CHAPTER NINETEEN

Diet Composition, Foraging, and Feeding Behavior in Relation to Habitat Disturbance: Implications for the Adaptability of Ruffed Lemurs (*Varecia v. editorium*) in Manombo Forest, Madagascar

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INTRODUCTION

The effects of hurricanes and the process of forest recovery have been well-studied in the Caribbean, especially in Puerto Rico (e.g., Sanford et al., 1991; Walker et al., 1991; Walker, 1995). However, long-term investigations of the effects of severe

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natural disaster upon forest recovery processes have received only limited study to date in most tropical rainforests. Behavioral strategies used by species or groups of species experiencing natural disasters are important with respect to their subsequent recovery in the particular forest affected. It can be extremely useful to determine how different species have responded to the cumulative impact of human activities and natural disturbances of their natural habitats (e.g., cyclone, flooding, windstorms, fires, or drought) in order to improve species management for conservation purposes. Primates are an excellent group of animals to study when attempting to understand the impact of habitat alterations on the fauna of a tropical forest (Struhsaker, 1997). They can be relatively easy to census, and individual species in a given community often respond differently to habitat disturbance (Lovejoy et al., 1986; Ganzhorn, 1994; Estrada and Coates-Estrada, 1996; Tutin et al., 1997). Indeed, primates respond in complex and varied ways to different types and levels of disturbance (Dunbar, 1988). Obviously, the effects of habitat disruption on a primate population depends upon the nature and extent of forest alteration, the time since such alteration took place, as well as the requirements and adaptability of each primate species inhabiting an area (Wilson and Wilson, 1975; Cowlishaw and Dunbar, 2000). Nevertheless, studies on primate communities show that some species are more adaptable and resistant than others in response to habitat disturbance (Cody, 1981; Ganzhorn et al., 1999).

It is also important to remember that dietary flexibility is an important feature of ecology of all primates, even though species can be characterized as favoring one type of diet (Cowlishaw and Dunbar, 2000), as dietary category of a particular species can vary from one habitat to another. For example, gorillas in Rwanda are typically terrestrial folivores, whereas those in Gabon are typically arboreal frugivores (Tutin et al., 1991).

Obtaining food of appropriate quality and quantity, and avoiding predators are often considered to be conflicting goals for animals living in the wild (van Schaik and van Hooff, 1985; Koivula et al., 1995). The difficulty of reconciling these conflicting goals may be aggravated when pristine forests become fragmented and/or altered. Currently, there is growing interest in learning how primates cope with extreme forest degradation and destruction (see Johns, 1986, 1991; Estrada and Coates-Estrada, 1996; Cowlishaw and Dunbar, 2000).

Empirical studies have demonstrated that the combined effects of natural catastrophe (e.g., cyclone or wind storm) and anthropogenic disturbance can cause levels of habitat destruction to increase spatially and temporally. Consequently, favored foods become less abundant, and different primate species must employ different behavioral strategies in response to environmental change. de Ruiter (1986) demonstrated that large groups of *Cebus olivaceus* may travel farther than small groups, and forage less on fruit, and large groups can compensate for loss of fruit by foraging more on invertebrates. Such behavior demonstrates the ability of *C. olivaceus* to feed opportunistically on available food resources. Research on *Callithrix flaviceps* indicates that this species can substitute gum for fruit as a source of carbohydrates during periods of food scarcity. This strategy enables *C. flaviceps* to survive in small patches of highly disturbed habitats (Ferrari and Diego, 1995).

The rainforest habitats of Madagascar constitute a good starting point for studying behavioral responses in lemurs, as habitat disturbance is not restricted to anthropogenic pressures. Indeed, natural disturbances are common, and are of great concern (Jolly, 1989; Richard and Connor, 1997; Wright, 1997). However, little has been written about the impact of natural disasters of this island, or the adaptive responses of lemurs to highly altered habitats. Therefore, in this study, I am interested in behavioral response strategies used by black-and-white ruffed lemurs (*Varecia variegata*) to the combined effects of human-induced pressures and natural disturbances. Long-term studies of ruffed lemurs have only been conducted in pristine, less disturbed forests and in captivity. It appears that *V. variegata* is susceptible to habitat disturbance to a far greater degree than are most other lemur taxa (White et al., 1995; Ratsimbazafy, 1999).

The ruffed lemur is one example of a group-living prosimian that exhibits great flexibility in grouping patterns (group size: 2–31) (Morland, 1991a,b; Rigamonti, 1993; Balko et al., 1995; Vasey, 1997; Balko, 1998; Ratsimbazafy, 2002a; Louis et al., 2005; Lehman et al., 2005). Ruffed lemurs are highly frugivorous (nearly 75% of their diet is fruits), but they can supplement fruits with varying amounts of other food resources (e.g., leaves, flowers, nectar) during times of food shortage (see Morland, 1991a; Rigamonti, 1993; White et al., 1995; Balko, 1998; Ratsimbazafy, 2002a,b; Ratsimbazafy et al., 2002; Mittermeier et al., 2006). *V. variegata* has been described as the most reproductively stressed of all primates because of its high maternal investment (Tilden, 1994). In other words, *Varecia* is an ideal candidate for this natural experiment (Ratsimbazafy and Ratsirahonana, 1998).

From June to July 1997 and from February 1999 to July 2000, research was conducted on the southernmost population of black-and-white ruffed lemurs, at Manombo forest, in southeastern Madagascar. Manombo is a good location to carry out investigations on lemur behavioral responses, as this environment combines human pressures with a history of stochastic windthrow damage from the annual cyclone season.

In this chapter, I discuss foraging and feeding behavior in relation to food availability used by *Varecia v. editorium* living in an abruptly disturbed habitat. In addition to collecting data on activities such as feeding, foraging, traveling, resting, and others (e.g., social and agonistic), I examined the relative use of different plant species by each individual during different seasons and throughout the study. In this way, I could document not only the proportions of fruits, leaves, nectar, and other items in the diet, but also individual preferences for certain plant species and families, and the role of alien plant species in the *Varecia* diet. My data were also compared with data on the same species collected in undisturbed habitats.

METHODS

Study Site Description

The study was conducted in a southeastern lowland rainforest in Madagascar, the Manombo forest. Manombo forest is comprised of the Manombo Special Reserve (MSR) and the Manombo Classified forest (MCF). Manombo is located in the province of Fianarantsoa at 23° 02'S and 47° 44'E (Figure 1). The MSR and CFM cover 14,000 ha, but only 9000 ha remains forested (Ratsimbazafy, 2002a). The elevation of the forest ranges between sea level and 137 m.

The climate of Manombo is characterized by high rainfall throughout the year, with heaviest rainfall during the cyclone season, from January through March. During this period, the area is subject to cyclones from the Indian Ocean, causing flooding, stream-course changes, and extensive tree falls (Donque, 1975).

In January 1997, cyclone "Gretelle," with winds up to 245 km, hit Manombo forest for 12 hours causing extensive damage: uprooting trees, breaking trunks

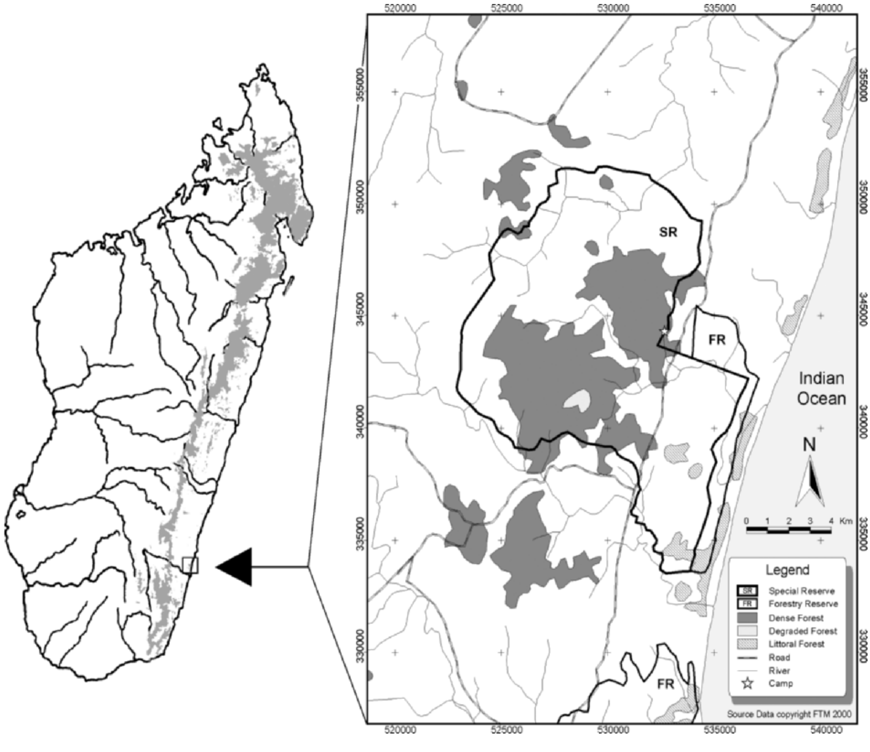

Figure 1. Location of Manombo Forest study area in Madagascar. Madagascar map: forest cover after Green and Sussman (1990). Inset: GIS data courtesy of ANGAP (Laborde Projection)

and large branches, toppling the canopy trees, and defoliating most of the remaining canopy. Postcyclone botanical transect studies revealed 85% canopy loss. Three years after the cyclone, alien plant species have invaded more than 40% of the total forested area. Currently, seven species of plant invaders have become potential threats to the native vegetation, especially in forested areas already subject to anthropogenic disturbances. As such, Manombo forest provides a unique environment in which to study habitat disturbance.

Study Individuals

Following a 2-month habituation period, I continuously studied two groups of *V. variegata* for a period of 18 months. Although the composition of each group did not change during the study, only one adult male that was present in Group I during a 3-month survey in 1997 survived to 1999. Group I comprised three members (one male, Redy-M, and two females, Boloa-F and Silvera-F), while neighboring Group II consisted of two members (a male, Grina-M, and a female, Kolara-F).

Individual scans on the study groups were taken 10 days each month for a total of 1431 hours of observations on 188 days (total scans = 17,171). Data are unavailable on Grina-M for the months from April to June 1999, and in July 2000. In addition, Kolara-F was missing during the months of April and May 1999, and in July 2000. Boloa-F disappeared during June 1999 and again in April 2000. Comparisons between groups were not always possible (as each group has relatively few individuals in each age/sex class); therefore, comparisons were made between individuals in statistical analyses.

Behavioral Methods

Data collection procedures involved focal animal sampling (Altmann, 1974). With the help of field assistants, groups were followed for a full day's activities whenever possible. Each day, a different focal animal was chosen in order to obtain a representative sample among individuals and across sexes. Individual scans on the study groups were taken 10 days each month for a total of 1431 hours of observations on 188 days (total scans = 17,171).

The activity of a focal animal was recorded at 5-minute intervals during daylight hours ("instantaneous" samples, Altmann, 1974). Behaviors were described at a general level (forage, feed, travel, rest, other). Specific behaviors provided more detailed records of these general activity categories. Each of the activity states was scored as an activity record for the corresponding 5-minute interval. The percentages of time spent at each activity were then calculated in relation to the total activity records for each 5-minute interval (Milton, 1980).

Feeding activity was defined as: reaching for, picking, placing in the mouth, chewing, and swallowing food items, whereas foraging was defined as moving slowly with attention directed toward a food source or manipulating substrates in search of foods (Whitten, 1983; O'Brien and Kinnaird, 1997). As feeding data are based on scans, they are measures of the frequency in which the focal animal fed on each item every 5 minutes. The food item and the part eaten were categorized and described as ripe or unripe fruit (only the fleshy part and/or the seed or both), young or mature leaves, flower parts, or miscellaneous materials (e.g., sap, bark) (see Overdorff, 1993).

The availability of different food was estimated using Importance Values (IV) (Curtis and McIntosh, 1951). The IV takes into account *relative tree density*, distribution (*relative frequency*), and *relative dominance* (basal area). The IV data were taken from a postcyclone survey of 665 trees. The IV are calculated by the equation

Importance value ($IV_{\text{tree species } i}$) = $RD + RF + RDo$
where
RD = (number of individuals of species i/total individuals of all species) x 100
RF = (number of species at which species i occurs/total number of points sampled) x 100
RDo = (total basal area of species i/total basal area of all species) x 100
[Basal area (cm^2) = $(\text{dbh})^2$ x (0.7854)]

Rainfall and temperature (maximum and minimum) were recorded daily at the study site and the mean monthly values were calculated. Combining these two climate parameters resulted in a total of eight seasons. The following criteria were used to define seasons:

"Rainy": average monthly precipitation (AFM) > 400 mm; "Moist" if AFM 400 – 200 mm; and "Dry" if AFM < 200 mm.

"Hot": temperature (T) > 20°C; "Cool" if (T) 20–15°C; and "Cold" if (T) < 15°C.

RESULTS

Dietary Patterns

Overall: Combining data from five individuals, black-and-white ruffed lemurs were observed to feed on a total of 83 different plant species during the dry and rainy seasons combined (see Table 1). This is about 12% of the total number of species recorded in my seven sample transects. Among the species eaten, 70 were used as fruit sources, 17 as leaf sources, 2 as nectar sources, and 4 as other item sources. Thus, the number of species used as fruit sources is more than four times the number of leaf species and more than 11 times the number of nectar and other items together. As Table 1 shows, only 1% of those 82 species was used for food sources in all three categories (fruit, leaf, and nectar), 4% for foods in two categories (fruit and leaves), and 79% for foods in only one (fruit), 12% only

Table 1. List of food species eaten by *Varecia variegata* at Manombo forest

Family	Scientific name	Vernacular name	Part eaten[a]	Importance value
Annonaceae	*Monanthotaxis pilosa*	vahatsimatra	Fr	—
	Polyalthia oligosperma	ramiavitoloha	Fr, Lv	73.1
	Xylopia sp.	fotsivony	Fr	—
Apocynaceae	*Landolphia platyclada*	vahateso	Fr	—
	Plectaneia sp.		Fr	—
Aspleniaceae	*Asplenium nidus*	betoboka (velomiato)	Lv	—
Burseraceae	*Canarium madagascariensis*	ramy	Fr	72.6
Clusiaceae	*Symphonia urophylla*	haziny	Fr, Lv	—
	Garcinia aphanophlebia	kimba	Fr, Lv	14.8
	Mammea sp.	kimba	Fr	43.3
	Garcinia chapelieri	kimba	Fr	—
Combretaceae	*Hirtella tamenaka*	tamenaka	Lv	—
	Terminalia mentaly	masomposaina	Fr	—
Connaraceae	*Agelae pentagyna*	vahibe	Lv	—
Cunnoniaceae	*Weinmania rodoxylon*	varikanda	Fr	—
Cyperaceae	*Cyperus latifolius*	harana	Fr	—
Ebenaceae	*Diospyros platicalyx*	hazomainty	Lv	43.6
Erythroxylaceae	*Erythroxylon sphaeranthum*	menahihy	Lv	28.8
Euphorbiaceae	*Uapaca louvelii*	voapaky	Fr	75.7
	Anthostema madagascariensis	baby (raloto)	Fr	79.8
	Cecropia peltata	tanatana	Fr	—
	Cleisthanthus bovianum	taimbarika	Lv	28.9
Fabaceae	*Cynometra cloiselii*	variotra	Lv	—
	Calliandra alternans	ambilazona	Lv	—
Flacourtaceae	*Aphloia theaformis*	fandramanana	Fr	—
	Hemalium sp.	tsimbotry	Fr	—
Hypericaceae	*Harungana madagascariensis*	harongana	Fr	—
Icaninaceae	*Apodytes* sp.	malanimanta	Fr	58.0
Lauraceae	*Cryptocaria* sp.	vitano	Fr, Lv	—
	Ocotea sp.	varongy	Lv	43.4
Linaceae	*Hugonia* sp.1	vahamavo	Fr	—
Melastomaceae	*Clidemia hirta*	voatrotrokala	Fr	217.5
	Memecyclon sp.	tomizo	Lv	86.8
Menispermaceae	*Burasia madagascariensis*		Fr	29.0
Moraceae	*Ficus baroni*	amontana	Fr	14.4
	Ficus reflexa	laza	Fr	—
	Ficus rubra	vahinonoka	Fr	—
	Bosqueia boiviniana	kivozoala	Fr, Lv	—
	Pachytrophe dimepate	andrimena	Fr	—
	Treculia sp.	hazosavoa	Fr	—
Myrtaceae	*Eugenia emimense*	rotra	Fr	—
	Syzigium sp.1	rotra fotsy	Fr, Lv	—
Oleaceae	*Norohnia myrtoides*		Fr	—
	Norohnia sp.2	silaitra	Fr	15.9
Palmae	*Dypsis gracilis*	varaotry	Fr	—
	Dypsis nauseosa	mangidibe	Fr, Ex	—
	Vonitra thouarsii	vonitra	Fr	—
	Dypsis sp.1	vakaky	Fr, Br, Ex	—

(Continued)

Table 1. List of food species eaten by *Varecia variegata* at Manombo forest—Cont'd.

Family	Scientific name	Vernacular name	Part eaten[a]	Importance value
Pandanaceae	*Pandanus* sp.1	tsiriky	Fr	57.7
	Pandanus sp.2	tsiriky	Fr	—
Polyporacea (fungus)	*Polyporus* sp.	olatra	other	—
Rubiaceae	*Coffea* sp.1	maranitrantany	Fr	—
	Rothmania sp.1	bevoa	Fr	29.2
	Rothmania sp.2	fotsikatry	Fr	—
	Gaertnera stipula	belakevo	Fr	43.7
	Breonia chinense	valotra mainty	Fr	87.0
	Breonia sp.1	valo— drano	Fr	—
	Gaertnera sp.	hazondambo	Fr	43.7
Rutaceae	*Vepris* sp.1	kalavelo	Fr	—
Sapindaceae	*Sapindacus* sp.	hazomby	Lv	—
	Macphersonia madagascariensis	sanirafotsy	Fr	59.7
	Prothorus ditimena	sandramy	Fr	—
	Prothorus sericea		Fr	—
	Tina sp.1	lanary	Lv	—
Sapotaceae	*Labramia louvelii*	nato	Fr	1.0
	Gambeya madagascariensis	harongampanihy (rahiaka)	Fr	—
Sarcolaenaceae	*Schizolena cauliflora*	foto	Nr	—
Sterculiaceae	*Dombeya lucida*	hafomena	Fr	—
	Dombeya sp.	hafotra	Fr, Lv	—
	Sterculia tavia	aboladitra	Fr	—
Strelitziaceae	*Ravenala madagascariensis*	ravinala	Nr	43.3
Tiliaceae	*Grewia* sp.	hafopotsy	Fr	—
Ulmaceae	*Trema orientalis*	andrarezina	Fr	—
Verbenaceae	*Vitex cauliflora*	mazambodiala	Fr	—
Unknown	11 unknown sp.		Fr	—

[a] Fr: fruit; Lv: leaves; Nr: nectar; Br: bract (modified leaf in the inflorescence); Ex: exudates.

leaves and 5% only nectar (if data collected in 1997 also included). *Varecia* were never observed to eat animal matter or soil, but they were seen licking exudates. Furthermore, they consumed only flower nectar, not sepals or petals. From general observations, there was a significant loss of both flowers and fruit, and even shrubs declined after the cyclone. *Varecia* drank water occasionally in the morning from tree holes when the temperature was very hot. Eighty-four percent of the *Varecia* food sources came from trees, 6% from lianas or vines, and the remaining 10% from epiphytes, shrubs, and shelf fungi.

Thirty-five percent of available food species were used as food sources on only one day during the entire study. More than half of the food sources of *Varecia* were eaten over fewer than 4 days during the entire study. In contrast, only three species of food sources were consumed more than one-fifth of the total number of the study days. The fruits of a nontree species, *Clidemia hirta*, were eaten most frequently by *Varecia* (80 days or 42% of the total days of study), followed by the leaves of two tree species, *Polyalthia oligosperma* (40%) and *Cynometra cloiselii* (23%).

The average percentage of each food type used was calculated for each individual using instantaneous sampling at 5-min intervals containing feeding data throughout the sample period (Redy-M *n* = 849, Grina-M *n* = 551, Boloa-F *n* = 449, Kolara-F *n* = 746, and Silvera-F *n* = 687). For all five focal animals, there were no consistent differences between seasons in time spent foraging or feeding. However, when considering the use of individual food species, there were consistent differences in intensity of use across focal animals from day to day and month to month. In other words, on different days of the month and different months of the year, *Varecia* devoted different amounts of time feeding on particular species. Overall the dietary diversity ranges from 1 to 11 species per day and 5–26 species per month. Generally, the number of species eaten was greater during the hot rainy season.

***Fruit*:** At Manombo forest, fruit was a basic part of the *Varecia* diet and was eaten on nearly every sample day throughout the study. *Varecia* were observed eating fruit on 165/188 study days (or 88% of the total observations). In addition, a great proportion of the feeding time each day was devoted to fruit eating. When data from the five focal animals were combined, fruits constituted 75% of the amount of time spent feeding (Figure 2). Seven of the ten top foods during the total 18 months were fruits. Because of the low relative density of preferred food trees, most fruits eaten by *Varecia* were consumed while still unripe. Unripe fruits comprised 22.5% of all observations. Some fruit trees were depleted before fruits ripened. Although *V. variegata* are primarily frugivorous, they were not ripe fruit specialists, at least not at Manombo during this critical time.

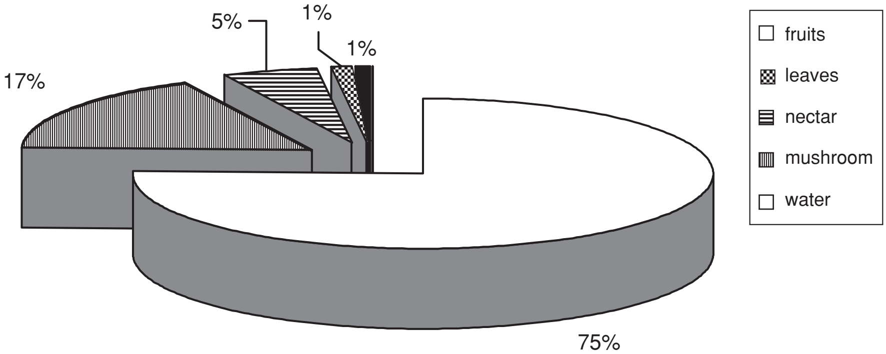

Figure 2. Representation of food types in the diet of *Varecia variegata editorium* at Manombo forest.

Seventy-eight percent of *Varecia* food trees consisted of berries and 22% were drupe. While *Varecia* fed on a wide range of fruit colors (seven different colors), most fruit consumed were green. Black-and-white ruffed lemurs at Manombo utilized fruits of all sizes as did the *Varecia* groups on Nosy Mangabe (Morland, 1991a).

During the study, the mean percentages of fruits in the diet of each individual were as follows: Redy-M male, 72% from 34 different species; Grina-M, 81% from 30 species; Boloa-F, 57% from 25 species; Kolara-F, 83% from 42 species; and Silvera-F, 77% from 33 species. Overall, *Varecia* fruit sources were obtained from 70 species of trees, shrubs, and vines.

***Leaves*: ** Combined data on all individuals revealed that 17% of *Varecia's* diet consisted of leaves, but only of a few tree species. A great proportion of time was spent eating the leaves of two plant species, *Polyalthia oligosperma* and *Cynometra cloiselii*. Young leaves were overwhelming preferred over mature leaves. Leaves were consumed on 45 of the study days (24% of total observations, n = 188). Only six food species were exclusively leaf sources. During the sample period, the mean percentages of folivorous material in individual diets were: Redy-M 20%, Grina-M 14%, Boloa-F 21%, Kolara-F 11%, and Silvera-F 17%.

***Nectar*:** Although the mean average of nectivory was low overall (5%), it was an important food source from September 1999 to February 2000. *Varecia* did not feed on the nectar of all of the flowers available in the forest, but specialized on two species, *Humbertia madagascariensis* and *Ravenala madagascariensis*, which flowered at the end of the dry season. During one day, a single *R. madagascariensis* tree could be visited four to five times. It appears that *R. madagascariensis* trees were visited only to feed, as I never saw any individuals using those trees as resting places.

***Shelf fungi*:** Shelf fungi comprised only a small percentage (1%) of the Varecia diet. The mean percentage of shelf fungi in the diet of each individual was as follows: 0.4% for Redy-M, 1.1% for Grina-M, 1.3 for Boloa-F, 2.1% for Kolara-F, and 1.5% for Silvera-F, and the focal animals ate only one species, *Polyporus* sp. (Polyporaceae), which occurred at low densities throughout the forest. Shelf fungi were eaten on 22/188 days, by both females and males.

***Miscellaneous items*:** (bark and exudates): Bark and exudates played a very small role in the diet of *Varecia*. The total amount of those two items combined was insignificant (0.5%), perhaps because they were eaten opportunistically, and not by all animals. Grina-M was seen feeding on bark of *Dypsis* sp. in the wet and hot season. Kolara-F was observed consuming the bark of *Garcinia aphanophlebia* in a dry month (November 1999). Redy-M, Boloa-F, and Silvera-F were also seen feeding opportunistically on plant exudates around the pedicels in the moist, cool season (September–October 1999).

Water**:** Water was used especially during the hottest season, between the months of February and April of 1999. I did not observe *Varecia* drinking water directly from a stream, but they did drink water from holes within trees, either by leaning their heads into larger tree holes or by placing their hands into holes too small for the head to fit into, and licking the water off of their hands.

Family and Species Preferences

As noted earlier, *Varecia* at Manombo were observed to eat at least 83 plant species. Seventy-nine of these species were identified to family level. In total, *Varecia* food trees are distributed throughout 43 families (about 2 species per family on average). The families most frequently represented were Moraceae (7 of the 10 species recorded), Rubiaceae (7 of the 27 species recorded), Annonaceae (4 of the 4 species recorded), and Clusiaceae (4 of the 9 species recorded).

DISCUSSION AND CONCLUSIONS

Severe drought years have been shown to impact dry, western forests in Madagascar (Gould et al., 1999). But droughts also affect the rainforest by extending the dry season and reducing annual rainfall (Wright, 1999). Drought in rainforests has resulted in high canopy tree mortality (Milton et al., 1994; Condit et al., 1995), reproductive failure (Struhsaker, 1997), fruit crop failure (Foster, 1980; Leighton and Wirawan, 1986), and decrease in young leaf abundance (Leighton and Wirawan, 1986; Struhsaker, 1997). No long-term studies have been conducted yet on the effects of natural disasters such as drought and cyclones on fauna and flora in the Manombo region. However, direct cyclone hits can result in complete defoliation, blowdowns of all canopy trees, landslides, and flooding (Ganzhorn, 1995a,b). As a consequence, neither fruits nor leaves may be available for consumption until the following spring, leaving only crisis foods, such as epiphytes, for the lemurs to eat (Ratsimbazafy, 1999).

In the pristine forests of Madagascar, the mean tree crown diameter (patch size) of fruit trees fed in by lemurs is 12 m (Overdorff, 1996; Balko 1998; Hemingway, 1998). In Manombo, cyclone Gretelle had two effects on the food supply of *Varecia*. First, surviving native trees suffered an average crown loss of 85%, and broad crowned trees are generally toppled first by the high winds generated by a cyclone (Wright, 1999). Six months after the cyclone of 1997, the mean crown diameter of trees from the seven sample plots was 3 m (range: 0.5–9 m; $n = 439$). These losses represent a greater than 70% reduction in the fruit-producing vegetation of the forest. Ninety percent of the few remaining trees forming the upper layers of the forest are still producing new leaves and new branches. Moreover, after the cyclone, there were significant losses of flowers and fruits among trees, and shrubs. The recovery of endemic species after this natural disaster is still very slow, but *Varecia* are able to survive in this highly disturbed forest by adjusting their feeding strategies.

It has been well-demonstrated that seasonal peaks in the abundance and scarcity of food used by lemurs are variable from year to year in Malagasy rainforests, as many canopy species produce flowers on prolonged, irregular, and asynchronous or alternate year cycles (Morland, 1991a, 1993; Hemingway, 1995; Powyzk, 1997). In the rainforest at Manombo, a study of the phenological sequence of 120 trees of 24 plant species consumed by *Varecia* over almost 2 years demonstrated that this irregularity of fruiting pattern is reflected in variable annual food availability, i.e., more species produced fruits in May 1999 than in May 2000. As noted by Wright (1999), this pattern of unpredictability requires lemurs to be able to adapt to energetic constraints at almost any time of the year. Manombo presents an extreme case of the effects of habitat disturbance; therefore, it is important to determine how an obligate frugivore like *V. variegata* copes in such a highly disturbed habitat. Did the ruffed lemurs at Manombo exhibit diet similarities with their conspecifics living in undisturbed forests?

Comparisons with undisturbed forests indicate that there are general similarities in the ruffed lemurs' diets in different habitats with regards to the overall food categories eaten. Field research on the diets of *Varecia* at different sites have shown that this species is highly frugivorous (see Table 2). When the data for both sexes are combined from studies on wild *V. rubra*, diets are similar from season to season, comprised mainly of fruits (Vasey, 1997). In the present study, it was expected that *Varecia* living in highly disturbed habitats would have general dietary patterns different from those living in undisturbed habitats. My results demonstrated that they remain predominantly frugivorous regardless of habitat type. This confirms that *Varecia* is an obligate frugivore (Balko, 1998). While dietary diversity fluctuated monthly, the percentage of fruit in the diet always outnumbered the percentage of nonfruit items, except during the month of November 1999 (the second driest month of the study). *Varecia* could feed heavily on young leaves when they were available. In other words, it is not necessary that *Clidemia hirta* be consumed when other foods are available. As fewer trees bore fruits (due to serious cyclone damage), *Varecia* at Manombo devoted much of their feeding time on fruits from shrubs and vines. For instance, the exotic shrub species *C. hirta* can provide a fairly constant source of fruits throughout the year. This became a staple food source and an essential fruit for 3 years after cyclone Gretelle hit Manombo. Ruffed lemurs living in undisturbed sites have not been reported to feed on *C. hirta*, although it is eaten by *Hapalemur griseus* in Valohoaka/Ranomafana (Grassi, 2001). As noted by Vasey (1997), during the transitional cold season *V. rubra* feeds exclusively on fruit.

Results from this study indicate that *Varecia* are able to diversify their diets in terms of the number of fruit species consumed, but the ability to digest and detoxify leafy material and other nonfruit items is limited. A comparative study of the gastrointestinal tract of five lemur species (*Propithecus tattersalli*, *Propithecus verreauxi coquereli*, *Varecia variegata*, *Hapalemur griseus*, and *Lemur catta*)

Table 2. Diets of *Varecia variegata* at different sites

Study Site[1]	Species	Seasons observed	Fruit	Nectar	Flowers	Leaves	Young Leaves	Other
Nosy Mangabe Morland (1991)	*V. v. variegata*	all	74%	21%			5%	2.7%[2]
Ranomafana White (1991)	*V. v. editorium*	cold rainy	71%	15%	3%	11%		
Ambatonakolahy Rigamonti (1993)	*V. v. rubra*	cold rainy, hot dry	74%		5%	18%	3%	[3]
Ranomafana Balko (1998)	*V. v. editorium*	all	90%	4%			6%	
Andranobe Vasey (1997)	*V. v. rubra*	all	88%		6%	1%	3%	2%[4]
Manombo (This study)	*V. v. editorium*	all	74%	6%		17%		3%[5]

[1] Study lengths vary: Morland (1991), 12 months over 18-month period; White (1991), 2 months; Rigamonti (1993), 7 months; Balko (1998), 18 months over four-year period; Vasey (1997), 13 months; Ratsimbazafy (this study), 18 months White's percentages are based on percent food patches used. Percentages for other studies are based on time point samples.

[2] Flowers, buds, shoots, shelf fungus, unidentified (0.9%).

[3] Mushroom.

[4] Unidentified (2%).

[5] Bracts, exudates, fungus.

shows that *Varecia* has the least structural complexity, as determined by the lack of tenaie and subsequent sacculations (Campbell et al., 2000). These authors suggest such a lack of sacculations may explain the inability of this species to subsist on a diet high in secondary compounds, such as those found in leaves. Compared with other sites, *Varecia* living at Manombo had the highest percentage of folivorous material in the diet through every season, yet they concentrated on the leaves of only two plant species, *Polyalthia oligosperma* (ramiavitoloha) and *Cynometra cloiselii* (hazomby). These two species are present in Ranomafana, but only ramiavitoloha is listed in the food species of *Varecia* in that site.

Even living in a harsh environment, *Varecia* spent an overwhelming percent of their feeding time on seasonal rather than perennial foods, as demonstrated by the high percentage of feeding time spent on fruits and young leaves, and a preference for nectar and shelf fungi. The abundance, distribution, and availability of a given food in the habitat may influence feeding behavior, but there is strong evidence in *Varecia* that seasonal foods are much preferred.

Comparing food species in disturbed (Manombo) and pristine (Nosy Mangabe, Ranomafana) forests, ruffed lemurs concentrated their feeding on relatively few tree species in the undisturbed forests. At these different sites, total food species utilized by ruffed lemurs were as follows: In Ranomafana, the three study groups used 27 plant species in 17 different families, 16 species in 12 families, and 14 species in 9 families; on Nosy Mangabe, 67 species in 24 families; and in Manombo, 83 species in 43 families. Preliminary data from a plant inventory study of the Nosy Mangabe rainforest indicate that this forest has very high species diversity (Gentry, 1988). In Manombo, although long-term effects of logging activities limit food choices, there is increased plant diversity due to massive invasions of various new plant species. This allows animals to diversify the number of food species ingested. Additionally, because different species fruit asynchronously, but within a species-specific 2- to 3-month period, feeding diversity is important to any animal with a small home range (Milton, 1980). The two study groups used mainly four small core areas of about 3 or 4 ha during this study, but the entire area used by each group was summed, and the home range was quite large: estimated at 70 and 30 ha for Groups I and II, respectively. Nevertheless, the food species chosen by *Varecia* at Manombo indicates that they were opportunistic feeders. Results of this study demonstrate that 35% of food species were used on only 1 day, and more than half of all food sources were eaten on less than 4 days of the entire study. This further underscores the opportunistic strategy used by ruffed lemurs at Manombo.

Varecia may travel less, and broaden the species they ingest as a strategy to cope with disturbed habitats (Milton, 1980; Terborgh, 1983; Dunbar, 1988). There are two possible explanations for this strategy: (1) to better guard and control food patches both from intraspecific competitors, and from other species at Manombo such as the brown collared lemur (*Eulemur albocollaris*) and frugivorous birds; and (2) to minimize use of the home range and distance traveled thereby conserving energy. It is important to note that the two study groups at

Manombo were not prevented from ranging farther and could have adopted an alternative strategy, traveling and foraging more if needed. Moreover, solitary foraging seemed to be another strategy for *Varecia* at Manombo, to avoid or reduce direct competition between group members, thus maximizing foraging success. Indeed, this allows a species to survive in areas where the distribution of resources would not support a cohesive group (de Thoisy and Richard-Hansen, 1997).

It is also important to note that even though the use of *C. hirta* tallied higher than any of the other food sources during the whole study, this does not necessarily mean that *C. hirta* was preferred, because when other food sources became available, its role was reduced. However, the two alien species, *C. peltata* and *C. hirta*, could be considered as "important foods," because these two species were eaten on many days during the study. Neither of these species is listed in the diet of *Varecia* at other sites. Overall, 38% of the total amount of feeding time was spent on those two species at Manombo. The survival of this frugivorous lemur in the highly disturbed Manombo forest seems to be related mainly to the availability of fruits of these two exotic plant species, because many of the endemic plant species did not produce fruits.

In comparing the five most important food families among the three sites (Manombo, Ranomafana, and Nosy Mangabe), no single family was present in all three (Table 3). Individually, Manombo shared one family (Clusiaceae) with Ranomafana and one family (Moraceae) with Nosy Mangabe. That Clusiaceae family at Ranomafana was consumed by the group living in selectively logged areas. Once again, this demonstrates changes in diet composition correlated with changes in the forest quality.

Some of the foraging strategies exhibited by the ruffed lemurs at Manombo forest can be explained by the high relative abundance of few plant species within the animals' territory. For instance, each time a preferred tree-food became less

Table 3. Comparison of top five plant families exploited by *Varecia variegata* groups at various sites in Madagascar

	Site		
	Nosy Mangabe (Morland, 1991b)	Ranomafana [a] (Balko, 1998)	Manombo (Ratsimbazafy, 2002a)
Plant family	Ebenaceae	Anacardiaceae	Annonaceae
	Lauraceae	Clusiaceae	Arecaceae
	Moraceae	Lauraceae	Clusiaceae
	Myrtaceae	Monimiaceae	Moraceae
Sapotaceae	Myrsinaceae	Rubiaceae	
		Proteaceae	
		Sapotaceae	
		Tiliaceae	

[a] Combined top five food families for three separate study groups.

abundant, *Varecia* supplemented their diets with the nontree food *C. hirta* and/or sometimes with *Pandanus* spp. Likewise, *Varecia* may have reduced their daily range by feeding on these shrub food sources. Moreover, during this study, Kolara-F was seen in the same *Ficus rubra* tree the entire day for 10 successive days, and Boloa-F was found in an unidentified fruit tree for 8 days. It is also the case that a single *Ravenala madagascariensis* tree was visited four to five times in 1 day by Boloa-F.

In this study, I did not have clear evidence as to whether *Varecia* at Manombo fed before dusk, or outside of daytime observation periods in general. It is possible that they did, as they were sometimes heard calling in warm seasons while it was still very dark in the early morning hours, but nocturnal vocalizations alone do not confirm nocturnal activity. No systematic nocturnal studies of ruffed lemurs in the wild have been conducted. On only two occasions did I see *Varecia* continuing to feed after dark (at 6:30 pm and 7:30 pm). Morland (1991a) also made limited observations of nocturnal activity in ruffed lemurs. She described seeing one female feeding and another feeding and moving. If *Varecia* does exhibit significant nocturnal activity, it will be interesting to investigate how such behavior may correlate with other ecological factors (e.g, food availability, food competition, or predation).

ACKNOWLEDGEMENTS

I would like to acknowledge the National Association for the Management of Protected Areas (ANGAP) and the Department of Waters and Forests (DEF) for permission to work at Manombo Special Reserve and the Classified Forest. Thanks to the Malagasy Institute for the Conservation of the Environment Tropical (MICET) and the staff of the Institute for the Conservation of Tropical Environments (ICTE) at SUNY Stony Brook and the Durrell Wildlife Conservtion Trust Madagascar. I am grateful to the Department of Anthropology and the Department of Botany of the University of Antananarivo, and in particular to the late Pr. B. Rakotosamimanana and Dr. V. Jeannoda. My thanks also go to Drs. P. Wright, L. Godfrey, W. Jungers, D. Krause, C. Janson, J. Fleagle, J. Ganzhorn, L. Gould, M. Sauther, R. Sussman, S. Lehman, and J. Durbin. I appreciate the help and advice of numerous colleagues, notably S. Zeeve, M. Irwin, K. Samonds, N. Stevens, P. O'Connor, and S. Nash. I gratefully thank L. Balko, H. Simons, F. Kerridge, and N. Vasey. This study would not have been possible without the assistance of Paul Rasabo, F. Razafy, T. Ramarolahy, Lezo, Jean Denis, Tsilefa, E. Louis, E. Larney, R. Zaonarivelo, H. Ramarosandratana, G. Randriatahina, N. Ravololomanana, B. Rakotonirina, R. Lala, H. Rabarison, R. Edmond, J. Burns, J. Ratsirarson, and the late Romule. Special thanks to all of the reviewers for their various comments and excellent advice for improving this article. Funding and support for the project were provided by the Wildlife Trust, the Rockefeller Foundation, the Margot Marsh Biodiversity Conservation Foundation, Primate Conservation Inc., the Wildlife Conservation Society, and the Brookfield Zoo.

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