumferences deviate positively from the overall averages. Positive deviations in body weight are closely tracked by positive deviations in tail circumference during this period.

Monthly frequencies of mouse lemurs in four different size classes

An initial inspection of the monthly histograms indicates that most male and female mouse lemurs trapped are in the 30-50 g size range (excluding pregnant and lactating females) (Figures 5.7 and 5.8). Size classes on either side of this range appear during certain periods of the year:

a) Decreased body weights are observed between February and May when individuals in the 20-30 g size class make their appearance. Because of their low body weight and/or the fact that they are being trapped for the first time (in the case of

individuals trapped in 1994), I assume that these individuals are the new crop of weaned young from the year's breeding season.

A single female, first trapped in July, accounts for the 20-30 g weight class appearing in July, August and October 1993. Though she remained under 30 g she did go through estrus during the breeding season, indicating that she was a mature, albeit lighter-weight individual.

b) Increased body weights (individuals >50 g) in both sexes are observed at the onset of the dry season, i.e. between February and June in 1993, and February and May in 1994. Some heavy individuals do appear outside of this period. Although I excluded females who were obviously pregnant or lactating, the one >50 g female, trapped in December and included in this analysis, may have been lactating as evidenced by the lack of fur around the nipple area.

Males >50 g were trapped in August and September 1993. Of these individuals, two males were heavier (88 g and 74g) when trapped at the onset of the dry season than when they were subsequently retrapped for the first time following this season. However, they remained over 50 g (53 and 51 g respectively) even after their weight loss. In addition, two males gained weight over the dry season: M34 was active throughout the dry season, gaining weight from an average in April 1993 of 33 g, to 51 g in September, while M12, last trapped in April at 42 g, was retrapped at 55 g in August. Three other >50 g males had no trap history prior to August. Any or all of these five males (the two who gained weight and the three for whom no data exist prior to August) may have been individuals who were new to the population and who increased in weight as part of their maturation and integration into the pool of breeding males.

Comparison of adult male and female average body weights and tail circumferences

In order to investigate sexual differences in body fat changes, I compared average body weight and tail circumference in September-October 1993 to that in February-May 1994 separately in males and females. February-May represents that period of relatively high resource abundance when some individuals undergo seasonal fattening, while September - October is the period just following seasonal torpor when some individuals are expected to have reduced body fat.

In females, average body weight and tail circumference differed significantly between these two periods (Student t-test: body weight, $t=-5.8$, $df=47$, $p<0.0001$; tail circumference $t=-3.0$, $df=43$, $p<0.005$), with the average weight in February-May 1994 being approximately 32% higher than in September-October 1993, and the tail circumference approximately 16% higher.

In contrast, in males, there was no statistically significant variation in body weight between the two periods (t-test: $t=-1.5$, $df=94$, $p=0.128$). Compared to females, male average body weights differed only by approximately 6%. However, tail circumferences differed by 17%, and were statistically significant (t-test: $t=-3.2$, $df=26$, $p<0.005$).

Changes in sex ratio

The ratio of males to females trapped fluctuated over the course of this project (Table 5.11). There appear to be several distinct periods when these changes occur. From February to May 1993, the average sex ratio is 1.0. This ratio increases dramatically to 3.7 during the period from June 1993 up to and including September 1993. Additionally, due to short leaves from the field which I took in June, August and September 1993 newly captured individuals were not marked by the guides who

continued trapping. Therefore, they could not be identified if recaptured. In the majority of cases these unmarked individuals were male and their inclusion in the analysis would have contributed to intensifying the sex ratio in favor of the males.

The period between October 1993 and December 1993 also demonstrates more male than female presence. From January to March 1994, the sex ratio is in favor of the females. In May 1994 the frequency of males more than doubles.

Apart from the variation in sex ratio, another interesting point is that the absolute numbers for both sexes were dramatically decreased between December and February. I attribute this to the effects of the breeding season, when perhaps both males and females stayed closer to nest sites. An alternative explanation whereby increased rainfall negatively affects trappability is not consistent with results in March 1993 and 1994, when both rainfall and number of individuals trapped were high.

Discussion

Annual Cycles in Body Fat Accumulation and Activity Levels in *Microcebus rufus*

The aims of the research described in this chapter were to determine if annual cycles in body fat and activity level occurred in *M. rufus* and to reveal which individuals of the population were characterized by these behaviors. I hypothesized that some, but not all, mouse lemurs captured would exhibit seasonal body fat increase and reduction in activity level, as manifested by an increase in body weight and tail circumference and a lack of trap capture during some part of the dry season. Recapture would be characterized by body fat decrease. I discovered that a certain number of male and female *M.rufus* exhibited these changes. Support for my hypothesis came from analysis of both longitudinal and monthly population averages. Since individuals

included in each month's size classes are not necessarily the same ones, changes in their proportions from month to month may reflect seasonal changes in body weight, demographic changes such as the addition of new individuals of different sizes into the population, or even chance error due to sampling variation. Therefore, longitudinal data are of value as they allow one to monitor known individuals and therefore to pinpoint when and why the changes may be occurring.

Body Fat Fluctuations in Group Two Males

Longitudinal data for mouse lemurs in 1993, and in 1994, demonstrated body weight and tail circumference increase at the beginning of the dry season. In 1993, when I recaptured these male mouse lemurs following a period of absence from the traps, their body weight and tail circumference were reduced. Interestingly, some male mouse lemurs captured in August had even more reduced body fat values when recaptured in September, and further reduced values when recaptured in October.

A similar situation has been reported in adult male woodchucks (Snyder et al., 1961). Like male mouse lemurs they emerge from hibernation 1 month earlier than females and continue to lose weight following resumption of activity due to decreased food availability and the preparation for reproduction. Female woodchucks conserve some body fat by staying in hibernation, but lose weight after emerging.

Fietz (1997), to the contrary, reports an **increase** in body weight from August to October in male *M. murinus* captured in a west coast dry forest. Differences between the results of my study and that of Fietz may be due to differences in resource availability. In Ranomafana, I have shown that the number of trees in fruit declines from August to October, and insect availability is low. On the west coast, where the dry season can last from six to eight months, it has been found that peak fruit production

occurs during the dry season (Sörg and Rohner, 1996). However, it is not clear if fruit production is high specifically in August through October, when males are increasing in body weight.

It is not possible to know with certainty whether all the males who underwent fattening in 1993 were older individuals or ones born to the population that year who were in the process of maturing or dispersing. In woodchucks (*Marmota monx*), even the young of a given year (approximately three months following their birth) accumulate fat and disappear from above-ground activity, presumably to hibernate (Snyder et al., 1961). In any case, by virtue of being trapped in January, which is too early for young individuals to be independent and to have an adult body weight, at least two of these individuals, M01 and M02, were adult, at least one year of age.

There were some indications that individuals who adopt the behavior of fattening and entering torpor one year may not do so the next. For instance, there were males who underwent seasonal fattening in 1994 but had not undergone seasonal fattening in preparation for the dry season in 1993. M40 and M63 were trapped throughout the dry season of 1993, demonstrating little change in body fat at that time. In addition, M11, who belonged to Group Two in 1993, was at a very low body weight when last trapped, at the end of April 1994. At that time in 1994, he weighed 37 g and had a tail circumference of 2.5 cm, whereas at the same time in 1993, he weighed approximately 45 g and had a tail circumference of 3.1 cm. However, it is possible that this male fattened and entered torpor after I discontinued data collection. The trap history of the other Group Two males in 1993 ended between September and November, and, therefore, could not be compared with the behavior of M11.

Body Fat Fluctuations in Group Two Females

As with the males, Group Two females underwent seasonal fattening and were absent from the traps for part of the dry season of 1993. F22, who was among the 1993 Group Two individuals who had undergone seasonal fattening, demonstrated similar increase in 1994. Another Group Two individual, F13 was recaptured once in 1994, heavier in weight than she had been at approximately the same time in 1993. Three others, F08, F10 and F32 had shown no weight increase by the time of their last capture at the end of April 1994. Therefore, it is possible that the same females who fatten one year may not do so each year.

Body Fat Fluctuations in the Population

Seasonal body fat changes occurred in both males and females, as demonstrated by the fluctuations in the monthly average population values. These values generally increased between February and May 1994. Furthermore, results from the monthly frequencies of body weight classes demonstrate the existence of several groups of individuals who may either be following different annual life-history strategies or be in different phases of their life cycle:

1. The most prevalent size classes of mouse lemurs, the 30-40 g and 40-50 g groups, are found throughout the annual cycle.

2. Individuals who make up the 20-30 g size class when it is present are presumably the new crop of weaned individuals from the year's breeding season.

3. Lastly, the individuals who form the heaviest, over-50 g, weight class of mouse lemurs occur almost exclusively during the period just prior to or at the onset of the dry season, i.e between February and June in 1993, and between February and

May in 1994. This suggests a seasonal pattern of increasing body weight which characterizes only a subset of mouse lemurs.

Comparison of Male and Female Body Measurements

As discussed in the introduction to this chapter, *M. rufus* females have been shown to have significantly longer skull lengths than males (Jenkins and Albrecht, 1991) and greater body weights (Kappeler, 1991). It has even been argued that the rapid (26% in 25 days) increase in weight observed in one free-ranging *M. murinus* female is an example of how females achieve dominance over males (Pagès-Feuillade, 1988). Other studies examining various body size values in *M. murinus* (Fietz, 1997) and comparing body weights in *M. rufus* (Harcourt, 1987) point to monomorphism in mouse lemurs. My study also found that no sexual dimorphism existed between adult males and females in terms of body weight or tail circumference, nor between juvenile males and females. However, the standard deviation for body weight was much greater in adult females than in adult males (7.6 compared to 4.4) due to the wider range in body weights of adult females captured (26.8 g-61.0 g versus 34.0 g-56.0 g in males).

Although body weight differences between the sexes are commonly used to measure sexual dimorphism (e.g. Gaulin and Sailer, 1984; Kappeler, 1991) it has been argued that this value is not an appropriate indicator of body size since it undergoes seasonal variation (Fietz, 1997). Jenkins and Albrecht (1991) assert that temporal, geographic and taxonomic effects introduce variance when attempting to determine the existence of sexual dimorphism in prosimians where differences may be slight anyway. A combination of any of these factors may account for the lack of consistency concerning indications of the existence of sexual dimorphism in mouse lemurs.

Fluctuations in Activity Level and Sex Ratio

In my study of brown mouse lemurs, I captured more males than females, and at almost all the trap sites the total number of male individuals captured was greater than females. In contrast, Martin (1972) reported that between July and December, when he conducted his field study, more female than male grey mouse lemurs were observed. He concluded that mouse lemurs lived in "population nuclei" with excess males occupying the fringes of these populations. However, I found that caution is needed when drawing conclusions about mouse lemur behavior because it so strongly seasonal. This was clearly demonstrated by the seasonal fluctuations in the sex ratio during the course of my study. The highly biased sex ratio primarily occurred in the period between June and September. Similar results have been found in previous studies on the brown mouse lemur: Harcourt's (1987) study which took place in Ranomafana between June 22 and July 29, also found captures to be highly male-biased, (23 males to 5 females), and, extracting only the brown mouse lemur data from Martin's study, revealed that, in Perinet, between August and September, more males were captured than females (7:1).

Biased birth sex ratios are known to occur in primates (Johnson, 1988; Paul and Thomen, 1984; MacFarland Symington, 1987) and captive female *M. murinus* living in groups with other females produced more male offspring (Perret, 1990). Thus, one explanation for the sex ratio which I observed is that with the addition of the new mouse lemurs from the year's breeding season to the population, a bias in the sex ratio was introduced. However, since trap data reflect post- weaning sex ratio and not the birth sex ratio it is impossible to conclude that free-ranging *M. rufus* produce a male-biased birth sex ratio, especially such a strong one. In any case, young individuals have

already made their appearance much earlier than May and June when the biased sex ratio first appears. In addition (and this is only verified for 1994 when juvenile individuals could be determined with some certainty), although new females made their appearance much earlier in the traps than males and with lower body weights, by the middle of May when the project terminated, the number (and weight) of male and female juveniles was the same.

Sex ratio and its fluctuations, as reflected through trapping, may be indicative of intersexual differences in activity levels, generally or seasonally, rather than true biases in the core population. One study, which took place between August and October, and was conducted on west coast gray mouse lemurs, revealed a sex ratio in favor of males and was thought to be indicative of differing sexual strategies for surviving the austral winter's period of food scarcity (Fietz, 1997). It was also suggested that one can account for the presence of mouse lemurs throughout the austral winter or dry season as the result of active males who are preparing for the reproductive period by establishing hierarchical order while the females are inactive. However, results from analysis of the longitudinal data in this study, which followed individuals for a longer period of time, revealed that both sexes can increase body fat and not appear in the traps during part of the dry season. And yet the fact remains that individuals trapped between June and September are, in their preponderance, male.

I propose that the sex bias between June and September is due to increased activity of males who are dispersing from their natal range. No data exist on dispersal patterns in mouse lemurs but it is known to occur in other nocturnal prosimians (Clark, 1978; Bearder, 1987). Among mammals, males tend to be the sex that disperses (Greenwood, 1980). This is true in primates where many females are philopatric and remain within their maternal homerange (Pusey and Packer, 1987; Johnson, 1988),

and in small mammals where dispersal is known to be dependent on season, density and life-history events (e.g. Lidicker, 1985; Gaines and Johnson, 1987).

In addition to increased activity due to dispersal, male *M. rufus* may be generally more active than females, with larger home ranges, as has been found for *M. murinus* (Barre et al., 1988; Pagès-Feuillade, 1988; Martine Perret, pers. com.). Captive data indicate that juvenile animals follow similar patterns to those of adults, juvenile females behaving like their less active mothers and juvenile males like the more active adult males (Martine Perret, pers. com.). This may explain why, in June, July and August, more new-to-the-trap-population males are captured than are females. Presumably, these males are the additions from the breeding season of that year. This combination of factors may result in males entering the traps before females reach them.

In my study the highly biased sex ratio continued into the months of August, September and October. However, the magnitude of the skewness decreased over time (from 4.7 in August, to 1.9 in October) as the number of females increased and the number of males eventually decreased (from 33 in August, to 44 in September, to 28 in October). This period of time coincides with the beginning of the breeding season. In captive mouse lemurs, females become active when their sexual activity begins, during late September, while males increase their activity from mid-July to August prior to the beginning of their sexual activity (Martine Perret, pers. com.).

It is also known that in some small mammals, males emerge from torpor earlier than females (e.g. jumping mice and woodchucks; see Godin, 1977; Snyder et al., 1961). Therefore, an additional factor contributing to the biased sex ratio of August to October is that males may be emerging earlier from their period of lethargy, a statement confirmed by the longitudinal data with male mouse lemurs reappearing in

the traps one month earlier than the females. As mentioned earlier, captive *Microcebus murinus* males establish a strict hierarchy based on their relative body weights (Perret, 1992). Therefore, *M. rufus* males may also take the opportunity, before females emerge, to establish breeding hierarchy.

The biased sex ratio between October and December 1993, which constitutes the main period of the breeding season, may be the result of males ranging further in search of females in estrus, and pregnant and lactating females staying closer to their nests.

The few months when the sex ratio was biased in favor of the females (January 1994 to March 1994) is probably due to the earlier capture of females new-to-the-population than males new to the population as previously noted.

Conclusions

It is frequently stated that a consideration of the relationship between seasonality and lemur life histories is important to understand the peculiarities of strepsirhine behavior. Seasonality based on rainfall (e.g. Hladik et al., 1980; Petter-Rousseaux, 1980; Pereira, 1993) and, more recently, on temperature (Morland, 1993), has been suggested as an explanation of strict cyclical variations in lemur behavior in many different kinds of Malagasy climates (Richard and Dewar, 1991).

Pereira (1993) discusses how the strict seasonality of *Lemur catta* behavior, even in captivity, is directly related to the distinct climatic cycles of southern Madagascar, where rain is limited to four months per year. Reproduction, which is under tight photoperiodic control, is synchronized with seasonal rainfall occurring during the period of highest food availability. The readily available resources decrease

competition in this group-living species, ensuring that the young have an adequate food supply during the first stages of their life and thereby reducing juvenile mortality rates.

My study has demonstrated that cyclical variations in behavior can also occur in a solitary foraging rainforest species. Even in the east coast rain forests, resource availability for mouse lemurs declines during certain months of the dry season and is accompanied by a decrease in ambient temperature and rainfall (see Chapter 3). *M. rufus* individuals are faced with reduced resources, stressful climatic conditions and increasing thermoregulatory costs during some parts of the year. It is perhaps for these reasons that, as in ring-tailed lemurs, mouse lemurs inhabiting both the dry west and the more humid east coast rainforests synchronize their breeding season so that lactation and maturation of the young take place during periods of peak rainfall and food availability. (An additional explanation for strict seasonality in reproduction has been proposed by Martin (1990), who suggested that it was a way to saturate local predators. Because they face a high risk of predation (Goodman et al., 1991, 1993) this suggestion may apply to mouse lemurs, in addition to the one proposed above based on resource stress).

I have also shown that individual mouse lemurs do not all follow the same annual behavioral patterns. Some, but not all, mouse lemurs, both male and female, undergo seasonal fattening, enter torpor and reappear in the traps with decreased body fat values. In addition, the same individuals, male or female, can behave differently from one annual cycle to the next (as did individuals who fattened in 1994 but not in 1993).

As previously stated, the trap history of Group Two males, other than M11, ended between September and November 1993. The eventual absence of these

males from the trapped population may be the result of chance fluctuations in trapping success. However, if males who fatten and enter torpor are the resident males, their subsequent absence may be indicative of demographic changes in the population, perhaps due to an influx of new males outcompeting previously established ones.

The question which remains to be further explored is which individuals are able to fatten and enter torpor and which are not, or, why some do and others don't. One consideration is the fact that the trap history of a large section of the trapped population (those in Group One) was incomplete. It is likely that a much larger segment of the population adopts the seasonal behavior described. Yet the fact remains that among mouse lemurs whose trap history is long-term and continuous enough to be revealing, there are those who enter traps throughout the dry season (as do some Group Three individuals) and those who do not, and those who fatten dramatically and those who do not (once again, as is demonstrated by certain Group Three individuals).

Martin (1972) has invoked the existence of different size classes in free-ranging male mouse lemurs which he thought may reflect social status. On the other hand, the existence of behavioral differences based on age, has been observed in one study conducted on captive males (Russell, 1975). In that study, during the period which corresponded to the austral winter (or dry season) in Madagascar, adult males who were at least 30 months in age had consistently lower body temperatures than the younger males who were exactly 18 months in age. Furthermore, young males were never observed at rest during the night while the other animals could remain lethargic. Therefore, observed behavioral differences in my study may be, at least partially, explained by differences in the level of maturity of the individuals in the population. It is perhaps younger males, who are dispersing, that accounted for most of the activity during the mid-dry season months of July and August 1993. I further speculate that

perhaps it was only the older individuals (those who had been in the population from at least the previous year) who were able to exhibit the behavior of seasonal fat increase and torpor.

Torpor during part of the dry season has been studied in the west coast *Microcebus* species. All mouse lemurs that were part of that study underwent periods of daily torpor but aroused themselves and were active as usual during each nocturnal phase (Ortmann et al., 1997). This conforms with observations that mouse lemurs can be seen active in the forest all year round. Based on my longitudinal data, I found that mouse lemurs who undergo seasonal fattening are absent from the traps for part of the dry season. It is likely that all mouse lemurs are able to undergo daily torpor but that only a subgroup is able to sustain torpor for a longer period of time, though the duration of such a state remains unknown. Moreover, it is possible that those mouse lemurs that do undergo deep torpor, maintain overall lethargy even if they are aroused. Their decreased state of activity may prevent them from entering the traps.

In another captive study, *M.murinus* notably decreased activity and food consumption during the winter but without ceasing either (Bourlière and Petter-Rousseaux, 1966). The degree to which mouse lemurs become inactive may be related to resource availability. Captive *Cheirogaleus medius* followed photoperiodic cues and underwent seasonal body weight changes but did not totally cease activity under conditions of constant temperature and food supply (Foerg and Hoffmann, 1982). The propensity to reduce activity and enter torpor in captive hedgehogs (*Atelerix frontalis*) varied depending on degree of temperature reduction and level of food restriction (Gillies et al., 1991). The combination of both low temperatures and reduced food availability produced the greatest degree of hypometabolism. Based on

trapping success, it was noted that winter activity in a population of the little pocket mouse (*Perognathus longimembris)* ranged from zero to five months depending on the year (Kenagy, 1973). Experiments on captive animals confirmed that food availability determined the extent to which torpidity was utilized, if at all, in the winter.

Physiological field studies are unavailable for east coast mouse lemurs but would aid in determining whether the trap data are indicative of real differences in annual behavioral cycles among mouse lemur individuals. I predict that east coast mouse lemurs may indeed differ in their behavioral responses to seasonal changes. This may be related to differences in the behavior of the sexes, to age, to individual responses to resource availability or to a combination of any of these factors.

My study was unique both in the length of the study and in its reliance on longitudinal data rather than population averages. I would not have been able to detect the existence of different behavioral patterns on the basis of a shorter study of, for example, three months duration. On the other hand, it is evident that an even longer-term study is required to observe fluctuations in the behavioral patterns of the same individuals from year to year, and to discover why there may be inter-individual differences in behavior within an annual cycle.

Table 5.1. Group Two male *M. rufus with* increasing body weight (g) and tail circumference (cm) values* in February-June 1993, followed by a decrease in these values when retrapped in August or September, after at least one month's absence from traps.

	1993										1994			
Male	Feb-93	Mar-93	Apr-93	May-93	Jun-93	Jul-93	Aug-93	Sep-93	Oct-93	Nov-93	Dec-93	Jan-94	Feb-94	Mar-94	Apr-94
M01 weight		44.0		50.7			47.5	43.5							
tail circ.		2.5		3.4			3.4	2.7							
M02 weight	46.0		88.0				52.0	48.8							
tail circ.	2.7		4.2				3.2	2.8							
M07 weight	56.0	54.7					48.3	47.6	48.0	43.5					
tail circ.	4.5	3.6					3.2	2.8	2.6	2.6					
M11 weight		37.3	38.6	49.3	50.0		40.8	39.2	39.0	37.4	42.0		41.0	40.7	37.6
tail circ.		2.5	2.7	3.2	3.5		2.8	2.5	2.4	2.5	2.5		2.7	2.7	2.7
M22 weight		43.0	74.0					52.0							
tail circ.		2.5	3.7					2.6							
M60 weight				66.0				43.5	42.0						
tail circ.				4.1				2.5	2.5						

*Data shown are monthly averages in contrast to data in Table 5.2 which are single data points.

Note that averaged values may not clearly demonstrate the rapid changes in body weight and tail circumference that can characterize mouse lemurs.

Table 5.2. Differences in body weight (g) and tail circumference (cm) values in Group Two* male M. rufus between time of last capture in April, May or June 1993 and first recapture in August and/or September 1993, at Talatakely, RNP (After at least one month's absence from traps)

Male	Last capture: weight	First recapture weight: August	Difference between last capture and Aug. recapture: weight	First recapture weight: September	Difference between last capture and Sep. recapture: weight
M01	53	48	5	43	10
M02	88	53	35	49	39
M07	55	45	10	46	9
M11	50	40	10	38	12
M22	74			48	26
M60	66			42	24

Male	Last capture: tail circ.	First recapture tail circ.: August	Difference between last capture and Aug. recapture: tail circumference	First capture tail circumference: September	Difference between last capture and Sep. recapture: tail circumference
M01	3.8	3.4	0.4	2.7	1.1
M02	4.2	3.4	0.8	3.1	1.1
M07	3.7	3.2	0.5	2.7	1.0
M11	3.5	2.8	0.7	2.6	0.9
M22	3.7			2.6	1.1
M60	4.1			2.5	1.6

*Group Two males are those demonstrating an increase in body weight and tail circumference during the first months of the dry season in 1993, followed by a decrease in these values when retrapped later in the season.

Table 5.3. Group Three male *M. rufus* monthly average body weight (g) and tail circumference (cm) values in 1993 and 1994, at Talatakely, RNP.

	1993											1994				
Male	Feb-93	Mar-93	Apr-93	May-93	Jun-93	Jul-93	Aug-93	Sep-93	Oct-93	Nov-93	Dec-93	Jan-94	Feb-94	Mar-94	Apr-94	May-94
M05 weight	32.7						48.0									
tail circ.	2.4						3.6									
M09 weight	43.0		43.0				53.0	45.0	41.3	39.6			47.0			
tail circ.	2.5		2.6				3.6	2.7	2.5	2.5			3.0			
M12 weight		42.0	42.0				54.5	44.8	45.3							
tail circ.		2.5	2.6				3.8	2.6	2.5							
M14 weight		43.5						46.9	44.3	44.7				67.5		
tail circ.		3.3						2.9	2.6	2.6				4.8		
M16 weight		34.0	34.0	39.0	39.0	39.5	41.5	46.8	41.3	40.6				51.0		
tail circ.		2.4		2.5	2.5	2.6	3.0	2.7	2.4	2.4				3.5		
M19 weight		32.0				37.0		44.0	40.0							
tail circ.		2.3				2.5		2.9	2.5							
M32 weight			45.3				48.0	43.0								
tail circ.			3.2				3.2	3.0								
M36 weight			40.0	41.5	40.0	37.1	42.6	42.8	41.3	41.0						
tail circ.			2.5	2.6	2.9	2.7	2.6	2.6	2.5	2.5						
M40 weight			37.5	40.4	39.6	39.9	43.1	40.9	37.8	37.4	43.0	44.0	43.0	43.3	45.4	55.0
tail circ.			2.3	2.6	2.9	3.0	2.9	2.6	2.4	2.4	2.4	2.5	2.7	2.6	3.0	4.2
M44 weight			49.0				46.6	42.3	41.5	41.5						
tail circ.			3.0				3.3	2.6	2.5	2.5						
M48 weight				41.0	39.0	39.9	41.4	40.7								
tail circ.				2.5	2.7	2.5	2.5	2.4								
M63 weight					31.5	31.6	33.4	38.7	37.0	35.0				40.0	37.0	57.0
tail circ.					2.4	2.4	2.4	2.5	2.3	2.4				2.7	2.5	3.3
M70 weight						33.6	41.1	37.1	37.8	33.7	39.0	40.0		41.0		
tail circ.						2.7	2.6	2.5	2.4	2.3	2.4	2.7		2.9		
M79 weight								42.8	40.8	39.5		47.0			65.0	
tail circ.								2.7	2.6	2.5		2.8			5.0	

*see text for description of Group Three males.

Table 5.4. Comparison of body weight (g) and tail circumference (cm) values between last capture and first recapture in Group Two male and female *M. rufus,* at Talatakely, RNP.
Results from t-tests and Wilcoxon sign rank statistical tests.

Sex	Group	Comparison	Body weight or tail circumference	Sample size	z-statistic	z-statistic p	z-statistic results
male	2	Last capture to August recapture	Body weight	4	-	-	-
male	2	Last capture to August recapture	Tail circumference	4	-	-	-
male	2	Last capture to September recapture	Body weight	6	-2.201	0.028	significant
male	2	Last capture to September recapture	Tail circumference	6	-2.207	0.027	significant
female	2	Last Capture to first recapture	Body weight	6	-2.226	0.026	significant
female	2	Last Capture to first recapture	Tail circumference	5	-	-	-

con't

Sex	Group	Comparison	Body weight or tail circumference	t-statistic	t-statistic p	t-statistic alpha--Bon.	t-statistic results
male	2	Last capture to August recapture	Body weight	2.71	0.015	0.05	significant
male	2	Last capture to August recapture	Tail circumference	3.553	0.006	0.025	significant
male	2	Last capture to September recapture	Body weight	3.213	0.009	0.017	significant
male	2	Last capture to September recapture	Tail circumference	8.12	0.000009	0.0083	significant
female	2	Last Capture to first recapture	Body weight	3.927	0.00076	0.01	significant
female	2	Last Capture to first recapture	Tail circumference	5.365	0.000064	0.013	significant

Table 5.5. Group Two female *M. rufus with* increasing body weight (g) and tail circumference (cm) values* in February-June 1993, followed, in some cases, by a decrease in these values when retrapped** in September, October or November after at least one month's absence from traps.

	1993											1994				
Female	Feb-93	Mar-93	Apr-93	May-93	Jun-93	Jul-93	Aug-93	Sep-93	Oct-93	Nov-93	Dec-93	Jan-94	Feb-94	Mar-94	Apr-94	May-94
F08 weight	36.5	35.0	34.0	43.0	54.0			34.0	33.0	37.0				45.0		
tail circ.	2.4	2.3		2.6	3.1				2.4	2.4				2.5		
F10 weight	52.0	46.7	43.0	65.0						42.6		44.5	41.0	41.0		
tail circ.	3.1	2.6	2.5	3.7						2.5		2.5	2.5	2.6		
F13 weight		43.0	49.0	62.0										51.0		
tail circ.		2.7	3.0	4.0										3.5		
F19 weight		39.0	37.0	43.0												61.0
tail circ.		2.5	2.4	2.7												4.0
F22 weight		46.7	53.5						48.0	47.0		53.0		53.0	59.0	
tail circ.		3.0	3.3						3.0	2.5		2.7		3.6	4.0	
F29 weight		30.0	37.0	41.0	52.0											
tail circ.		2.4	2.4	2.8	3.4											
F32 weight			50.0						34.0					42.0		
tail circ.			3.6						2.6					2.6		
F38 weight			51.0						43.0							
tail circ.			3.2						2.7							
F42 weight				40.0				32.0	31.5							
tail circ.				3.0				2.5	2.4							
F49 weight					42.0			34.0								
tail circ.					2.9			2.4								

*Data shown are monthly averages in contrast to data in Table 5.6 which are single data points.
Note that averaged values may not clearly demonstrate the rapid changes in body weight and tail circumference that can characterize mouse lemurs.
**no recapture data for F13, F19 and F29

Table 5.6. Differences in body weight (g) and tail circumference (cm) values in Group Two* female *M. rufus*, between time of last capture in April, May or June 1993 and first recapture** in September, October, or November 1993, at Talatakely, RNP. (After at least one month's absence from traps)

Female	Last capture: weight	First recapture: weight	Difference between last capture an first recapture: weight	Last capture: tail circ.	First recapture recapture: tail circumference	Difference between last capture and first recapture: tail circ.
F08	54	34	20	3.1	2.40	0.7
F10	65	42	23	3.7	2.50	1.2
F13	62			4.0		
F19	43			2.7		
F22	54	48	6	3.3	3.00	0.3
F29	52			3.4		3.4
F32	50	36	14	3.6	2.60	
F38	51	43	8	3.2	2.70	0.5
F42	40	32	8	3.0	2.50	0.5
F49	42	34	8	2.9	2.40	0.5

*Group two females are those demonstrating an increase in body weight and tail circumference during the first few months of the dry season in 1993, followed by a decrease in these values when retrapped later in the season.

**no recapture data for F13 and F29 (but increase in values from February to May).

Table 5.7. Group Three female *M. rufus* monthly average body weight (g) and tail circumference (cm) values in 1993 and 1994, at Talatakely, RNP.

	1993												1994				
Female	Jan-93	Feb-93	Mar-93	Apr-93	May-93	Jun-93	Jul-93	Aug-93	Sep-93	Oct-93	Nov-93	Dec-93	Jan-94	Feb-94	Mar-94	Apr-94	May-94
F04 weight		52.0	47.5						41.0	44.0	48.0	53.0			51.0	51.0	
tail circ.		3.05	2.6							2.5	2.5	2.7			2.7	3.5	
F20 weight			33.0	32.5	42.0	41.8	34.0	36.0	32.0	33.5				45.5	46.0		
tail circ.			2.3	2.3	2.5	2.5	2.3	2.5	2.3	2.4				2.5	2.5		
F25 weight			35.7	36.5	39.9	40.0	38.0	41.5	39.0	35.0	40.0					52.5	
tail circ.			2.4	2.3	2.6	2.7	2.6	2.6	2.6	2.3	2.4					3.4	
F27 weight			45.0	40.5					42.0		42.0						
tail circ.			2.5	2.5					2.9		2.7						
F37 weight				36.0	39.0				35.0	33.5	37.0		47.0				
tail circ.				2.2	2.6				2.5	2.4	2.4		2.4				
F47 weight					37.0	39.0	35.5	40.0	36.5								
tail circ.					2.6	2.8	2.7	2.5	2.6								

*see text for description of Group Three females.

Table 5.8. Body weight (g) and tail circumference (cm) averages of *Microcebus rufus* captured between February 1993 and May 1994 at Talatakely, RNP.

	Category	Body weight	Sample size	Standard deviation	Range	Tail circ.	Sample size	Standard deviation	Range
1	All males, Feb 93-May 94	41.27	319	6.57	30-88	2.67	313	0.38	2.2-5.0
2	All females*, Feb 93-May 94	41.13	167	9.31	20-76	2.66	163	0.42	2.2-4.4
3	Adult males, June 93-May 94	41.90	220	5.32	31-67.5	2.70	214	0.36	2.2-5.0
4	Adult females, June 93-May 94	40.82	82	8.20	26.7-72	2.68	78	0.42	2.25-4.4
5	Adult males, Aug 93-May 94	43.47	155	4.44	34-56	2.69	157	0.40	2.2-5.0
6	Adult females, Aug 93-May 94	42.02	32	7.59	26.8-61	2.68	58	0.45	2.25-4.4
7	Pregnant and lactating females	47.28	31	8.47	37-73	2.57	31	0.14	2.3-3.0
8	Juvenile males, April-May 1994	34.44	17	2.79	30-39	2.40	17	0.10	2.3-2.7
9	Juvenile females, Feb-May 1994	31.00	16	5.00	20-40	2.36	17	0.12	2.2-2.6
10	Juvenile females, April-May 1994	33.90	7	4.10	29-40	2.40	7	0.09	2.3-2.6

*excluding pregnant and lactating individuals

Table 5.9. Comparison of population averages for body weight (g) and tail circumference (cm) values as presented in Table 5.6 for *Microcebus rufus* at Talatakely, RNP. Results from t-test statistics.

Type of comparison	t-statistic	p	alpha Bonfer.	df	Result
All males to all females, body weight (no. 1 to no. 2 in Table 5.6)	t=0.19	0.85		484	ns
All males to all females, tail circ. (no. 1 to no. 2)	t=0.05	0.96		474	ns
June 93-May 94 males to August 93-May 94 males (no. 3 to no. 5)	t=-2.0	0.046		273	ns
June 93-May 94 females to August 93-May 94 females (no. 4 to no. 6)	t=-0.71	0.47		112	ns
August 93-May 94 males and females (no. 5 to no. 6)	t=-0.98	0.33		44	ns
1994 juvenile males to 1994 juvenile females, body weight (no. 8 to no. 9)	t=2.46	0.02	0.055	31	ns
1994 juvenile males to 1994 juvenile females, tail circ. (no. 8 to no. 9)	t=1.11	0.28		32	ns
April-May 1994 juvenile males to April-May 1994 juvenile females, body weight (no.8 to no.10)	t=0.41	0.69		22	ns
April-May 1994 juvenile males to April-May 1994 juvenile females, tail circ.(no.8 to no. 10)	t=-0.62	0.54		22	ns

Table 5.10. Percentage deviation of monthly average body weight (g) and tail circumference (cm) values from annual averages for adult male and female *Microcebus rufus* at Talatakely, RNP.

Month	Male Monthly average body weight	Sample size	% deviation from annual av body weight of 43.47g	Male Monthly average tail circ.	Sample size	% deviation from annual av tail circ. of 2.67cm
Aug-93	43.3	33	-0.39	2.90	30	7.24
Sep-93	43.9	44	0.99	2.67	39	0.00
Oct-93	41.8	27	-3.84	2.47	28	-8.91
Nov-93	39.6	24	-8.90	2.46	24	-9.35
Dec-93	42.1	7	-3.15	2.43	7	-10.70
Jan-94	43.7	3	0.53	2.67	3	0.00
Feb-94	45.3	4	4.21	2.78	4	3.24
Mar-94	45.2	10	3.98	2.95	10	8.81
Apr-94	43.5	13	0.07	3.10	7	13.23
May-94	47.0	16	8.12	3.23	5	16.72
Month	Female Monthly average body weight	Sample size	% deviation from annual av body weight of 42 g	Female Monthly average tail circ.	Sample size	% deviation from annual av tail circ. of 2.67 cm
Aug-93	37.0	7	-11.95	2.54	7	-5.22
Sep-93	35.9	11	-14.56	2.54	8	-5.22
Oct-93	37.4	16	-10.99	2.52	15	-5.97
Nov-93	41.4	7	-1.48	2.47	4	-7.84
Dec-93	53.0	1	26.13	2.70	1	0.75
Jan-94	47.0	1	11.85	2.40	1	-10.45
Feb-94	47.5	3	13.04	2.47	3	-7.84
Mar-94	46.9	10	11.61	2.77	10	3.36
Apr-94	54.5	5	29.70	3.56	5	32.84
May-94	44.8	4	6.62	2.94	4	9.70

Table 5.11. Monthly trapping of individual *Microcebus rufus* and ratios of males to females captured at Talatakely, RNP.

Month	Total number of trap nights	No. of males trapped	No. of females trapped	Ratio of males to females trapped	Notes
Feb-93	10	9	11	0.8	
Mar-93	7	23	25	0.9	One unidentified male not included.
Apr-93	15	27	21	1.3	
May-93	15	23	21	1.1	
Jun-93	14	34	11	3.1	Maximum of 14 unidentified males not included (min.3);max 4 females (min.1).
Jul-93	11	24	8	3.0	
Aug-93	14	33	7	4.7	Maximum of 5 unidentified males (min. 1) not included.
Sep-93	8	44	11	4.0	Maximum of 3 unidentified males (min. 1) not included.
Oct-93	4	28	15	1.9	One unidentified male not included.
Nov-93	9	24	18	1.3	
Dec-93	7	7	2	3.5	
Jan-94	7	3	6	0.5	
Feb-94	5	4	8	0.5	
Mar-94	4	10	16	0.6	One unidentified male and one female, not included.
Apr-94	10	13	11	1.2	
May-94	7	16	6	2.7	

Figure 5.1. Body weight (g) and tail circumference (cm) change between last trap capture in April 1993 and first trap captures in August and in September in Group Two M02.

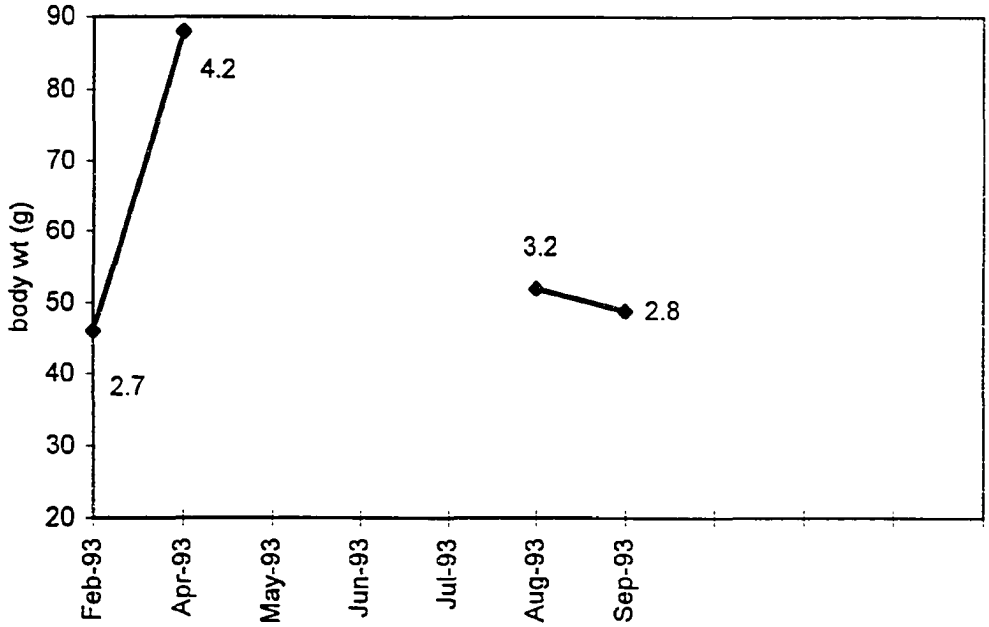
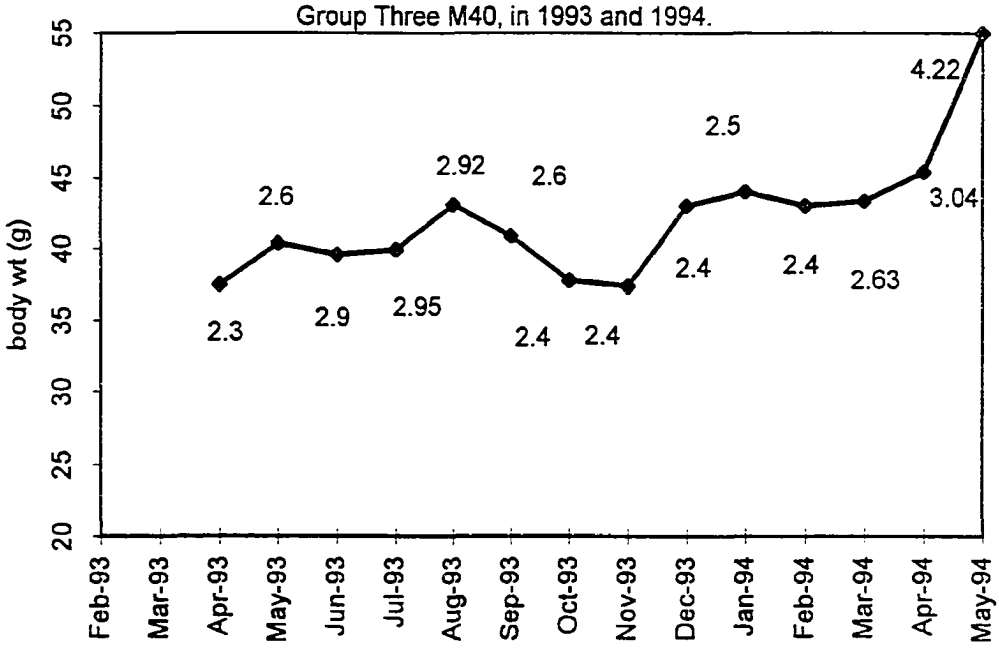


Figure 5.2. Body weight (g) and tail circumference (cm) values in Group Three M40, in 1993 and 1994.



Tail circumference found next to corresponding body weight value.

Figure 5.3. Body weight (g) and tail circumference (cm) change between last trap capture in June 1993 and first recapture in September in Group Two F08.

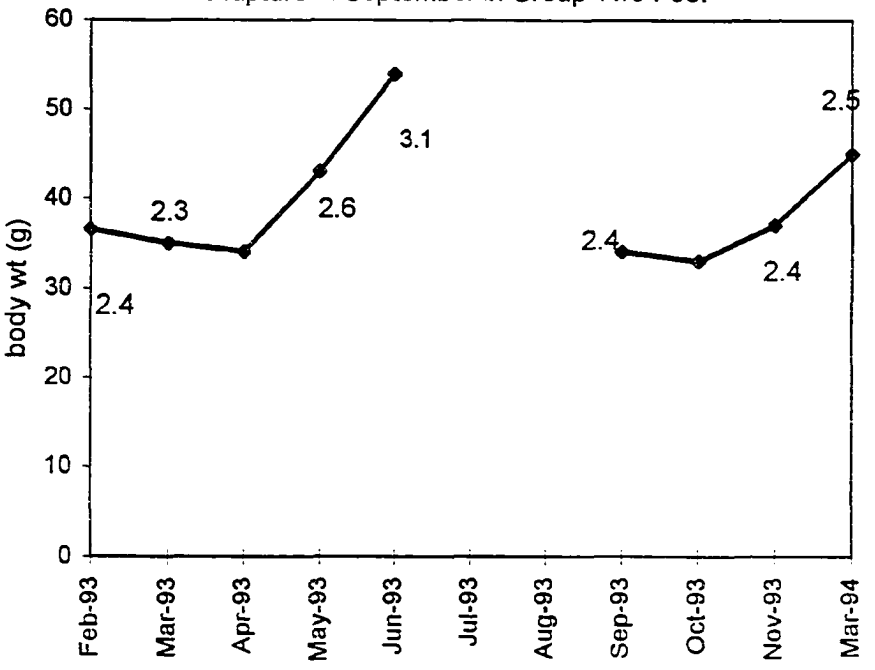
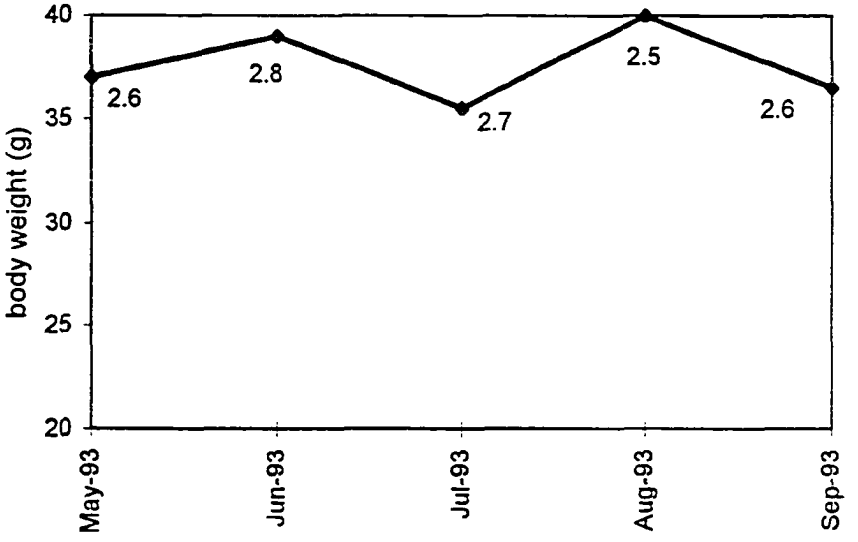


Figure 5.4. Body weight (g) and tail circumference (cm) values in Group Three F47, in 1993.



Tail circumference found next to corresponding body weight value.

Figure 5.5. Percent deviation of monthly body weight (g) and tail circumference (cm) averages from the annual averages in male *M. rufus* at Talatakely, RNP

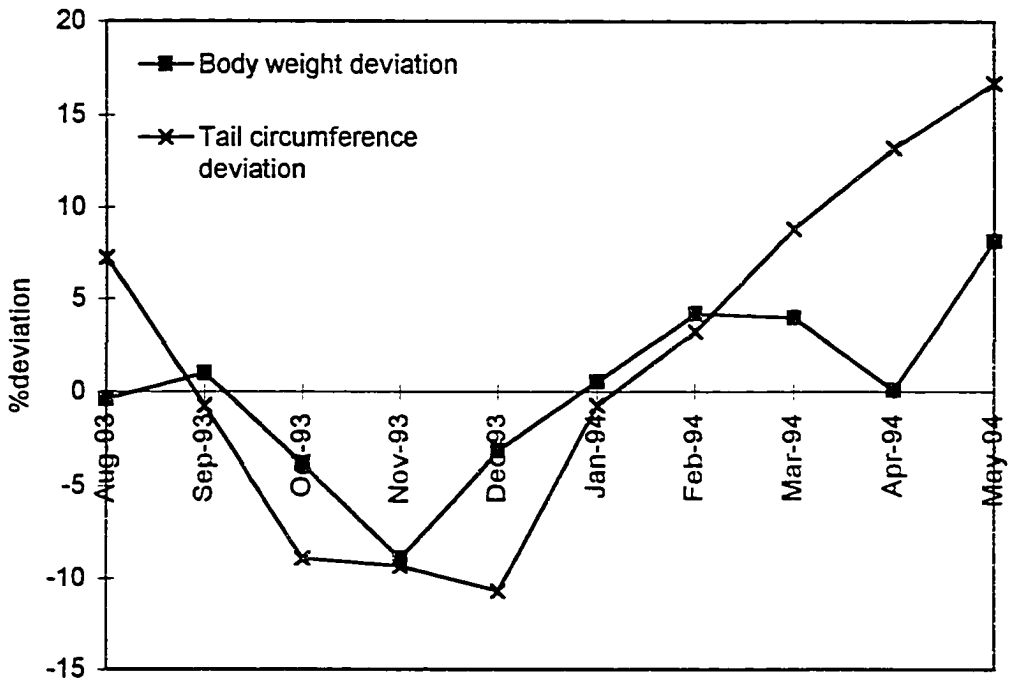


Figure 5.6. Percent deviation of monthly body weight (g) and tail circumference (cm) averages from the annual averages in female *M. rufus* at Talatakely, RNP

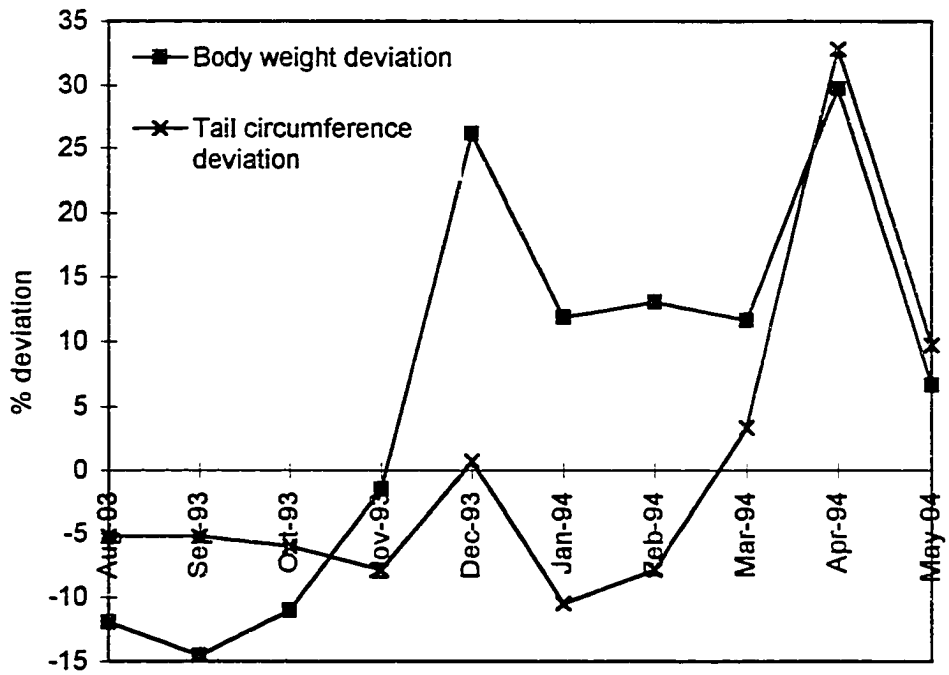


Figure 5.7. Monthly frequencies of four body weight (g) classes in male *M. rufus* at Talatakely, RNP.

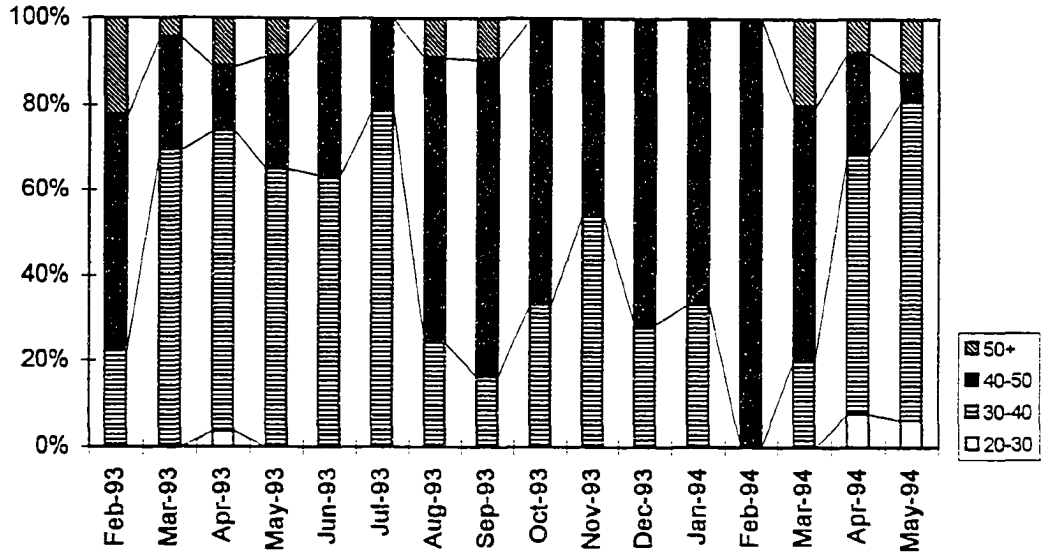
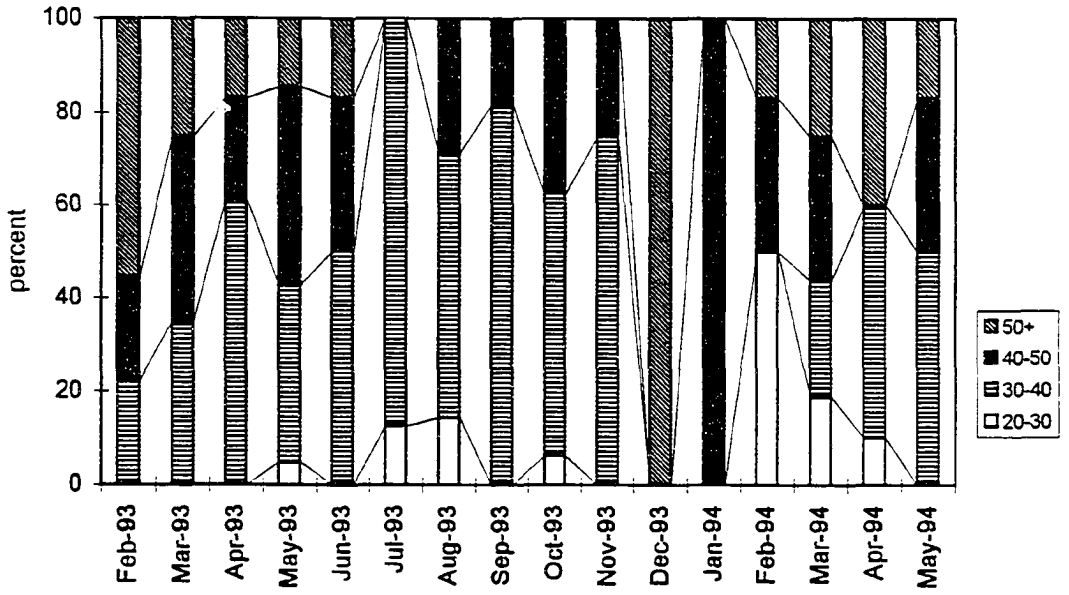


Figure 5.8. Monthly frequencies of four body weight (g) classes in female *M. rufus* at Talatakely, RNP



CHAPTER SIX

SUMMARY AND CONCLUSIONS

Data Collection

The goal of this study was to investigate the behavior and ecology of free-ranging brown mouse lemurs, *Microcebus rufus*. For this purpose, I collected data for a period of 17 months on a population of mouse lemurs located at the Talatakely Research Station in Ranomafana National Park, Madagascar.

I took a general approach to this study because this species of mouse lemur has rarely been the subject of any research, in captivity or in the wild. The methods I used provided important information on this species but rarely in a direct manner. Diet was inferred from material (primarily seeds and chitin remains) found in fecal samples which were easily collected from trapped animals, and, more rarely, from direct observation of animals feeding. Seasonal changes in activity levels were inferred from presence or absence in traps. Reproductive state was monitored through changes in testicular size and vulval activity in captured individuals. Litter size was inferred from ventral palpation of pregnant females. Information on nesting was collected by locating daytime nests and counting individuals who emerged following disturbance. Night ranging data were collected by triangulating the position of radiocollared individuals. Data on home-range size were collected by radiotracking, by measuring distances between nest locations when the individual occupying the nest was known and by measuring the distances among different trap sites where individuals were captured. Various body measurements were collected directly on captured individuals. Social behavior had to be inferred from data on nesting occupancy and home-range overlap, since direct observation of individuals for any length of time was rarely possible.

I collected a wider range of data than was analyzed in this dissertation, but to which I will refer in this synopsis in order to tentatively flesh out the picture of the natural history of this species. Analysis of the data included here should help to elucidate the behavior of the different species of mouse lemur, compare their behavior in the context of their different environments and interpret the behavior of other little-studied nocturnal primates. Furthermore, the broad array of data which I collected can serve as a baseline for future research which will focus more intensively on such topics as social behavior and reproduction.

Aims

The primary aims of this research and analysis were twofold:

a. To investigate feeding behavior, especially to determine fluctuations in the quantity and quality of fruit and insects eaten. Data on fruit and flower phenological cycles and insect availability complement this part of the study by relating feeding patterns to resource availability.

b. To collect information from trapped individuals on body fat and activity levels, which are known to fluctuate seasonally in west coast mouse lemurs, in order to determine if annual cycles also occurred in this east coast rainforest species.

Hypotheses

I hypothesized that mouse lemurs have preferred food resources. Based on this hypothesis, I predicted that specific plant and insect resources would be incorporated into the diet irrespective of what might be generally available. Furthermore, I hypothesized that, as part of the mouse lemur annual cycle, some, but not all, individuals of both sexes would exhibit seasonal increase in body fat and subsequent reduction in activity during some part of the dry season. I predicted that

there would be individuals of both sexes whose trap history would be interrupted for part of the dry season and who would exhibit weight loss when recaptured following this interval.

Summary of Results

a. I found that contrary to certain predictions based on body size, *Microcebus rufus* relies heavily on fruit, consuming a large variety of vernacular species (24 which were taxonomically identified and an additional 40-52 which remained unidentified). Mouse lemurs increased the quantity and diversity of fruit intake during the rainy season when fruit productivity was high. This coincided with the period of seasonal fattening in preparation for the dearth in resources of the dry season and with the time when young mouse lemurs began to feed independently.

Microcebus relied heavily on several varieties of the epiphytic semi-parasite *Bakerella*, a mistletoe which was eaten all year round irrespective of the availability and abundance of other fruit. Other epiphytic plants were also part of the diet of mouse lemurs. Mouse lemurs increased intake of *Bakerella* when its availability increased regardless of whether the availability and consumption of other fruit also increased. *Bakerella's* high fat content, which has twice the energy content of carbohydrates, renders it an ideal staple resource which is possibly essential to mouse lemur survival. This study is the first to discover the importance of mistletoes as food sources for mouse lemurs. The relationship between mistletoes and mouse lemur ecology remains to be further investigated, especially the way by which a normally difficult-to-digest resource is utilized by a small-bodied non-specialist species.

In contrast to fruit consumption, insect consumption did not increase during the rainy season when insect abundance was at its highest. Instead, beetles (Coleoptera)

were consumed regularly all year round, indicating that these insects are another staple resource.

In conclusion, *Microcebus rufus* can broadly be described as a "frugivore-faunivore" with seasonal patterns in fruit intake and a preference for beetles which along with one high lipid fruit act as a dietary staples.

b. This study was unique in using longitudinal data from free-ranging mouse lemurs rather than population averages to examine body fat and activity level fluctuations. I established, for the first time, that a rainforest-dwelling species of mouse lemur follows similar seasonal behavioral patterns to those of its west coast dry forest congeners. I found that some members of both sexes of the brown mouse lemur, increased body weight and tail circumference (which I used as indicators of body fat) and then underwent winter lethargy as suggested by their total absence from traps. These mouse lemurs resumed activity having lost the body fat that they metabolized during their period of absence. I determined that not all mouse lemurs were characterized by this behavior. One group of males was absent from the traps during part of the dry season, only to return with increased weight and tail circumference. Other individuals remained active throughout the dry season without changes in body fat. Furthermore, there were hints that particular individuals did not adopt the same behavior each year.

In addition, between the months of June and September, almost all mouse lemurs captured were males. I have suggested that some of these individuals were new to the population from that year's breeding season and that they were dispersing from their natal area, a phenomenon common to many mammals, including primates.

The Relationship of Environmental Conditions to the Annual Cycle in Mouse Lemur Behavior

One species of mouse lemur, *M. murinus*, has been extensively studied in captivity. Among others, Perret (e.g. 1972, 1974, 1977, 1992) has closely studied the annual endocrinological cycle of captive *M. murinus* and its effect on behavior. In another long-term study, Glatston (1979) focused on the details of reproduction in both *M. murinus* and *M. rufus*, and its association with certain aspects of social behavior. In captive populations, where individuals can be closely monitored, these researchers found that mouse lemurs have annual endocrinological cycles which are closely synchronized with changes in daylength. Shortening of daylength served as a cue for changes in endocrine activity and behavior. Immediately prior to the period of shortened daylength, feeding activity increased while the activity of the thyroid began to decrease (Perret, 1974). This permitted animals to store fat. With endocrine functions decreasing, metabolism, body temperature, sexual activity and overall activity were decreased and individuals became more socially tolerant, nesting together in large groups (Perret, 1972, 1992; Glatston, 1979). Normal endocrine functions resumed when daylength began to increase. This signaled the beginning of the reproductive season when mouse lemurs became sexually active. Male testicular development increased, female estrus commenced and individual oxygen consumption became higher. In males, testicular development was sometimes accompanied by loss of body weight (Perret, 1977). At the end of the reproductive season when daylength began to shorten once again, the cycle began anew.

How are annual cycles in mouse lemur behavior associated with the seasonal changes in climate and resource availability in the natural environment?

As I discussed in chapter five, the function of these cycles in *Microcebus* and other small mammals is to reduce exposure to stressful climatic and resource conditions. In the case of mouse lemurs, these conditions in Madagascar occur during the dry season and they are thought to be more intense in the west coast dry deciduous forests. Most studies conducted on mouse lemurs have taken place on the west coast species, *M. murinus*, either in the wild or in captivity. The marked dry season in the west coast is believed to have a greater influence on behavior in the gray mouse lemur than the presumably less dire conditions of the rainforest environment have on the brown mouse lemur. The endocrine and behavioral changes described are viewed as adaptations to the intense seasonal fluctuations of the west coast.

Climatic and resource data from studies on east and west coast forest environments do not necessarily validate these assumptions. Sörg and Rohner (1996) conducted a long-term study on the climate and phenology of the Morondava forest located in western Madagascar. In this dry deciduous region most of the annual precipitation, concentrated between December and March, averaged 699 mm, while total rainfall from April through November averaged 100 mm (calculated from Table 1, Sörg and Rohner, 1996). There is approximately an 85% decrease in precipitation between the rainy and dry seasons. In Ranomafana, precipitation in the rainy season, December through March, was 3149 mm. It averaged 1334 mm in the dry season, April through November. This represented a decrease of 57%. In terms of temperature, Sörg and Rohner, found a mean monthly temperature of approximately 27 ° C during the rainy season and 23.5 ° during the dry season representing a decrease of

approximately 14%. In Ranomafana, averaging minimal and maximal temperatures (from Table 3.2), I calculated a mean temperature of 20.3 ° in the wet season and 16.8 ° in the dry season representing a decrease of approximately 17%.

In brief, although precipitation is much higher in the rainforest than in the dry forest, both over an annual cycle as well as when comparing season-by-season, the rainforest environment undergoes a decrease in rainfall in the dry season, though this decrease is less distinct than in the dry forest. Furthermore, the reduction in average temperature from the wet season to the dry season is slightly greater in the rainforest than in the dry forest, and average temperatures in the rainforest are, overall, lower than those of the dry forest.

In chapter three, I also demonstrated that despite Ranomafana's higher precipitation in the dry season compared to the minimal precipitation of the west coast, there is a marked decrease in fruit and insect availability and abundance between the wet and dry seasons. I therefore suggest that east coast rainforest-dwelling mouse lemurs, like their west coast congeners, are subject to seasonal climatic and resource stresses that have resulted in behavioral adaptations during the annual cycle to reduce the effects of the dry season.

Based on these observations, what is known of the biology of mouse lemurs through captive studies, and what I discovered about the ecology of *Microcebus rufus,* I attempt below a reconstruction of an annual cycle in the life of this species in Ranomafana (Figure 6.1).

The Annual Cycle of *Microcebus rufus*

In Ranomafana, fruit and insect resources become abundant primarily within the rainy season. December signals the start of the wet season with increased rainfall and

temperature and the occurrence of the first peak in diversity of fruit availability. In mid-rainy season, February-March, the diversity of fruiting trees and shrubs peaks while March through May are characterized by peak fruit abundance. Between January and May various important fruit sources for *M. rufus* are in high abundance, including *Bakerella.* January is also a month of peak availability for insects, both with respect to fresh weight and number of insects captured. During this period of abundance, mouse lemurs increase their fruit consumption in both quantity and diversity without, however, increasing their intake of insect matter.

Increased fruit intake overlaps with two important events in the life cycle of the brown mouse lemur: a period of seasonal fattening and the time when young mouse lemurs begin to feed independently.

With regard to the former, population averages for body weight and tail circumference are higher than annual averages, and individuals weighing over 50 g make their appearance. Specifically, from April through June, a number of individual male and female mouse lemurs show marked seasonal fattening. These individuals then decrease their activity entering a state of torpor during part of the dry season. The reduction in behavioral activity is attributed to a reduction in metabolic activity which allows animals to store and use fat over the course of the dry season when average rainfall, temperature and resource abundance are at their minimum. Individuals remain inactive for a minimum of one month, though the exact length of this period varies.

Other males and females continue to be active throughout the dry season. However, more males are active than are females. The sex ratio, approximately 1:1 between January to April, begins to change in May. From May through September it is highly biased in favor of males. Mouse lemurs born into the population from that year's

breeding season make their appearance as independent individuals in February through May. Some of the new males may remain active throughout the dry season as they disperse from their natal ground. Preliminary analysis of trap data shows that a large number of individuals, up to 15, can be captured at a single trap location, suggesting that there may be a high degree of home-range overlap in east coast mouse lemurs. This contrasts with greater territoriality presumed for the west coast species, *Microcebus murinus*. However, if male dispersal is indeed occurring, further analysis is required to discriminate between possible transients and resident occupants. Since at some (but not all) of these trap locations the sex ratio is biased in favor of the males, it is possible that trap data will be better explained by, and even further support, the dispersal, rather than the home-range overlap, hypothesis.

In July, a month of relatively higher rainfall within the dry season, there is once again a peak in diversity of fruit availability, but this is accompanied by an increase in consumption only of *Bakerella*.

In the period between August and October, previously torporing males and females resume activity. Males do so in August and September, perhaps in order to establish mating hierarchy, while females reappear in September and October ready for sexual activity. Both sexes resume activity with weight loss as compared to their pre-torpor state. The bias in sex ratio does not begin to decrease substantially until October, when members of both sexes have come out of torpor and dispersal activity has either decreased or stopped.

Based on preliminary analysis of reproductive data, I found that, in August, all males show signs of testicular development while some females show vulval perforation. Testicular development continues and is greatest in September and

October. In November, the last month of the dry season, testicular size begins to decrease and resumes pre-reproductive size in December. Females with fetuses or who are already lactating are first detected in mid-November. [Glatston (1979)reports a gestation length of approximately 60 days]. The end of November marks peak timing for pregnancies. Females I examined carried one to three fetuses.

The sex ratio increased in December, the result of pregnant or lactating females staying closer to their young in the nests. My observations indicate that nest occupancy ranged from 1 to 5. During the months of January and February some nests were shared by adults and young individuals.

The period of greatest fruit availability, in February through May, occurs at the same time as the appearance of lighter weight individuals (20-30 g) presumably representing the newly weaned young of the season. This implies that the young are born at the beginning of the rainy season so that the period in which they prepare to feed independently coincides with the time of maximum food availability. There are indications that a small minority of females undergo two estrous cycles in some years. For some females, lactation continues in April and a few undergo vulvul perforation during this month. The annual cycle begins anew with all mouse lemurs profiting from the increase in resource availability.

Comparing Mouse Lemurs to Other Small Mammals

Within the order Primates, where most species weigh more than 5 kilograms (Smith and Jungers, 1997), the combination of small body size, nocturnality and non-gregarious behavior is relatively rare. And yet, small mammals, under 5 kg, constitute the majority of species within most mammalian orders and the majority of species in all mammal orders combined (Bourlière, 1975; Fleming, 1979). Although debate exists as

to the degree to which life-history attributes are directly related to body size (Western, 1979) or to ecological factors (Promislow and Harvey, 1990; Kozlowski and Weiner, 1997; Purvis and Harvey 1997), small body size undeniably creates a common set of ecological constraints (e.g. see Golley et al., 1975). Consequently, it is not surprising that within the general context of small mammal ecology mouse lemur behavior is far from unique. Small mammal species are frequently confronted with seasonally unfavorable conditions when food supply declines, which makes it a challenge to maintain a balanced physiological state (Fleming, 1979). Under these conditions, many small mammals respond by eating concentrated foods when available, storing body fat when food is abundant and relying on hypothermia for varying lengths of time to decrease energetic costs (Bourlière, 1975; Fleming, 1979). The Cheirogaleidae are the only primates which enter periods of seasonal fat increase and torpor. Additionally, *Microcebus rufus* reliance on high-lipid food sources parallels the reliance of other small mammals on concentrated foods. Thus, a collateral finding of this chapter has been that the life cycle of mouse lemurs appears to be similar to that of many other small non-primate mammals.

Nevertheless, the similarities between other mammals and mouse lemurs do not cover all aspects of life-history. To illustrate, I compare certain shared attributes of several families of small-bodied rodents characterized by dormancy, the Heteromyidae, Sciuridae and Zapodidae, to mouse lemurs. Among small-bodied rodents, these taxa have the lowest reproductive rate (less than 2.3 litters per individual per season), the lowest densities (0.54 to 15 per hectare) and the longest life span (7.5 to 12.5 months) (French et al., 1975; although Whitaker, 1963 cites a report of 24 months for *Zapus hudsonius*). The reproductive rate of mouse lemurs is slower (one, rarely two litters per

year). Available data for density vary, but based on trap and radiotracking data for *M. murinus* (Hladik et al., 1980; Pagès-Feuillade, 1988), I roughly estimate it to be 1.2 to 4 animals per hectare (home ranges have been estimated to be 0.2 to 3.5 hectares per individual depending on the environment where the study took place) denoting a lower density than the groups discussed above. Lastly, with regard to life span, in captivity (which admittedly can be much longer than in the wild) female mouse lemurs are known to survive for an average of 6-8 years (Perret, 1990).

Therefore, despite certain similarities that mouse lemurs have with non-primate small mammals, they share along with the other members of their order certain distinctively primate features. Specifically, *Microcebus* has a longer lifespan and slower reproduction than other mammals of comparable body size as well as greater encephalization. These characteristic features of primate life-history (Shea, 1987) affect the process of socialization and establishment of extensive social networks and long term social ties (Pereira and Altmann, 1985). The social systems of non-gregarious primates were thought to be primitive, but this notion is changing as more data accumulate (e.g. Clark, 1985; Harcourt and Nash, 1986a; Nash and Harcourt, 1986; Pagès-Feuillade, 1988). However, more research remains to be conducted in order to understand how mouse lemurs establish and maintain their non-gregarious social networks, how the life history cycles which are similar to those of non-primate small mammals affect their social patterns, and how the details of their social behavior compare to generally accepted patterns of primate sociality.

Avenues for Further Research

Quantification of fruit and insect matter in the diet

In chapter two I referred to some of the difficulties involved in measuring the amount of fruit and insect matter in fecal remains. The methods which I eventually used were based on values which allowed a comparison of the fluctuations in levels of frugivory and insectivory over time, but were not conducive to a direct comparison of quantities consumed. One suggested method is to compare ingested biomass of fruit with ingested biomass of insect matter (Korschgen, 1969). This requires data on the size and weight of the fruits and insects eaten in addition to the number of items ingested. Data from this study are currently insufficient to apply this method. However, the description of the feeding habits of *Microcebus rufus* could be enriched by applying the method outlined in order to better evaluate the importance of fruit versus insects in the diet of this species.

Seasonal increase of body fat and decrease in activity in Microcebus rufus

In chapter five, I noted that the question of why particular individuals fatten and enter torpor is unresolved. However, I speculated that age may be one criterion distinguishing those individuals which undergo seasonal fattening from those which do not, i.e. that only individuals who had been in the population for one year or more and therefore were known to be adult, were able to adopt this behavior. This does not answer the question of why the same individual will fatten one year and not the next, assuming that this does indeed occur. However, it provides a working hypothesis for future research. It requires that the same population of mouse lemurs be followed over at least two annual cycles (and perhaps several June to September periods) so that

individuals trapped during the first cycle can be considered, without hesitation, to be adult by the time of the second cycle; their behavior can then be evaluated according to the age hypothesis.

The social behavior of Microcebus rufus

Although the study of social behavior was not part of this project, future analysis of trapping, radiotracking and nest-site data which I collected may reveal social patterns not previously described for mouse lemurs. Based on my trap data, I suggest that the degree of home range overlap is rather high based on what is known so far for solitary species. Radiotracking of more individuals, both males and females, simultaneously, will provide detailed information on the extent of social interaction and home range overlap. Reliance on radiotracking for more information implies that better ways to insulate equipment from rain damage need to be explored.

Dispersal in Microcebus rufus

In this dissertation I proposed that the high male bias in the sex ratio during part of the dry season may be due to young males born into the population that year who are dispersing from their natal ground. These males may account for some of the individuals who remain active throughout the dry season. In diurnal primates it is possible to observe dispersal activity. With small nocturnal species, one can infer dispersal by examining the change in composition of the trappable population and by monitoring the number of males trapped at different times of the annual cycle, as I did in the present study. However, in order to distinguish new-to-the-population males from older males, one also needs to know which individuals were part of the population from the previous year. As in the case of determining if age is involved in who fattens and enters torpor, a study covering at least two annual cycles remains to be conducted.

***The ranging behavior of* Microcebus rufus**

The hypothesis that social organization is influenced by the distribution of food resources of a species has frequently been tested in primates (e.g. Clutton-Brock and Harvey, 1977b). Solitary ranging behavior in many small nocturnal primates has been linked to a diet emphasizing insects, a widely dispersed resource requiring individual skill to obtain (Jolly, 1985). Insect secretions, available during the austral winter, determined the spatial distribution of one population of *M. murinus* (Corbin and Schmid, 1995).

In this study, I discovered that the ranging patterns of mouse lemurs may be influenced by flower availability possibly because of the abundance of insects attracted to them. Therefore, in light of the high frugivory in *M. rufus*, one needs to consider that ranging behavior, at least on a proximate level, may be influenced by the spatial distribution of **plant** food resources and not necessarily only by insect distribution as has been traditionally maintained for small solitary species. This is probably particularly true for important plant food resources such as *Bakerella* which may influence nightly ranging behavior as well as the general size and location of home ranges. There is some evidence to support this from Ganzhorn (1988) who found that sightings of *M. rufus* depended heavily on the presence of fruiting plants.

Comparison of seasonal feeding and activity patterns in east and west coast species of mouse lemur

I suggest that *Microcebus murinus*, a west coast dry forest species of mouse lemur, and *M. rufus,* the east coast rainforest species, have similar feeding and activity patterns despite differences in general environmental conditions. Specifically, a period of seasonal fattening achieved through a diet primarily rich in carbohydrates, and which

precedes that part of the dry season when at least some mouse lemurs enter torpor, has now been documented in both these species (Andriantsiferana and Rahandraha, 1973; Russell, 1975; Hladik et al., 1980; Petter-Rousseaux, 1980; Petter-Rousseaux and Hladik, 1980; Schmid, 1996; this work). As previously discussed, torpor is considered a strategy to cope with highly seasonal environmental conditions that are stressful for small mammals. Earlier in this chapter, I suggested that east coast mouse lemurs, like west coast species, face seasonal stresses. These stresses incur physiological and behavioral adaptations. My study infers the existence of torpor indirectly through seasonal body fat and activity level changes, but torpor has not been studied in *M. rufus* as it has been in west coast mouse lemurs. An investigation of this nature is essential to understanding whether the underlying physiological mechanisms and environmental cues are the same as those for *M. murinus* or *M. myoxinus*. One subject to be investigated is the flexibility of the torporing ability in the rainforest environment and whether or not there is a climatic or resource threshold above which animals may or may not enter torpor. A similar study should also be conducted to test the flexibility of seasonal body fat accumulation. For instance, in *M. murinus* feeding patterns persist even under controlled laboratory conditions with constant food sources present (Hladik et al., 1980).

The nutritional value of resources

To determine what constitutes a high quality diet for a small primate, one needs to consider the specific availability and abundance of food items, their nutritional value and how they fullfill the needs of the primates themselves. Factors such as deviant metabolic rates or the presence of food resources that can constitute nutritionally sustaining staple dietary items need to be considered. Harding (1981) proposed that

estimates of nutritional requirements can include measuring metabolic rates under various conditions and conducting controlled food test experiments to see how foods are digested and nutrients assimilated. These methods are especially pertinent to mouse lemurs who vary their thermoregulation depending on environmental conditions and who, at least in the case of the population I studied, rely on a food source, *Bakerella*, which may require special adaptations to digest. In addition, all varieties of *Bakerella* should be biochemically analyzed for nutrient content and compared to other fruits, especially with respect to lipid and protein levels. These analyses need to be conducted in parallel with studies of the seasonally changing nutritional needs of mouse lemurs (related to changing activity levels). A similar analysis may be conducted for Coleoptera, which mouse lemurs also consume preferentially.

The influence of* Microcebus rufus *on forest ecology

M. rufus plays an important role in seed dispersal of *Bakerella*, thus demonstrating a direct relationship between mouse lemurs and the ecology of the epiphytic vegetation of this rainforest. To gain information on this important component in the diet of *Microcebus* this relationship should be researched by concentrating on clarifying long-term cycles of availability of the various species of Loranthaceae as well as other epiphytes such as the Viscaceae. As an additional contribution to understanding Ranomafana's long-term ecological dynamics, a study on the composition, abundance and nutrient concentration of epiphytes needs to be considered.

Concluding Statement

Twenty years ago, Martin signaled the need for more information on the behavior of mouse lemurs. He stressed that this was necessary not only because of

the lack of data on nocturnal prosimians in general, but also to test the proposal that mouse lemurs along with bushbabies may be suitable analogs for the ancestral primate.

This dissertation summarizes the first long-term continuous field study on the behavior of any mouse lemur. It comes in the wake of recent innovative field studies on the physiology of mouse lemurs, the rediscovery of *Microcebus myoxinus* and possibly even the discovery of new species of mouse lemur (P. Wright pers.comm.). And yet, the cluster of studies conducted on mouse lemurs in their natural habitat, especially in the east coast rainforests, remains small and our knowledge limited. For example, we still cannot answer the question of how close mouse lemurs may be to the ancestral primate condition. Nor, can we assert with confidence that mouse lemurs thrive in the secondary growth which, due to deforestation, characterizes much of Madagascar's forests today. If we wish to present a reasonable argument on mouse lemur similarity to early primates or to understand the conservation status of this taxon, much more basic data are required on its natural history. For example, more analysis is required to effect a quantitative comparison between plant and animal matter consumed in order to more accurately determine the importance of fruit and insects in the diet, and then to use what is known about mouse lemurs to better infer aspects of the ancestral primate condition. Another feature which needs to be studied, both to understand the behavior of the modern mouse lemur as well as to compare it to what we expect the ancestral primate to be, is its social behavior. The high degree of home range overlap suggested by my trap data probably indicates less territoriality than previously thought for this species. In addition, a high degree of home range overlap requires the establishment and maintenance of extensive social networks which,

although they do not render this taxon gregarious in the sense applied to a group-living primate, do point to greater social interaction. Furthermore, concerning the conservation status of this primate, although it is frequently stated that it is the most abundant lemur species, little is known about the basic ecological requirements to sustain a population of mouse lemurs. Given the difficulty of studying a small, nocturnal primate in the wild, especially in a rainforest, the recent interest in both east and west coast mouse lemur species suggests that these difficulties are not insurmountable.

I suggest that both in the Kirindy forest and in Ranomafana, studies on nocturnal species have been successful because they took place within the context of established research sites. In addition, the well-organized nature of these research sites promoted collaborative efforts among researchers, foreign and Malagasy. More important, however, is the participation of the local people in research activities. Local people have accumulated knowledge on the fauna and flora of the forest which not only enhances the research but makes it possible in the first place. I can state with conviction that without the assistance of a team of several local field guides, the present project would have been much more limited in scope. This may be reassuring to those new students of primate behavior who are hesitant to undertake the challenge of studying a nocturnal species. Working side by side with local people makes this type of research possible as well as promoting conservation efforts, not to mention goodwill and friendship among different cultures.

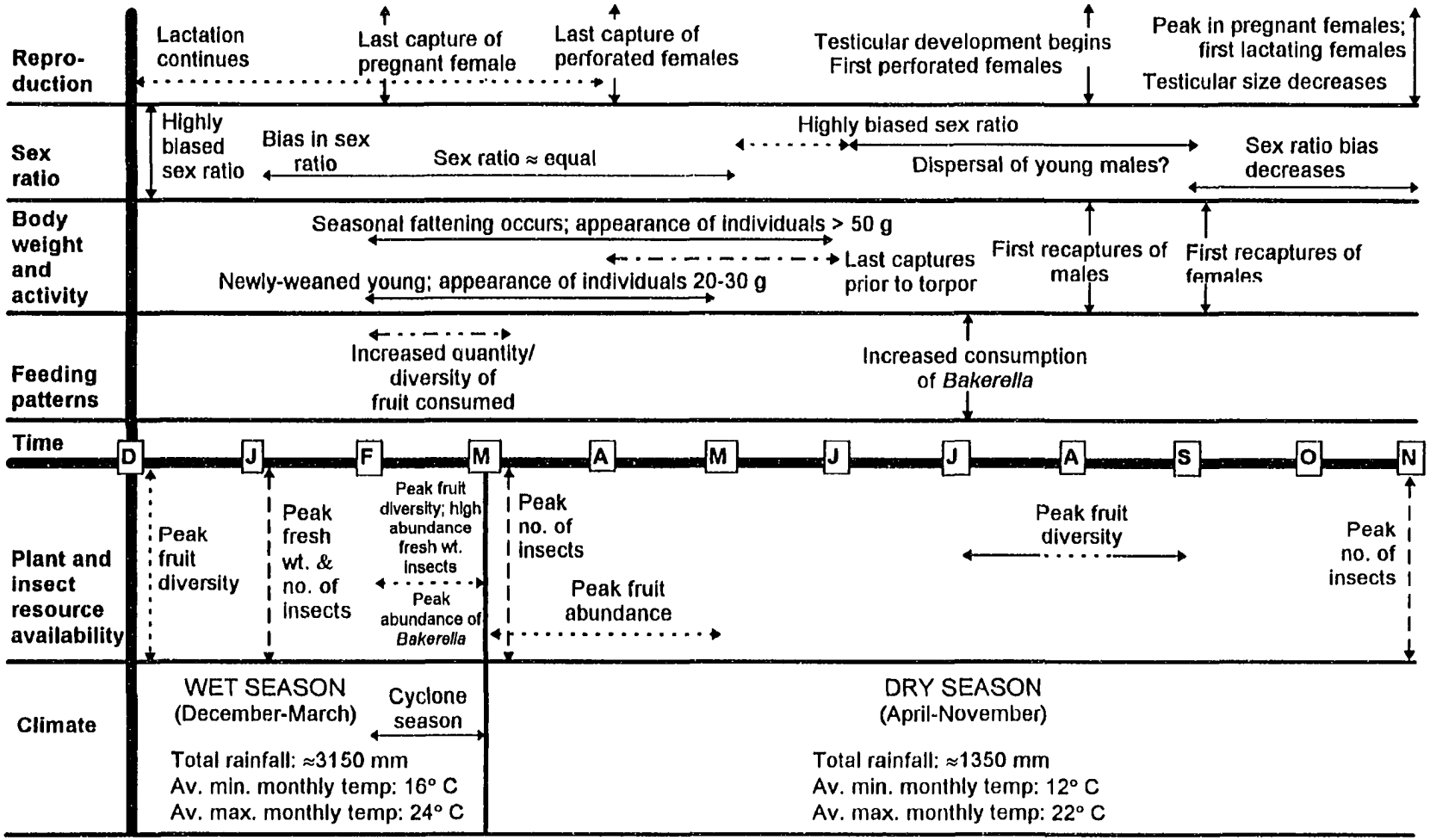


Figure 6.1. The annual cycle of *Microcebus rufus* at Ranomafana National Park.
An event represented by a vertical arrow occurs only within the month designated by the arrow.
An event represented by a horizontal arrow occurs during the months spanned by the arrow.
Different line styles are intended solely to differentiate the lines, not to provide additional descriptive information.

Appendix 1. Vernacular species level analysis of basal area and dominance of trees and shrubs in 4 botanical plots at RNP*.

Vernacular species	Genus	Family	Number of stems used in calculation	Basal area of vernacular species in cm²	Percent of basal area (relative dominance) of vernacular species
Maka	*Weinmannia*	Cunoniaceae	36	15977	20.982
Valotra	*Breonia*	Rubiaceae	3	4626	6.076
Sisitra	*Weinmannia*	Cunoniaceae	1	4283	5.625
Hafitra	*Dombeya*	Sterculiaceae	32	2991	3.928
Kalafambakaka	*Oncostemon*	Myrsinaceae	79	2981	3.915
Tambonetra	*Tambourissa*	Monimiaceae	57	2924	3.840
Tavolomalady	*Ravensara*	Lauraceae	24	2473	3.248
Voambana	*Dalbergia*	Fabaceae	19	2243	2.946
Varongy	*Ocotea*	Lauraceae	19	2219	2.914
Voanananala	*Psychotria*	Rubiaceae	99	2167	2.846
Tarambitona Madinidravina			12	1936	2.542
Vatsilambato	*Cussonia*	Araleaceae	5	1922	2.524
Vatsilana		Araleaceae	15	1801	2.364
Lalona	*Weinmannia*	Cunoniaceae	7	1767	2.321
Tavolorano	*Ravensara*	Lauraceae	11	1601	2.103
Mahanoro		Moraceae	23	1555	2.041
Dikiana	*Allophylus*	Sapindaceae	10	1523	2.000
Lambinana Special	*Nuxia*	Loganiaceae	8	1457	1.913
Fatora	*Mussaenda*	Rubiaceae	10	1418	1.862
Kibolany		Monimiaceae	33	1408	1.850
Hafitra Taikalalao	*Grewia*	Tiliaceae	10	1357	1.782
Harina	*Bridelia*	Euphorbiaceae	11	1347	1.769
Vitanona	*Calophyllum*	Clusiaceae	17	1335	1.753
Fanadramanana	*Aphloia*	Flacourtiaceae	47	1301	1.709
Hazondrano	*Ilex*	Aquifoliaceae	7	1052	1.382
Voararano	*Ficus*	Moraceae	4	935	1.228
Kimbaletaka	*Mammea*	Clusiaceae	11	822	1.079
Rotra	*Eugenia*	Myrtaceae	15	629	0.826
Tsingotrodrano	*Dichaetanthera*	Melastomatace	2	593	0.779
Hazotoho		Rubiaceae	14	530	0.696
Ambora	*Tambourissa*	Monimiaceae	11	503	0.661
Bararata	*Gaertnera*	Rubiaceae	16	494	0.649
Vanandahy	*Sloanea*	Elaeocarpacea	4	476	0.624

Appendix 1. Vernacular species level analysis of basal area and dominance of trees and shrubs in 4 botanical plots at RNP*.

Vernacular species	Genus	Family	Number of stems used in calculation	Basal area of vernacular species in cm²	Percent of basal area (relative dominance) of vernacular species
Fanorafa			5	425	0.558
Apaly	*Streblus*	Moraceae	7	354	0.464
Faritraty	*Eugenia*	Myrtaceae	2	319	0.419
Lanary		Sapindaceae	1	311	0.408
Maniny		Araleaceae	14	296	0.388
Ramy Special	*Canarum*	Burseraceae	2	248	0.326
Vitanoharongana	*Calophyllum*	Clusiaceae	3	238	0.312
Ramiavotoloho		Annonaceae	2	236	0.310
Tsirika	*Pandanus*	Pandanaceae	9	218	0.286
Ambiaty	*Vernonia*	Asteraceae	5	184	0.242
Tavolomanitra	*Ravensara*	Lauraceae	2	180	0.237
Bemalemy		Araleaceae	4	163	0.213
Ambovisikia	*Pittosporum*	Pittosporaceae	7	154	0.203
Odimamo		Rubiaceae	3	150	0.197
Hazombahy			3	134	0.176
Voakiringy			5	115	0.151
Tavolopina	*Ravensara*	Lauraceae	3	106	0.139
Rotravoabe		Myrtaceae	1	99	0.129
Amboralahy	*Decarydendron*	Monimiaceae	6	93	0.122
Sandramifotsy	*Protorhus*	Anacardiaceae	1	92	0.121
Malanimanta	*Micronycia*	Anacardiaceae	1	85	0.112
Dendemy	*Anthocleista*	Loganiaceae	6	79	0.103
Voangy	*Citrus*	Rutaceae	2	76	0.100
Famakilela	*Ficus*	Moraceae	7	72	0.095
Hazonovy		Euphorbiaceae	1	68	0.089
Fanikara	*Dypsis*	Arecaceae	4	66	0.087
Fahavalonkazo	*Zanthoxylum*	Rutaceae	4	60	0.078
Goavy Gasy	*Psidium*	Myrtaceae	4	59	0.077
Voara Special	*Ficus*	Moraceae	2	57	0.075
Voasarigasy	*Citrus*	Rutaceae	1	56	0.073
Mandravasarotra			4	53	0.069
Kaboukala	*Cabucala*	Apocynaceae	1	42	0.055

Appendix 1. Vernacular species level analysis of basal area and dominance of trees and shrubs in 4 botanical plots at RNP*.

Vernacular species	Genus	Family	Number of stems used in calculation	Basal area of vernacular species in cm²	Percent of basal area (relative dominance) of vernacular species
Kalafana Special	*Oncostemon*	Myrsinaceae	1	42	0.055
Hasina Vevetiravina	*Dracaena*	Liliaceae	1	40	0.053
Tongely		Rubiaceae	3	39	0.051
Solaipotsy		Euphorbiaceae	3	39	0.051
Hafidahy		Sterculiaceae	1	33	0.044
Fatsikahitra		Rubiaceae	1	32	0.042
Sandramy	*Protorhus*	Anacardiaceae	1	32	0.042
Fanalamangidy			2	31	0.041
Hazoharaka	*Anisophyllea*	Anisophyllacea	2	31	0.041
Mandravalanonana	*Diospyros*	Ebenaceae	2	29	0.039
Mananitra	*Brachylaena*	Asteraceae	1	28	0.037
Mokaranana	*Macaranga*	Euphorbiaceae	2	27	0.036
Kimba Special	*Symphonia*	Clusiaceae	1	22	0.029
Malambovony	*Erythroxylum*	Erythroxylacea	2	21	0.028
Tavilona	*Vernonia*	Asteraceae	2	20	0.027
Tavolomatso	*Ravensara*	Lauraceae	1	20	0.027
Sana	*Elaeocarpus*	Elaeocarpacea	1	18	0.024
Zahatavoka	*Pyllarthron*	Bignoniaceae	1	18	0.024
Ramandriana			1	17	0.022
Disohasaka		Bignoniaceae	1	16	0.020
Fatsy	*Carissa*	Apocynaceae	1	12	0.016
Amboratambalakoko	*Tambourissa*	Monimiaceae	1	11	0.014
Sehana	*Micronychia*	Anacardiaceae	1	11	0.014
Voalatakakohoala	*Clerodendrum*	Verbenaceae	1	9	0.012
Volomborona	*Albizia*	Fabaceae	1	9	0.012
Hazonasity			1	8	0.011
Sevatenany	*Solanum*	Solanaceae	1	8	0.010

*Based on total basal area of 76148 sq.cm. and 831 trees. Note that basal area values are rounded to integers but percents calculated on original two decimal place calculations.

Appendix 2. Genus level analysis of basal area and dominance of trees and shrubs in 4 botanical plots at RNP.

Genus	Number of stems used in calculation	Number of vernacular species	Basal area of genera in cm²	Percent of basal area (relative dominance) of genera
Weinmannia	44	3	22028	28.927
Breonia	3	1	4626	6.076
Ravensara	43	5	3968	5.211
Tambourissa	69	3	3438	4.515
Oncostemon	80	2	3023	3.970
Dombeya	32	1	2991	3.928
Dalbergia	19	1	2243	2.946
Ocotea	19	1	2219	2.914
Psychotria	99	1	2167	2.846
Tarambitona*	12		1936	2.542
Cussonia	5	1	1922	2.524
Streblus	30		1908	2.506
Vatsilana*	15		1801	2.364
Calophyllum	20	2	1572	2.065
Allophylus	10	1	1523	2.000
Nuxia	8	1	1457	1.913
Mussaenda	10	1	1418	1.862
Kibolany*	33		1408	1.850
Grewia	10	1	1357	1.782
Bridelia	11	1	1347	1.769
Aphloia	47	1	1301	1.709
Ficus	11	3	1065	1.399
Ilex	7	1	1052	1.382
Eugenia	17	2	948	1.245
Mammea	11	1	822	1.079
Dichaetanthera	2	1	593	0.779
Hazotoho*	14		530	0.696
Gaertnera	16	1	494	0.649
Sloanea	4	1	476	0.624
Fanorafa*	5		425	0.558
Lanary*	1		311	0.408

Appendix 2. Genus level analysis of basal area and dominance of trees and shrubs in 4 botanical plots at RNP.

Genus	Number of stems used in calculation	Number of vernacular species	Basal area of genera in cm²	Percent of basal area (relative dominance) of genera
Maniny*	14		296	0.388
Canarum	2	1	248	0.326
Ramiavotoloho*	2		236	0.310
Pandanus	9	1	218	0.286
Vernonia	7	2	205	0.269
Bemalemy*	4		163	0.213
Pittosporum	7	1	154	0.203
Odimamo	3		150	0.197
Hazombahy*	5		134	0.176
Citrus	3	2	132	0.173
Protorhus	2	2	124	0.163
Voakiringy*	5		115	0.151
Rotravoabe*	1		99	0.129
Micronychia	2	2	96	0.126
Decarydendron	6	1	93	0.122
Anthocleista	6	1	79	0.103
Hazonovy*	2		68	0.089
Dypsis	4	1	66	0.087
Zanthoxylum	4		60	0.078
Psidium	4	1	59	0.077
Mandravasarotra*	4		53	0.069
Cabucala	1	1	42	0.055
Dracaena	1	1	40	0.053
Tongely*	3		39	0.051
Solaipotsy*	3		39	0.051
Hafidahy*	1		33	0.044
Fatsikahitra*	1		32	0.042
Fanalamangidy*	2		31	0.041
Anisophyllea	2	1	31	0.041

Appendix 2. Genus level analysis of basal area and dominance of trees and shrubs in 4 botanical plots at RNP.

Genus	Number of stems used in calculation	Number of vernacular species	Basal area of genera in cm^2	Percent of basal area (relative dominance) of genera
Diospyros	2	1	29	0.039
Brachylaena	1	1	28	0.037
Macaranga	2	1	27	0.036
Symphonia	1	1	22	0.029
Erythroxylum	2	1	21	0.028
Elaeocarpus	1	1	18	0.024
Pyllarthron	1	1	18	0.024
Disohasaka*	1		16	0.020
Carissa	1	1	12	0.016
Albizia	1	1	9	0.012
Clerodendrum	1	1	9	0.012
Ramandriana*	1		8	0.011
Hazonasity*	1		8	0.011
Solanum	1	1	8	0.010

*Unknown genus

Note that basal area values are rounded to integers but percents calculated on original two decimal place calculations.

Appendix 3. Family level analysis of basal area and dominance of trees and shrubs in 4 botanical plots at RNP.

Family	Number of stems used in calculation	Number of vernacular species	Basal area of families in cm^2	Percent of basal area (relative dominance) of families
Cunoniaceae	44	3	22028	28.927
Rubiaceae	149	8	9456	12.418
Lauraceae	62	5	6599	8.666
Monimiaceae	108	5	4940	6.487
Araliaceae	38	4	4181	5.490
Sterculiaceae	33	2	3025	3.972
Myrsinaceae	80	2	3023	3.970
Moraceae	41	5	2973	3.904
Clusiaceae	32	4	2416	3.173
Fabaceae	20	2	2252	2.958
Tarambitona*	12		1936	
Sapindaceae	11	3	1834	2.408
Loganiaceae	14	2	1535	2.016
Euphorbiaceae	17	4	1481	1.945
Tiliaceae	10	1	1357	1.782
Flacourtiaceae	47	1	1301	1.709
Myrtaceae	22	4	1105	1.452
Aquifoliaceae	7	1	1052	1.382
Melastomataceae	2	1	593	0.779
Elaeocarpaceae	5	2	493	0.648
Fanorafa*	5		425	
Burseraceae	2	1	248	0.326
Annonaceae	2	1	236	0.310
Asteraceae	8	3	233	0.306
Anacardiaceae	4	4	219	0.288
Pandanaceae	9	1	218	0.286
Rutaceae	7	3	192	0.252
Pittosporaceae	7	1	154	0.203
Hazombahy*	3		134	
Voakiringy*	5		115	
Arecaceae	4	1	66	0.087

Appendix 3. Family level analysis of basal area and dominance of trees and shrubs in 4 botanical plots at RNP.

Family	Number of stems used in calculation	Number of vernacular species	Basal area of families in cm^2	Percent of basal area (relative dominance) of families
Apocynaceae	2	2	54	0.071
Mandravasarotra*	4		53	
Liliaceae	1	1	40	0.053
Bignoniaceae	2	2	34	0.044
Fanalamangidy*	2		31	
Anisophyllaceae	2	1	31	0.041
Ebenaceae	2	1	29	0.039
Erythroxylaceae	2	1	21	0.028
Verbenaceae	1	1	9	0.012
Ramandriana*	1		8	
Hazonasity*	1		8	
Solanaceae	1	1	8	0.010

*Of unknown family

Note that basal area values are rounded to integers but percents calculated on original two decimal place calculations.

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