

Forest restoration in Masoala National Park, Madagascar: The contribution of the red-ruffed lemur (*Varecia rubra*) and the livelihoods of subsistence farmers at Ambatoladama

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Abstract

Madagascar is among the most diverse places on earth, with 100% of the primates (lemurs), 99% of the amphibians, 95% of the reptiles, and almost 90% of the plants found nowhere else in the world. It is also rich in exploitable resources. Precious hardwoods like rosewood grow in the eastern rain forest. Deposits of sapphires, quartz, nickel, graphite, and gold are available. Yet it is one of the poorest countries, ranked in the lower 1/5 by the United Nations Development Program (UNDP 2009). Much of the original forest cover has been converted to agriculture, pasture, or degraded forest as a result of past non-renewable reliance on its natural resources.

The government of Madagascar, with substantial support and influence from the international community, has developed a network of areas throughout the country protecting the diverse ecosystems. This is the backdrop for the present study. My dissertation research focuses on seed dispersal by the largest diurnal lemur in Masoala National Park (MNP), the red-ruffed lemur (*Varecia rubra*), and the attitudes of the local farmers in an effort to assess the sustainability of a forest restoration project in the Ambatoladama forest corridor in MNP. Can the park rely on lemurs to restore natural forest habitat? Do the farmers in the region understand and respect park regulations well-enough to ensure long-term compliance and acceptance of forest protection and restoration?

In the first chapter, I report on the diet and activity budget of *V. rubra* during two field seasons in 2006 and 2007. The behavior of seed dispersers greatly affects the seed shadow of forest species; for example, the distance traveled in a day, the habitats lemurs travel through, the types of food eaten, and the amount of time resting can influence the deposition sites of passed seeds.

The second chapter describes how *V. rubra* contribute to forest restoration through their seed dispersal capabilities. I analyzed the seed dispersal quality and quantity, including the spatial distribution, diversity, and germination success of passed seeds within the Ambatoladama corridor.

Finally, the third chapter elaborates on the attitudes towards the park held by subsistence farmers living in the Ambatoladama region at the time of the study. I was interested in how people can help or hinder the future sustainability of MNP. However,

between the completion of my field work and the present, Madagascar has undergone dramatic changes in its government and thus environmental legislation. The military-backed coup in 2009 led to logging in the northeast and legalized the shipment of unprocessed rosewood and palissandre logs. This has led to massive increases in rosewood and palissandre cutting within the boundaries of MNP. I therefore analyzed the interview data from 2007 in light of the current situation in MNP.

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List of Abbreviations, Acronyms, and Malagasy (*mg*) Terms

ANGAP	<i>Association National pour la Gestion des Aires Protégées</i> , National Park Service in Madagascar
CARE	Cooperative for Assistance and Relief Everywhere
COGAP	<i>Code de Gestion des Aires Protégées</i> , national policy for management of protected areas in Madagascar
DBH	diameter at breast height
<i>Eaux et Forêts</i>	<i>Ministère des Eaux et Forêts</i> , the Ministry of Waters and the Forests in Madagascar
GELOSE	<i>Gestion Locale Sécurisée</i> , Secured Local Management of Natural Resources policy
GPS	Global Positioning System
ICDP	Integrated Conservation and Development Program
IUCN	World Conservation Union
<i>la zone tampon</i>	buffer zone
MNP	Masoala National Park
NEAP	National Environmental Action Plan
NGO	non-profit organization
<i>Savoka</i>	abandoned cleared land or secondary forest vegetation (<i>mg</i>)
<i>Tavy</i>	slash-and-burn agriculture (<i>mg</i>)
USAID	United States Agency for International Development
WCS	Wildlife Conservation Society
ZDU	<i>les zones de droits d'usage</i> , the zones with usufruct rights
ZOC	<i>les zones d'occupation contrôlée</i> , the zones of controlled occupation
ZUC	<i>les zones d'utilisation contrôlée</i> , the zones of controlled use

Chapter 1: The effects of reduced frugivory on the activity budgets of *V. rubra* in a regenerating rain forest site in Masoala National Park, Madagascar

Introduction

Activity budgets summarize the allocation of time to various activities and provide an important summary of behavior and energy use by primates. The activity budgets of primates result from interactions between food quality and food distribution (Terborgh 1983, Strier 1987, Overdorff 1996, Stevenson *et al.* 2000, Kaplin 2001, Vasey 2005a), group size (Strier 1987), and risk due to predators (Grassi 2002, Stojan-Dolar & Heymann 2010). The activity budgets of primates are directly related to metabolism and variable energetic needs (Coelho 1986, Vasey 2005a). Some primates are more frugivorous than others, and during periods of edible fruit scarcity, highly frugivorous primates might react by conserving energy, for example by traveling shorter distances, spending less time traveling, and spending more time resting (Terborgh 1983, Doran 1997, Stevenson *et al.* 2000, Kaplin 2001). Frugivorous primates might also behave in ways that appear to counter energy-conservation, by ranging farther or traveling more in search of alternative food sources (Clutton-Brock & Harvey 1977). In the tropics where fruit is spatially and temporally patchy (van Schaik *et al.* 1993), primates with a more frugivorous diet expend more energy than primates with a more folivorous diet (Strier 2007) since edible fruit patches are more likely to be widely distributed than patches of edible leaves. Thus, the degree of frugivory in primates generally correlates positively with time spent traveling, daily path length, and home range size (Strier 2007).

Fruits are a basic source of caloric energy for primates, which are typically high in nonstructural carbohydrates (Milton 1980, Strier 2007). Frugivorous diets are considered higher quality than folivorous diets because primates obtain more usable energy from fruits. As the proportion of leaves in the diet increases, travel requirements decrease; palatable leaves are presumably less patchy than fruits in the tropics and the travel time needed for foraging decreases, but leaves also provide less readily usable energy, so primates have less energy to allocate to traveling in order to find food (Strier 2007).

Folivorous diets are considered low quality because both young and mature leaves can be low in nonstructural carbohydrates, which are readily usable for energy by primates (Milton 1980). Leaves provide essential amino acids, vitamins, and minerals and young leaves are the most easily digested source of plant protein because of the high protein to fiber ratio (Richard 1985). However, mature leaves tend to be high in cellulose, hemicelluloses, and lignin, collectively known as dietary fiber (Felton *et al.* 2009). Dietary fiber is difficult to break down for energy during digestion without a specialized gut and microbes. Although some primates can extract energy from dietary fiber, this is not well-supported by field studies (Felton *et al.* 2009) .

Given that fruit production is temporally and spatially patchy, seasonal dietary plasticity is common in primates (Strier 2007). In times of low fruit abundance, the highly frugivorous primates might feed on less common “fallback” foods, for example, they might consume a higher percentage of leaves, insects, flowers, fungi, or non-native fruit species (Hill 1997, Tutin *et al.* 1997, Kaplin *et al.* 1998, Brugiere *et al.* 2002, Strier 2007, Lappan 2009). In Madagascar, it is well-documented that fruit production in the eastern rainforests varies from year to year (Overdorff 1993, Ganzhorn *et al.* 1999, Wright 1999) and some tree taxa produce fruit on irregular, asynchronous, or alternate year cycles (Morland 1991, Overdorff 1993, Powzyk 1997, Balko 1998, Ratsimbazafy 2006).

Varecia is considered to be the most frugivorous Lemurid (Vasey 2000b). During the seasonal period of fruit scarcity in Masoala National Park (June-August), a previous study of *Varecia rubra* in an undisturbed forest site, Andranobe, found that they spent less time traveling, exhibiting an energy conservation activity budget, but they did not increase the time spent feeding, or exhibiting an energy accumulation activity budget (Vasey 2005a) . During the fruit scarce season, fruit comprised 100% of the diet of *V. rubra*—seasonal dietary flexibility was not observed at the undisturbed site of Andranobe (Vasey 2002). However, *V. rubra* females did feed on more young leaves during lactation (October-December) presumably for the protein (Vasey 2005a) ; but high-protein foods require more time and energy for nutrient extraction (Richard 1985).

In the present study, at the Ambatoladama forest corridor in Masoala National Park (MNP), *V. rubra* groups were observed in 2006 during what has been described by Vasey (1997) as the hot-dry season and in 2007 during the transitional dry to hot-dry season in MNP. The site is a relatively disturbed forest near agricultural settlements. The forest in MNP is composed of a mosaic of young secondary forest, regenerating forest and mature forest. I tested the hypothesis that the activity budget of *V. rubra* was affected by diet on a daily basis. Predictions based on previous studies of primate energetics were: 1) *V. rubra* would exhibit an energy conservation activity budget by spending less time traveling and more time resting with a more folivorous diet and 2) There would be a positive correlation between the dependent factors of distance traveled and time spent traveling and the independent factor of percent fruit in the diet on a daily basis (Strier 2007). I also provide behavioral evidence that the observation period in 2007 was a time of fruit scarcity for *V. rubra*.

Methods

Study site

The Ambatoladama forest corridor is about 2.5 km by one km located in Masoala National Park (MNP) in northeastern Madagascar located between 50°0'5.83" east, 15°16'42.85" south and 50° 1' 38.15" east, 15° 17' 32.52" south (Figure 1). The vegetation is tropical dense evergreen forest and the altitude at the site ranges from 300-700 m. The climate of the peninsula is tropical humid with annual rainfall for the park ranging from 2200-7000 mm, relative humidity above 80%, and an annual temperature range of 21-24 °C (Hatchwell 1999). Climatological data from the National Climatic Data Center (US Department of Commerce) for Antalaha, which is 50 km NE of Ambatoladama, in 2006-2007 is displayed in Figures 2 and 3. Antalaha is located along the coast of the Indian Ocean and the two locations probably differ in rainfall amounts, but this is the closest location with available data. Ambatoladama is the site of a forest restoration program (see Chapter 2 for a description) where regenerating, secondary forest patches are interspersed within mature rain forest. Subsistence farmers live on the edge of the forest corridor at Ambatoladama and there are about 15 households outside of MNP boundaries and within 2 km of the forest corridor.

Study organisms

The red-ruffed lemur is endemic to the Masoala Peninsula and is closely related to the black and white ruffed lemur (*Varecia variegata* spp.). *V. rubra* was recently declared a distinct species rather than a sub-species of *V. variegata* (Mittermeier *et al.* 2006) and *V. rubra* is classified by the World Conservation Union as “Endangered” (Andrainarivo *et al.* 2009). *V. rubra* is described as living in multimale/multifemale communities that has a fission-fusion social organization including subgroups, affiliates, core groups, and a community social network (Vasey 2006). During the study periods at Ambatoladama, *V. rubra* appeared to range within core groups of two to six individuals (Table 1, Chapter 2). Two of the core groups we observed (JJ and Piste) were likely part of the same community as their ranges overlapped and the females interacted socially; I therefore pooled the behavior data for these two groups. The third group, JP, was likely part of a different community since they never overlapped with the other two core groups. In this paper, I refer to the core groups as “groups” and they are the unit of analysis.

To collect data on the behavior of *V. rubra*, the team of Dr. Ed Louis, DVM, of the Henry Doorly Zoo (Omaha, Nebraska) conducted the capture and immobilization of *V. rubra* at Ambatoladama in November 2006. Following a standard protocol (Glander *et al.* 1991), lemurs were captured using a CO₂-powered dart gun. A dose of 25mg/kg of Telazol® (or 0.3 ml per 2.5-3 kg animal) effectively immobilized adult *V. rubra*. Telazol is a non-narcotic, non-barbiturate, injectable anesthetic and known to be a safe drug for primates (Glander *et al.* 1991) and lemurs (Glander *et al.* 1992). We affixed Telonics brand MOD-205 radio collars (Telonics Inc, Mesa, Arizona) to four adult females and one adult male from two core groups. Lemurs were released after the Telazol wore off sufficiently, about two to three hours after injection. The capture and immobilization methodology was approved by the University of Minnesota’s Institutional Animal Care and Use Committee, Protocol number 0603A83626.

Vegetative composition and food availability of the corridor

In order to quantify the vegetative composition of the forest corridor at Ambatoladama, I created seven linear transects ranging from 700 m to 1040 m in length by 10 m wide (Table 1). Locations of transects were selected randomly from a grid

overlaying a map beyond the requirement of being at least 50 m from the start of another transect. Five transects started at the western forest edge in agriculture or secondary forest and two transects started in primary forest. Two transects ran due east and the remaining five ran 45° northeast. We recorded the following information for all stems with the diameter at breast height (DBH = 1.3 m from ground) greater than or equal to 10 cm along transects: estimated tree height from ground, phenology, location along transect, vernacular name, and family (if known). When possible, specimens of unknown trees were collected, pressed, and preserved in 70% alcohol for identification in Antananarivo by parataxonomists at the Tsimbazaza Zoo. I randomly chose fourteen 10 m x 10 m plots along each transect and collected the same information for all stems with a DBH 1-10 cm. Phenological data were collected opportunistically at Ambatoladama during the study seasons; I did not have a phenology trail that was systematically monitored. However, at a site 65 km south of Ambatoladama near Fampotobe on the Masoala Peninsula (Figure 3), monthly phenological data was collected on 38 tree species from July 2006 - November 2007 (partial list, Appendix 5). These species were chosen because they were identified by local guides and in the literature as *V. rubra* food species (Rigamonti 1993, Vasey 1996, 2000a). Although the behavioral study was conducted at a different site, the data provide insight into fruit availability of some food trees during the study period.

I quantified the number of stems of all taxa with DBH between 1-10 cm in subplots totaling 7000 m², and the number of stems of all taxa with DBH ≥ 10 cm within 53,000 m² (Table 1). I extrapolated the number of stems per hectare from the seven transects. The basal area of trees was calculated using the equation: $\pi \left(\frac{DBH}{200}\right)^2$; this equation converts the DBH from square centimeters to square meters. Stand basal area, m²/ha, was calculated by adding the basal areas for each tree and dividing by the total number of hectares surveyed along transects.

Analysis of activity budget, diet, and daily path length

From November 2006 through January 2007, teams observed the behavior of the three core groups of *V. rubra* during either all-day sessions (called “follows”) between 0600-1800 hr or half-day follows between 0600-1200 hr. In 2006, three observation

teams were composed of BTM, an American field technician (Jeff Kloppenburg), or my colleague Mrs. Onja Razafindratsima, plus three local farmers trained to use GPS units, collect lemur feces, measure DBH, and track lemurs with radiotelemetry equipment. In 2007, observation teams were composed of BTM, an American field technician (Claire Catania), two trained local farmers (Georges Betandra and Jean Charles), plus three local farmers trained to use GPS units, collect lemur feces, measure DBH, and track lemurs with radiotelemetry equipment. All people collecting behavioral observations trained together with BTM until we were 95% in agreement of observed behaviors.

From November 2006-January 2007, we followed the core groups on a rotating schedule of an all-day follow, a half-day follow, and a day of no observations. I refer to this as the “2006 season.” One radio-collared adult female from the JJ group perished in 2007 between January and August. From August-November 2007, we observed the behavior of two core groups, Piste and JP. I refer to this as the “2007 season.” We did not follow the third group, JJ, as the female that perished was the only one collared in her core group. Two teams conducted all-day follows of both groups simultaneously from three to six times per week.

Teams collected the activity budget data of the groups during scans every ten minutes. At each ten minute sampling point, we sampled the behavior by all individuals within sight of the focal female in the group (Altmann 1974, Ratsimbazafy 2002). An ethogram for *V. rubra* behavior is based on activity budget data collected on *Varecia* species by Vasey (1997), Morland (1991) and Ratsimbazafy (2002). We recorded behaviors for all visible individuals, including: resting, traveling, moving, feeding, grooming, or out of sight. The “out of sight” category was noted when an individual was known to be in the vicinity of the group but obscured by vegetation so that the behavior was not visible. We also noted all occurrences of less-common social behaviors like vocalizing, cuffing, chasing, infant playing, and scent-marking. Other variables collected every ten minutes were GPS location of observer and horizontal distance to focal animal, group size, group composition, and a description of the forest type (i.e. primary, secondary, edge, or regenerating parcel). We recorded the GPS location of every food tree and food patch for items that were parasitic lianas or shrubs.

We attempted to get the coordinates of all trees even if the lemurs fed on the items outside of the instantaneous scan sampling.

The activity budgets represent the proportions of each activity (resting, traveling, moving, and feeding) divided by the total number of activity records for each individual within the group per day. Data are referred to as “scores.” Activity budget data were analyzed on a daily basis and in this paper reported for adults only, as there was a significant difference between the behaviors of non-reproductive adults and adults (Pearson’s χ^2 : $\chi^2=443.2$, $df = 4$, $P < 0.0001$, $N = 21,209$ scores). I used both full and half days for the analyses. A group was followed for at least three hours to twelve hours per day. There was no significant difference between the activity budgets of the Piste and JJ groups in 2006, thus these two groups were pooled in the analyses (Pearson’s χ^2 : $\chi^2=9.01$, $df=4$, $P=0.06$, $N=11,538$ scores). Their range overlapped and on multiple occasions the adult females interacted socially, therefore I treated them as members of the same group. I analyzed data by group because the JP group ranged within more mature forest than the Piste group; the home range of the Piste group included more area of regenerating parcel than the home range of the JP group (see Chapter 2). For some analyses, traveling and moving were pooled, under the assumption that both activities require high energetic inputs. I excluded the “out of sight” behavior from the analysis as this information does not provide insight into the activity budget of the lemurs—I am assuming in these analyses that the behaviors lemurs engaged in when “out of sight” follow the same distribution as the behaviors when in sight.

In order to determine the effect of diet on the activity budget on a daily basis by group and year, I categorized the percent feeding time on leaves into high (100-66.7%), medium (66.7-33.3%) and low (33.3-0%) categories. I used the proportion of time spent on leaves in the daily diet as the independent variable because in order to obtain carbohydrate energy, structural carbohydrates like hemicellulose in leaves must be fermented in the gut, which requires more time and energy than extracting carbohydrate energy from fruit pulp (Lambert 2007).

Daily path lengths were calculated based on the GPS locations, which were collected every ten minutes, of groups during all-day follows greater than eight hours. I

analyzed only the full days since a half-day would only give a snapshot of a daily path length. I used Hawth's Tools "Create path from points" tool within ESRI ArcMap 9.1. This tool sequentially connected and measured distances between locations on a daily basis.

To evaluate differences in activity budgets and percent leaves in diets, which are represented as frequencies, I used bivariate and multivariate analyses. I report the test statistics of either the Cochran-Mantel-Haenzel for contingency tables greater than three-dimensions, the Mantel-Haenzel test with continuity correction for three-dimensional contingency tables, or the Pearson's chi-squared test for two-dimensional contingency tables (Sokal & Rohlf 1995). The null hypotheses for the analysis of frequencies using these test statistics are that the distribution of the activity budget does not differ by group, year, group and year, or percent leaves in daily diet. Analyses were run in R version 2.9.1 using the "mantelhaen.test" or "chisq.test" commands.

To test if either of the dependent variables, daily path length or daily percent time spent traveling, were positively correlated with the daily proportion of time spent feeding on fruit, I conducted regression analyses. The daily path length was log-transformed to better fit the assumptions of normality. Analyses were run in R version 2.9.1 using the "cor.test" command.

Results

Degree of frugivory by year and group

Based on the scan data for all groups, during the 2006 season, *V. rubra* spent 88% of the feeding time consuming fruits and 10% of the feeding time consuming leaves. In 2007, the groups consumed fruit 50% of the feeding time and 37% of the feeding time was spent consuming leaves (Table 2). There was a significant difference in the time spent feeding on fruits, leaves, and nectar or flowers when the data were subdivided by group and field season (Mantel-Haenzel test: MH= 9.0, df=1, P=0.003, N=2,449 scores). The JP and Piste groups differed in the time spent feeding on fruits or leaves within the 2007 but not the 2006 season (2007: Pearson's χ^2 : $\chi^2=57.3$, df=1, P<0.01, N=2121 scores; 2006: Pearson's χ^2 with Yates' continuity correction $\chi^2=2.2$, df=1, P=0.14, N=320 scores) (Figure 4, Table 2).

Table 3 lists the top five food taxa consumed by group and year based on the percentage of the daily total group feeding scans. It also shows the number of individual trees in which the lemurs fed within each food species. Productive food patches in the JP range included a parasitic *Ficus* plant (Moraceae), vernacular name Mandrisy, and a *Callophyllum milvum* tree (Clusiaceae), vernacular name Vintanona. The JP group spent 19% and 25% respectively of the total feeding time in these two food trees. There was one productive *Callophyllum milvum* tree that the Piste group spent 13% of the total feeding time feeding on in 2007. The Piste group spent more time, 14%, feeding on the immature leaves of 13 different *Dialium unifoliolatum* trees (Fabaceae), vernacular name Zagnamena. Also, in 2007, the Piste group spent 11% of their feeding time consuming the ripe fruits of *Clidemia hirta*, a non-native pioneer shrub that is common in disturbed, open canopied areas like the regenerating forest patches within the Ambatoladama corridor and the forest edge (see Chapter 2).

Activity budgets

There was a significant difference between the activity budgets of adults when data were subdivided by group and year (Mantel-Haenzel test: MH=207.8, df=1, P <0.0001, N=11,538 scores; Figure 5). When the two groups are pooled, there was still a significant difference in the activity budgets of *V. rubra* in 2006 vs. 2007 (Pearson's χ^2 : $\chi^2=433.5$, df=4, P<0.0001, N=11,538 scores; Figure 6).

Activity budget and diet

On a daily basis with both years pooled, there was a significant difference between the activity budget of *V. rubra* and the proportion of time spent feeding on leaves (Pearson's χ^2 : $\chi^2=127.6$, df=4, P <0.0001, N=10,731 scores; Figure 7). When the data were subdivided by season and group, there was a significant difference between the activity budget and the proportion of time spent feeding on leaves in the diet on a daily basis (Cochran-Mantel-Haenzel: $M^2=836.4$, df=2, P<0.0001, N= 10,731 scores; Figure 8).

Daily path length, diet, and activity budget

In 2006, the mean daily path lengths during full days greater than eight hours were 758 m (SD=278 m, N = 22 days) and 785 m (SD=435 m, N = 9 days) for the Piste

and JP groups respectively, and in 2007 the mean daily path lengths were 826 m (SD= 582 m, N = 56 days) and 539 m (SD= 358 m, N = 45 days) for the Piste and JP groups respectively (Figure 9). The variation was great in daily path lengths, as the distances ranged from 0 m to 3,413 m in a full day of eight hours or more (Table 4). I log-transformed the daily path length data to make the data fit a normal distribution. The log transformed mean daily path lengths by group and year differed significantly ($F=3.457$, $df=3$ and 128 , $P<0.05$) with a highly significant effect of the JP group in 2006 ($t = 21.77$, $P < 0.001$; Table 5).

There was a significant positive correlation between the percent time spent feeding on fruit in the diet and the percent of the daily time budget spent traveling, however the correlation coefficient is not large (Correlation coefficient = 0.36, $t = 4.45$, $df = 130$, $P < 0.0001$; Figure 10). There was not a significant correlation between the percent time spent feeding on fruit and log-transformed daily path length (Correlation coefficient = -0.040, $t = -0.4581$, $df = 130$, $P = 0.6476$).

Fruit scarcity

The phenological data collected in this study at Ambatoladama makes it difficult to compare between study periods to determine if fruit from potential food sources was scarce in 2007 versus 2006 (Appendix 5). In the case of the two short field seasons at Ambatoladama, I suggest that the behavior of the *V. rubra* groups in the 2007 supports that it was a time of fruit scarcity. The fact that *V. rubra* spent less time traveling and spent more time consuming leaves in 2007 than 2006 lends evidence towards fruit scarcity in 2007. That the Piste group in 2007 spent 11% of the total feeding time eating the ripe fruits of the non-native pioneer shrub, *Clidemia hirta*, which grows in the open-canopy regenerating forest parcels, lends more evidence to the hypothesis of fruit scarcity.

Discussion

Diet

V. rubra spent more time consuming fruit than leaves and other items in the 2006 season versus the 2007 season when data from both groups were combined. Within the 2007 season, the JP group spent significantly more time consuming fruits

than leaves when compared to the Piste group. I attribute this difference between the groups to two productive food patches in the JP range; a parasitic *Ficus* plant (Moraceae), vernacular name Mandrisy, and a *Callophyllum milvum* tree (Clusiaceae), vernacular name Vintanona. The JP group spent 44% of the total feeding time in the 2007 season in these two food patches. The *Ficus* species attracted a number of *V. rubra* individuals presumably all within the same core group as the JP group; on one day in September 2007, twelve *V. rubra* were observed simultaneously feeding on the *Ficus* fruits. There was one productive *Callophyllum milvum* tree that the Piste group in 2007 fed on, but they spent only 13% of the total feeding points in this tree. The Piste group spent more time, 14%, feeding on the immature leaves of 13 different *Dialium unifoliatum* trees (Fabaceae), vernacular name Zagnamena. The Piste group spent 11% of their feeding time exploiting the abundant patches of *Clidemia hirta*. This shrub produces fruit year-round and can be considered a “fall-back” food during times of food scarcity. *V. variegata* in Manombo was observed feeding on the fruits of *C. hirta* after a cyclone devastated many of the food trees (Ratsimbazafy 2002).

Daily activity budget and diet

The activity budgets were significantly different among the different groups and study seasons. This result does not control for the effects of weather or food availability. Behaviors involving locomotion, in this case traveling and moving, are estimated to be the most energetically costly for primates (Coelho 1986, Altmann & Muruthi 1988). The data from Ambatoladama showed that overall *V. rubra* devoted more time to feeding, less time to traveling, and more time to resting in 2007, when less time was devoted to consuming fruit, than in 2006. This pattern, of less travel, more rest, and more feeding, suggests an activity budget geared towards energy conservation or energy accumulation in 2007 (Vasey 2005a). At Andranobe, an undisturbed site in MNP, *V. rubra* had an activity budget described as accumulating energy during gestation (July-October) and an activity budget described as high energy expenditure, more traveling and less resting, during lactation (November-December) (Vasey 2005a). The activity budget data at Ambatoladama in 2006 were consistent with this as *V. rubra* was lactating and caring for infants during the 2006 season, and infants were not born in October or November of the 2007 season. Lactating *V. rubra* spend more time traveling and less time resting

because they often return to stashed infants between feeding bouts rather than traveling directly to another feeding tree (Vasey 2005a). We suspected that the females were pregnant in 2007, but they had not given birth by the end of our field season; this was unusual given that they typically give birth at the end of October-early November (Vasey 2007). At Andranobe in MNP, observed *V. rubra* also did not give birth to infants in 2007 (Vasey & Borgerson 2009). *V. rubra* may have been gestating, and this could explain the difference in activity budgets between years, however, the evidence suggests the observed *V. rubra* never gave birth to infants in 2007, and the energy-conserving activity budget in 2007 was in response to other environmental factors.

The evidence from Ambatoladama in this study suggests that the diet accounted for some of the variation in the daily activity budgets of *V. rubra* between the two observation periods of 2006 and 2007. Primates that have relatively fast gut processing times are expected to feed on fruits, which are high in readily available energy in the form of soluble carbohydrates compared to leaves, which require specialized guts that can ferment and extract energy from tough plant cell walls (Milton 1979, Lambert 1998). The mean transit time for a variety of seeds passing through the gut of *V. rubra* at Ambatoladama is 3.4 hr (Chapter 2) and 1.7 hr for a chromium oxide marker in a captive group of *V. rubra* (CabreVert & Feistner 1995). Compared to similar sized primates, this is a relatively fast gut passage time (Lambert 1998). A primate gut requires more time to extract comparable amounts of energy from a more folivorous diet than frugivorous diet, and this is apparent in the different activity budgets based on the percent leaves in the daily group diet. When the daily diet was at least 2/3 leaves, *V. rubra* groups spent less time traveling and more time resting than on days when leaves constituted 1/3 or less of the diet. This difference in activity budgets due to diet has been observed in other primate species. One species of gibbon (*Nomascus concolor jingdongensis*), which is a typically more folivorous primate, decreased energy consumptive activities like traveling, singing, and playing and increased feeding time when they consumed more leaves in their diet (Fan *et al.* 2008). Woolly spider monkeys (*Brachyteles arachnoides*) also alter their ranging patterns along with diet; they travel shorter distances on days when they consume higher proportions of low quality but abundant leaves or when they consume high quality fruits in large patches (Strier 1987).

In 2007, *V. rubra* spent more time feeding on leaves than in 2006, and in general they spent more time resting and less time traveling. However, the daily activity budgets differed significantly across the three categories of leaf consumption (high, medium, and low) in the daily diet and between the two seasons. If the proportion of leaves in the daily diet was the only factor affecting the difference in the activity budgets in 2006 and 2007, then I would expect to see a consistent pattern of activity when lemurs were eating a large amount of leaves versus a small amount of leaves. It might also be that a daily time scale does not capture the relationship between the percentages of time spent feeding on leaves or fruits and the activity budget, as some studies found a difference in activity budgets based on the time of day (Erkert & Kappeler 2004).

Daily path length and activity budget

There was an overall significant difference between the mean log daily path lengths by group and season, however this difference is mainly driven by a significant effect of the JP group's activities in 2006; there is a lot of variation by group and season. There was one day in October 2007 where the JP group did not travel during a 10hr 20min observation period. The group stayed within the previously mentioned *Callophyllum milvum* (Clusiaceae) tree alternating between bouts of foraging on the ripe fruits and resting in the tree. In this particular case, *V. rubra* was not conserving energy due to a need for extra time to digest a high percentage of leaves in the diet; they spent 66% of the time points resting and 23% of the time points feeding on the ripe fruits of *C. milvum*. Rather, *V. rubra* was exploiting a productive food source. The second shortest distance traveled in a full day was by the JP group one day in August 2007, 54.3 m, during 10hr of observation. On that day, the group fed only on mature and immature leaves in two patches. They spent 80% of the observation time resting and 13% of the time feeding on leaves, fitting the prediction of less time spent traveling and more time spent resting when the diet is composed of a high proportion of leaves. The longest daily path length for a group was one day in September 2007 by the Piste group at over 3,400 m. On that particular day, the group spent most of the feeding time in six patches of ripe fruit trees and less feeding time in one patch of immature leaves over an observation period of 11hr 10 min. The activity budget for that day was 21%

traveling, 16% feeding, and 50% resting. That day supports the prediction of a positive correlation between the distance traveled and the percent time spent feeding on fruit.

However, overall there was not a significant positive correlation between the daily path length and the time spent traveling. There was a significant but relatively weak correlation between the time spent traveling and the percent fruit in the diet on a daily basis. It is evident from the plot in Figure 8 that on days in which the groups fed only on fruit, there was variation in the amount of time spent traveling, from 2% to 38%. Likewise, on the days when the groups did not spend time traveling, the percent of time spent feeding on fruit ranged from 20% to 88%. The interesting part of this plot is the empty space in the lower right section; on days when groups spent more than 18% of their daily activity budget traveling, time spent feeding on fruit was always at least 50%. *V. rubra* were either able to travel this much because they were eating a high-energy diet or they were spending time traveling to get to spatially patchy fruit resources.

Evidence of food scarcity

In disturbed habitats, primates may spend less time traveling between food patches and instead diversify the species they consume (Milton 1980, Terborgh 1983, Riley 2007). Two possible explanations for this strategy are to better guard and control food patches from intra and interspecific competitors at food patches and to minimize the use of the home range and distance traveled thereby conserving energy (Ratsimbazafy 2006). Likewise, primates might spend more time traveling because they need to travel further and longer to find food patches in disturbed habitats (Chapman 1988, Overdorff 1996). Overall at Ambatoladama, the time spent traveling, resting, and feeding looked most like what was observed in *V. rubra* at Andranobe during the food-scarce “cold-rainy” season (June – August) in MNP (Vasey 2005a), with 14% time traveling, 23% time feeding, and 62% time resting at Ambatoladama. The cold-rainy season in MNP is characterized by low fruit availability, heavy rainfall (i.e. over 550 mm rainfall per month), and relatively low temperatures (average 19-20° C) (Vasey 1997). Other frugivorous primates are known to spend more time feeding and less time traveling during colder seasons with seasonal low fruit availability: *Cebus albifrons*

(Terborgh 1983), *Eulemur fulvus rufus* and *Eulemur rubiventer* (Overdorff 1996), and *Pan troglodytes verus* (Doran 1997).

The nature of the phenological data collected in this study at Ambatoladama makes it difficult to compare between study periods to determine if fruit from potential food sources was scarce in 2007 versus 2006. One common method for measuring food availability is to measure food patch size using the tree DBH as a proxy for patch size (Wich *et al.* 2002). This measure can be based on the phenology of predicted food taxa or based on primate behavior (Isbell *et al.* 1998, Wich *et al.* 2002). In either case, in short-term studies, one might either over or underestimate food availability depending on a chosen protocol. In the case of the two short field seasons at Ambatoladama, I suggest that the behavior of the *V. rubra* groups in the 2007 supports that it was a time of fruit scarcity. The fact that *V. rubra* traveled less and consumed more leaves than in 2006 lends evidence towards fruit scarcity. The Piste group spent a considerable amount of time feeding on the non-native pioneer shrub, *Clidemia hirta*, which grows in the open-canopy regenerating forest parcels and lends more evidence to the hypothesis of fruit scarcity during the 2007 field season. The high proportion of leaves in the daily diets, foraging on *C. hirta*, and spending more time traveling in the 2007 season was evidence that the time period was a time of fruit scarcity, especially for a genus that is described as one that is "...highly frugivorous, uses the highest forest strata and the largest feeding trees..." (Vasey 2005b) and has only been observed feeding extensively on *C. hirta* in a highly anthropogenic and cyclone-disturbed forest site (Ratsimbazafy 2002). Another possible indicator of fruit scarcity is the fact that *V. rubra* did not have infants in 2007, as inadequate resources could lead to a lack of infants. In previous studies, howler monkey (*Alouatta seniculus*) reproduction was reduced on small islands (Terborgh *et al.* 2001) and bearded saki monkeys (*Chiropotes satanas chiropotes*) did not successfully reproduce in small 10 ha forest fragments (Boyle & Smith 2010).

There are other environmental and sociobiological factors that I did not address in this study but that may also affect the activity budget of primates, and in turn confound the effects of the diet on the activity budgets of *V. rubra*. For example, in some primate species, group size affects the activity budgets in that larger groups tend to spend more time feeding, searching for food, and traveling (de Ruiter 1986, Overdorff

1996), they travel further than smaller groups (Dunbar 1992, Wrangham *et al.* 1993), and they spend less time scanning for predators (de Ruiter 1986).

Conservation implications

Ambatoladama is a disturbed rain forest habitat with a behaviorally flexible community of *V. rubra*. The fact that the typically highly frugivorous *V. rubra* has the capacity to spend 100% of their daily feeding time consuming leaves or non-native fruits bodes well for their conservation, assuming they are acquiring the necessary nutrients. However, the high-leaf and low-fruit diet of *V. rubra* during the observational period in 2007 is correlated with a low-birthing season—*V. rubra* in the study groups did not give birth to infants in 2007. The site at Ambatoladama has an active restoration program and the long-term sustainability of that program in part relies on *V. rubra* depositing seeds of interior forest trees into the most degraded areas. Overall, the seasonality of fruit production at the site and the effects on the activity budgets of *V. rubra* makes it difficult to predict when the restoration program can be left to the lemurs. More long-term research is needed to determine if a high-leaf diet does affect *V. rubra* reproductive success, and therefore to understand the population dynamics within degraded landscapes. However, an encouraging result of this research is that *V. rubra* exhibit dietary flexibility during periods of interior forest fruit-scarcity by feeding on non-native pioneer fruits and mature or immature leaves.

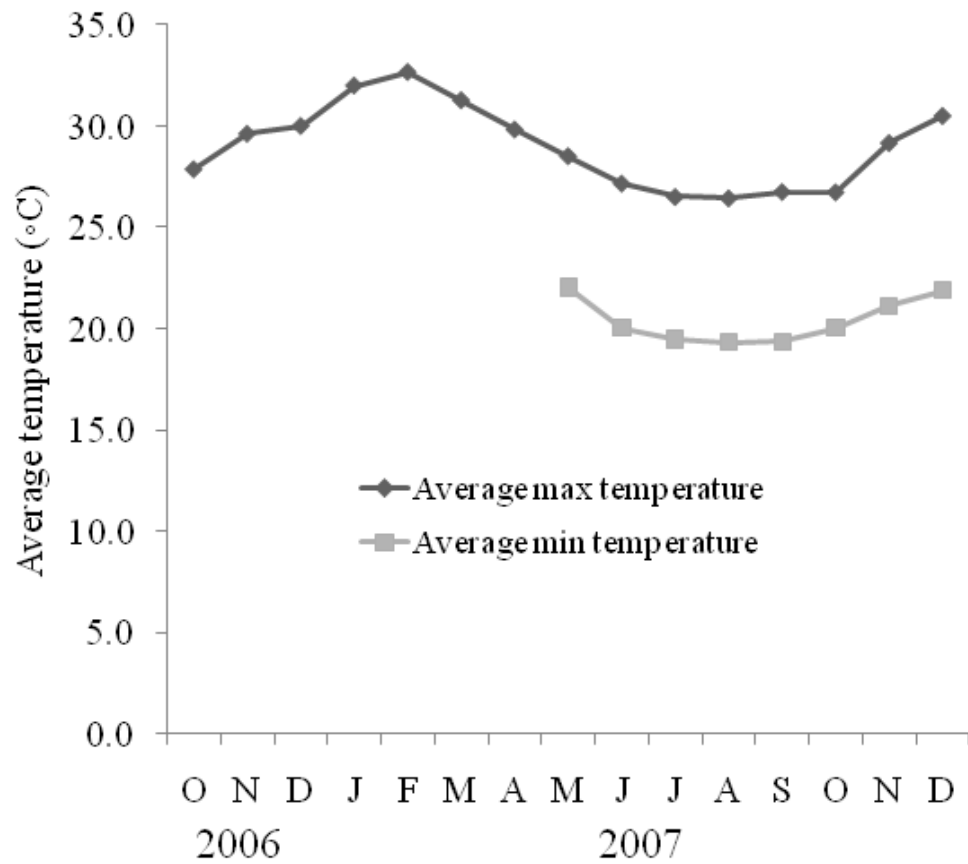


Figure 2. Average monthly temperatures for Antalaha in 2006 and 2007. Data were not available from January-September 2006 and the minimum average temperatures were not available from October-April 2006. Antalaha is located about 50 km NE of Ambatoladama. The study period was November 2006 – January 2007 and August – November 2007. Data from NCDC (National Climatic Data Center) of the US Department of Congress, accessed 26 April, 2010.

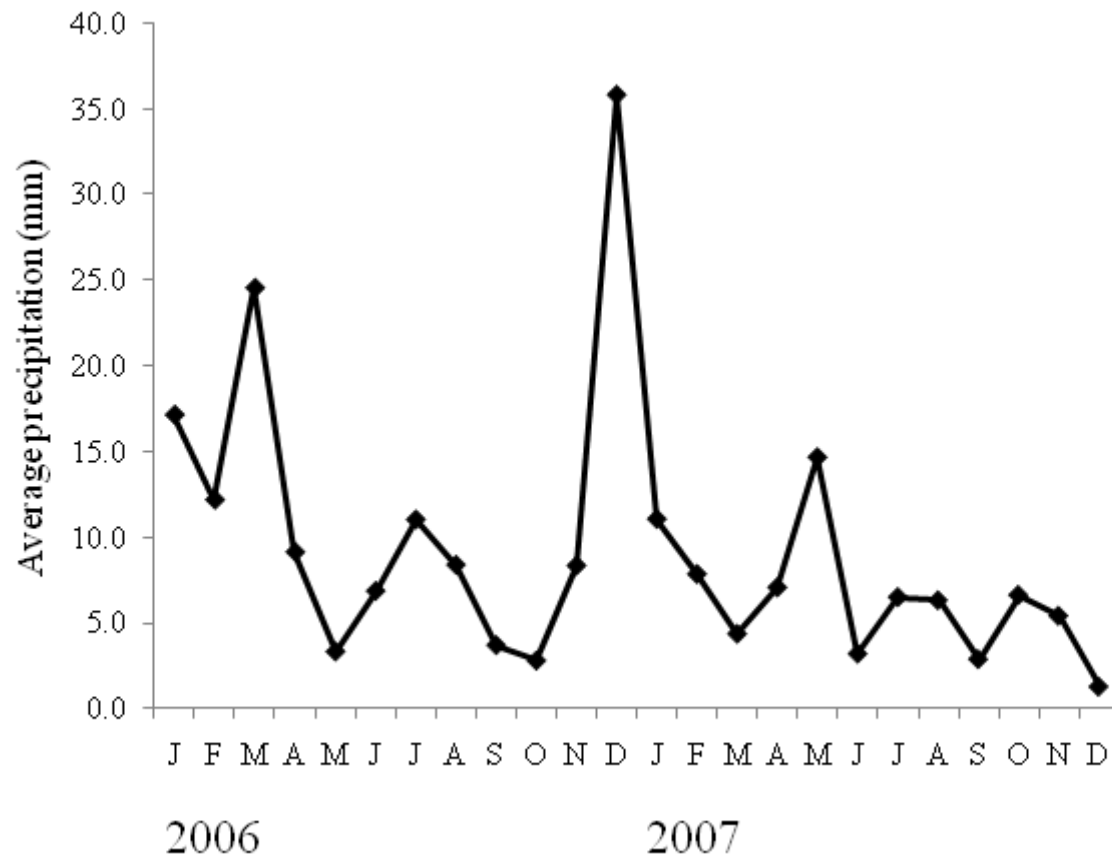


Figure 3. Average monthly rainfall for Antalaha 2006-2007. Data from NCDC (National Climatic Data Center) of the US Department of Congress. Antalaha is located about 50 km NE of Ambatoladama.

Table 1. Botanical data from the transects in the corridor at Ambatoladama. DBH = diameter at breast height (1.3 m).

Transect	Transect size, m ²	Mean DBH, trees ≥ 10 cm, ±SD	Maximum DBH	Total stems ≥ 10 cm	Mean height, m, ±SD	Area of plots without trees ≥ 10cm DBH, m ²	Stand basal area, m ² /ha	Stems per ha DBH ≥ 10 cm	Percent area without trees DBH ≥ 10 cm	Total stems DBH 1-10 cm	Area of sub-plots, m ²
TBA	10,400	19.8 ±13.3	142.0	626	11 ±5	3,725	26.3	602	23		
TD	7,000	22.0 ±15.2	146.2	382	12 ±7	2,225	30.5	546	32	373	1,400
TG	7,000	21.2 ±14.5	198.8	577	11 ±5	1,075	42.5	824	15	855	1,400
TJ	7,000	21.0 ±12.1	91.0	559	13 ±5	1,450	36.9	799	21	654	1,400
TJA	7,000	20.1 ±16.8	168.0	363	11 ±6	1,650	27.9	519	24		
TP	7,600	22.4 ±15.7	169.0	419	12 ±8	2,475	32.5	551	33	342	1,400
TR	7,000	20.5 ±10.4	83.0	492	12 ±5	350	29.0	703	5	542	1,400
Totals	53,000			3,418		12,950		4,543		2,766	7,000

Percent area without trees ≥ 10 cm DBH 24%

Stems per ha, DBH ≥ 10 cm 645

Stems per ha, DBH 1-10 cm 3951

Average basal area all plots, m²/ha 32.2 ±5.7

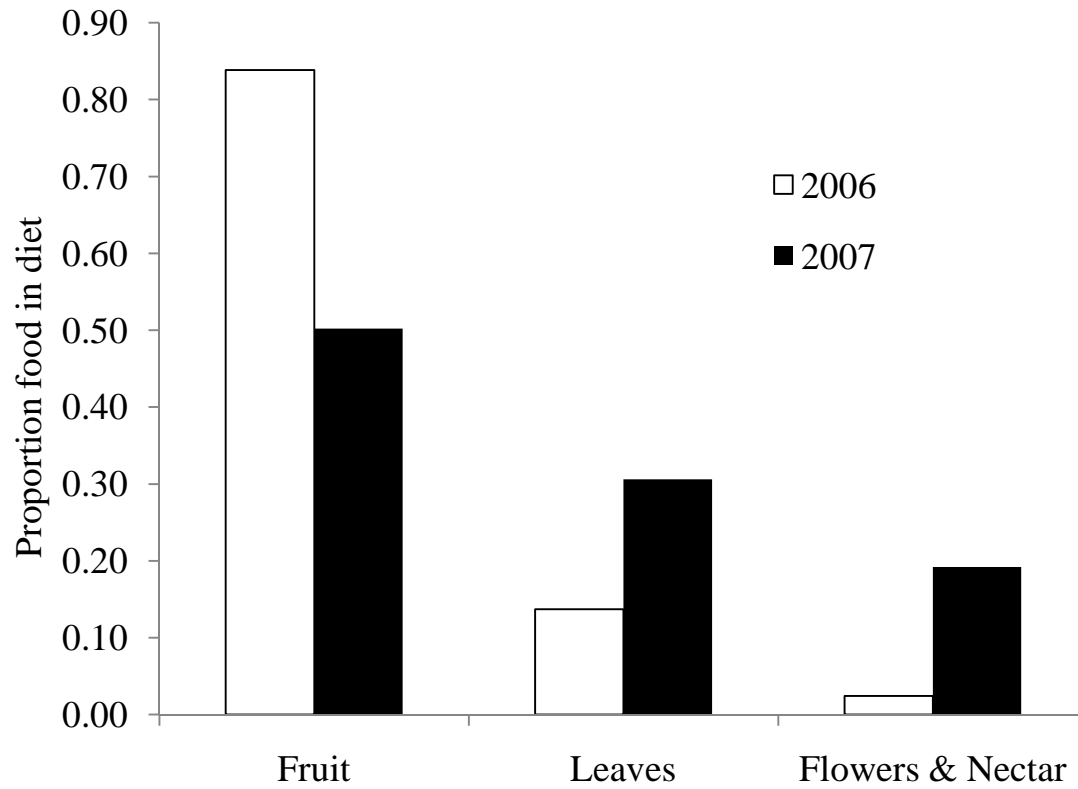


Figure 1. Diet within the two seasons as represented by the proportion of feeding scores for each food type during scan samples. The data is pooled by groups. There is a significant difference between seasons: $\chi^2=134.4$, $df=2$, $P<0.0001$, $N = 2,449$ scores.

Table 2. Proportion of total feeding scores for each group in each season feeding on fruits, leaves and flowers or nectar. There was a significant difference in time spent feeding on the food types when data is subdivided by year and group (MH=9.0, df = 1, P=0.003, N=2,449).

Group	Year	Proportion fruit	Proportion leaves	Proportion flowers and nectar	Total feeding time scores
JP	2007	0.51	0.24	0.25	1043
Piste	2007	0.50	0.37	0.14	1078
JP	2006	0.88	0.10	0.02	130
Piste/JJ	2006	0.81	0.16	0.03	198

Table 3. The number of individual trees (first number) and the percent of total group feeding time points spent consuming the following food items. The top five food items, based on the percentage of feeding time points, are listed for each group and year. Food parts consumed are: LM = mature leaves, FL = flowers, FRR = ripe fruit, FR = fruit, either ripe or unripe, LIM = immature leaves.

Family	Genus Species	Vernacular name	Part consumed	Piste 2006	JP 2006	Piste 2007	JP 2007
Malvaceae	<i>Dombeya sp.</i>	Alampona fotsy	LM, FL				2/5.7%
Lauraceae	<i>Potameia sp.</i>	Antaivaritra	FRR		4/7.1%		
Cluciaceae	<i>Symphonia fasciculata</i>	Azinina	FL				8/17.3%
Melastomataceae	<i>FRR, LIM</i>	Trotrobaritra	FRR			NA/11.0%	
Moraceae	<i>Ficus sp.</i>	Mandrisy				8/8.1%	8/19.4%
Moraceae	<i>Ficus sp.</i>	Nonosay	FRR		2/11.0%		
Strelitziaceae	<i>Ravenala madagascariensis</i>	Ravinala	Nectar	7/2.5%			
Lauraceae	<i>Cryptocarya sp. or Aspidostemon sp.</i>	Tapiky	FR	9/17.3%	4/7.1%		
Lauraceae	<i>Cryptocarya sp.</i>	Tavolo	FRR	8/2.5%			
Euphorbiaceae	<i>Domohinea perrieri or Tannodia sp.</i>	Tsivoangivoagny	FL, LIM, LM				7/7.1%
Clusiaceae	<i>Callopyllum milvum</i>	Vintanona	FRR			7/13.3%	9/25.2%
Clusiaceae	<i>Garcinia verrucosa</i>	Vongobe	FRR	71/41.6%	11/38.6%		
Fabaceae	<i>Dialium sp.</i>	Zagnamalotra	LIM, LM	5/3.5%		6/5.9%	
Fabaceae	<i>Dialium unifoliolatum</i>	Zagnamena	LIM, LM		4/8.7%	13/14.4%	

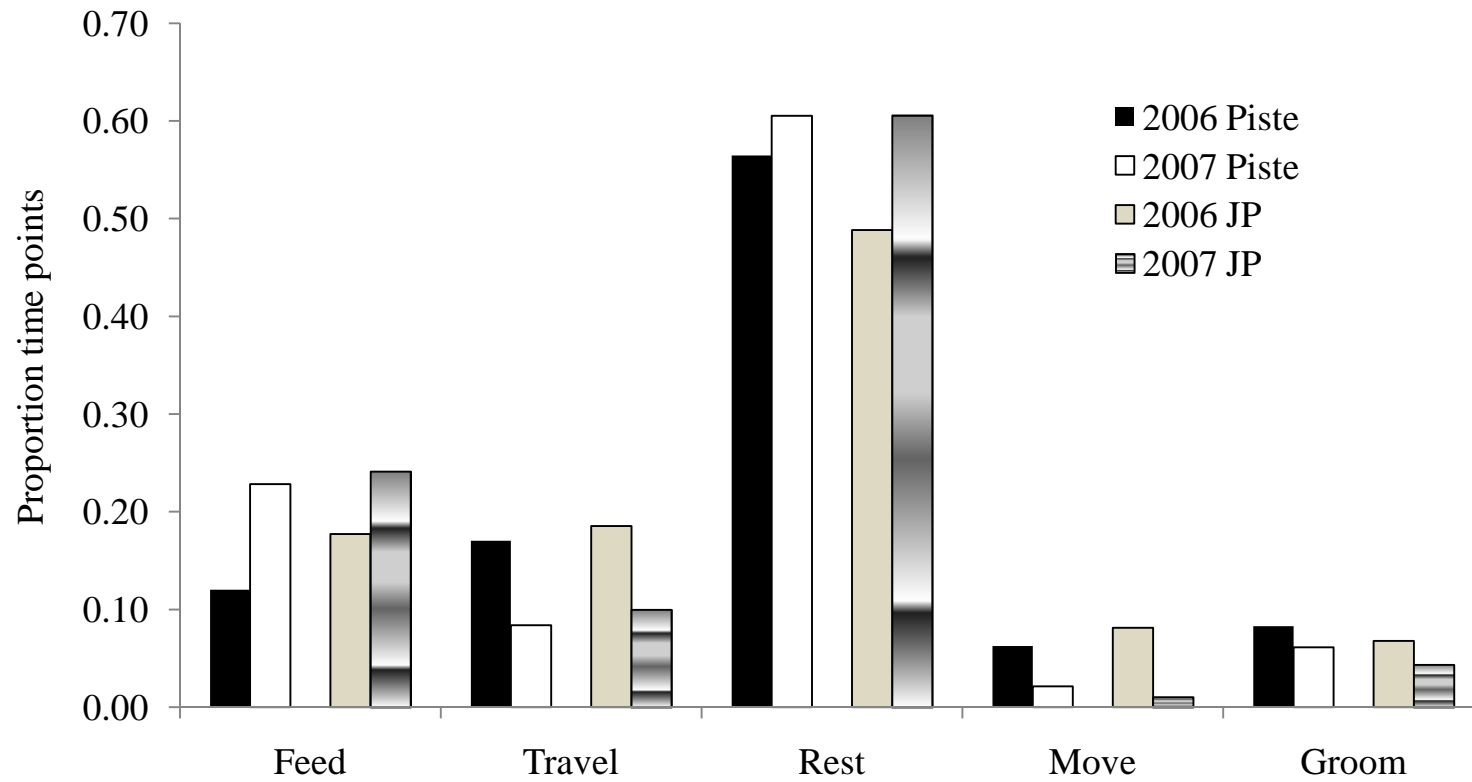


Figure 2. Activity budget of the two groups by season. MH=207.8, df=1, P<0.0001, N = 11,538 scores.

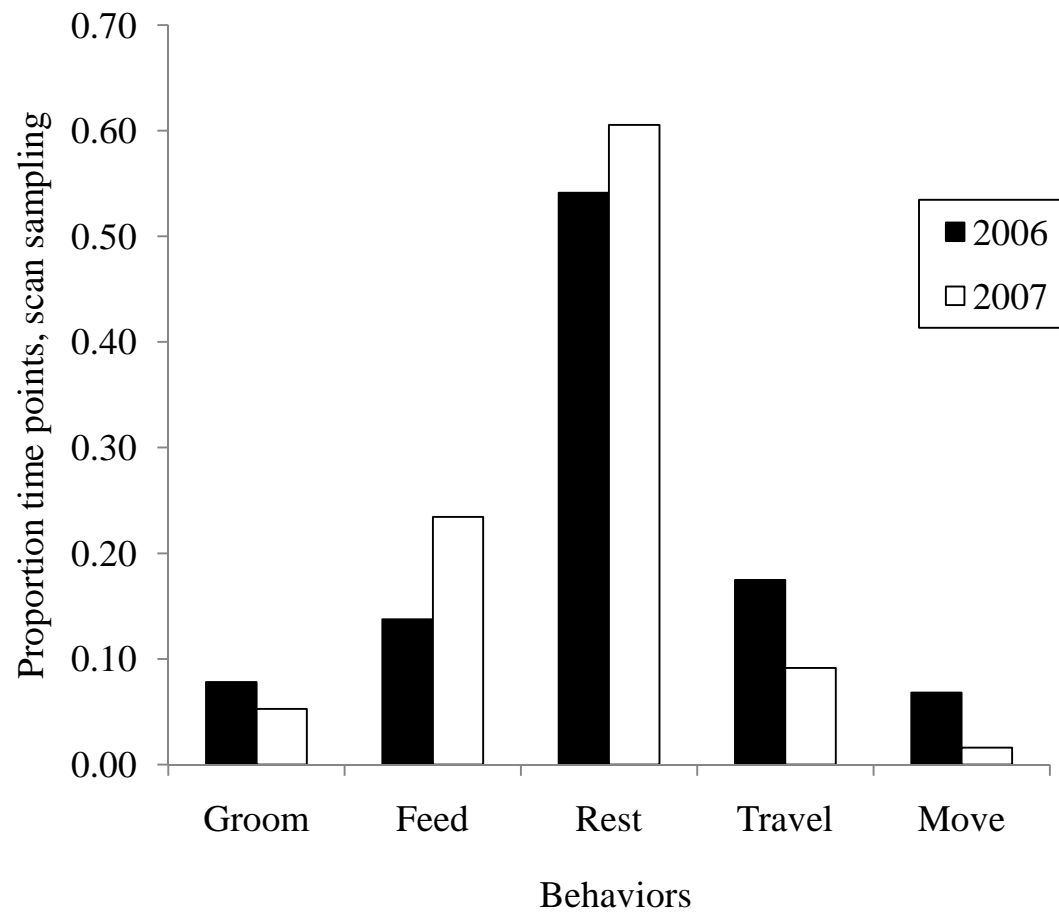


Figure 3. Activity budgets for adult *V. rubra* in 2006 and 2007, groups combined. Pearson's $\chi^2=433.5$, $df=4$, $P<0.0001$, $N=11,538$.

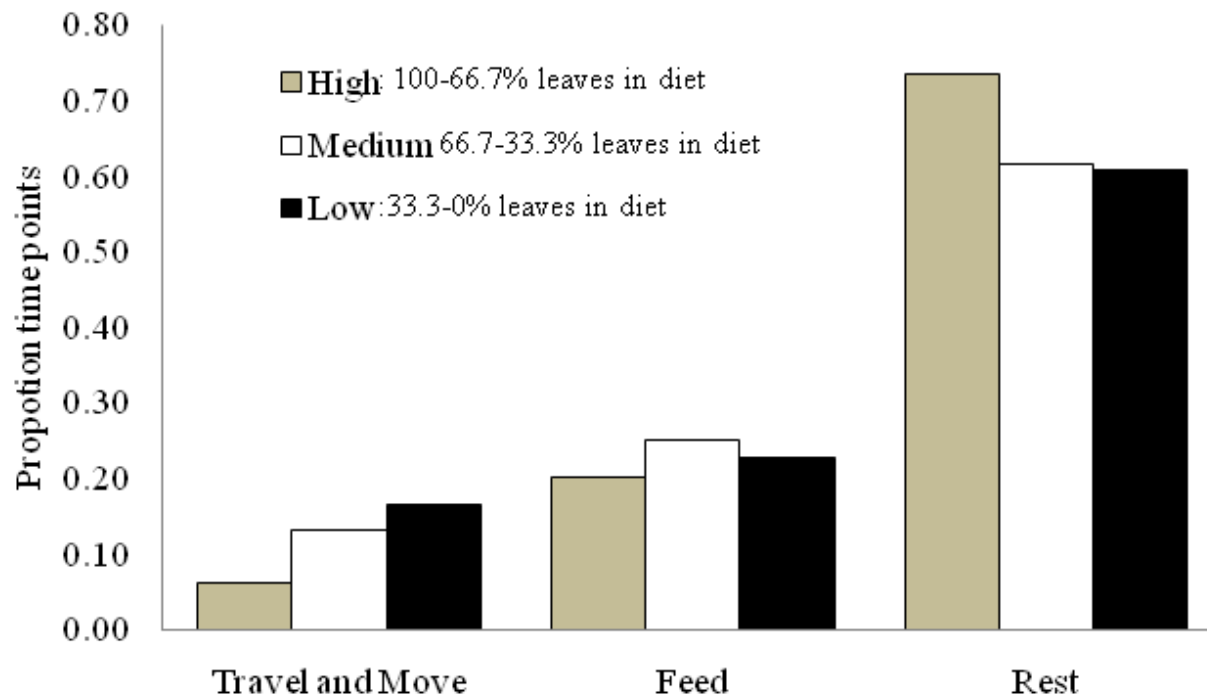


Figure 4. Daily activity budgets for adult *V. rubra* in both years based on the proportion of leaves in diet. High = 100-66.7%, Medium = 66.7-33.3%, Low = 33.3% - 0%. The remaining proportion of food in the diet is fruit, flowers, or nectar. Pearson's $\chi^2=124.6$, $df=4$, $P<0.0001$, $N=10,731$.

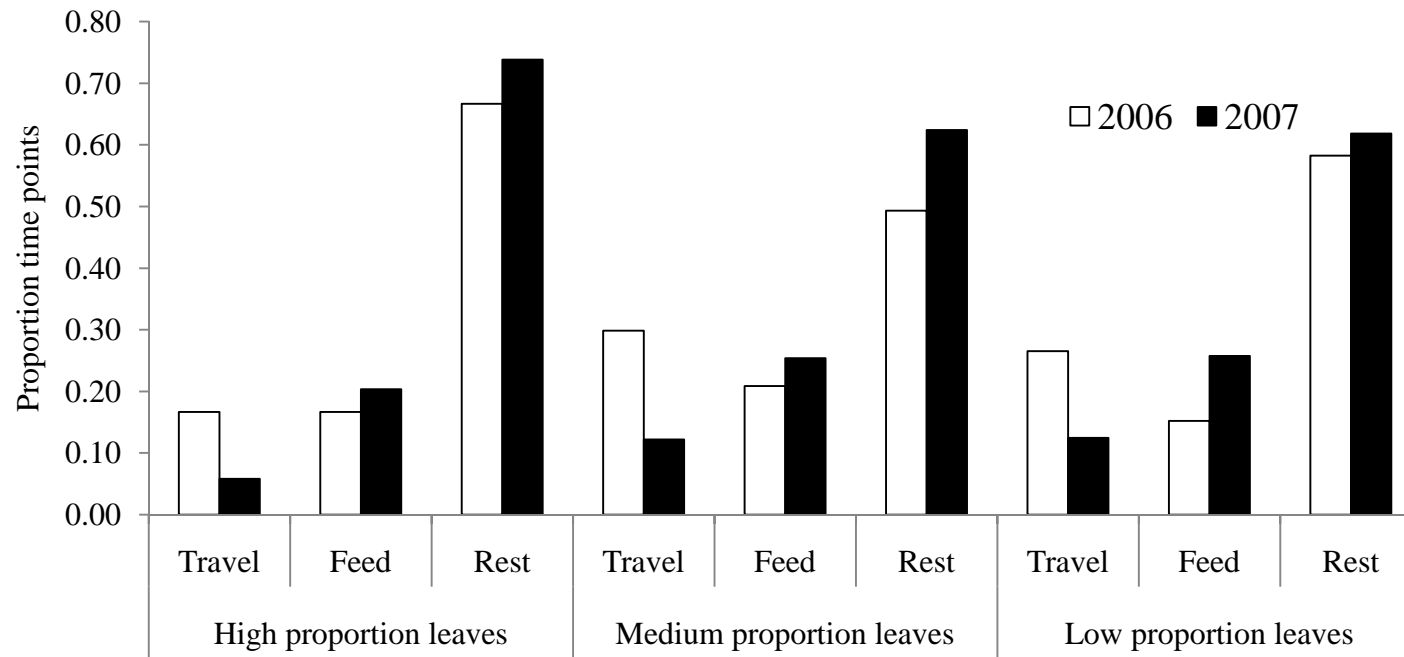


Figure 5. Activity budget of *V. rubra* by year and daily proportion of leaves in diet. CMH=836.4, df=2, $P < 0.0001$, N= 10,731 scores.

Table 4. Daily path lengths for each group by year, standard deviation, minimum and maximum distances in meters traveled during all-day follows (≥ 8 hour days). ANOVA table for the log daily path length for each group and year. The only statistically significant effects are the JP group in 2006; their daily path length differs from the mean from all combinations of groups and years at $785 \pm SD 435$ meters. The log daily path length of the JP group in 2007 is moderately significantly different from the mean—they had the smallest mean daily path length at $539 \pm SD 358$ meters.

Year	Group	Mean \pm SD	Minimum	Maximum	N days	Estimate	Standard error	t value	P
2006	Piste and JJ	758 \pm 278	79	1568	22	-0.1333	0.3585	-0.372	0.7106
2006	JP	785 \pm 435	436	1636	9	6.5757	0.302	21.774	<0.001
2007	Piste	826 \pm 582	60	3414	56	0.6646	0.4018	1.654	0.1005
2007	JP	539 \pm 358	0	1636	45	-0.6282	0.3308	-1.899	0.0598

Residual standard error: 0.906 on 128 degrees of freedom
 Multiple R-squared: 0.07495, Adjusted R-squared: 0.05327
 F-statistic: 3.457 on 3 and 128 DF, P-value: 0.01847

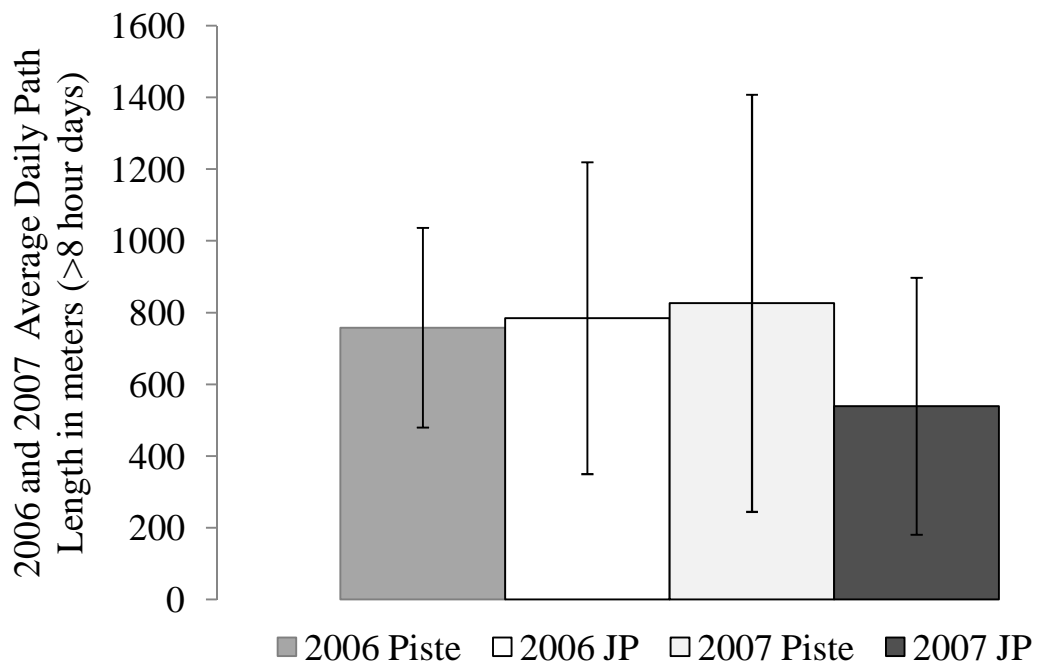


Figure 6. Daily path lengths in meters for each group by year with standard deviation bars. $F=3.457$, $df=3$ and 128 , $P<0.05$.

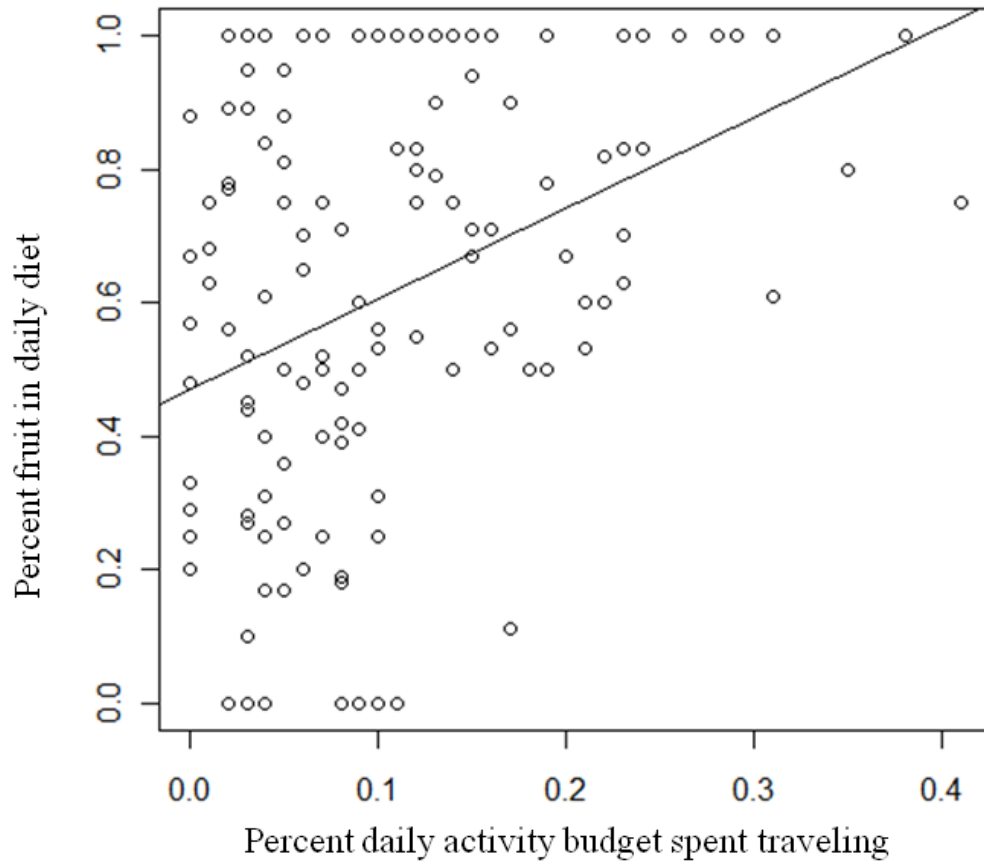


Figure 7. Correlation between the daily proportion of fruit in the diet of *V. rubra* groups and the proportion of time spent traveling during the daily activity budget. Correlation coefficient = 0.36, df = 130, $P < 0.0001$.

Chapter 2. Are lemurs able to assist in their own habitat restoration? Foraging and seed dispersal in the regenerating forest corridor at Ambatoladama, Masoala National Park, Madagascar

Introduction

More than half of the eastern evergreen rain forest in Madagascar has been converted to agriculture or secondary forest since 1953 (Dufils 2003). However, one site in Madagascar's Masoala National Park (MNP) is being restored to forest from former agricultural plots through a combination of forest plantings and the promotion of seed dispersing frugivorous lemurs.

Many frugivorous primates are important seed dispersers for tropical tree species (Estrada & Coates-Estrada 1984, Tutin *et al.* 1991, Chapman 1995, Dew & Wright 1998, Garber & Lambert 1998, Kaplin & Lambert 2002, Wehncke *et al.* 2003). In undisturbed sites, the foraging and ranging patterns of frugivores affect the spatial distribution of successful seedling recruits (Bleher & Bohning-Gaese 2001, Wehncke *et al.* 2003). The efficacy of a seed disperser, or the quality and quantity of dispersed seeds, affects the recruitment of plants and forest dynamics (Howe & Smallwood 1982, Schupp 1993). But dispersal effectiveness varies across primate species, depending on their physiology, behavior and morphology (Howe 1989).

Lemur species are important frugivores in the rain forests of Madagascar and they may be the primary seed dispersers in those forests (Dew & Wright 1998, Overdorff & Strait 1998, Birkinshaw 2001, Wright *et al.* 2005, Lahann 2007). Within MNP, the large-bodied frugivorous red-ruffed lemur, *Varecia rubra*, is considered to be a prime seed dispersal agent (Holloway 2000). However, few studies have actually examined the efficacy of seed dispersal by lemurs in Madagascar in degraded landscapes (Scharfe & Schlund 1996, Ganzhorn *et al.* 1999, Lahann 2007). In order to predict the success of a program that uses lemurs as agents in the restoration of their own habitat, research is necessary to understand the quality and quantity of seed dispersal by *V. rubra*.

Seed dispersal quantity is characterized by the amount and diversity of seeds defecated, including the diversity of taxa dispersed and the proportion of large to small seeds dispersed (Schupp 1993, Kaplin & Moermond 1998, Kaplin & Lambert 2002). Quality of seed dispersal affects the probability of recruitment of seeds to trees, including the processing of seeds in the disperser's mouth and gut, and the spatial pattern of deposition (Schupp 1993).

The present study evaluates whether the sustainability of a restoration project in the forest corridor at Ambatoladama, MNP (herein referred to as Ambatoladama), may be enhanced by the seed-dispersal capabilities of frugivorous lemurs. The site is a narrow forest corridor within a matrix of agriculture and secondary forest. Interspersed within the forest corridor are former agricultural parcels, which are now covered in secondary forest species and planted forest tree saplings, most of which were planted because they are suspected lemur foods. To quantify seed dispersal enhancement by the lemurs, I studied the behavior of the largest of the frugivorous species in MNP, *Varecia rubra*, specifically the quality and quantity of seed dispersal *sensu* Schupp (1993). I examined the spatial patterns of their food trees and dispersed seeds, in particular the proximity of passed seeds to the forest edge and regenerating parcels, the distance seeds are dispersed away from potential parent trees, germination success of passed seeds, and the diversity of passed seeds.

Previous studies suggest that *V. rubra* are primarily frugivores that spend between 86% (N=12 months) (Vasey 1997) and 74% (N=7 months) (Rigamonti 1993) of their foraging time on fruits. However, some physiological or behavioral barriers might inhibit *V. rubra* from dispersing seeds along the forest edge or into the regenerating parcels. Previous research has shown that *V. rubra* feed primarily on fruits within relatively tall and large trees (Vasey 2000b) and they have been characterized as sensitive to disturbed forests (Balko & Underwood 2005, Ratsimbazafy 2006). Of the lemurs studied in edge habitats, most are either "unwilling or unable" to travel through grasslands or agricultural fields between forest patches (Dehgan 2003, Lehman 2007). Finally, forest-dwelling primates might be more at risk of predation in open areas like the regenerating parcels and therefore avoid them (Duncan & Chapman 2002).

The main questions my research addresses are: How effective are red-ruffed lemurs as seed dispersers at a restoration site in MNP in terms of (1) quantity and (2) quality of seed dispersal, per Schupp (1993)? To evaluate quantity of seed dispersal, I assessed the proportion of fruit in the diet, the amount and diversity of seeds passed by *V. rubra*, the proportion of large to small and seeds passed by *V. rubra*, and the diversity of foods consumed by the lemurs compared to passed taxa. To explore quality of seed dispersal, I assessed the spatial pattern of seed deposition relative to the coarse scale land classes of the hard-edge of the forest and agricultural matrix, the regenerating parcels, and the hard-edge of the regenerating parcels and forest. I also assessed the probability that seeds are moved away from the potential parent tree and the germination success of passed seeds within an experimental nursery.

Methods

Study site

The Ambatoladama corridor is about 2.5 km by one km located in Masoala National Park (MNP) in northeastern Madagascar located between 50°0'5.83" east, 15°16'42.85" south and 50° 1' 38.15" east, 15° 17' 32.52" south (Figure 1). The vegetation is tropical dense evergreen forest and the altitude at the site ranges from 300-700 m. The climate of the peninsula is tropical humid with annual rainfall for the park ranging from 2200-7000 mm, relative humidity above 80%, and an annual temperature range of 21-24 °C (Hatchwell 1999).

There are about 15 subsistence farming households living within 1 km south and southwest of the border of MNP in the Ambatoladama region. The Wildlife Conservation Society (WCS) initiated a forest restoration project in the forest at Ambatoladama in 1997 called the *Masoala Corridors Restoration Project* (Holloway 2000). The forest at Ambatoladama is narrow, about 2.5 km in width, surrounded by agriculture and a matrix of secondary forests (*savoka*) of various ages (Figures 2&3). The forest at this location is referred to as a corridor since it physically connects larger forested sections of MNP. Prior to park creation, the corridor was occupied by subsistence farmers. Those former agricultural plots are now the regenerating parcels in the WCS-sponsored restoration program. The initial goal of the restoration project in 1997 was to entice frugivorous lemurs into the regenerating plots so they could disperse

seeds from interior forest trees (Holloway 2003). There are seven restoration parcels within MNP where park staff actively plant and maintain saplings, mostly of species expected to be lemur food trees, from 14 families (Figure 3; WCS, unpublished data). In 2006, with the exception of the oldest parcel, Parcel One, the regenerating parcels had a discontinuous canopy, an understory of native and non-native shrubs with a maximum height of two meters, few naturally-recruited remnant trees that were left standing while the area was in agriculture, and lines of planted saplings ranging in age up to eight years old. A recent report noted a closed canopy in Parcel One and fewer *Afromomum angustifolium* (Zingiberaceae) shrubs in the understory, but the maximum age of planted trees was ten years at the time of this study (Holloway 2008).

Savoka is the Malagasy term used to describe land that was formerly used for rice cultivation and is currently fallow. Typically rice is grown for one season and then the land is left fallow for 3-8 years; pioneer secondary forest vegetation takes about 7-8 years to grow to three meters in *savoka* (Dokolahy 2004). *Savoka* of different ages (20-42 years old) in the corridor at Ambatoladama all have the shrub *A. angustifolium* in common (Dokolahy 2004). Other common species found in *savoka* are the non-native shrub *Clidemia hirta* (Melastomataceae), the tree *Harugana madagascariensis* (Clusiaceae), and the tree *Dombeya andapensis* J. Arenes (Malvaceae) (Dokolahy 2004; Martinez unpublished data). All of the regenerating parcels were *savoka* at the time of this study since they were all former agricultural plots; the areas of the parcels are noted in Figure 1. Some representative families of hardwood trees in the primary forest within the corridor include Pandanaceae, Ebenaceae, Clusiaceae, Euphorbiaceae, Sapotaceae, and Rubiaceae (Appendix 4). The agricultural matrix that borders MNP contains plantations of dry and wet rice, banana, vanilla, coffee, and patches of litchi, mango and clove trees.

Study organisms

The red-ruffed lemur (*Varecia rubra*) is endemic to the Masoala peninsula and is closely related to the black and white ruffed lemur (*Varecia variegata* spp.). *V. rubra* was recently declared a distinct species rather than a sub-species of *V. variegata* (Mittermeier *et al.* 2006) and *V. rubra* is classified by the World Conservation Union as “Endangered” (Andrainarivo *et al.* 2009). *V. rubra* is described as living in

multimale/multifemale communities with a fission-fusion social organization including subgroups, affiliates, core groups, and a community social network (Vasey 2006). During the study seasons at Ambatoladama, *V. rubra* appeared to range within core groups of two to six individuals (Table 1). Two of the core groups we observed (JJ and Piste) were likely part of the same community as their ranges overlapped and the females interacted socially. The third group, JP, was likely part of a separate community since they never overlapped with the other two core groups. In this paper, I refer to the core groups as “groups” and they are the unit of analysis. Groups were habituated from August-November 2006.

Behavior

From November 2006 through January 2007, teams observed the behavior of the three groups of *V. rubra* during either all-day sessions (called “follows”) between 06:00-18:00 or half-day follows between 06:00-12:00. In 2006, three observation teams were composed of BTM, an American field technician (Jeff Kloppenburg), or my colleague Mrs. Onja Razafindratsima, plus three local farmers trained to use GPS units, collect lemur feces, measure tree DBH, and track lemurs with radio telemetry equipment. In 2007, observation teams were composed of BTM, an American field technician (Claire Catania), two trained local farmers (Georges Betandra and Jean Charles), plus three local farmers trained to use GPS units, collect lemur feces, measure tree DBH, and track lemurs with radio telemetry equipment. All people collecting behavioral observations trained together with BTM until we were 95% in agreement of observed behaviors.

From November 2006-January 2007, we followed the groups on a rotating schedule of an all-day follow, a half-day follow, and a day of no observations. I will refer to this as the “2006 season.” One radio-collared adult female from the JJ group died in 2007 between January and August. This female had a prolapsed birth canal at the time of capture in 2006 and it did not heal during that season; her death was likely due to infection or complications from this ailment. From August-November 2007, we observed the behavior of two core groups, Piste and JP. I refer to this as the “2007 season.” We did not follow the third group, JJ, as the female that perished was the only one with a radio collar in her group. Two teams conducted all-day follows of both

groups simultaneously from three to six times per week. We opportunistically collected feces and feeding observations (limited to food patch location and food species) of the sympatric white-fronted brown lemur, *Eulemur albifrons*, but we did not have any habituated groups for collecting other behavioral data.

Teams collected the feeding behavior and seed dispersal data of the radio-collared adult females from the three groups. I focused on the adult females because in the genus *Varecia*, females are dominant to males in social and feeding contexts, therefore I expect the females to feed on preferred foods compared to males (Kaufman 1991, Morland 1991). We recorded all-occurrence feeding data (Altmann 1974) by the radio-collared focal females in each group; this method involved recording every feeding bout the focal female engaged in. Each time the focal female started to feed on an item, we recorded the start and end time of feeding, tree vernacular name, diameter at breast height (DBH), height of tree from ground, feeding height of focal animal, plant part eaten, GPS point of food tree (Garmin GPSMAP® 60CS), and forest type (primary, secondary, edge, or parcel). We attempted to collect every fecal sample from all lemurs during follows and a GPS point of the feces location. Fecal samples were stored in plastic bags and later washed at camp to extract and identify seeds. The length and width of seeds with a length greater than one millimeter were measured with calipers. We also collected the GPS locations of the lemur groups every ten minutes.

Analysis: quantity of seed deposition

The proportion of fruit in the diet is reported as the time the focal females spent foraging on fruits divided by the total time spent foraging on all foods. These data come from the all-occurrence feeding observations of the focal females. Food items in the analyses included the trees where we observed *V. rubra* focal females and associated group members feeding on the fruits, leaves, nectar or flowers for more than one minute. Previous studies show *V. rubra* feed on mature interior forest trees and some lianas (Appendix 3). I refer to the food items as patches, as lemurs fed in trees, lianas, and shrubs, and each food patch was stored as a GPS point in the dataset.

The number of seeds defecated by *V. rubra* was the sum of all seeds with a length greater than one millimeter extracted from all collected feces. Seeds less than one millimeter in length were counted as occurrences in feces and they were not included in

the reported value for the total number of seeds. A measure of diversity other than taxa was seed size. Seeds were classified into three categories per Dew and Wright (1998): large seeds were those greater than ten millimeters in length, medium seeds between five and ten millimeters in length, and small seeds less than 5 millimeters in length. Most food items and passed seeds were identified to the family level, as related taxa have similar seeds. We were not always able to collect voucher specimens of unknown food trees due to tree height. Finally, I also classified passed seeds with respect to their importance to forest restoration—whether they were novel within the parcels, planted within the parcels, or pioneer species already common within the parcels and along forest edges.

Analysis: quality of seed deposition

To determine the probability of seed deposition into the different land classifications, I first calculated the home range for each group by year using the minimum convex polygon (MCP) method. This was calculated within ESRI ArcMap 9.1 using the Hawth's Tools extension (Create Minimum Convex Polygons tool.) Every GPS location recorded for each group in both years was used to create the accompanying MCP (Figure 3). I divided the MCP into four land categories, which have assumed different probabilities of seed germination success and microclimates: the regenerating parcels, the ten meter parcel buffer, the ten meter forest edge buffer, and the remaining forest. A ten meter buffer was chosen to designate the edges since the average GPS error of all locations was 11.0 m (SD=5.0 m, N=764). Parcel edges differed from forest edges because most of the perimeter of the parcels was bordered by mature forest, whereas the forest edges bordered secondary forest and active agricultural fields. The final category, forest, was the remaining area within the corridor and MCPs that did not fall within parcels, parcel buffers, or forest edge buffers. The canopy in the forest category was generally continuous and the pioneer species found in the regenerating parcels (i.e. *Harungana madagascariensis* and *Afromomum angustifolium*) were rare in the mature forest. The areas of the parcels, ten meter parcel buffers, and ten meter forest edge buffers were also determined using Hawth's Tools (Polygon in Polygon tool) in ArcInfo 9.1. This tool calculated the area of overlap in the polygons of the buffers and parcels with the MCP polygons.

Spatial Distribution of passed seeds

A first measure of dispersal quality was the distribution of the number of feces containing seeds within the four land classes compared to the expected percentages based on the relative area of land classes for each group in both years. A second measure of dispersal quality was the spatial distribution of the occurrences of seeds in feces; this variable was calculated per feces, for example, if feces had five seeds of one taxon and 100 seeds of a second taxon, there would be two occurrences of passed seeds for the feces. A third analysis involved the amount of time lemurs spent in the four land types relative to the area of that land type. The variable “time spent” was the number of 10-minute time points during which the group associated with the focal female spent in a GPS location that was within one of the four land classifications. Differences by year and group for the above analyses were determined using a Chi-Square Goodness of Fit test. Data points for groups were either pooled or kept separate depending on whether the mean distances of food items to the forest edge or parcels differed significantly since that is an indication of whether the parcels and edges are within the home range of a group.

To include the information about seed deposition distances relative to the forest edge or parcel edges, I calculated the probabilities of the Euclidian distances between feces containing seeds to the nearest parcel edge and forest edge for each group in both years. Differences in distances were also determined by a Chi-Square Goodness of Fit test.

Seed dispersal relative to parent tree

For some tree taxa, the chances of seed germination and recruitment increase when seeds are dispersed away from the parent tree (Nathan & Muller-Landau 2000). I could not always confirm the parent tree of a passed seed, therefore, I calculated the probability of seed deposition away from conspecific “potential parent trees” using similar methods to previous studies of primate seed dispersal (Stevenson 2000, Lambert 2001, Wehncke *et al.* 2003). Seed taxa occurrences within feces were matched with food patches that had been fed upon by the lemurs earlier in the same day. Next, I calculated the probability distributions of the differences in foraging time to time of seed deposition for a measure of retention time. I also calculated the probability distribution

of the Euclidian distances from conspecifics to seed deposition sites. This latter analysis was not a measure of effective dispersal distance (distance of passed seed to nearest tree of the same species), but rather it was a measure of dispersal from a tree that was visited by the lemurs based on the time of foraging and time of deposition within the daily observational periods. Following the low-end of gut passage time as recorded in captive individuals, potential parent trees were those in which a seed of that taxon was passed at least 30 minutes after the start of foraging on that taxon (CabreVert & Feistner 1995). Since lemurs frequently fed on multiple trees of the same taxon on the same day, some passed seeds have multiple possible parent trees and these points were included in the distributions. Food patches were defined as those in which the focal females fed for at least one minute. The feces containing seeds in this analysis may have come from the focal female or other individuals in the group. The other individuals typically fed in the same tree as the focal female, but it was not always possible to identify the source of synchronously falling feces. All groups and years were pooled in this analysis.

Potential seed dispersal sites

I also determined the probability distributions of the first recorded distance and time to travel away from a food source after fruit consumption. I calculated the time difference and Euclidian distance from the foraging site to the first different GPS location where the lemurs traveled. The first GPS location was either a 10-minute scan location or the next food tree location that did not correspond with a 10-minute time point. The distribution does not reflect actual passed seeds, only movement of the lemurs away from the parent tree reflecting opportunities to pass seeds. When the distance moved was zero, lemurs remained in the foraging tree for at least 2.5 hours and until the end of the daily observation.

Germination success

The effect of seed processing via germination success was studied by my collaborator, Onja Razafindratsima, (Razafindratsima and Martinez, unpublished data). She created an outdoor nursery adjacent to the forest corridor within the agricultural matrix to study the difference in germination success of passed versus non-passed seeds. Passed seeds were cleaned and we collected an equal number of non-passed seeds of the same taxon; when this was not possible, those seeds were left out of the

statistical analysis. Following the methods of the park staff who maintained the nursery, seeds were placed on the top of non-forest soil and covered with river sand one millimeter thick to minimize insect predation and to keep a more constant temperature. The seedlings in the nursery were shaded by a roof of *Afromomum* leaves that withered and eventually fell off over time; this cover was not replaced. We collected seeds from feces and trees between November 2006 and January 2007. Seedling germination was monitored on a monthly basis until September 2007. Local guides collected data on time of germination and seedling height.

Results

Quantity of seed deposition: frugivory and distribution of food patches

Groups were observed for a total of 65,911 minutes during the follows (daily mean = $588 \pm \text{SD } 124$ minutes) over 99 days in 2006 and 2007 (Table 1). Based on the focal behavior data, the Piste group in 2006, pooled with the JJ group, spent 87% of foraging time consuming fruit and 10 % leaves (N=2,180 minutes). However, in 2007 the Piste group spent less time consuming fruit, 48%, and more time consuming leaves, 39%, than in 2006 (N=8,776 minutes). The JP group in 2007 had a similarly low percent of time consuming fruit, 53%, and 26% of foraging time feeding on leaves (N=6,466 minutes) compared to 2006 with 87% foraging time eating fruit and 10% eating leaves (N=717 minutes) (Table 2). There was a significant difference between the time spent feeding on leaves, fruits, or other items by year and group (Mantel-Haenszel χ^2 test: $\chi^2 = 341.96$, $P < 0.0001$, $df=1$, N=18,139 minutes). This is driven mainly by the significant difference in the diets of the JP and Piste group in 2007 ($\chi^2=320.69$, $P < 0.0001$, $df=2$) and the significant difference between the diets in 2006 and 2007 ($\chi^2=1352.69$, $P < 0.0001$, $df=2$); the diets are the same by groups in 2006 ($\chi^2=1.17$, $P=0.55$, $df=2$). The Piste group spent more time consuming leaves and less time consuming fruit than the JP group in 2007.

V. rubra fed on taxa from 31 different plant families in both seasons (Appendix 1). They passed the seeds of at least 28 and 19 different fruit taxa in 2006 and 2007 respectively, not including the unidentified seeds (Appendix 2). One particular food taxon dominated the diets of *V. rubra* in 2006, the ripe fruit of *Garcinia verrucosa*

(Cluciaceae) (45%, N=2,897 minutes). *V. rubra* ate the fruits of *G. verrucosa* whole or in large bites (Table 3). The three groups of *V. rubra* visited 95 different *G. verrucosa* trees, comprising 41% of all food patches visited by all groups in 2006 (N=231 food patches). *V. rubra* was not the only species dispersing the seeds of *G. verrucosa*: 38% of the opportunistically collected feces of the sympatric white-fronted brown lemur, *Eulemur albifrons*, contained *G. verrucosa* seeds (N=45 feces). The mean number of *G. verrucosa* seeds per feces was $2.3 \pm \text{SD } 1.8$ (N=400 seeds in 169 feces). The seeds were relatively large, with an average length of $34.9 \pm \text{SD } 3.7$ mm (N=435; Razafindratsima and Martinez, unpublished data).

The second most frequent food source consumed in 2006 was the fruit of *Cryptocarya* sp. (Lauraceae) at 8% of their foraging time. *V. rubra* did not store any seed species in their cheeks as other primates do; I observed them dropping seeds while feeding, but it was not clear if those seeds were processed in the lemurs' mouths to define the handling as "spitting" (Lambert & Garber 1998).

In 2007, the two most frequently consumed foods were the ripe fruits of *Callophyllum milvum* (Cluciaceae) (18%, N=15,205 minutes) and the young leaves and ripe fruits of a *Ficus* species (Moraceae) (13%) locally called "Mandrisy" (Table 3). The fruits of *C. milvum* contained one seed and are readily depredated beneath the parent tree by an unidentified insect (Martinez personal obs.). *V. rubra* fed in the parent tree, eating fruits whole and they appeared to swallow seeds whole rather than masticating or spitting seeds. The two lemur groups fed on 16 individual *C. milvum* trees, comprising only 5% of the total food patches (N=307 trees). *E. albifrons* also fed on this taxa and dispersed the seeds; 21% of collected feces contained seeds of *C. milvum* (N=127).

Distribution of food patches

The mean distances of food patches fed in by group and year to the forest edge differed significantly (Anova: $F=18.8$, $df=3$ and 520 , $P<0.001$). There was a significant effect of group and year with the distance to the edge, with the JP group in 2006 foraging on food patches closer to the forest edge than (Tables 4 and 5). Likewise, the mean distances of food patches by group and year to the nearest parcel edge differed significantly (Anova: $F=52.76$, $df=3$ and 488 , $P<0.001$, Table 6). There was a

significant effect of year and group on the mean distance of food patches to the parcel edge, with the Piste group in 2007 foraging in patches closest to the parcel edges. In 2007, the Piste group foraged in 187 food patches (trees or shrubs) within the corridor representing 46 unique taxa in 21 families (Table 2). Of those patches, only two grew within 10 m of the forest edge, but both were also located within a regenerating parcel, and the mean distance to the nearest forest edge of food patches was $263 \pm \text{SD } 105$ m (N=187). Likewise, 4% of food patches grew in the 10 m parcel edge buffer with and the mean distance of all food patches was $74 \pm \text{SD } 41$ m (N=158) to the nearest parcel edge (excluding patches growing within the regenerating parcels). This group foraged on 11 unique food taxa from eight different families within four of the seven regenerating parcels. Most of the food patches were fruits, 45% (N=28 patches), and 70% of the feeding bouts were spent consuming fruits of the non-native pioneer species, *Clidemia hirta* (Melastomataceae) (Table 7).

Diversity of passed seeds

We extracted 2,125 passed seeds with a length greater than one millimeter from 569 fecal samples in 2006-2007. Disseminated seed taxa belonged to 14 families distributed into 46 unique taxa, but eight could not be identified (Appendix 2). The percentage of taxa of passed seeds from the fruit we observed being consumed in 2006 and 2007 was 61% and 57% respectively. Zero to four seed taxa were extracted per feces. Average passed seed size, excluding those less than one millimeter in length, was considered “large” at $21.5 \pm \text{SD } 9.2$ mm in length by $13.7 \pm \text{SD } 4.5$ mm in width (N=2,106; Appendix 2), based on previously published seed size classes (Dew & Wright 1998). The largest passed seed taxon was represented by a liana named locally “Vahanonoka,” *Ampelosicyos humblotii*, (Cucurbitaceae) with a mean length of $47.84 \pm \text{SD } 1.66$ mm and width of $24.71 \pm \text{SD } 3.44$ mm (N=19). Results demonstrated that 66 % of collected seeds fell in the “large” size category with a width between 10 – 20 mm and 41% with length 20 – 30 mm (Razafindratsima and Martinez, unpublished data).

Quality of seed deposition: locations of passed seeds

The home ranges of the groups in both years, as determined by the minimum convex polygons, overlapped with some regenerating parcels, the 10 m forest edge buffers, and the 10 m parcel buffers (Table 8).

Seed dispersal by group: Piste and JJ group

In 2007, feces containing seeds passed by the Piste group were not distributed in space randomly relative to the areas of regenerating parcels, 10 m forest edge buffers, 10 m parcel buffers, and forest within the MCPs ($\chi^2=21.77$, $P=0.0001$, $N=331$) (Table 8). Most feces with seeds were passed in the forest outside of the parcels, while slightly fewer than half the number of expected feces with seeds fell into the parcels (28 of 58). In 2006, the deposition of feces with seeds did not differ significantly from the null hypothesis of random distribution by land class ($\chi^2=4.95$, $P=0.1753$, $N=137$).

The Piste group in both years spent significantly different amounts of time than expected in the four land classes relative to their area (Figure 4). The Piste group spent more time in the 10 m parcel buffer than expected (609 vs. 231 time points, $\chi^2=796.01$, $P<0.0001$, $N=3,818$). In 2006, the Piste group also spent more time than expected in the 10 m parcel buffer (41 vs. 24 time points, $\chi^2=64.96$, $P<0.0001$, $N=1,190$). These values indicated that lemurs passed seeds in regenerating parcel buffers and the forest slightly more than expected, but they passed seeds four times less than expected into the 10 m forest edge buffer and 1.8 times less than expected into the parcels. They appeared to be avoiding the forest edge and parcels based on seed defecation data.

The Piste group in 2007 dispersed feces with seeds on average $57\pm SD 40$ m from the nearest parcel edge (excluding feces with seeds passed in the parcels, $N=309$) and $216\pm SD 91$ m to the nearest forest edge ($N=331$, Figure 5, Table 9). In 2006, the Piste group dispersed feces with seeds on average $121\pm SD 84$ m (excluding feces with seeds passed in the parcels, $N=114$) and $332\pm SD 144$ m ($N=115$) to the nearest parcel edge and forest edge respectively.

The Piste group in 2007 dispersed the most seeds into the regenerating parcels but overall the number was not large—within 28 feces there were 48 instances of seeds from at least 8 taxa and 6 families (Table 10). Half of the taxa were already planted in the parcels and most of the seeds, 63%, were in the small size category. In 2007, V.

rubra fed more on leaves, flowers, and nectar and the fruits of the non-native pioneer shrub *Clidemia hirta* (Melastomataceae) (7%, N=15,247 minutes) than large-seeded interior forest species. We observed only the Piste group foraging on *C. hirta*. The lemurs ate the fruits whole, choosing the purple, ripe fruits (Figure 6). *V. rubra* foraged within Parcel Two for extended bouts, up to $115 \pm \text{SD } 30.5$ minutes (mean=29 min, N=38 bouts).

JP group

The locations of the JP group's feces with seeds were not randomly distributed by land classification in 2006 but they were randomly distributed in 2007 (2006: $\chi^2=18.51$, $P=0.0003$, N=72; 2007: $\chi^2=11.14$, $P=0.01$, N=190; Table 8). Most of the feces with seeds fell within the forest and not in the regenerating parcels, 10 m parcel buffers, or 10 m forest edge buffers.

In an analysis of actual time points spent in the different land classes relative to area, the JP group in 2007 spent significantly different amounts of time than expected in the four land classes relative to their area; slightly more time was spent in both the 10 m edge buffer (61 vs. 53 time points) and the forest (2548 vs. 2449 time points) ($\chi^2=145.0$, $P=0.00$, N=2633; Figure 4). The JP group in 2006 did not spend a significantly different amount of time than expected in the land types ($\chi^2=5.7$, $P=0.13$, N=908).

The JP group in 2007 passed seeds on average $318 \pm \text{SD } 233$ m from the nearest forest edge (N=190) and $297 \pm \text{SD } 219$ m from the nearest parcel edge (excluding feces passed in parcels: N=188). In 2006, JP feces with seeds were passed closer to the forest and parcel edges: $220 \pm \text{SD } 79$ m (N=71) and $144 \pm \text{SD } 53$ m (N=71) respectively.

Groups combined

When the data for both seasons and all groups were pooled and the analysis was by the occurrences of seeds rather than feces with seeds, I found there was a significant difference in the locations of passed seeds ($\chi^2=34.1$, $P<0.0001$, N= 1,105; Table 11). *V. rubra* passed seeds in the forest and 10 m parcel buffers slightly more than expected. They passed seeds four times less than expected into the 10 m forest edge buffers and 1.8 times less than expected into the parcels.

Distances of passed seeds from potential parent trees

For all groups in both years, the median distance *V. rubra* carried seeds from conspecific trees was 36 m (mean=73 m, SD=107 m, N=1,281 occurrences). A large percentage of seeds, 42%, fell within 10 m of a conspecific adult tree. The farthest distance a passed seed was moved from a conspecific adult was 582 m. When the seeds passed between 0-30 minutes from feeding on a conspecific were removed from the analysis, the median distance that seeds were deposited away from the potential parent trees (or conspecific) was slightly more at 43 m (mean=81 m, SD=111 m, N=1,141 occurrences; Figure 7). Thirty minutes after the start of feeding, the percentage of seeds that fell within 10 m was still relatively high at 38% but the majority, 62%, of seeds were dispersed at least 10 m away from the parent tree (Figure 7).

Based on an analysis of the most likely parent tree for passed seeds, the median time from fruit consumption to when seeds show up in feces was 185 minutes (about 3 hours; mean=203 minutes, SD=141 minutes, N=1,332). However, this included seeds that were theoretically passed between 0-30 minutes. When these values were removed from the analysis (11% of the points), the median time to passing seeds was slightly longer at 208 minutes (about 3.5 hours; mean=227 minutes, SD=133 minutes, N=1,187; Figure 8). Only 35% of the seeds showed up in feces during the gut passage range found by CabreVert and Feistner (1995) between 30 minutes to 2.5 hours in a captive group of *Varecia*.

The median distance to the first recorded location of the groups after feeding on fruits in both years was 45 m (mean=64 m, SD=64 m, N=709 locations; Figure 9). For a small percentage of the feeding observations, 5%, lemurs moved only between 1-10 m from the foraging location after consuming fruits. In 4% of the observations, lemurs did not move away from the food tree between 2.5 hours to the end of the observational period for that day.

The median time it took for lemurs to move away from a fruit tree was 31 minutes (mean=74 minutes, SD=97 minutes, N=689 locations; Figure 10). Assuming a gut passage rate of 30-150 minutes (CabreVert & Feistner 1995), 36% of the observations occurred within this interval. For 51% of observations, the lemurs left the

parent tree before 30 minutes, and by 150 minutes 85% of the observations show the lemurs moved away from the parent tree.

Germination success

In the nursery, 65% passed seeds germinated (N=444) whereas 41% of non-passed germinated (N=430). Seeds that passed through the gut of *V. rubra* had greater germination success than non-passed seeds ($\chi^2 = 44.561$, $df = 1$, $P = 0.0001$, $N = 874$, Razafindratsima and Martinez, unpublished data).

Discussion

Quantity of seed deposition: Frugivory rate and diversity of passed seeds

The degree of frugivory of *V. rubra* varied between the two study periods in 2006 and 2007; the study periods were not the same seasons, and these observations show that the time frame of a study can produce different conclusions about the efficacy of primates as seed dispersers. The previously published diets of *Varecia* species reported high rates of frugivory (Rigamonti 1993, Dew & Wright 1998, Vasey 2002) (Table 12), but during the 2007 season at Ambatoladama, *V. rubra* spent much less time consuming fruit. However, when *V. rubra* did feed on fruits, the present study shows they passed seeds and moved them away from the suspected parent food patch. Also, when there are multiple and synchronous patches of food, as in *G. verrucosa* in 2006 (95 known feeding patches), *V. rubra* effectively increased the seed shadow of consumed seeds from this taxon and others. They moved between patches and did not concentrate their feeding effort in one location.

It is important to note that most of the seeds passed by *V. rubra* fell within the “large” seed category (length greater than 10 mm). Previous studies have found that fruits with a single large seed have fewer potential seed dispersers (Kitamura *et al.* 2002). In MNP, *V. rubra* is likely the only mammal to consume and disperse seeds away from the parent trees of the largest fruits and seeds given their relatively large gape; the cranium size of *Varecia* spp. is 104.7 mm versus 88.5 mm for *Eulemur fulvus* (Tattersall 1982), the latter being similar in size to the other large frugivore in MNP, *E. albifrons*. The diversity of dispersed seeds by *V. rubra* at Ambatoladama was much like that of *V. variegata* at Ranomafana (Dew & Wright 1998) (Table 10). Compared to

sympatric species, *V. variegata* consumed the greatest diversity of foods, passed mostly “large” seeds, and passed 77.8% of consumed seeds intact (Dew & Wright 1998). Likewise, *V. rubra* in this study consumed a diversity of fruit taxa, passed mostly “large” seeds, and passed the intact seeds from 60.9% of consumed fruits. Elsewhere, large-seeded tree species tend to be canopy or primary forest species (Kitamura *et al.* 2002).

Dispersal quality: Use of the parcels and edges

It is expected that in a regenerating rain forest the spatial distribution of food patches and the home ranges of dispersers will affect the survival probability of dispersed seeds (Schupp 1993). Project managers at Ambatoladama designed the restoration program under the assumption that the lemurs would disperse seeds into the regenerating parcels or along the hard edge of forest and agriculture. This idea was integrated into the original restoration plan when park employees planted a mixture of lemur food patches, fast growing trees, trees used sustainably by local farmers, and trees locally threatened or over-exploited by people (Holloway 1997). The first trees for the restoration program were planted in 1997, and in 2006 trees planted in the oldest Parcels (Parcels One and Two) had an average height of 3.6 m and an average DBH of 4.4 cm (WCS, unpublished data). However, none of the trees planted in the parcels were producing fruit during the 2006-07 field seasons.

Instead, the lemurs were drawn into the parcels by the fruits of the non-native shrub species *C. hirta*, the ripe fruits of one remnant *Ficus* sp. tree, ripe fruits of one remnant *Callophyllum* sp. tree, and the mature leaves of at least two *Croton* sp. trees (Euphorbiaceae). This is not what the park managers expected, but it is not to say that the restoration program is a failure. As the trees in the parcels mature, we now know *V. rubra* is not behaviorally averse to foraging in the open areas. *V. rubra* obviously feeds on a diversity of fruiting trees and is dispersing seeds around its home range. When fruits from interior forest trees are scarce, as was apparently the case during the 2007 season (Martinez, unpublished data), *V. rubra* will supplement their diet with leaves, flowers, or nectar and the fruits of the non-native pioneer shrub *C. hirta*.

At Ambatoladama, the largest patches of *C. hirta* were found in Parcel Two. *C. hirta* grows close to the ground with a maximum height of 2 m in the parcel, and lemurs

forage while locomoting quadrupedally on the ground. Parcel Two is also characterized by an open canopy where planted trees averaged 2.5 m in height in 2006 (WCS unpublished data). We observed only the Piste group foraging on this shrub. Previous field studies found that *V. rubra* spent 94% of its time in the tree crowns and fed on the fruits or leaves of relatively large trees, with a year-round average DBH of 50 cm (Vasey 2000b, 2002). The observations at Ambatoladama suggest that in a degraded landscape, *V. rubra* is not behaviorally restricted to foraging in tall trees within the forest. This is also not the first observation of *Varecia* sp. feeding on *C. hirta*. At a more southerly site in Madagascar the closely related *V. variegata* was observed feeding on *C. hirta* after most of the lemurs' habitat and interior forest food patches were destroyed by a cyclone (Ratsimbazafy 2006).

The most recent report on the restoration project noted that the original design strategies to lure seed dispersing lemurs into the parcels were overlooked, including (1) creating funnels from the forest edge leading into the parcels, (2) planting a suite of tree species that fruit year round, and (3) creating “a network of linked clusters of planted trees” (Holloway 2008). However, without these design elements, lemurs ventured into Parcels One, Two, Three and Four to feed on either remnant trees or *C. hirta*. Foraging in patches of *C. hirta* in Parcel Two required extensive terrestrial travel. In Parcels One and Three the lemurs foraged on trees within 5 m of the parcel edge, which did not require extensive travel through secondary forest vegetation. In Parcel Four, the lemurs foraged on a large fruiting *Callophyllum* tree, which required a combination of terrestrial and arboreal travel through young secondary vegetation and the planted trees. Perhaps with the design elements in place the lemurs would use the parcels more efficiently and disperse more seeds. However, with ten years into the restoration program, it is beneficial that *V. rubra* is behaviorally flexible to feed and travel within patches that are not mature forest.

Other animals forage on *C. hirta* and are therefore probably also passing interior forest seeds into the parcels. I found that 52% of the feces of *E. albifrons* contained the seeds of *C. hirta* in 2007 (N=127 feces). Because the fruits and seeds are small, 9-10 mm in length and 0.5 mm diameter, a number of other fauna forage on this fruit and disperse the seeds, including birds (Wester & Wood 1977, Linnebjerg *et al.* 2009) and

the seeds of *C. hirta* have better germination success once they passed through the gut of a bulbul (Linnebjerg *et al.* 2009). Each fruit contains 700-1,200 seeds, thus a foraging bout on *C. hirta* results in a greater number of seeds dispersed compared to an equal bout on a large-seeded forest tree like *G. verrucosa* or *Callophyllum* sp. There were too many *C. hirta* seeds in *V. rubra* feces to quantify, on the order of a thousand seeds per feces. The ecology of *C. hirta* has not been studied in depth in Madagascar. However, in Hawaii the shrub is known to germinate and thrive in areas ranging from full sunlight to 100% canopy cover (Wester & Wood 1977). I did not quantify ground cover in the corridor at Ambatoladama but anecdotally, *C. hirta* grows in the forest in light gaps, and it is most dense in open areas like Parcel Two, *savoka*, and the forest edge.

There are positive and negative aspects to lemurs feeding on and dispersing the seeds of *C. hirta*. In the short-term, foraging on *C. hirta* is beneficial for the restoration project at Ambatoladama since *C. hirta* provides fruits year-round (Wester & Wood 1977) and draws lemurs into at least one parcel, allowing the opportunity to disperse the seeds of forest trees. Elsewhere, studies found that early-successional shrubs were important for the initiation of forest regeneration (Nepstad *et al.* 1991, Vieira *et al.* 1994, Zahawi & Augspurger 1999, Duncan & Chapman 2002). However, during the present study, *V. rubra* tended to carry the seeds of *C. hirta* back into the forest and add to the seed bank. Since this plant grows densely in open areas, it could out-compete interior forest species in light gaps, affecting the future structure of the forest, as the success of dispersed seeds is limited by the existence of invasive plants at Ambatoladama (Dokolahy 2004).

Dispersal of seeds into Parcels and forest edges

In degraded landscapes, a major factor preventing forest regeneration is the lack of seed dispersers in the degraded areas (Nepstad *et al.* 1991, Holl *et al.* 2000). A logical expectation is that large-bodied vertebrate frugivores will be important agents in the restoration of their habitat by dispersing large-seeded forest tree species into degraded areas (Kaplin & Lambert 2002). This was the assumption behind the success of the restoration program at Ambatoladama. Although the Piste group spent time foraging and resting in the parcels on multiple occasions, the actual time points indicated that all

groups avoided the regenerating parcels and they avoided ranging within 10 m of the forest edges; finally, they were never observed in the non-forest matrix (i.e. the active agricultural patches). When lemurs did range within the regenerating parcels, a majority of the passed seeds were in the “small” seed size category, like *Ficus* sp. and *C. hirta*, and only one dispersed seed taxon was novel compared to what was planted in the parcel (Table 10). A similar scenario was observed in degraded patches within Kibale National Park; only 14% of seeds dispersed by all seed vectors in degraded agricultural plots adjacent to forest were tree species, and 99.9% of those seeds were early-successional species that were already established in the agricultural plots (Duncan & Chapman 1999).

There was likely overlap in the most commonly *V. rubra*-dispersed seeds into the parcels at Ambatoladama. Elsewhere in Madagascar, fruit bats, *Pteropus rufus* and *Eidolan dupreanum*, consume fruits and pass seeds of *Ficus* spp. (Long & Racey 2007, Picot *et al.* 2007). Also, *E. dupreanum* pass seeds within the range of 0.9-6.9 mm (Picot *et al.* 2007), in the small and medium categories. Both bat species are present in MNP (MacKinnon *et al.* 2003) and probably also disperse the smaller seeds at Ambatoladama. Further study is necessary on the seed rain into the parcels by all seed vectors (Holloway 1997). Studies of this type have not yet been implemented at Ambatoladama.

Spatial distribution of dispersed seeds and germination success

A large percentage of seeds fell within 10 m of a conspecific adult tree but more seeds were dispersed at least 10 m away from the parent tree. It is significant that most of the seeds were passed at least 10 m away from the potential parent tree or a fruiting conspecific since elsewhere in the tropics seed survival is greater when seeds are moved at least 5 m away from the crown of an adult conspecific (Schupp 1988). However, there is also evidence that the Janzen-Connell model of density dependent mortality of seeds under the parent tree does not apply to all forest tree species (Chapman & Chapman 1996, Lambert 2001). Germination success of a large-seeded tree species in Uganda relied more on whether the red-tailed guenon (*Cercopithecus ascianus*), cleaned the pulp off of fruits before spitting the seeds under the parent tree; the cleaning avoided fungal infections of the seeds (Lambert 2001).

In captive studies, *V. rubra* has a relatively short gut retention time of 0.5-2.5 hours (CabreVert & Feistner 1995). This attribute may not ensure wide (or long) seed shadows of trees unless the animal travels away from a food tree soon after a feeding bout. In this study, nearly 50% of the observations revealed that after 30 minutes, lemurs had moved away from the parent tree, therefore *V. rubra* does have the potential to disperse seeds some distance from parent trees, creating lengthened seed shadows. *V. rubra* lies on the low end of the spectrum of frugivorous primate gut retention times. For example, guenons (*Cercopithecus* sp.), have average gut retention times of greater than 26 hours (Maisels 1993, Lambert 1997), *Lemur catta* has an average gut retention time of 4.8 hours and *Hapalemur* spp. average 18.2 hours (CabreVert & Feistner 1995). Gut retention time is influenced by feeding frequency, ambient temperature, reproductive state, and age (Lambert 1998) and seed characteristics (Tsuji *et al.* 2010). Results from this study suggested a mean gut retention time for seeds of 3.8 hours (227±SD 133 minutes). Although this relatively short gut retention time, the probability that *V. rubra* moved at least 10 m away from the parent tree after 3.8 hours was 0.86.

The nursery study showed that passed seeds germinated more successfully than seeds extracted from fruits. A number of other studies found similar results regarding seeds passed by primates (Dew & Wright 1998, Lambert 2001, Stevenson *et al.* 2002, Wehncke & Dalling 2005, Valenta & Fedigan 2009). We know that seeds at Ambatoladama have a greater germination success in *savoka* (Holloway 1998). Therefore, it would seem that successful restoration of the parcels at Ambatoladama depends on lemurs dispersing seeds away from the parent tree into open areas. Perhaps the recruitment of particular trees benefits from the short gut-retention time and the probability that lemurs do not move away from the food tree before seeds are passed. A deeper analysis by tree taxa is necessary to support this hypothesis.

Conclusions

In many ways, *V. rubra* can be a useful agent in its own habitat restoration at Ambatoladama: (1) they passed more than half of the seed taxa consumed, (2) they dispersed mostly large-sized forest species, (3) a significant fraction of the seeds are dispersed at least 10 m from the parent tree, (4) they entered the regenerating parcels to access food sources, (5) they do not always remain in food patches beyond gut retention

time, and (6) passed seeds are more likely to germinate than non-passed seeds. In other ways, *V. rubra* are not the most effective seed dispersers for habitat restoration: (1) the average gut retention time is relatively low compared to other primate seed dispersers, (2) the probability was still relatively high that seeds would fall under the parent tree or a conspecific, (3) they avoided forest edges and the interior of the regenerating parcels at Ambatoladama, and (4) fruit consumption was highly variable and unpredictable.

For the restoration program at Ambatoladama to become self-sustaining, it is necessary that seeds not only get dispersed into the parcels and along the forest edge to increase the diversity of trees that were already planted by the park staff, but those seeds must also successfully germinate and recruit (Holloway 2003). A pilot study at Ambatoladama showed that germination success can be relatively high in the parcels given the high light levels (Holloway 1998). However, high light levels and other factors can reduce germination and recruitment success of forest taxa passed within the parcels or along the hard forest/agriculture edges, for example, competition with small-seeded faster growing pioneer species, high winds, or warmer soil that favors gap-dependent species (Murray 1988, Davies-Colley *et al.* 2000). The results of the present study on *V. rubra* feeding and seed dispersal ecology will be useful to the park employees and the future management of the restoration program at Ambatoladama. A recent report on the status of the restoration program outlined the management recommendations to attain the goal of restored parcels that no longer need human input (Holloway 2008). Specific recommendations for the regenerating parcels included: continued weeding of *A. angustifolium* and other non-forest plants that compete with forest trees until planted stems reach 3-4.5 m in height, increase the diversity of lemur food trees in the regenerating parcels so that at least three tree species are in fruit year round, increase the density of planted trees to expedite canopy closure, and plant trees in an arrangement that will create pathways for seed dispersers to access the interior of regenerating parcels (Holloway 2008). These recommendations were drawn up without knowledge of the present ecological research on *V. rubra*.

In light of the data and analyses presented here, I recommend that managers not spend much effort designing an ideal tree planting arrangement to lure animals into the interior of regenerating parcels, because when lemurs moved about in Parcel Two, they

traveled on the ground and with the aid of the relatively small pioneer *Harungana* trees. Cutting back all non-forest species in the regenerating parcels is probably counterproductive to restoration. This is especially true in Parcel Two, where the ground cover of *C. hirta* lured lemurs into the area of restoration. Instead of cutting back *C. hirta*, the park staff, with minimal training, can occasionally follow the already habituated lemurs into the regenerating parcels to mark the locations of feces. At those locations, they can cut back *C. hirta*, cage the passed seeds to prevent depredation, and monitor germination success. As for adding diversity to the tree species planted in the parcels, the restoration plan specifically states they need trees that produce fruit during the months of October-November (Holloway 2008). Based on the data we collected at Ambatoladama, I suggest planting more *Garcinia verrucosa* trees since the lemurs were highly dependent on the fruits in November-January 2006. Other important species that produce fruit during the months of October-December are *Callophyllum milvum* and *Cryptocarya* species.

I also recommend that the data and methods of the present study be incorporated into a long-term monitoring program to be established at the site. This would include tracking the growth of a sampling of replanted trees in the regenerating parcels, recording vegetative characteristics of trees in plots of forest, regenerating parcels, and non-intervention sites, recording the changes in seed rain over time into these different plots, recording seed rain around planted trees in regenerating parcels, recording observations of seed dispersers in regenerating parcels, and tree phenology (Holloway 2008). In this study, I tracked lemurs in the regenerating parcels and collected data on seed rain by *V. rubra*. Local farmers assisted on my project and it would take little training to create a long-term monitoring program that includes the community members.

Finally I recommend that similar studies be conducted elsewhere in the world, to learn how native animal species can be used as agents in their own habitat restoration.

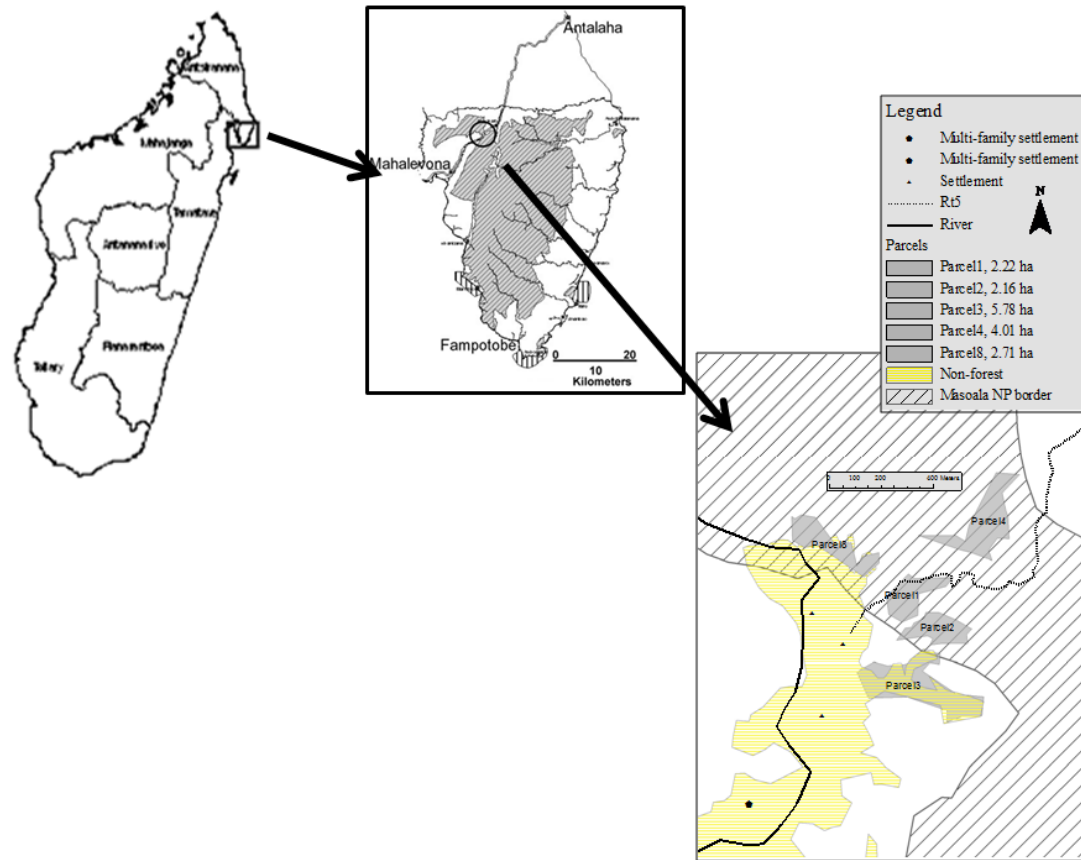


Figure 1. Map of Madagascar showing the location of the Masoala Peninsula (middle image) and the corridor at Ambatoladama (bottom image). The hatched area on the Masoala Peninsula image is the boundary of Masoala National Park. In the bottom image, the white area is forested. The shaded area is non-forest, either agriculture or *savoka* and the hatched area is MNP. Maps redrawn from WCS Madagascar.



Figure 2. Ground view of the corridor at Ambatoladama. The line shows the edge between *savoka* (regenerating forest) and mature forest. There is a recently cleared area within the *savoka*. Irrigated rice paddies are in the foreground.

Table 1. Composition of groups of *V. rubra* studied and observations at Ambatoladama.

2006	Adults	Infants	Other	Total observation time, minutes	Total focal feeding bouts, minutes	Total days observed	Total scans
Piste	1♀, 1♂	3		8,135	1,533	25	810
JJ	1♀, 1♂	4		6,918	647	12	688
JP	1♀, 1♂	2	1 juvenile ♀ born before 2006	6,596	717	10	656
2007	Adults	Infants	Other				
Piste	1♀, 1♂	0	2 juveniles	25,866	8,776	63	4087
JJ	1♀ died in 2007		Not observed				
JP	2♀, 1♂	0	2 juveniles	15,258	6,466	49	3033

Table 2. Diet of *V. rubra* 2006 and 2007 represented as percentages of total feeding bouts for the focal females. There was a significant difference between the diets subdivided by group and year (MH = 341.96, df = 1, P < 0.0001). Also noted is the number of different taxa, unknown taxa, and diversity of families consumed by the focal females. “Total observation minutes” are the total minutes the focal and her associated group was followed during the study period.

Group	Year	Percent Fruit	Percent Leaves	Percent Flowers & Nectar	Number of different taxa consumed	Unknown taxa	Number of families consumed	Total bout minutes	Total observation minutes
Piste (and JJ)	2006	87	10	3	46	6	21	2,180	15,053
Piste	2007	48	39	13	57	10	21	8,776	25,866
JP	2006	87	10	3	26	3	14	717	6,596
JP	2007	53	26	21	36	6	19	6,466	15,258

Table 3. Top five foods consumed by *V. rubra* in 2006 and 2007. FRR= ripe fruit, LIM=young leaves, FL=flower. The percent time forage is based on total bouts for focal individuals. Percent feces with seeds represents presence of any number or species of seeds in the feces: 2006 N=245 feces and 2007 N=557 feces. Total food patches represent trees, shrubs, or lianas with a known GPS location: 2006 N = 231 and 2007 = 307. The percent total food trees is based on the number of trees and lianas, which were discrete locations. **C. hirta* is a shrub and GPS locations do not accurately represent the number of patches, therefore the percent of total food patches was not quantified.

Year	Food taxa, Family	Genus species	Vernacular name	Part eaten	% time forage	% total food trees	% feces with seeds
2006	Clusiaceae	<i>Garcinia verrucosa</i>	Vongobe	FRR	45	41	62
	Lauraceae	<i>Cryptocarya sp. 1</i>	Tapiky sp. 1	FRR	8	6	2
	Lauraceae	<i>Cryptocarya sp. 2</i>	Tavolo	FRR	7	3	15
	Euphorbiaceae	<i>Uapaca sp.</i>	Vapakafotsy	FRR	6	6	7
	Lauraceae	<i>Potameia sp.</i>	Antaivaritra	FRR	3	5	7
2007	Clusiaceae	<i>Callophyllum milvum</i>	Vintanona	FRR	18	5	43
	Moraceae	<i>Ficus sp.</i>	Madrisy	FRR, LIM	13	4	7
	Fabaceae	<i>Dialium unifoliolatum</i>	Zagna mena	LIM	8	5	n/a
	Clusiaceae	<i>Symphonia fasciculata</i>	Azinina	FL	8	5	n/a
	Melastomataceae	<i>Clidemia hirta</i>	Trotrobaritra	FRR	7	*	27

Table 4. ANOVA table for the response variable of distance in meters of food patches to forest edge.

	Estimate	Standard error	t value	P(> t)
JP 2006	208.81	18.99	10.996	< 0.001
JP 2007	121.11	23.26	5.208	< 0.001
Piste 2006	125.16	22.33	5.606	< 0.001
Piste 2007	-207.23	28.19	-8.102	< 0.001

Residual standard error: 147.1 on 520 degrees of freedom

Multiple R-squared: 0.098, Adjusted R-squared: 0.093

F-statistic: 18.8 on 3 and 520 DF, P-value: < 0.001

Table 5. Mean distances of food trees with standard deviation to nearest parcel edge and forest edge for all groups in both years.

Group	Year	Parcel edge			Forest edge		
		distance (m) ± SD	N		distance (m) ± SD	N	
Piste	2007	74 ±41	158		256 ±105	187	
Piste&JJ	2006	133 ±101	156		334 ±156	157	
JP	2007	287 ±199	118		330 ±200	120	
JP	2006	152 ±72	60		209 ±102	60	

Table 6. ANOVA table for the response variable of the log normalized distance in meters of food patches to nearest parcel edge.

	Estimate	Standard Error	t value	Pr(> t)
JP 2006	4.88	0.106	45.94	< 0.001
JP 2007	0.43	0.13	3.31	<0.001
Piste 2006	-0.28	0.125	-2.26	0.02
Piste 2007	-0.9534	0.16	-5.95	< 0.001

Residual standard error: 0.823 on 488 degrees of freedom

Multiple R-squared: 0.245, Adjusted R-squared: 0.240

F-statistic: 52.76 on 3 and 488 DF, P-value: < 0.001

Table 7. Foods eaten by the Piste group in 2007 in the parcels. All of the species except *C. hirta* are remnant trees that were not planted by park staff for the restoration program. Food parts: FRR=ripe fruit, LIM=young leaves, LM=mature leaves, FL=flowers. The percent bout is limited to the total minutes fed in the parcels.

Family	Genus, species	Vernacular name	Food part	% Bout in parcels
Melastomataceae	<i>Clidemia hirta</i>	Trotrobaritra	FRR	70
Fabaceae	<i>Dialium unifoliolatum</i>	Zagna mena	LIM	14
Malvaceae	<i>Dombeya sp.</i>	Alampona	LM	5
Clusiaceae	<i>Callophyllum milvum</i>	Vintanona	FRR	3
Moraceae	<i>Ficus lutea</i>	Amotana	FRR	3
Sapotaceae	<i>Faucherea sp.</i>	Nanto	FRR	1
Strelitziaceae	<i>Ravenala madagascariensis</i>	Ravinala	LM	1
Lauraceae	<i>Cryptocarya sp.</i>	Tapiky	FRR	1
Melastomataceae	<i>Dichaetantera cordifolia</i>	Trotroka	FL	0.4
Fabaceae	<i>Cynometra commersonii</i>	Mampay	LIM and FL	0.1
Euphorbiaceae	<i>Domohinea perrieri</i> or <i>Tannodia sp.</i>	Tsivoangivoangy	FL	0.1
Total bout time in parcels:		1450 minutes		

Table 8. Number of feces with seeds passed within each of the four land categories for each group in both years. A Goodness of Fit test was applied to the numbers of feces with seeds that were deposited in each land type relative to the size of those areas. The expected values are in parentheses. The JP group in 2007 deposited fewer feces with seeds than expected in the parcels, parcel edges, and forest edge. The Piste group in 2007 deposited fewer feces with seeds than expected in the parcels and forest edge, but slightly more than expected in the parcel edges and forest. For the JP group in 2006, the expected numbers were near zero for feces with seeds in the parcels, parcel edge, and forest edge; one feces with seeds in a parcel caused the expected to differ from the observed.

Feces with seeds deposited by area							Area in hectares						
Group	Year	Parcels	10m parcel buffer	10m edge buffer	Forest	Total feces with seeds	Home range, MCP	Overlap with Parcels	Overlap with 10 m Edge	Overlap with 10 m Parcel	Overlap with Forest	χ^2	P
Piste	2007	28(58)	22(20)	1(5)	281(253)	331	24.47	4.30	0.3340	1.4842	18.35	21.77	0.0001
Piste& JJ	2006	1(6)	2(3)	0(0.3)	134(128)	137	18.84	0.83	0.0345	0.3733	17.60	4.95	0.1753
JP	2007	2(9)	0(4)	2(4)	186(177)	190	55.55	2.71	1.24	1.1116	51.73	11.14	0.01
JP	2006	1(0.05)	0(0.4)	0(0.4)	71(72)	72	8.13	0.01	0.0471	0.0427	8.09	18.51	0.0003

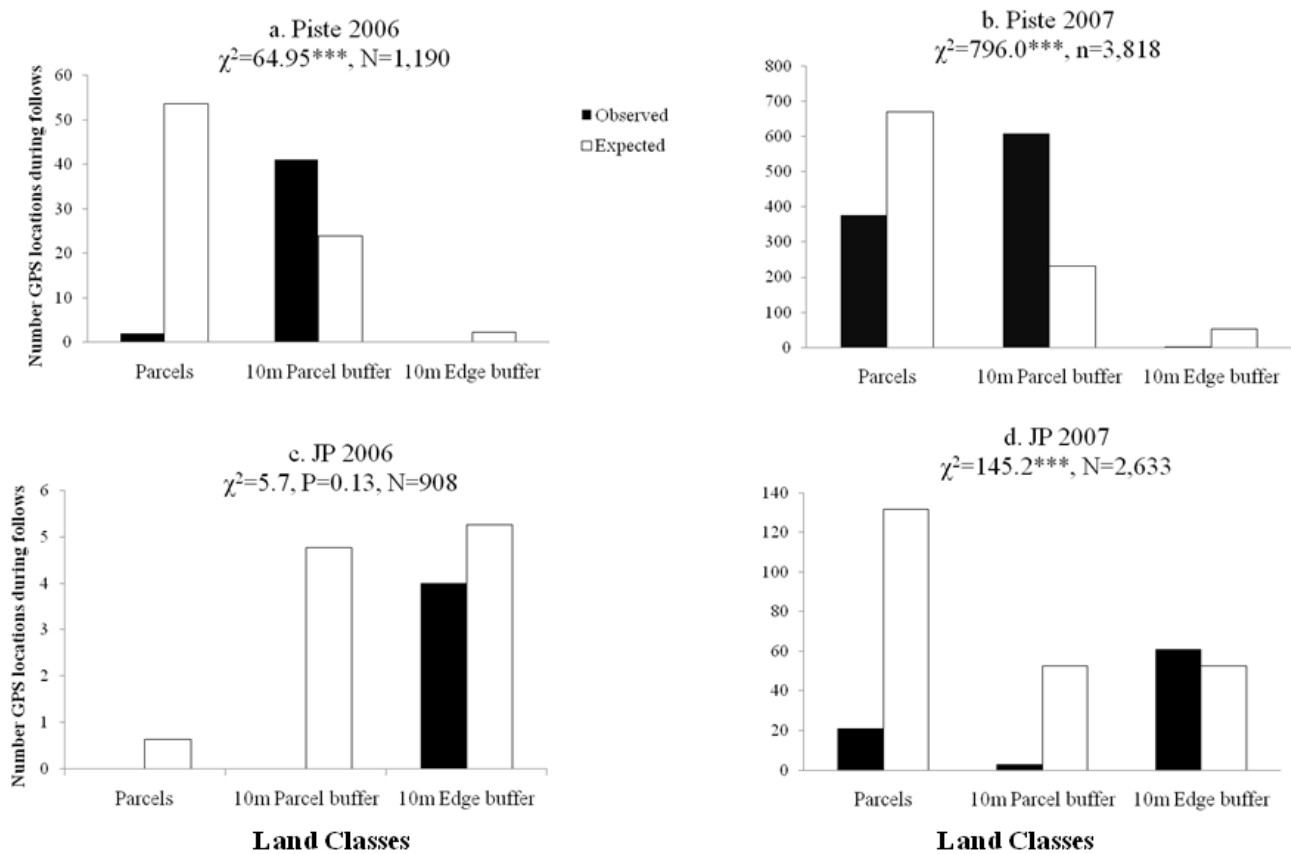


Figure 4. Observed and expected values of the number of GPD locations during follows where groups were found within one of four habitat types by area within their respective minimum convex polygons. The expected and observed values for the forest are not included in the figures since those values changed the scale so that the differences in the smaller areas are not obvious. They are as follows: a. Piste 2006 (and JJ), expected = 1,111, observed = 1147, b. Piste 2007, expected = 2,918, observed = 2,831, c. JP 2006, expected = 902, observed = 904, d. JP 2007, expected = 2,449, observed = 2,548. ***P<0.0001.

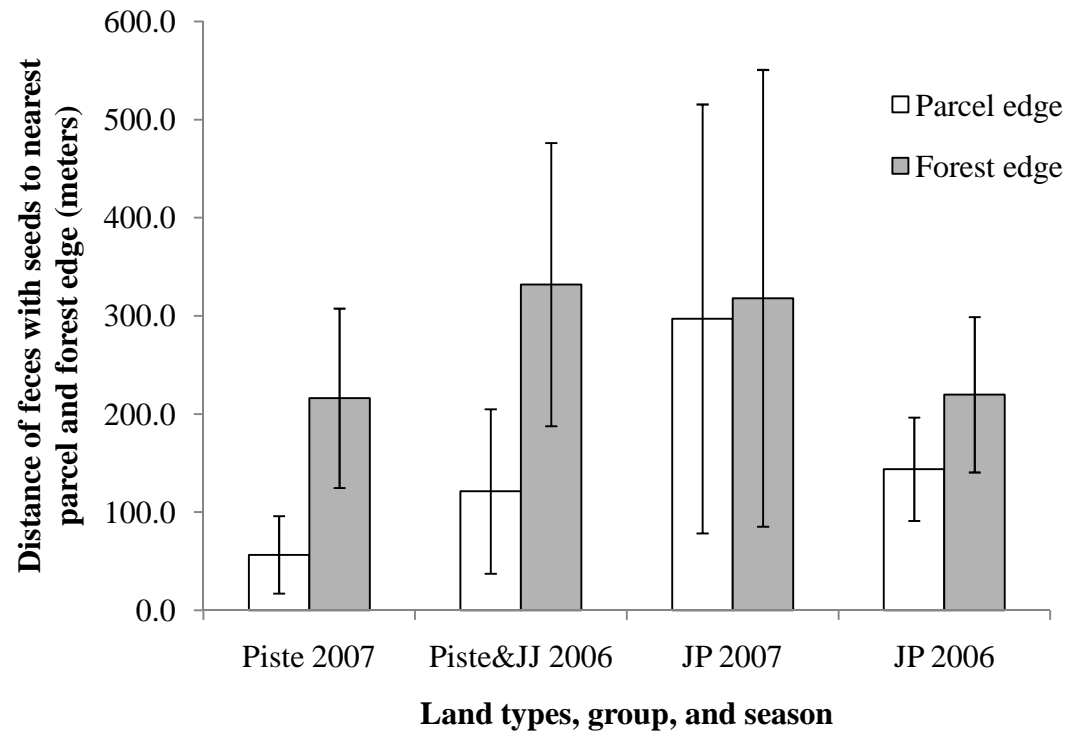


Figure 5. Mean distance of feces with seeds to nearest parcel edge and forest edge for all groups in both years. Error bars are the standard deviations.

Table 9. Mean Euclidian distances of feces with seeds to the nearest parcel edge and nearest forest edge. The distances to the nearest parcel edge exclude feces found within a parcel.

Group	Year	Parcel edge		N	Forest edge		N
Piste	2007	57 m	±40	309	216 m	±91	331
Piste&JJ	2006	121 m	±84	114	332 m	±144	115
JP	2007	297 m	±219	188	318 m	±233	190
JP	2006	144 m	±53	71	220 m	±79	71

Table 10. Seed taxa dispersed into the parcels by Piste group 2007. The “percent instances” is the percentage of feces containing that seed taxa and does not reflect the actual number of seeds in each feces. Number of instances of seeds in feces = 48 and number feces passed in the parcels by the Piste group in 2007 = 28. Excluding the unknown *Ficus* species, only one seed taxa is novel in the parcel.

Family	Genus species	Vernacular name	Percent Instances	Seed size	Habit and parcel status of taxon
Melastomataceae	<i>Clidemia hirta</i>	Trotrobaritra	40%	Small	Non-native pioneer shrub
Moraceae	<i>Ficus lutea</i>	Amotana	21%	Small	Liana, not planted in parcels
Rubiaceae		Valotra	13%	Small	Liana, not planted in parcels
Clusiaceae	<i>Callophyllum milvum</i>	Vintanona	13%	Large	Tree, planted in parcels
Moraceae		Unknown ficus	4%	Small	Tree or liana, not planted in parcels
Lauraceae	<i>Cryptocarya</i> sp.	Tavolo madinidravina	4%	Large	Tree, planted in parcels
Moraceae	<i>Ficus</i> sp.	Nonosay	4%	Small	Tree, not planted in parcels
Myrtaceae	<i>Eugenia</i> sp.	Ompa	2%	Medium	Tree, same genus planted in parcels



Figure 6. *V. rubra* feeding on the ripe fruits of *C. hirta* in Parcel Two. ©Barbara Martinez, 2007.

Table 11. Land classification type where seeds were dispersed. Values are occurrence of all seed taxa in feces and not the actual numbers of seeds or feces dispersed—there were a total of 1,105 occurrences of seed taxa from all collected feces. For example, one feces containing a *Garcinia verrucosa* seed and hundreds of *Clidemia hirta* seeds was counted as two occurrences. All groups and both years are lumped in the analysis.

Land classification	Observed: number of occurrences of defecated seeds	Expected: number of occurrences of passed seed
Forest	1009	944
Parcel	51	90
10m Parcel buffer	40	33
10m Edge buffer	5	20
χ^2	34.1	
P <	0.00001	

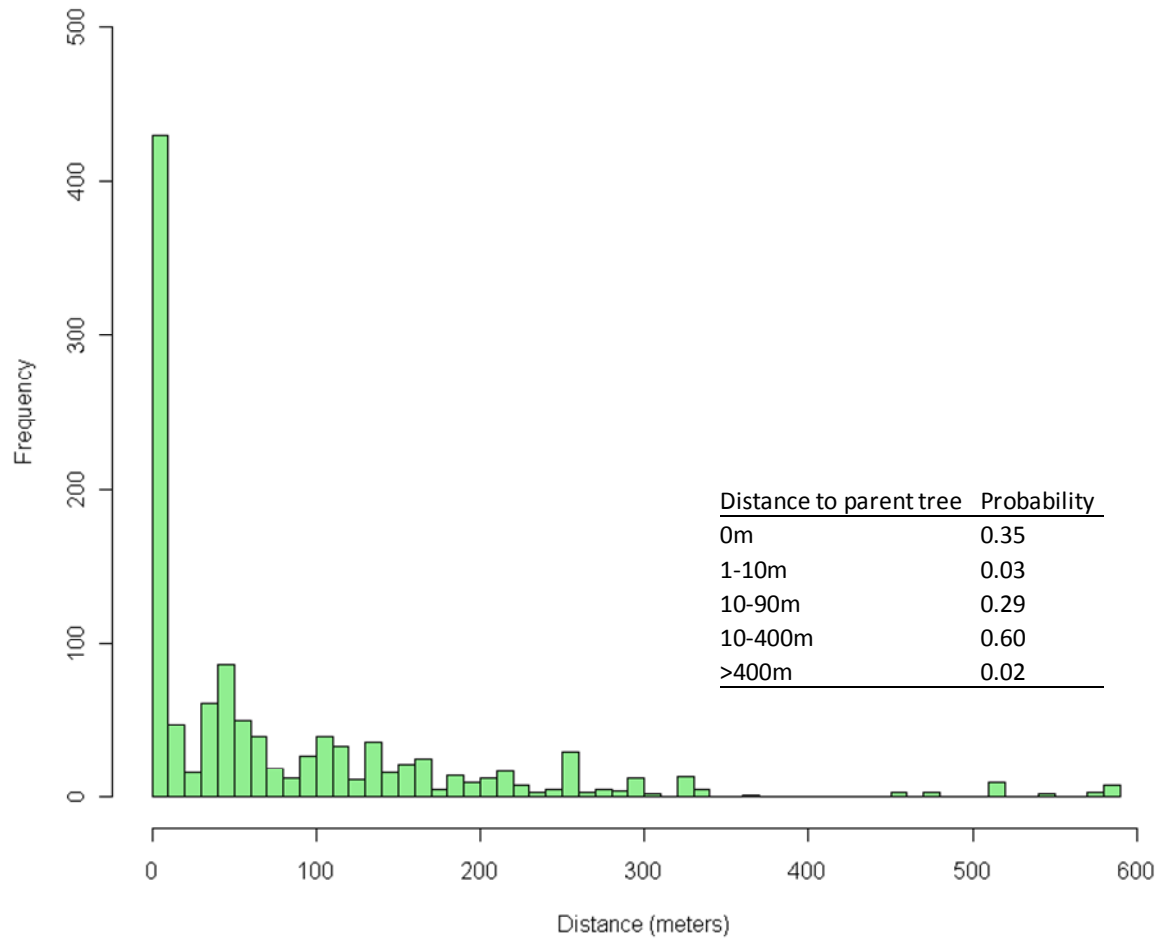


Figure 7. Distance of passed seeds from the most likely parent tree 30 minutes after the start of feeding in tree and probabilities. Mean=90±SD 101 m, median=44 m, range 0- 582 m, N=1,142.

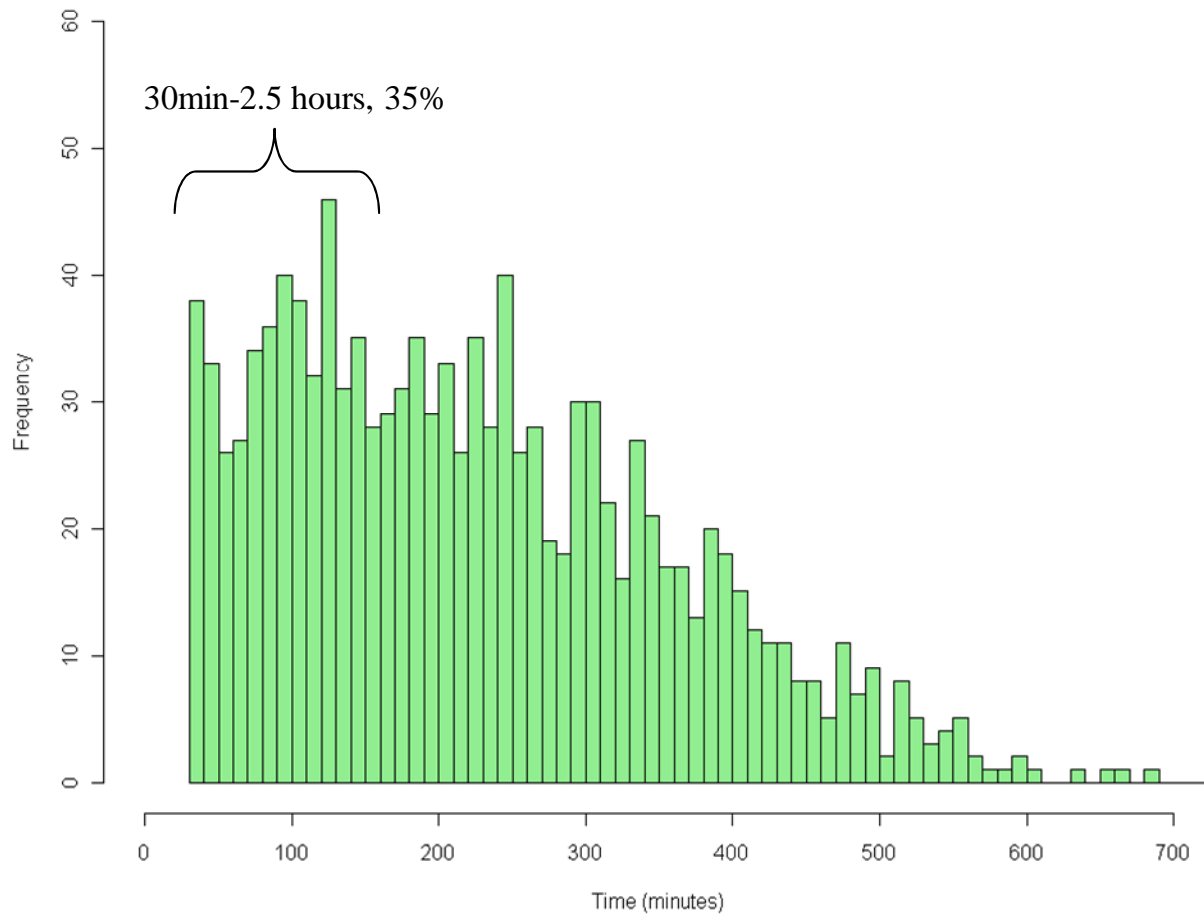


Figure 8. Time from start of fruit consumption to when seeds show up in feces, excluding seeds linked to suspected parent tree that are passed within the first 30 minutes. Mean= $227 \pm \text{SD } 132$ minutes, median=208.0 minutes, range=30-690 minutes, N=1187 seeds.

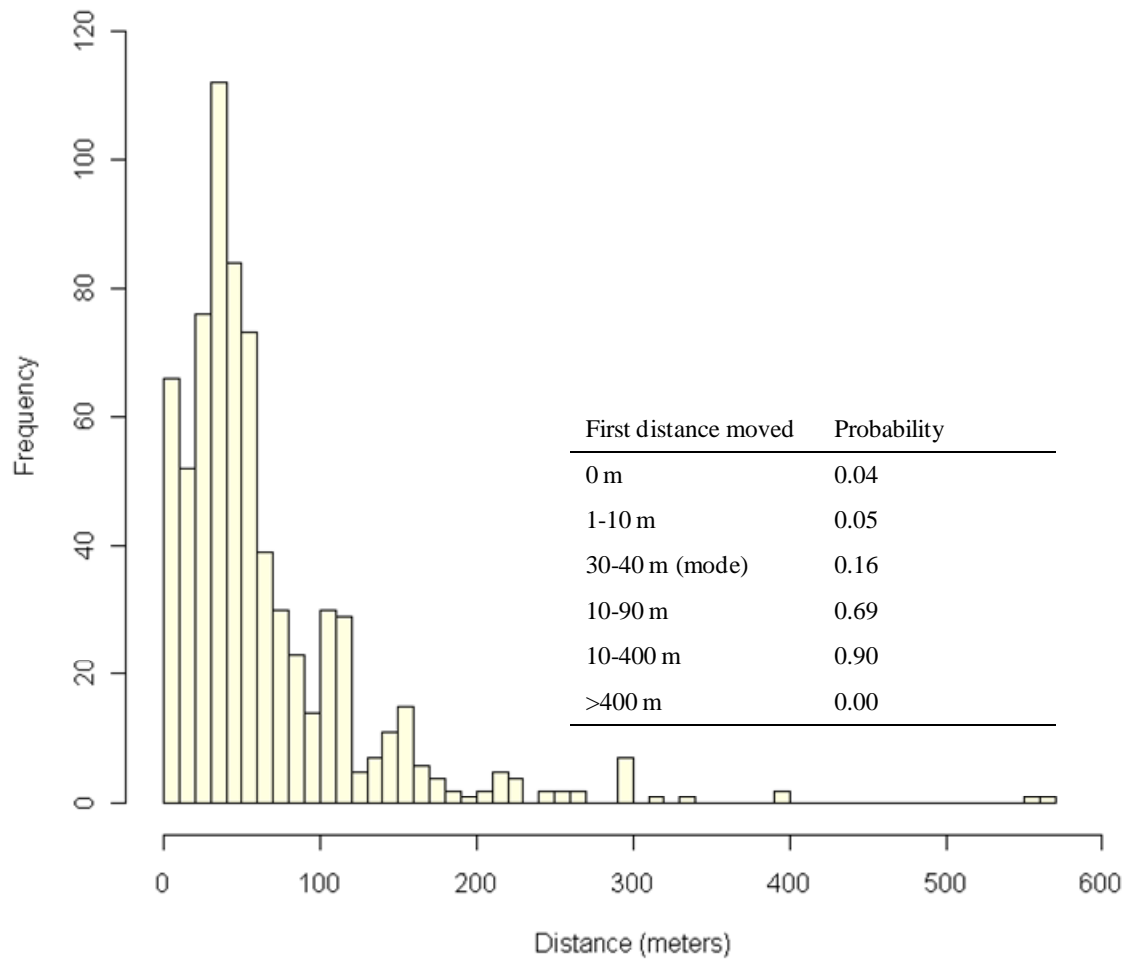


Figure 9. Distribution of the first recorded distances traveled after foraging on fruit and probabilities for selected distances for all groups in both years. Mean=64 m, median=45 m, range=0-568 m, SD=64 m, N=709.

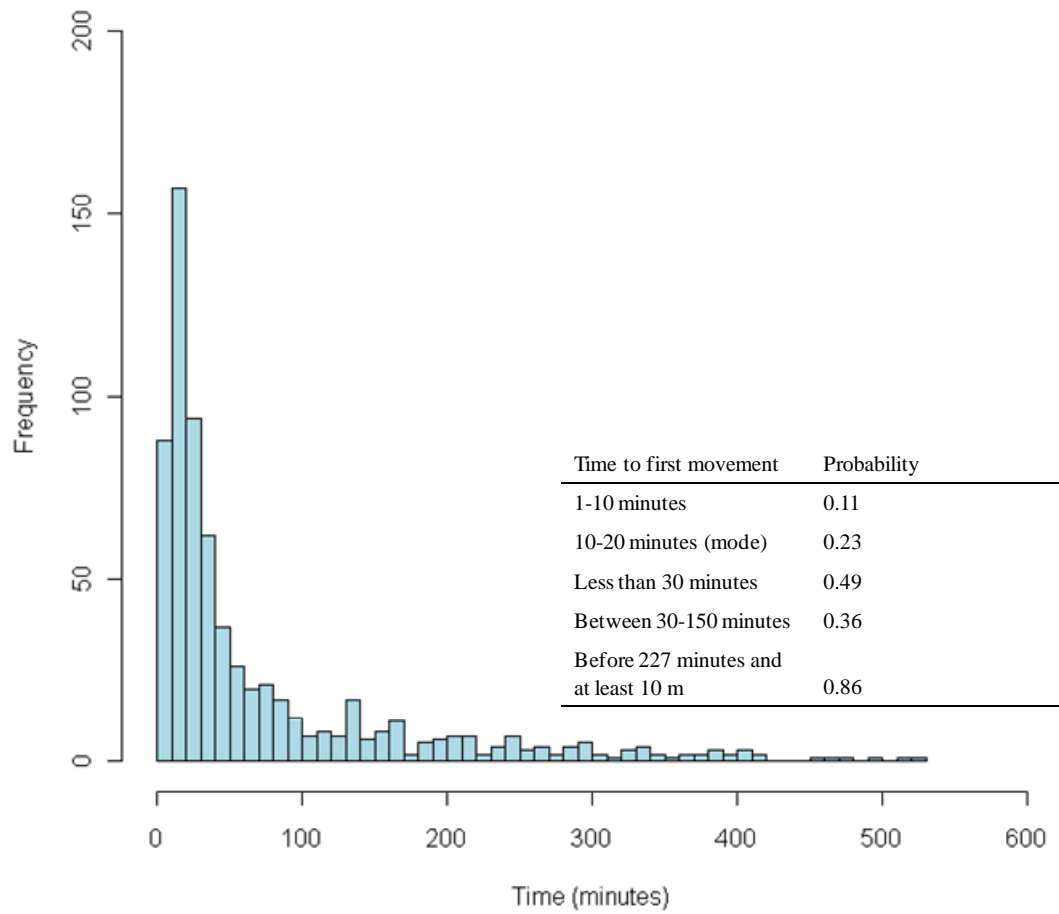


Figure 10. Distribution of the first recorded time to travel after foraging on fruit for all groups in both years. Mean=74±SD 97 min, median=31 min, range=1-529 min, N=689.

Table 12. Comparisons of seed dispersal quantity and germination success among lemur species. Seed sizes for *V. rubra* and *E. albifrons* are based on Dew and Wright (1998) categories. The time periods differed for each study: Dew and Wright (1998) August-November 1991; Birkinshaw (2001) November 1991-March 1993; Vasey (2002) November 1993-January 1995. Seed length: <5mm = small; 5-10mm = medium; >10mm = large (Dew and Wright 1998). Birkinshaw (2001) used different size classes: <10mm = small; 10-20mm = medium; >20mm = large.

Species	Frugivory rate	Number of fruit taxa consumed	Number seed taxa passed	Average seed size passed & (percent Large seeds passed)	Percent germination success	References
<i>Eulemur albifrons</i>	69%*	-	11†	Medium†	82.4% †	†Martinez and Razafindratsima , unpublished data; *Vasey, 2002
<i>E. fulvus</i>	80.6%	11	9	Large (44%)	60%	Dew and Wright, 1998
<i>E. macaco</i>	-	70	57	Large	37%	Birkinshaw, 2001
<i>E. rubriventer</i>	66.8%	11	7	Large (71.4%)	80%	Dew and Wright, 1998
<i>Propithecus diadema</i>	30%	13	2	Small	0%	Dew and Wright, 1998
<i>V. rubra</i>	47.8%-87.7%	37-39	46	Large (84.7%)	60.9%	This study
<i>V. variegata</i>	70.8%	18	14	Large (76.5%)	66.6%	Dew and Wright, 1998

Chapter 3. Subsistence farmers near the boundaries of Masoala National Park: perceptions and conflict

Introduction

Madagascar is considered a biodiversity “hotspot” due to the high diversity of endemic plants and animals (Myers *et al.* 2000). For example, 100% of the primates (lemurs), 99% of the amphibians, 95% of the reptiles, and almost 90% of the plants are found nowhere else in the world. With its hotspot status, conservation in Madagascar has an abundance of international stakeholders including multilateral donors, nongovernmental organizations, and foreign governments. These provide large funding packages, often with policy stipulations to advance conservation goals. The traditional conservation narrative in Madagascar centers on the threats to biodiversity by agricultural expansion (Koechlin 1972, Green & Sussman 1990, Kremen *et al.* 2000, Styger *et al.* 2007), specifically, shifting slash and burn agriculture called “*tavy*,” which is practiced mainly by subsistence farmers. However, many factors other than slash-and-burn agriculture threaten biodiversity, including an international demand for precious hardwood trees (rosewood, ebony, and *pallisandre* or *Dalbergia* species) (Schuurman & Lowry 2009), hunting mammals for local consumption (Golden 2009), and mining of quartz, gold, and other minerals (Sarrasin 2006). The threats to biodiversity have driven recent environmental policy in the country, but the country also has a long history of forest protection driven by other factors (Raik 2007).

Extraction of resources and agricultural expansion on a large scale in and around protected areas is generally believed to be detrimental to the rain forest ecosystem; laws based on conservation theory prohibit most extractive and agricultural activities within protected areas in Madagascar (Raik 2007). The people living on the borders of protected areas are largely subsistence farmers often at the center of the international conservation debate; they rarely hold power in the decision making (Kull 1996), yet they are impacted by changes to the land they rely on for their livelihood. Powerful stakeholders working without direct regard for the goals of biodiversity conservation (including the international markets for natural resources and agricultural products like

cloves and vanilla) provide income to the poor subsistence farmers living near protected areas. However, they are power-brokers themselves, making choices, both legal and illegal, about the use of their land and negotiating with international markets that provide opportunities for income.

Despite a conscious effort to include people living on the Masoala Peninsula in the creation and management of Masoala National Park (MNP), conflicts abound. The non-governmental organizations of WCS and CARE and the country of Madagascar itself collaborated to establish the park with input from residents of Masoala Peninsula in an effort to avoid the typical pitfalls that lead to conflict, for example, instituting forced removals of entire villages to draw park boundaries or removing access to culturally significant sites (Kremen *et al.* 1999). The physical boundary of MNP covers 536 km. As of 2007, park staff had not completed the task of marking this via painting red lines on trees along the boundary, signage, or cutting a three-meter wide swath of vegetation. Park management and subsistence farmers living on the border of the park are in conflict over the physical Park boundaries and the current and future permitted uses of land in and outside of the park.

In Masoala National Park, questionnaire research and field observations revealed that subsistence farmers were engaged in debates with Park managers over the location and meanings of Park boundaries, as well as current and future land use in the park and the surrounding buffer zone. But these disputes, at the time of my study, did not appear to manifest themselves in the form of widespread disregard of park rules; rather, farmers primarily complained about the restrictions and envisioned other possibilities for the park. It is necessary to give some background of the environmental history in Madagascar to better understand the current situation in MNP.

Brief history of forest protection in Madagascar

The contemporary restrictions on forests set aside for protection are not the first to be imposed on subsistence farmers on the east coast of Madagascar. In fact, for at least the past two centuries, rulers have imposed various restrictions. In the early 1800s, people living within and near the eastern rain forest were ruled by the Merina monarchy, which was based on the high plateau near the current capital of Antananarivo. During his reign from 1745-1810, King Andrianampoinimerina banned

the cutting of live trees for firewood, banned the burning of forest for agriculture (*tavy*), declared all forests in his kingdom as royal property, and forbade people from congregating in forests due to a fear of people clandestinely taking up arms and rebelling against the monarchy (Ratovoson 1979, Raik 2007). His son, King Radama I, unified the Merina kingdom in the early 1800s after he conquered most of the island with the aid of the British military (Kull 1996). As part of an effort to control the Betsimisarika¹ people living near the coastal eastern rain forest, the Merina monarchy imposed strict legislation on them in 1881 in the Code of 305 Articles (Cole 2001). The Articles stated that the Betsimisarika could not build houses in the forest without government authorization; they could not clear the forest using fire to create agricultural plots; and they could not cut or damage trees growing next to the ocean (Cole 2001). These restrictions were not created for conservation to protect the forests, but rather they were meant to maintain the Merina political authority over the Betsimisarika (Cole 2001).

The French first attacked ports in Madagascar in 1883 (Esoavelomandroso 1985). After years of fighting, the French colonial regime began in 1896. The colonial government promptly established the Ministère des Eaux et Forêts (Ministry of Water and Forests, *Eaux et Forêts*) in 1896, and with that governmental department came the notion of “domain of the State” (*domaine de l’Etat*) (Henkels 2001). This declared all of Madagascar’s forests as national property, and clearing forested land for agricultural expansion continued to be illegal (Henkels 2001). Many pieces of legislation during the colonial period, 1896-1960, continued to ban *tavy* and imposed strict fines and sentences for infractions (Kull 2002). The state also outlawed the hunting of lemurs and established the first protected areas system in Africa in 1927, the ten “Strict Nature Reserves,” (*Reserves Naturelle Integrales*) (Kull 1996). However, during the colonial period, the government granted logging and forest concessions and French colonists had access to large land holdings for logging and agriculture (Cole 2001). A significant

¹ The Betsimisarika are recognized as an ethnic group in Madagascar who live along the east coast of Madagascar. They are described as “a heterogeneous lot, and what little unity that exists is a product of shared customs and shared historical experience, including being treated as a social entity by powerful outsiders” (Cole 2001, pg. 39). One of those powerful entities is the Merina, or people from the highlands of Madagascar.

portion of remaining primary forest was logged in the first 30 years of French rule (Jarosz 1993).

Independence from France in 1960 brought with it a “fairly complete set of environmental legislation” (Kull 1996) and the beginning of non-French foreign involvement by development and conservation organizations like the World Wildlife Fund (WWF) and the International Union for the Conservation of Nature (IUCN) in 1963. It was still illegal to burn forests for agriculture, but the government, through land tenure and land use laws in 1960-1964 meant to stress the “social obligation to develop land,” encouraged reverting fallow land back into cultivation (Kull 1996). Also in the 1960s, the independent government encouraged people to move from the highly populated south to the north-east coast where forested land and former French-maintained agricultural estates were available for use (Ghimire 1994). At that time, the government relaxed laws regulating access to forests for agriculture and the collection of forest products (Ghimire 1994).

In 1988, with funding from the World Bank and USAID, the government of Madagascar enacted the National Environmental Action Plan (NEAP). This three-part plan aimed to integrate conservation and development and was funded from 1990-2008. The first phase of the plan (1992-97), during which MNP was developed, created a framework for implementing ICDPs (Integrated Conservation and Development Program) near protected areas and the establishment of the Malagasy National Parks Association (*Association National pour la Gestion des Aires Protégées*, ANGAP). It was during this phase that MNP was created. Phase 2 of the NEAP (1998-2003) was characterized by the Secured Local Management of Natural Resources policy, or *Gestion Locale Sécurisée* (GELOSE, Law No. 96-025, 1996), which focused on creating community forests outside of protected areas (Raik 2007). The goal of the final phase of the NEAP (2004-2008) was to increase the acreage of protected areas from 1.6 million hectares to six million hectares by 2012 (10% of the whole area of Madagascar), with the goal of protected areas being co-managed by communities under GELOSE contracts and government agencies (Raik 2007).

To date, the State is the sole owner of all forest (with the exception of private forest held by legal titles) and access to forest resources is regulated by Decree Number

87-110 and the National Forestry Policy, Law 97-017 (08 August 1997). The Malagasy law, 2001-005 of 11.02.03, *Code de Gestion des Aires Protégées* (COGAP), is the legislation that formalized protected areas and buffer zones in Madagascar. It defines a National Park as:

...an area that aims to protect and conserve natural heritage and original culture while presenting a recreational and educational space. It is under the control of the state and its limits cannot be changed, nor any of its alienated parts except by the competent authority (Article 3, COGAP)².

The legislation furthers that protected areas are for “conservation, research, enhancement of natural and cultural heritage, education and recreation of the citizens, the promotion of ecotourism, and contribution to economic and social development” (Article 11). Restrictions within National Parks include land acquisition, clearing land by any means, collection of medicinal plants, collection of firewood or other construction products, hunting of wild boar, temporary settlements, livestock grazing, and capturing or diverting water (partial list from COGAP, Article 45). In this same piece of legislation the peripheral zone, or buffer zone (*la zone tampon*), is defined in Article 7 as “the land adjacent to the protected area where activities are limited and regulated to assure the best protection for the protected area.” There are different types of buffer zones described in the COGAP: the zones of controlled occupation (ZOC, *les Zones d’Occupation Contrôlée*), the zones of controlled use (ZUC, *les Zones d’Utilisation Contrôlée*), and service zones. The ZOC consists of villages or hamlets located within the boundaries of the national park. The ZUC consists of three areas: zones with usufruct rights (ZDU, *Zones de Droits d’Usage*), areas within the national park boundaries where some extractive activities are allowed (Table 1); areas for scientific research where “access is strictly prohibited to any foreign person for research”; and areas of tourist activities. Finally, service zones are locations where infrastructure for tourism, education, or park management will be built (Hatchwell 1999).

² Translated from the COGAP, “Un Parc National désigne une aire dont le but est de protéger et de conserver un patrimoine naturel ou culturel original tout en présentant un cadre récréatif et éducatif. Elle est placée sous le contrôle de l’Etat et ses limites ne peuvent être changées, ni aucune de sa partie aliénée sauf par l’autorité compétente.”

People and protected area conflicts

A number of factors can accumulate and lead to conflict between those managing protected areas and people living along their borders; for example, when there is a lack of communication between the park management and local people; international markets for natural resources; negative perceptions between different stakeholders; and differing goals or values (Hough 1988, Fabricius *et al.* 2001). One specific situation that leads to conflict is when people are expelled from their land for protected area creation (Moore 1998, McLean & Straede 2003, Mukherjee & Borad 2004, Cernea & Schmidt-Soltau 2006, Mombeshora & Le Bel 2009). Conflict also arises when people are forced to comply with restrictions that impinge on their livelihoods (Ghimire 1994, Fiallo & Jacobson 1995, Allendorf *et al.* 2007, Lee *et al.* 2009). Finally, conflict arises when wildlife venture out of protected areas. These problem wildlife raid crops and destroy the holdings of farmers, they attack people, or they are perceived to compete with domestic stock (Heinen 1993, Newmark *et al.* 1994, De Boer & Baquete 1998, Naughton-Treves 1998, Siex & Struhsaker 1999, Maikhuri *et al.* 2000, Nyhus *et al.* 2000, Rao *et al.* 2002, Gillingham & Lee 2003, Weladji & Tchamba 2003, Kagoro-Rugunda 2004, Gadd 2005, Tweheyo *et al.* 2005, Perez & Pacheco 2006, Wang *et al.* 2006, Wang & Macdonald 2006, Allendorf *et al.* 2007, Linkie *et al.* 2007, Warren *et al.* 2007, Graham & Ochieng 2008, Yihune *et al.* 2009).

Masoala National Park

Masoala National Park was created in 1997, and the total acreage within the core area of protection is about 217,560 ha (840 square miles). In the early 1990s, few protected areas could claim they were designed based on both biological and local socioeconomic conditions. In an attempt to consider the wants and needs of communities living on Masoala Peninsula, a group of Malagasy and American conservationists helped determine the boundaries of MNP based on socioeconomic and biological data collected throughout the Peninsula (Kremen *et al.* 1999). The funding for park creation was within the ICDP framework, which consisted of programs to encourage local people to switch from *tavy* to permanent agriculture in already deforested lands, and promoting forest conservation through multiple use (Kremen *et al.* 1999). Along with goals for ecological sustainability, this group, led by C. Kremen,

developed goals for socioeconomic sustainability: human settlements were not to exist within the park limits; wherever possible, the park boundaries would be placed outside of currently cultivated lands and traditional harvest zones while including room for expansion; the forest buffer outside the park would be large enough to meet the human population's commercial and subsistence needs for forest products; headwaters of rivers would be included in the park; limits would be easy to see and respect, following geographic features when possible; and there would be points of access for ecotourism and patrolling (Kremen *et al.* 1999). The final border of the park excluded 70,490 ha of a mosaic of forest interspersed with settlements on the eastern side of the peninsula (Figure 3); this area was left out of the borders since a modeling exercise determined it would likely be deforested in the next 9-24 years (Kremen *et al.* 1999). This area became referred to as "70% of the potential forestry zone," and leaving this area outside of the park boundaries could provide "better economic returns to local communities than slash and burn agriculture" (Kremen *et al.* 1999), thereby meeting one of the goals of maintaining a forest buffer outside the park to meet the population's needs for forest products.

The funding for the ICDP ended in 2000. The ICDP funded development projects in target villages on the Masoala Peninsula, but not all villages on the peninsula and therefore not all of the residents benefited from projects. Residents were likely confused about the goals of MNP when the funding no longer came from the ICDP framework (Ormsby & Kaplin 2005).

Subsistence farming and land use on the Masoala Peninsula

Rice is the major crop grown in Madagascar. In the Masoala Peninsula, people prefer growing irrigated rice in lowland sites; this preference causes human settlements to expand along river valleys (Hatchwell 1999). Once the flat, irrigable land is taken, people practice *tavy* along hillsides to grow rice and other products. *Tavy* is a culturally important agricultural system that was inherited by the ancestors of farmers in the eastern rainforest (Styger *et al.* 2007). The process of *tavy* as described by Koechlin (1972) and Styger *et al.* (2007) includes first cutting forest and then burning the remaining vegetation. Upland rice is the main crop planted in the first season after clearing land, followed by other crops in the second or third seasons, including maize or

manioc. After the first crop is harvested, the fallow land is colonized first by heliophilous shrubs like *Solanum mauritianum* (Family Solanaceae) and *Psiadia altissima* (Family Asteraceae). These shrubs are followed by the growth of two native pioneer trees, *Harungana madagascariensis* (Family Clusiaceae) and *Trema orientalis* (Family Ulmaceae). All of these species establish rapidly from seeds after the forest has been cleared. Gradually the secondary forest, called *Savoka*, becomes established; *savoka* is described as a shrubby fallow with a height of 2-4 m. *Savoka* is used to describe secondary forest but it is also a stage of land that is ideal for clearing to plant a second or third crop. The length of the fallow period is important for soil fertility and the sustainability of the *tavy* system. The longer land is allowed to remain fallow, the more productive are subsequent crops. In a location on the periphery of protected forests in eastern Madagascar, Styger *et al.* (2007) reported that fallow periods used to be 8-15 years in the 1970s, 6-10 years in the 1990s, and 3-8 years in the 2000s. In order for plots to remain productive and produce good rice crops, the length of fallow time needs to increase with each successive crop. A “good” rice crop is 1.5-2 tons/hectare (Styger *et al.* 2007) and the national average is 2.5 tons/ha (Minten *et al.* 2007). Research revealed that a fallow period should therefore last three years for the first two cycles of crops, 5 years for the third, 8 years for the fourth, 12 years for the fifth, and 20 years for the sixth (Styger *et al.* 2007). Thus, subsistence farmers who rely on *savoka* for growing rice must have multiple plots available in order to sustain productivity and avoid degrading the soils. When land is not available, people will shorten the fallow period and eventually soil nutrients will be depleted. Chemical fertilizers are not commonly applied to crops in Madagascar due to the marginal profitability of application, lack of access, and lack of extension (Minten *et al.* 2007).

Aside from the need for agricultural land, Kremen *et al.* (1999) calculated that households living on the periphery of MNP on average need 5 ha of forest for the sustainable collection of forest products, including firewood and construction materials. People living on the Masoala Peninsula use more than 290 species of plants for construction, firewood, medicine, crafts, food, and tools (Hatchwell 1999). At the time of park creation, about 20,000 ha were used for agricultural production on the Masoala Peninsula (Hatchwell 1999). In 1999, about 15% of the households sold surplus rice and

were referred to as “rich farmers” by the authors of the MNP draft management plan (Hatchwell 1999). Most people living on the peninsula are subsistence farmers; 70% of the population of Madagascar relies on subsistence farming (Holloway 2007).

Subsistence farmers also grow various cash crops on the Masoala peninsula, including coffee, vanilla, and cloves.

Potential sources of conflict, Masoala National Park

When MNP was being created, Park management was aware of the potential sources of conflict between the park and those people living along the periphery. They recognized potential sources of conflict as: the demand for land for subsistence farming and cash crops; collection of construction materials for houses; hunting of lemurs or wild boar for local or regional consumption; and logging of rosewood or palissandre (*Dalbergia* spp.) and ebony (*Diospyros* spp.) (Kremen *et al.* 1999, Ormsby & Kaplin 2005). When MNP was created, no one was evicted from permanently settled lands. However, 47 households were relocated because they were either deemed to be temporary settlements or their farms were located near the headwaters of several watersheds (Kremen *et al.* 1999), and at least one family was relocated from the forest corridor at Ambatoladama.

The draft management plan for MNP did not have qualitative or quantitative data on the attitudes of people who lived on the periphery of the Park regarding the Park, but the document recognized that residents of Masoala Peninsula probably considered the costs of the Park to be greater than the benefits (Hatchwell 1999). After park establishment, researchers collected data on the perceptions and attitudes of people living on the park periphery. Most residents living about 5 km from MNP were aware of the Park and spoke of it in positive terms (Ormsby & Kaplin 2005). People living in the villages targeted by the Masoala ICDP were “more inclined to be glad that the park exists” than interviewed residents of non-target villages (Marcus 2001). In general, residents who had negative attitudes about the park or conservation projects were those had higher resource demands on MNP (Ormsby 2003).

The disparity in wealth of people living on the periphery of MNP could lead to conflict between the residents and park management. A number of residents cultivate vanilla on the Masoala Peninsula and there is wide variation in wealth (as measured by

the monetary economy) among households (Marcus 2001). MNP is also one of the last areas where mature rosewood trees can be found. Farmers on the periphery of MNP can supplement their incomes through logging. Logging of rosewood in any protected areas within Madagascar was forbidden between 2002 and 2009. However, this did not prevent the practice on a relatively small scale (Ormsby & Kaplin 2005, Patel 2007). Policies regarding the export of ebony and rosewood has been somewhat chaotic since 2006; at least one Ministerial Order allowed some influential operators to export finished rosewood or ebony products (Anonymous 2009). Also, flaws in the process of obtaining permits to log ebony, palissandre, or rosewood allowed widespread abuse of the permitting system (Anonymous 2009). The recent political upheaval in the capital of Antananarivo created a climate for contradictory policies. An Inter-Ministerial order was passed in March 2009, soon after the military-backed coup d'état of Marc Ravalomanana's administration. This order granted exceptional rights for 13 particular operators to export raw rosewood, ebony, and palissandre from the SAVA region until April 30, 2009—but it was supposed to be limited to logs that were in storage. However, the order led to wide-spread illegal logging from the protected forests in the northeast, especially Masoala National Park, Mantadia Biosphere Reserve, and Marojejy National Park, collectively known as the SAVA region (Anonymous 2009). Inter-ministerial Order 38244 (21 September 2009) further allowed the operators to export 25 containers of ebony, rosewood, and palisandre after the April 30th deadline. People living on the Masoala peninsula have been illegally extracting logs in MNP for supplementary income since this legislation was passed (Anonymous 2009).

Methods

I was initially interested in how the long-term sustainability of MNP might be affected by perceptions people had of land ownership and park regulations. I wanted to understand if current perceptions held by farmers of the park might affect the long-term sustainability of MNP. At the time of the interviews, I did not anticipate the military coup of 2009 nor the current shift in forest policy and widespread extraction of timber from MNP that followed.

Study site

The estimated population of Masoala Peninsula in 1997 was 44,500 (Kremen *et al.* 1999) and 80,000 in 2004 (Dokolahy 2004). I focused on farmers living south of the forest corridor at Ambatoladama. In the Ambatoladama region, there are three small hamlets to the south of the corridor: one household at Ambatoladama less than 100 m from the park boundary, five households at Ampariandava 400 m from the park boundary, and nine households at Bevintanona about 300 m from the park boundary with an estimated 5-6 people per household (Dokolahy 2004) (Figure 1). These three small hamlets to the south were about the same size during the study period of 2006-2007. There is also the small village of Ankovana, which is about 4 km southwest of the corridor at Ambatoladama and about 1.5 km to the park boundary. This settlement has an elementary school and there are between 20-40 households in Ankovana. The oldest farmers in the area say they moved to the region in the 1960s, which coincides with the government's policies that encouraged people to move to the region post-independence.

Interviews

In October-November 2007, two Malagasy assistants conducted 26 structured interviews of subsistence farmers living within a buffer zone of MNP on topics of land ownership, use of their land, and use of the national park. Interviews lasted from thirty minutes to one hour and were conducted in the Betsimisarika dialect of the (Appendix 7); the interviewer was a guide for Masoala National Park who speaks English and he was accompanied by a local farmer who has a number of relatives in the region. The guide had no authority to punish people if they were to admit to breaking the rules of the National Park, and he made sure the participants understood this point. However, the participants probably associated the interviewer with the park and therefore their responses may have been influenced by the association. The final question was less-structured and was intended to give participants an opportunity to discuss issues related to the laws governing the park that they felt were important for us to know. If the participants seemed to not know how to respond to the open-ended question, the interviewer asked them again for their opinions of the park to try to continue the discussion. The assistants interviewed adult single men (N=9), single women (N=2), and couples (N=15) who identified themselves as "land owners." The participants

farmed along the Mahalevona River in a valley surrounded by MNP (Figure 1). The informants were briefed about the aim of the project, including their rights: their responses could not be traced back to them, they could refuse to answer any question, and they could choose to end the interview at any time. I translated the responses into English with the help of the interviewer who speaks English.

Results

Lack of communication: Awareness of the park boundary, restrictions, and goals of the park vs. people

Residents in the region responded that they are well aware of the Park's existence, but they perceive that the park boundaries are nonstationary in time and space. Although 62% (n=16) of respondents answered "yes" to the question "Do you know where the park limit is?" 56% of them stated the park is "far away" from their land (n=9). Three respondents defined "far" as between 1-2.5 km. Based on GIS layers of the park boundary³, the distance from the Mahalevona River east and southeast to the park boundary ranges between 50 m to 2 km; it is between this river and the park where a majority of interviewed residents have agricultural plots. The maximum distance north of the river to the park boundary is about 3.2 km; this area also contains agricultural plots, but the terrain is mountainous and there are fewer agricultural plots north of the river.

Although most residents claimed to have an idea of the park boundary location, no one directly mentioned a "Zone of Controlled Use" (la Zone d'utilisation Contrôlée, ZUC) or a buffer zone. The interview questions did not directly ask about the buffer zones, however, some respondents, 54% (N=14), mentioned the forested areas outside of the park and beyond their personal holdings in the context of land that they think is available or should be available for use (N=8) or is forbidden for use (N=7). Two respondents noted they knew they could obtain permits from Eaux et Forêts to expand their holdings onto land outside the park for agriculture or claim land to build a home. Three other respondents said they are allowed to use land outside the park, for example, to extract wood and palm leaves for construction and divert water for rice fields; they did not mention that permits were necessary for these actions. In general, people

³ GIS layer created by WCS, Madagascar, and obtained in 2003

seemed confused about what could be done with land that was outside of the park and not yet claimed by anyone. One respondent stated:

Project Masoala had a plan to give land for “*jinga*⁴” to the community. This piece of land is forest above my piece of land. The community can make *jinga*... The Masoala Project told me the forest (for *jinga*) is not for me. The community didn't work the land because the situation is not clear.

People expressed a range of knowledge about access and use of the park: 38% (N=10) of the respondents said it is forbidden to enter the park at all and 50% (N=13) said it is forbidden to either use the land or take things from inside the park. When asked “Who gives you permission to use land in the park?” 81% (N=21) responded that no one can give permission to use land in the park. The remaining five (one did not answer the question) respondents expressed hope that one day the park would open for the people. One respondent answered with a Bible quote that essentially translated to “nothing stays the same and everything can change.”⁵ The respondent further stated that someday the park will “open and give land to people since most Malagasy do not have enough land to work and survive on.” One respondent said that now they see the park limit goes down into their fields. Finally, one respondent stated that only the managers of the park (“*zare tompon andraikitra*”) can take materials from it.

Most of the people interviewed admitted they cleared forest for agricultural expansion without permits, either recently or when they first settled the land. Half of the respondents admitted to clearing forest when they acquired their land, (N=13). Less than half of these respondents, 46% (N=6), stated they had permission from Eaux et Forêts to cut the forest for agriculture. Of the seven respondents who did not have permission, one said their letter from Eaux et Forêts was lost in a fire. This respondent has lived in the region since the 1950s and he said he converted forest that was destroyed by a cyclone, which is typically allowed by permit. Two respondents without permission to cut forest stated that nobody stopped them from working the land in the past, and now their plantations prove ownership; these respondents have lived and worked in the region since the 1960s. Two more respondents without proof of

⁴ *Jinga* is a local word used to describe forest (primary or secondary) along hillsides that is to be converted to a dry rice plantation.

⁵ “*Ny menimeny eritrerita ambotraka mametraka tsisy raha maharitra mandrakizay doris amen.*”

permission stated that they did not ask Eaux et Forêts for permission and they have not been punished; they have lived in the region since the 1970s. Those respondents who cut forest for agriculture and have proof of authorization from Eaux et Forêts have worked land in the region from eight to 35 years.

The people interviewed understand that land use and agricultural expansion is not allowed in the park. In response to the question, “Who gives you permission to use land in the park,” 44% answered that no one can give permission to take or use the land in the park. However, the remaining 56% responded in ways that suggest a need for future flexibility on behalf of the park, as illustrated by one respondent:

If all the land outside the park is full of people then it is possible to get land inside the park. One day a person will be able to give authorization to take land from the park. But now there is no way to have land from inside the park.

Two respondents related a similar memory around the time when the park was being established in 1997. At that time, one respondent was a “chief” of his village. He had a discussion with “someone from the park” who said when the community increases they [the park] will move the limit. The respondent continued, “It is very difficult to know what the government is thinking and I would like to see the park managers move the limit of the park or the government provide another solution for the community to survive.” The other respondent with a similar memory remembers a speech by “someone” connected with the park. The speech included a statement like, “when the number of people in the community increases, it is possible to move the limit of the park.” However, this respondent continued that now he sees that the park limit has extended in the opposite direction into the community’s fields. The participant concluded,

I think now that no one can authorize people to cut the forest or enter the park. One day there will be people who can open and give permission to work and get land, because most Malagasy do not have enough land to work for survival. I think a lot to try to find a solution so I can get [land].

One interviewed family has cultivated land that is technically within the limits of MNP. This family participates in the restoration project at Ambatoladama when the park temporarily employs community members to plant trees or clear invasive

vegetation from the restoration parcels. When this family's interview began, the patriarch immediately asked in a defensive tone why ANGAP wanted to take his land when he did nothing wrong and he follows the rules of the park. He relayed the following story: Three years ago (about 2004) two ANGAP agents based in Maroantsetra came to Ambatoladama and told the participant that ANGAP wanted to extend the park limit to run right through his settlement. The limit was already set in 1997 and these two agents were the only ones to bring this up with him; they did not have documentation. The participant showed the two agents the location of the actual limit, which he helped map using a GPS one year earlier with a different ANGAP conservation agent. These ANGAP agents told participant he is a "small" person and the government is large and strong, and they will take his land. They claimed to represent the government. At the time of the interview (2007), the participant admitted those agents were exceptions to typical ANGAP agents and he referred to them as "corrupt"; he acknowledged that not all ANGAP agents are like that. However, he admitted that he is still scared that ANGAP could take his land because his land is not officially titled. Only one other respondent mentioned a fear of ANGAP. The participant was afraid to elaborate on the final open-ended question, which simply asked for other thoughts or opinions about the park, for fear of going to prison. This same participant also expressed fear associated with cutting any trees for land or for the wood.

Long-term subsistence on the periphery of the park: Perceptions of Livelihoods and survival on current land holdings

People interviewed perceive that they cannot survive on the land they currently have. They admit to wanting access to land that is in the park. The land in the park that is adjacent to people's current holdings are marginal for rice production due to steep slopes, but the subsistence farmers do not have many opportunities for alternate livelihoods. All twenty-six of the respondents answered that they and their families cannot survive on the food produced by their current land holdings. The question was phrased in such a way that probably restricted variation in the answer: "Does your land produce enough for you and your family all year?" Based on the answers to other questions, it seems like most respondents thought only of rice production for this answer and did not consider other food items grown on their land.

The interviewees were asked what they currently do in order to feed their family and how they might obtain more land. People responded that they rent land from other landowners to grow rice or other products (12%, N=3), they grow products other than rice (65%, N=17), they sell products that they grow including vanilla (69%, N=18), they sell rice for a profit (27%, N=7), and look for or have employment (23%, N=6). Some people's responses fit into multiple categories, but most people listed only one alternative to growing rice for subsistence. All of the respondents said they grow vanilla, however, only 69% mentioned that they sell vanilla in the context of the question about activities to supplement their incomes. More than half of the respondents grow the following items: coffee, bananas, potatoes, cloves, and sugarcane (Table 3). Aside from cloves, which is a cash crop meant for international markets; these products are both consumed and sold locally.

Respondents were asked about their options regarding obtaining more land, "Do you need more land? How do you obtain enough land to feed your family for one year?" Respondents answered the following: they want to buy land when it is available (73%, N=19), they want to or did ask Eaux et Forêts for more land (46%, N=12), they want to cut the forest for more land (38%, N=10), and finally one answered that they "do not think about getting more land. The object is to educate our children to find other jobs." Table 2 shows these results along with comments the same respondents made about the availability of land outside of the park. Of the ten respondents who said they want to cut the forest for more arable land, only two mentioned that forested land outside the park is available and two others acknowledged that the land is not available. Three more mentioned that they should be allowed access to the forested land outside the park. Twelve respondents said they want to or did approach Eaux et Forêts for more land; none of those respondents ever mentioned that using forested land outside the park is not allowed, while three made comments that suggest they think the land is either off-limits or permission is required to cut the forest outside of MNP. Four respondents lamented how they would have more land to cultivate if they could divert water from the park to irrigate their fields. One farmer exclaimed, "The park law forces me to be poor because I can't take water for the rice field."

In the Ambatoladama region, people do not have official titles to their land. When asked about proof of land ownership, the most common answer besides a lack of proof was that people have letters signed by community representatives that verified purchase of land (42%, Nn=11). The second most common reply was the possession of letters signed by the previous owners showing current ownership (31%, N=8), and four respondents with letters signed by community members also had letters signed by previous owners. Some people said that working the land is proof of ownership (19%, N=5); two of those respondents alluded to having letters showing proof of ownership in the past, but they were either lost or destroyed in fires.

There was a range of responses to the final open-ended question asking for people's thoughts on MNP, the regulations, and general opinions they had regarding the Park. Most of the responses focused on the needs and wants of local farmers. A number of people, 31%, brought up the importance of educating their children so they can get jobs other than farming. Some people, 23% (N=6) complained about the lack of facilities, teachers, and money for their children's educations. Some people, 23%, mentioned that they need medical care in the region. Four respondents, 15%, noted they are interested in forming local associations as means to be a stronger voice or create local business ventures. The farmers in this region live along National Route 5, which is designated as a major highway on the maps of Madagascar. However, it is merely a dirt footpath not wide enough for vehicles. Only five respondents, 19%, mentioned that the road needs to be improved so they can transport and sell their goods more easily.

Discussion

Confusion about Park boundaries and goals

I conducted the interviews in 2007, which was six years after A. Ormsby completed her research on the perceptions of residents in two different communities living at least 5 km from MNP (Ormsby 2003, Ormsby & Kaplin 2005). Despite her efforts to inform ANGAP and park staff of her findings through workshops and written recommendations, some of the same themes emerged from our interviews of people living on the park periphery, in particular, confusion on part of the local people regarding the Park. For example, people in Ormsby's study believed the park boundary could be and would need to change in the future "as resource needs increase" (Ormsby

& Kaplin 2005). The residents in the Ambatoladama region believed the same thing. However, the COGAP does not clearly support this supposition, as is stated in Article 3: “It [the National Park] is under the control of the state and its limits cannot be changed, nor any of its alienated except by the competent authority.⁶”

Awareness and acceptance of the park boundaries is fundamental to the long term sustainability of MNP. Other than where National Route 5, a footpath that cuts through the forest corridor at Ambatoladama, meets the park (Figure1), the boundaries are not well-marked in the region. Since there are regulations associated with the boundary, it would behoove both park management and farmers to know where in space those regulations take effect.

The creation of buffer zones within protected areas for use by local people was an application to try to address the problems associated with excluding rural people from access to natural resources (Lynagh & Urich 2002, Naughton-Treves *et al.* 2005). For MNP, the draft management plan outlined different buffer zones within MNP, each with their own set of restrictions and allowances. However, the people interviewed in the Ambatoladama region were confused about whether they can or where they can cut forest for agricultural expansion. They seemed to think that there is a flexible area, like a buffer zone, where materials can be collected and potentially forest can be cut for agriculture. However, because the boundaries are not marked, people have only a vague sense of their rights.

The group that helped create the park boundaries intentionally left unprotected “70% of the potential forestry zone;” this was a mosaic of forest and settlements located on the eastern boundary of MNP to meet the needs of the local people living on the park periphery (Kremen *et al.* 1999). The people in the Ambatoladama region cannot access this forestry zone due to the mountainous terrain and the national park separating the two (Figure 2). Thus, they are not privy to any economic benefits from that particular area. According to GIS layers provided by WCS, there is a “*Zone de Droits d’Usage*” (ZDU) with a total area of 2,063 ha in the Mahalevona river valley (Figure 3). It was evident through our discussions with people that the location and rights of this zone

⁶ Translated from Article 3 of COGAP: “... Elle [Un Parc National] est placée sous le contrôle de l’Etat et ses limites ne peuvent être changées, ni aucune de sa partie aliénée, sauf par l’autorité compétente. “

were either misunderstood or not communicated with the people in the Ambatoladama region. This is not due to a lack of oversight on behalf of the park planners, as the draft management plan listed the required actions related to park creation (Hatchwell 1999):

1. Marking the ZDU on the ground;
2. Monitoring the use of natural resources through regular patrols;
3. A systematic environmental education program in communities bordering the ZDU; and
4. A program to be developed in collaboration with the Masoala ICDP to provide concrete benefits of the park's creation to people living near ZDU.

Most of the actions were either not implemented or not memorable to people in the Ambatoladama region. Based on the interviews and comments made by the local guides, the only action that appeared to occur was the patrolling; people did relate stories of community members being arrested or fined for infractions like collecting medicinal plants, burning forest, or cutting trees inside the park boundaries.

Trust and better communication between people living near protected areas and park management could be mitigated through actions like following through with promised concessions or hiring local people as senior staff (Hough 1988). Interviewed people mentioned the need for hospitals, schools, and economic opportunities; I interpret these ideas as expectations of the park since the context of our questions concerned their feelings about the park. People may have heard of development promises as a result of MNP. Because the people in the Ambatoladama region are not seeing any of these developments, they probably do not trust the motives of the park. In another study of people living near MNP, a male focus group participant exclaimed,

They tell us you may not plant in the forest. We'll give you medicine that will help your plants grow quickly, but you can only plant near your village...The Project Masoala, since it began to work, has promised many things, but nothing is given. They promised to make our school better--fishing material, boats, but until now nothing (Marcus 2001).

Confusion about the objectives of the park might be linked to when the funding for the initial ICDPs finished and the goals of the park shifted towards biodiversity protection (Ormsby 2003). I did not specifically ask participants in the Ambatoladama region about the park's objectives, but it was clear from some responses that people

expect the park to provide basic needs or economic development opportunities in exchange for restricting access to resources within the park boundaries. Within the context of our interviews about MNP, people at Ambatoladama mentioned the need for hospitals, doctors, schools, support for associations, and more foreign researchers to provide jobs for locals. Conflicts could move beyond passive complaints when a governing entity does not follow through with promises that are associated with the creation of protected areas. For example, the Community Baboon Sanctuary in Belize has entered into voluntary agreements with local community members who farm in ways that conserve habitat for the area's howler monkeys. Revenues from tourism were promised, but there is a perceived uneven distribution of benefits with membership, thus, some have threatened to opt out of the agreement (Alexander 2000). In the case of MNP, people in the region have turned to illegal logging of precious hardwoods. Although the local farmers make the least amount of money along the supply chain (Anonymous 2009), some people probably recognized an economic opportunity that could provide funds for basic needs, which were not being met by the creation of the park.

The need for land

The residents of Ambatoladama feel like they cannot survive on the land holdings they had at the time of this study, and none of the interviewed participants have formal titles to their land. This puts them in a situation where the government or wealthier immigrants might have the power to legally take land from the farmers, for conservation or other purposes. Malagasy law does recognize customary tenure in some cases; if occupants can provide proof of ten-years of development (farming, for example) on the land, occupants of the land have a right to a definitive title (Hatchwell 1999). A number of studies suggest that when farmers in developing countries have secure land tenure, whether through customary norms or government-granted titling systems, people invest more time and energy into practices that will be better ecologically for the land (Feder & Nishio 1998, Fischer 2000, Heltberg 2002, Baird & Dearden 2003). In general, the interviewed people in the Ambatoladama region lack official titles for their agricultural plots, but most would probably be able to claim ownership under the customary tenure rules. However, in the Ambatoladama region, I

think the more immediate problem affecting ecologically beneficial investments in land use is the lack of options to expand their holdings and the lack of opportunities to diversify their farming techniques. Some of the interviewed people said they approached Eaux et Forêts requesting to expand their rice fields into forested areas, and none of them were granted permission. It is illegal to burn forest for agricultural expansion, but what is not clear to the farmers is whether it is illegal to cut trees for agricultural expansion outside of the National Park core or buffer zones. Farmers do grow crops other than rice, but as mentioned by a couple of the interviewees, they cannot easily get their products to larger markets because the infrastructure is not present.

International influences and sustainability of the Park

The people living on the periphery of MNP and the park managers are not the only stakeholders with a strong interest in the management of MNP. Park management is influenced by the international community through funding and the application of academic theories of conservation into environmental policy. There is also the international market for precious hardwoods. MNP is one of the few places where large rosewood, palissandre, and ebony trees grow (Schuurman & Lowry 2009). Back in 2001, Ormsby (2003) noted that “conflicts over resource use were increasing particularly over the issue of rosewood trade and, to a lesser extent, about lemur hunting.” During my field season at Ambatoladama, people in the region did not seem to be involved in the illegal rosewood trade or lemur hunting, but the fact that people did not discuss these activities in our interviews does not mean these activities were nonexistent. Previous to my field work in Ambatoladama, I spent time near Fampotobe in 2006, and evidence of lemur hunting and logging was more prevalent. I came across lemur traps, farmers with guns, and felled rosewood logs while conducting lemur surveys in the periphery of MNP and within the park boundaries. In that area, local farmers trusted me enough to inform me that a group of people living near the park borders had extracted rosewood logs from the park. They suggested that, for my safety, I not visit this particular village because Eaux et Forêts was notified of the infraction and were on their way to investigate. However, the location of the village was so remote that there was ample time for the loggers to hide the evidence before Eaux et Forêts was

able to organize a mission to get to the site. I was also informed that the loggers were tipped off by an ANGAP employee that Eaux et Forêts was on their way to investigate.

The recent changes in legislation in 2009 regarding the shipment of rosewood caused “thousands of loggers” to flood the protected areas in the SAVA region (Anonymous 2009). In fact, one former local farmer who worked on the red-ruffed lemur project with BTM at Ambatoladama drowned in a swollen river in MNP in early 2009 while searching for rosewood. The local farmers are admittedly poor; when the opportunities to make money from resources within MNP arise, neither the boundaries nor the restrictions associated with those boundaries are strong enough to prevent people from pursuing supplemental income. The money associated with the illegal logging industry in MNP is great compared to other opportunities that the climate in MNP became dangerous. Although illegal rosewood extraction probably occurred during the field season for this study, it was still illegal to ship large amounts of wood and those restrictions kept the logging in check. The situation has since become serious in MNP, as illustrated by the acknowledgement section of a recently published paper discussing the shipments of illegally logged rosewood out of ports in northeastern Madagascar: “we would like to thank our sources, most of whom have placed their lives at risk gathering information presented in this paper” (Schuurman & Lowry 2009).

Implications and recommendations for conservation

Ormsby (2003) conducted an extensive study of park perceptions of residents living within two communities near MNP. My study was based on a smaller sampling of subsistence farmers who live closer to the park boundaries, and who live in close proximity to a park-supported forest restoration program at Ambatoladama. The parallels between my study and Ormsby’s are interesting given the six-year difference between the two. I expected that people near Ambatoladama would have a clearer understanding of the park since many have taken part in the restoration program at Ambatoladama. Also, ANGAP agents live on-site and interact on a daily basis with a number of residents. In fact, the researcher who initiated the restoration program reported that people at Ambatoladama had an appreciation for the rainforest as a result of their participation in the restoration program:

MCR [Masoala Corridors Restoration Program] demonstrated that once people became aware of the link between their natural capital consumption and the resulting environmental damage they were willing to modify their behavior to improve their well-being and that of local ecosystems (Holloway 2007).

However, I found that in general the residents in the Ambatoladama region do not understand or know the restrictions and allowances that pertain to the park boundary, they think the park boundary is flexible, and they are not privy to development projects associated with the park. I am also not confident that people are willing to modify their behavior, that which is associated with feeling the need to expand their agricultural holdings, without continuing economic incentives to do so. The restoration program provided some assistance to farmers to grow supplemental food items other than rice for local consumption or to sell locally. There is a demonstration garden and most residents have relatively diverse gardens. Some people in the region are also growing native forest trees in nurseries to aid with the restoration program. A full economic analysis of their actions would be necessary to make any claims of success. Based on my observations, and the chaos that erupted after rosewood shipment laws changed, diverse gardens and tree nurseries are not sufficient to keep people from encroaching on the Park to maintain their livelihoods.

The Malagasy government and international funding agencies that support MNP need to simultaneously improve upon the development efforts for the subsistence farmers living along the borders of MNP. Much to the credit of the Malagasy government and the founding organizations, a number of progressive methods were used to establish MNP (Kremen *et al.* 1999). The park covers a vast amount of land and tens of thousands of people, mostly poorly-educated subsistence farmers, live along the borders and rely on resources found within the park's boundaries. The restoration program at Ambatoladama is one development effort that needs to continue to get funded. Other efforts in the region are necessary to improve the economic status of residents, and thus possibly decreasing their reliance on seeking more land or products from MNP. Tourism is a potential option for the Ambatoladama region, but this would not be an option that people could completely rely on. Although tourists would see red-ruffed lemurs up-close, Ambatoladama is at least a one and a half day hike from

Maroantsetra and Antalaha, two cities where tourists can access MNP. The park could employ extension officers, train ANGAP employees, or even deploy Peace Corps Volunteers to the more remote villages along the park periphery to give workshops on more efficient rice growing techniques. There are few doctors in the region, but occasionally a doctor will travel along Route 5 to remote villages to provide services for people. The park should employ a few of these traveling doctors and make it known to the residents that the park is the source of funding.

Masoala National Park is one of the few places where extremely valuable hardwoods grow. It is also home to a number of endemic plants and animals. Finally, the periphery of the park is occupied by people to tend to rely on natural resources provided by the park. It is a place worth investing time and energy to get the right balance of use and protection.

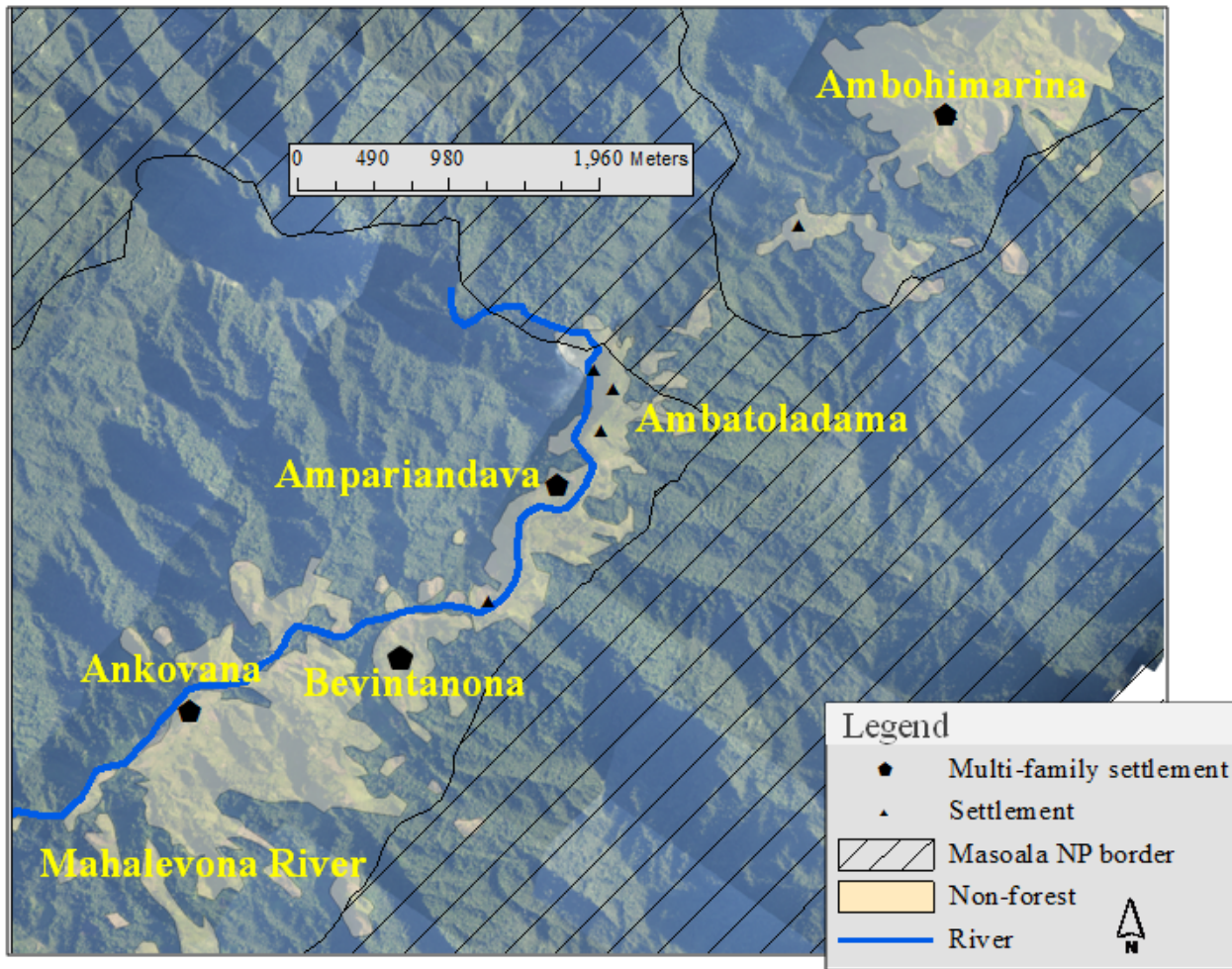


Figure 1. Map of the region near the Ambatoladama corridor in Masoala National Park. Aerial photograph and imagery adapted from WCS, Madagascar.

Table 1. Rules of use within the *Zones de Droits d'Usage*, ZDU buffer zones of Masoala National Park, from Hatchwell (1999). I obtained a copy of the draft management plan from its author, M. Hatchwell of WCS. I was unable to obtain the final draft.

Usage rules	Exceptions and activities not allowed
The collection of medicinal plants, fruits and food plants, without harming the parent plant.	Making settlements, temporary or permanent is not allowed
	Hunting is not allowed
	Collection of honey is not allowed
	Collection of wild potatoes (<i>ovybe</i>) is not allowed
The collection of palm leaves, without harming the parent plant.	Destruction of roots/base of palm (des pieds) to get the palm leaves or the hearts of palm
The collection of dead wood or burned wood (5th class only).	Clearing trees is not allowed
	Exploitation of <i>bilahy</i> (a tree used for making alcohol) is not allowed
Logging for construction, strictly only for non-commercial use, wood for coffins.	Must obtain permits, and it is prohibited to sell wood for profit
Cutting wood for canoe construction.	Must obtain permit
The removal of resin and latex, without harming the mother plant.	The cutting of trees for resins is not allowed
The passage of zebus allowed on the trails.	Zebus are not allowed to graze; they cannot be left for extended periods

Table 2. Responses to “Do you need more land? How do you obtain enough land to feed your family for one year?” cross-referenced with comments about whether forested or unforested land outside of the park boundaries can be aquired. N=26.

	Wants to buy land							
Wants to buy land	19, 73%	Wants to/did ask the government, Eaux et Forêts for more land						
Wants to/did ask the government, Eaux et Forêts for more land	0	12, 46%	Wants to cut the forest for more land					
Wants to cut the forest for more land	0	3, 44%	10, 38%	They will rely on children's education				
They will rely on children's education	0	0	0	1, 4%	Can use the forest outside the park			
Can use the forest outside the park	0	1, 4%	2, 8%	0	6, 23%	Cannot use the forest outside the park		
Cannot use the forest outside the park	0	0	2, 8%	0	0	7, 27%	Should be able to use land outside the park	
Should be able to use land outside the park	0	0	1, 4%	0	0	0	3, 12%	Eaux et Forêts should give permission to cut the forest outside the park
Eaux et Forêts should give permission to cut the forest outside the park	0	3, 44%	2, 8%	0	1, 4%	1, 4%	2, 8%	6, 23%

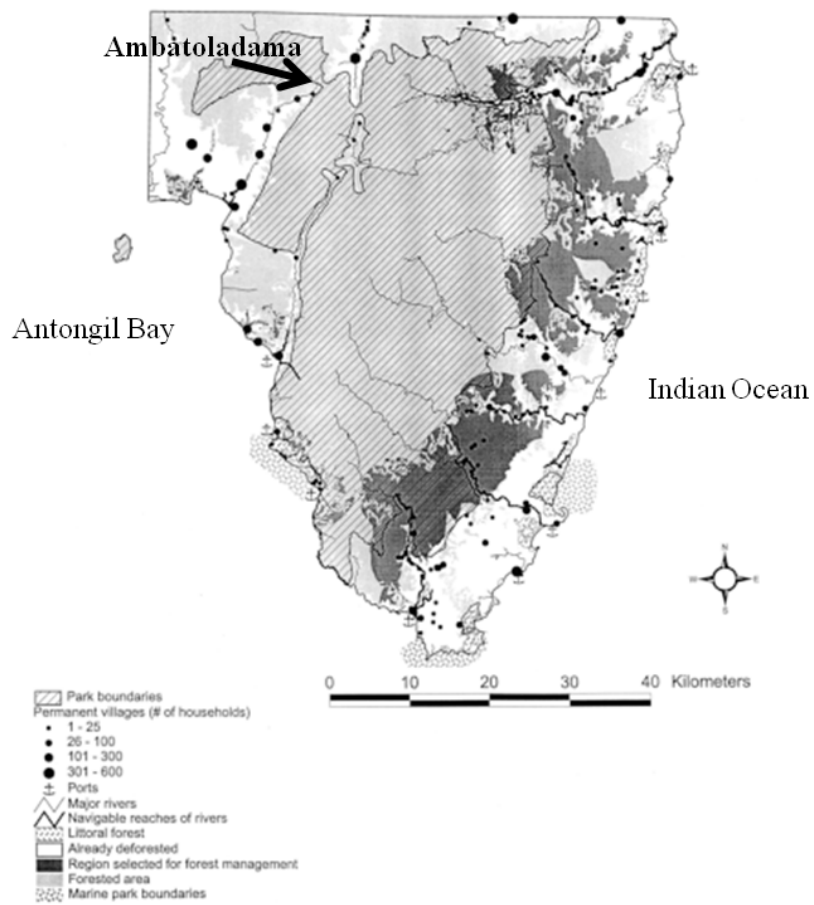


Figure 2. Map of Masoala National Park and the 71,400 ha of forest left outside of the park boundaries, referred to as the "Seventy percent of the potential forestry zone" in dark gray (adapted from Kremen et al. 1999).

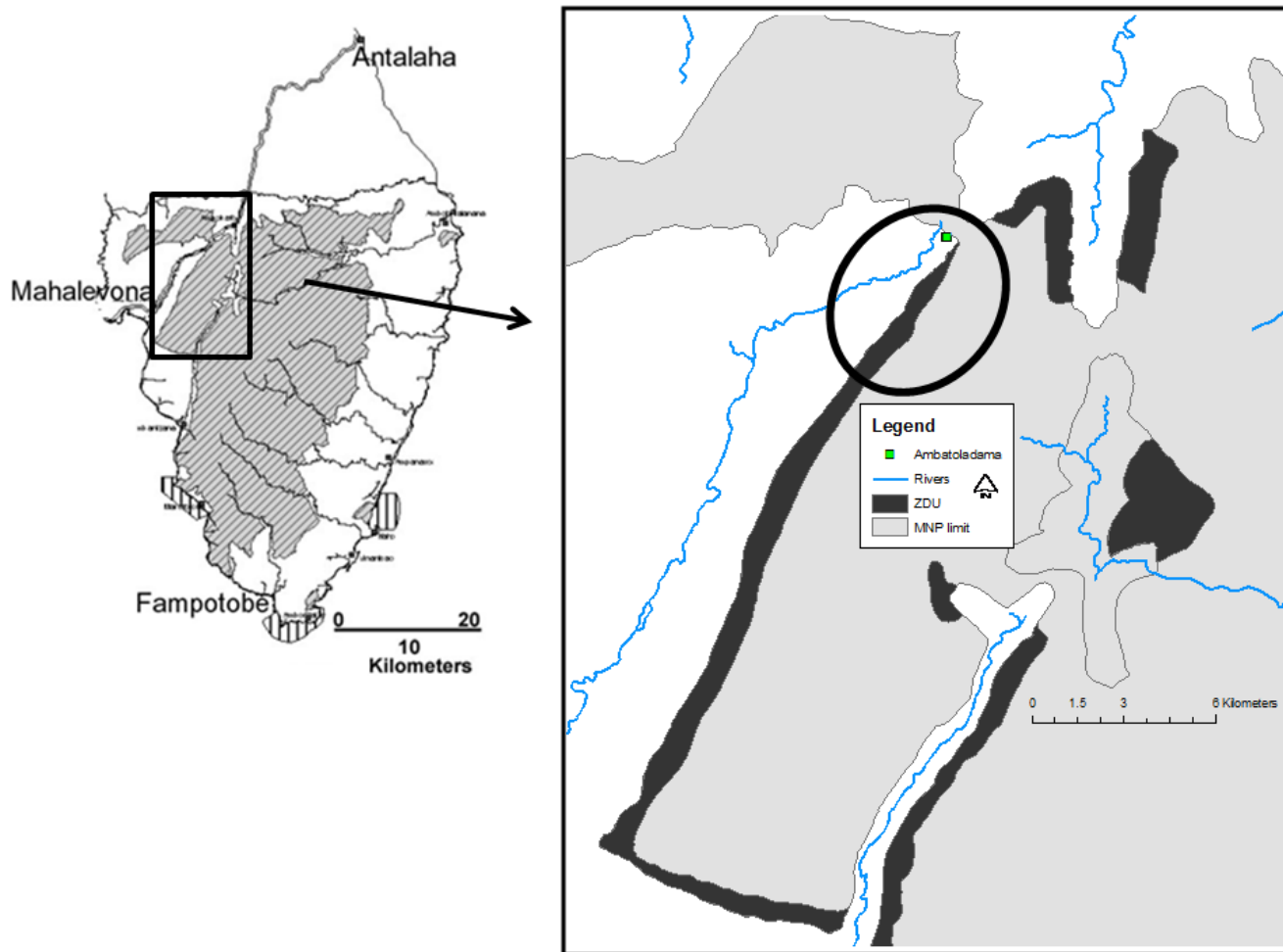


Figure 3. Map showing a few of the buffer zones, or the ZDU, within Masoala National Park. The circled area is the ZDU along the western edge of MNP where residents of the Ambatoladama would have the easiest access. Maps adapted from those provided by WCS, Madagascar.

Table 3. Cash and subsistence crops grown by respondents in the study (N=26) in addition to rice.

Products	Percent respondents who grow items
Vanilla	100
Coffee	92
Bananas	85
Potatoes	73
Cloves	62
Sugarcane	54
Fruits (mango, pineapple, litchi, orange, papaya)	35
Manioc (cassava)	23
Taro	15
Beans	8
Other vegetables	3

Appendix 1. Taxa consumed by *V. rubra* at Ambatoladama during the two seasons in 2006-2007 representing 31 different families. FRR=ripe fruit, FUR=unripe fruit, FR=fruit, unknown ripe or unripe, LM=mature leaves, LIM-immature leaves, FL=flower. There are 19 unknown taxa not included in this table.

Vernacular name	Family	Genus. Species	Parts eaten
Vongo madinidravina	Anacardiaceae	Protorhus sp.	FRR
Hazomamy	Anisophylleaceae	Anisophyllea fallax	LM
Morangavato	Annonaceae	Ambavia capuronii (Cavaco & Keraudren) Le Thomas	FRR
Moranga	Annonaceae	Xylophia sp.	FUR, LIM, LM
Ravintsira, Sira	Arecaceae	Dypsis sp.	FRR
Tsaravoasira	Arecaceae	Dypsis sp.	FRR
Vontro, Ravimbotro	Arecaceae	Pypsis sp.	FRR
Tsiaramiaramy sp2	Burseraceae	Protium madagascariensis	LIM
Tsiaramiaramy sp1	Burseraceae	Canarium boivinianum Engler	FRR
Aramitsitsiha	Burseraceae	Canarium boivini	FRR, LM
Aramy madinidravina	Burseraceae	Canarium madagascariensis Engler	LIM
Vintanona	Clusiaceae	Callophyllum milvum P. F. Stevens	FRR, LIM
Matahobaratra	Clusiaceae	Garcinia aphanophlebia H. Perr.	FRR, LM
Vongobe	Clusiaceae	Garcinia verrucosa Jum. Perr.	FRR
Azinina	Clusiaceae	Symphonia fasciculata	FL, LIM, LM
Mantady	Combretaceae	Terminalia ombrophila H. Perrier	FRR
Vahanonoko	Cucurbitaceae	Ampelosicyos humblotii (cozu) Jumelle et Perrier	FRR
Hazomafana	Ebenaceae	Diospyros sp.	FRR, FUR
Beandro	Erythroxylaceae	Erythroxylon sp	FL
Malazovoavy	Euphorbiaceae		LM
Varona	Euphorbiaceae	Antidesma petiolare Tul.	LM

Alampona beravina	Euphorbiaceae	Croton sp.	LM
Tsinoronoro	Euphorbiaceae	Deuteromallotus acuminatus (Baill)	FR
Tsivoangivoangy sp1	Euphorbiaceae	Domohinea perrieri Leandri	FL, FUR, LIM, LM
Tsivoangivoangy sp2	Euphorbiaceae	Tannodia sp.	FL, FUR, LIM, LM
Vapakafotsy	Euphorbiaceae	Uapaca littoralis, Uapaca bojeri	FRR, LIM
Vapaka	Euphorbiaceae	Uapaca thouarsii, Uapaca sp.	FRR, LM
Mampay	Fabaceae	Cynometra commersonii	LIM, LM. FL
Zagna malotra	Fabaceae	Dialium sp.	LIM, LM
Zagna mena, Zahamena	Fabaceae	Dialium unifoliolatum Capuron	LIM, LM
Mampay madinidravina	Fabaceae		LIM
Dindemona	Gentianaceae	Anthocleista amplexicaulis Bak	FRR
Tapiky sp2	Lauraceae	Aspidostemon sp.	FRR, LIM
Tavolo beravina	Lauraceae	Cryptocarya peirvillei	FRR, FUR, LIM
Tapiky sp1	Lauraceae	Cryptocarya sp.	FRR, LIM
Antafanonana sp2	Lauraceae	Ocotea leavis kostern	FL, FRR, LIM, LM
Antafanonana sp1	Lauraceae	Ocotea sp.	FL, FRR, LIM, LM
Tavolo madinidravina	Lauraceae	Ocotea sp.	FRR, LIM
Antaivaritra beravina	Lauraceae	Ocotea sp. Potameia velutina	FRR
Antaivaritra	Lauraceae	Potameia sp.	FRR, FUR, LIM, LM
Tavolo	Lauraceae	Ravensara acuminate, Cryptocarya sp.	FRR, LIM, LM
Alampona fotsy	Malvaceae	Dombeya sp.	FL, LIM, LM
Alampona sp1	Malvaceae	Hibiscus lasiococcus Bail	FL, LIM, LM
Trotrobaritra	Melastomataceae	Clidemia hirta	FRR
Trotroka	Melastomataceae	Dichaetantera cordifolia	FL
Somotrorana	Meliaceae	Astrotrichilia sp.	FRR
Amotana	Moraceae	Ficus baroni	FRR
Hodipaso	Moraceae	Ficus soroceoides	FRR
Mandrisy	Moraceae	Ficus sp.	FRR, LIM
Nonosay	Moraceae	Ficus sp.	FRR, FUR, LM
Tsimpalipaly	Moraceae	Ficus sp.	LIM, LM

Voara	Moraceae	Ficus sp.	FRR
Fotsidity	Moraceae	Pachytrophe sp.. Ficus politoria	LIM
Ompa	Myrtaceae	Eugenia cloiselii	FRR
Rotro beravina	Myrtaceae	Eugenia sp.	FRR, LIM, LM
Rotro madinidravina	Myrtaceae	Eugenia sp.	FRR, LIM, LM
Tantsitsiha	Myrtaceae	Eugenia sp.	LIM, LM
Rotro	Myrtaceae	Eugenia sp., Brochoneura sp., Sygziium sp.	LM
Menavogny	Ochnaceae	Diporidium sp.	LM
Tsilaitry	Oleaceae	Norhonia grandifolia H. Perr.	FRR
Tsilaitry beravina	Oleaceae	Noronhia sp.	FRR
Vatakasaka	Orchidaceae	Phayus sp.	LM
Rambo	Pandanaceae	Pandanus odoratissimus	FRR
Karaka	Pandanaceae	Pandanus sp.	FRR
Ravinavetro sp2	Rhamnaceae		LM, FUR
Tsiloparimbarika	Rubiaceae	Beonia madagascariensis	FRR, FL
Valotra	Rubiaceae	Breonia sp.	FRR
Tsifo	Rubiaceae	Canthium majas (br)	LIM, LM
Tsifo beravina	Rubiaceae	Genipa sp., Canthium majus	FRR
Mantalagnina sp2	Rubiaceae	Hyperacanthus sp.	FRR, FUR
Mantalagnina sp1	Rubiaceae	Pyrostria sp.	FRR, FUR
Hasina	Ruscaceae	Dracaena reflexa Lam.	LM
Kirandrambiavy	Salicaceae	Aphloia theaformis	FRR
Maimboloa. Mampandoa	Salicaceae	Casearia sp.	FRR
Ravinavetro sp1	Salicaceae	Scolopia sp.	LM, FUR
Mandritokana (Fagnonahona)	Sapindaceae	Deimbollia macrocarpa R.Capuron	FRR, LM
Fandifihana	Sapindaceae	Tinopsis phellocarpa	LIM
Nantodinga	Sapotaceae	Faucherea glutinosa	FRR
Nanto	Sapotaceae	Faucherea parvifolia Lecomte	FRR, LIM, LM
Nantovarantoala	Sapotaceae	Mimusops lecontei	FR
Ravinala	Strelitziaceae	Ravenala madagascariensis	LM, Nectar

Afopotsy	Malvaceae	Grewia sp.	LM
Ahaka			LM
Alampona maitso			LM
Alampona mena			FL, LM
Moranga beravina			FRR
Tamenaka			FRR
Tansetsy			LM
Tantsitsiha beravina			LIM, LM
Tsirakaomby			FRR
Vahinonetra			FRR
Valora			LIM, LM
Vamarana			LIM
Vankarabo			FL, Nectar
Vatakasina			LIM, LM
Vazagna			FRR

Appendix 2. Seeds passed by *V. rubra* and *E. albifrons* in 2006 and 2007 from 14 different families, including seed size measurements.

Vernacular name	Scientific name	Family	Season	Quantity of seeds extracted	mean width (mm)	mean length (mm)
Antafononana	Ocotea leavis	Lauraceae	06	5	11.98	20.6
Antaivaratra	Potameia sp1	Lauraceae	06, 07	73	13.7	21.5
Antaivaratra	Potameia sp2	Lauraceae	06, 07	18	15.31	25.02
Madinidravina						
Aramy	Canarium sp1	Burseraceae	07	1	21	33.3
Fagnoanaona	Tannodia sp1	Euphorbeaceae	07	1	24.2	20.2
Fandifihana	Allophylus cobbe	Sapindaceae	06	3	19.1	22.06
Hazondronono	Sideroxylon	Sapotaceae	06	10	17.58	12.92
Karaka*	Pandanus sp1	Pandanaceae	06	30	14.61	38.59
Mandrisy	Ficus sp1	Moraceae	07	Hundreds but not all measured		1.12
Mantadia			07	1	18	27.2
Mantalagnina	Pyrostria s or Hypercanthus sp.	Rubiaceae	07	11	5.01	6
Matahobaratra	Garcinia aphanophlebia H. Perr.	Clusiaceae	06	40	6.67	10.34
Morangavato	Xylopia oxyfolea	Annonaceae	06	4	18.47	23.37
Nanto	Mimusops sp. or Capurodendron sp. or Faucherea sp.	Sapotaceae	07	4	13.59	20.4
Nantodinga	Labramia sp.	Sapotaceae	06, 07	2	13.2	30.3

Vernacular name	Scientific name	Family	Season	Quantity of seeds extracted	mean width (mm)	mean length (mm)
Ombavy	Polyalthia sp.	Annonaceae	06, 07	4	11.63	17.91
Nanto Varanto	Labramia sp. or Mimusops sp.	Sapotaceae	06	13	15.65	26.95
Ompa	Eugenia sp.	Myrtaceae	07	356	8.22	9.68
Ramangitrika			07	2	16.4	23.65
Rambo*	Pandanus sp.2	Pandanaceae	07	24	16.47	32.23
Ravintsira	Dyopsis sp.1	Arecaceae	06	3	13.86	24.36
Rotro Beravina	Syzygium parkeri Baker	Myrtaceae	06	34	12.3	10.51
Somotrorana	Macphersonia madagascariensis Blume	Sapindaceae	06	3	19	18.16
Tapiky	Cryptocarya sp.1 or Aspidostemon sp.	Lauraceae	06	26	19.74	30.3
Tavolo	Cryptocarya sp.2	Lauraceae	06, 07	4	16.69	29.45
Tavolo	Cryprocarya sp3	Lauraceae	06, 07	188	12.18	18.24
Madinidravina						
Tsaravoasira	Dyopsis sp.	Arecaceae	06, 07	20	7.9	11.56
Tsiaramiaramy	Protium sp. or Canarium sp.	Burseraceae	06	2	16.7	12.5
Tsifo Beravina	Gaertnera sp.	Rubiaceae	06	5	9.1	17.44
Tsifo	Canthium boivianum	Rubiaceae	06	13	15.43	26.07
Madinidravina						
Tsilaitra	Noronhia sp.1.	Oleaceae	06	11	16.76	29.52
Tsilaitra	Noronhia sp.2	Oleaceae	06	2	18.42	30.08
Madinidravina						

Vernacular name	Scientific name	Family	Season	Quantity of seeds extracted	mean width (mm)	mean length (mm)
Vahanonoko	Ampelosicyos humblotii (cozu) Jumelle et Perrier	Cucurbitaceae	06, 07	18	24.74	47.96
Vahegny		Euphorbiaceae	06	5	5.34	12.72
Vapakafotsy	Uapaca sp.1	Euphorbiaceae	06	84	11.8	20.75
Vapakamena	Uapaca sp.2	Euphorbiaceae	07	9	8.63	15.82
Vongobe	Garcinia verrucosa	Clusiaceae	06	414	19.26	32.03
Vintanona	Callophyllum sp., Callophyllum milvum	Clusiaceae	06, 07	663	13.42	21.76
Not identified (08)				11		
Total extracted and measured seeds		2,125				

*Rambo and karaka might be the same taxon

Appendix 3. Known food species of *V. rubra* at Andranobe, in Masoala National Park. FR=fruit, FL= flowers, LIM=young leaves, LM=mature leaves, and SH=shoots. The life form of these food items were not specified except *vahegny* (unknown family) is the Malagasy work for liana; it is possible to assume none of the foods are shrubs and that foods are either trees or parasitic epiphytes as Andranobe is not a disturbed site. Vasey (2000, 2003) reported the percent time points feeding per on each food item and Rigamonti (1993) reported the percent of total feeding observations fed on each food item.

Family	Genus species	Vernacular name	Percent time points feeding	Part consumed
Moraceae	Ficus spp.	Amotana, Nonosay, Voara	35.928 ¹	FR
Myrtaceae	Eugenia spp.	Ompa, Rotro, Tantsitsiha	14.83 ^{2,3}	
Cluciaceae	Garcinia spp.	Vono (Vongo)	12.334 ¹	FR
Lauraceae	Cryptocarya sp.	Tavolo	11.6 ^{2,3}	
Lauraceae	Ravensara Pervillei, Ravensara sp.	Tavolo raventsara beravina or madinidravina	11.345 ¹	LIM, LM, SH, FR
Meliaceae	Lepidotrichilis sp.	Unknown	9.33 ²	
Moraceae	Ficus spp.	Amotana, Nonosay, Hodipaso, Voara, Tsimpalipaly, Mandrisy	8.532 ^{2,3}	FR
Burseraceae	Canarium sp.	Aramy, Aramitsitsiha	7.44 ^{2,3}	
Euphorbiaceae	Croton mongue	Alampona madinidravina	6.36 ¹	FL, FR
Lauraceae	Ocotea sp.2	Antaivaratra beravina	6.145 ¹	FR
Cluciaceae	Symphonia sp.	Azinina	4.26 ^{2,3}	
Cluciaceae	Symphonia spp.	Hazinina (Azinina)	3.78 ¹	FR, FL
Lauraceae	Ocotea macrocarpa	Tavolo beravina	2.836 ¹	LM
Sapotaceae	Capurodendron sp.	Nanto	2.75 ^{2,3}	FR
Theaceae	Asteropeia multiflora	Jody	2.45 ¹	LM, FR
Cluciaceae	Callophyllum drouhardi	Vintanona	2.42 ^{2,3}	FR
Sapindaceae	Filicium decipiens	Soretra beravina	2.149 ¹	FR, FL
Annonaceae	Polyalthia	Ombavy	2.08 ^{2,3}	

Family	Genus species	Vernacular name	Percent time points feeding	Part consumed
	humbertii			
Myrtaceae	Eugenia spp.	Ompa, Rotro	1.892 ¹	FR, LM
Sapotaceae	Gambeya	Famelona	1.805 ¹	FR
	madagascariensis			
Lauraceae	Cryptocarya sp.	Longotra	1.719 ¹	FR
Unknown	Unknown liana	Vahegny	1.547 ¹	FR, LIM, SH
Burseraceae	Canarium sp	Ramy tsytsiha (Aramitsitsiha)	1.461 ¹	FR, FL
Flacourtiaceae	Casearia sp.	Mampandoa	1.074 ^{2,3}	
Euphorbiaceae	Uapaca	Voapaka m.	0.817 ¹	FR
	Thonarsii			
Euphorbiaceae	Croton spp.	Alampona beravina	0.774 ¹	FL
Sapotaceae	Sideroxylon sp.	Nanto madinidravina	0.688 ¹	FR
Euphorbiaceae	Croton sp.2	Fotsyavadika	0.516 ¹	FL
Tilaceae	Grewia spp.	Hafomena, Hafopotsy, Hafotramena	0.473 ^{2,3}	
Lauraceae	Ocotea sp.1	Tavolo madinidravina	0.43 ¹	LM?, FR
Orchidaceae	Phayus sp.	Vatakasaka	0.43 ¹	?
Burseraceae	Canarium	Ramy beravina	0.387 ¹	SH
	madagascariensis	(Aramy beravina)		
Sapotaceae		Nanto antodingana	0.301 ¹	?
Rubiaceae	Canthium sp.	Tsifo madinidravina	0.258 ¹	FR
Ebenaceae	Diospyros spp.	Hazomainty	0.215 ¹	LM, FR
Liliaceae	Dracaena sp.	Asmibe	0.215 ¹	FR
Anacardiaceae	Pouparia	Rahiny	0.172 ¹	?
	chapidieri			
Sapotaceae	Sideroxylon	Nanto vasy	0.172 ¹	FR
	gerrardii			
Combretaneae	Terminalia sp.	Mantady beravina	0.129 ¹	FL, FR
Rubiaceae	Breonia	Tsiloparimbarika	0.086 ¹	FR
	madagascariensis			
Asclepiadaceae	Cryptostegia	Lombiry	0.043 ¹	FR
	madagascariensis			
Cluciaceae	Calophyllum sp.	Vintano (Vintanona)	0.043 ¹	?
Euphorbiaceae	Amyrea	Ampaliala	0.043 ¹	FR
	Humbertii	madinidravina		
Rubiaceae	Genipa sp.	Tsifo beravina	0.043 ¹	FR
Strelitziaceae	Ravenala	Ravinala	0.043 ¹	FR?
	madagascariensis			

Family	Genus species	Vernacular name	Percent time points feeding	Part consumed
Lauraceae	Ocotea sp.	Antafanonana ³		
Lauraceae	Ravensara sp.	Tavolo ³		

¹ Rigamonti (1993)

² Vasey (2000)

³ Vasey (2003)

Appendix 4. Tree taxa identified along the seven transects at Ambatoladama and the total basal area in square meters. Transect data were collected in 2006 and 2007 for trees with a DBH greater than 10 cm.

Family	Vernacular names	Stand basal area for each species in all transects DBH>10 cm, in m²
Anacardiaceae	Rahiny	0.87
Anacardiaceae	Sakoanala	0.06
Anacardiaceae	Tarantana	1.05
Anacardiaceae	Tarantana madinidravina	0.03
Anacardiaceae	Voasirindrina	1.43
Anisophylleaceae	Hazomalagny	4.88
Anisophylleaceae	Hazomamy	0.15
Anisophylleaceae	Masoavela	0.07
Annonaceae	Ampalibe	0.05
Annonaceae	Moranga	1.24
Annonaceae	Moranga madinidravina	0.02
Annonaceae	Moranga fotsy	0.02
Annonaceae	Morangamainty	0.03
Annonaceae	Morangavato	0.17
Annonaceae	Ombavy	0.82
Apocynaceae	Barabanja	0.58
Apocynaceae	Hazondranono	0.65
Apocynaceae	Taolanaomby	0.42
Apocynaceae	Voandregarena	0.06
Araliaceae	Voantsilana (Talendoha)	0.52
Arecaceae	Ravintsira (Sira)	0.28
Arecaceae	Sindro	0.04
Arecaceae	Tsaravoasira	0.56
Arecaceae	Unknown Arecaceae	0.02
Arecaceae	Vontro (Ravimbotro)	0.05
Asclepiadaceae	Lombiry	0.18
Asteraceae	Kisaka	0.12
Bignoniaceae	Antohiravina	0.09
Bignoniaceae	Unknown Bignoniaceae	0.01
Bignoniaceae	Tsikonjaza	0.14
Brexiaceae	Hasintohy	0.46
Brexiaceae or Myrsinaceae	Hasintohy beravina	0.03
Burseraceae	Aramibe	4.95

Family	Vernacular names	Stand basal area for each species in all transects DBH>10 cm, in m²
Burseraceae	Aramitsitsiha	2.11
Burseraceae	Aramy	5.18
Burseraceae	Aramy beravina	3.91
Burseraceae	Aramy madrinidravina	2.97
Burseraceae	Tsiaramiaramy	0.99
Clusiaceae	Arongana	1.48
Clusiaceae	Azinimboalavo	0.08
Clusiaceae	Azinina	2.70
Clusiaceae	Azinina be	0.09
Clusiaceae	Azinina beravina	0.01
Clusiaceae	Azininambohitry	0.02
Clusiaceae	Azinina Madinidravina	0.13
Clusiaceae	Azininambohitry	0.05
Clusiaceae	Haronganpanihy	0.16
Clusiaceae	Marompanihy	0.13
Clusiaceae	Matahobaratra	0.01
Clusiaceae	Vintanona	3.50
Clusiaceae	Vongo	0.93
Clusiaceae	Vongo beravina	0.04
Clusiaceae	Vongo maimbo	0.07
Clusiaceae	Vongo maitso	0.34
Clusiaceae	Vongo mena	0.87
Clusiaceae	Vongobe	5.10
Clusiaceae	Vongobe maimbo	0.10
Clusiaceae	Vongobe maitso	0.01
Clusiaceae	Vongobe maitso	0.06
Clusiaceae	Vongobe Mena	0.01
Clusiaceae or Anacardiaceae	Vongo madinidravina	0.02
Combretaceae	Mantady	0.06
Cunoniaceae	Lalona	1.68
Cunoniaceae	Lalonombary	0.53
Cyatheaceae	Fanjagna	1.28
Dilleniaceae	Tsilomparimbarika	1.89
Dracaenaceae	Ovotrasina (Hasina)	3.00
Ebenaceae	Hazomafana	0.14
Ebenaceae	Hazomainty	0.34
Ebenaceae	Hazomainty madinidravina	0.01

Family	Vernacular names	Stand basal area for each species in all transects DBH>10 cm, in m²
Elaeocarpaceae	Voatsanaka	0.63
Ericaceae	Maimboholatra (Maimbolatra)	0.04
Ericaceae	Mamoabokitra	0.28
Erythroxylaceae	Beandro	0.07
Erythroxylaceae	Sakaiala	0.13
Erythroxylaceae	Totokintsina	0.22
Euphorbiaceae	Arina	0.52
Euphorbiaceae	Fanavimangoka (Fanavimanjoko)	0.10
Euphorbiaceae	Malazovoavy	0.01
Euphorbiaceae	Mandravokiny	5.68
Euphorbiaceae	Mankaragnana	0.30
Euphorbiaceae	Tsinoronoro	4.28
Euphorbiaceae	Tsinoronoroala	0.36
Euphorbiaceae	Tsivoangivoangy	3.49
Euphorbiaceae	Vahegny (Vahambahegny)	0.04
Euphorbiaceae	Vapaka	1.34
Euphorbiaceae	Vapakafotsy	2.09
Euphorbiaceae	Vapakamena	1.73
Euphorbiaceae	Varona	0.03
Euphorbiaceae	Zemby	0.16
Fabaceae	Hazovola	1.00
Fabaceae	Hazovola mainty	0.04
Fabaceae	Mampay	1.65
Fabaceae	Sambahy	0.01
Fabaceae	Sambalahy	0.18
Fabaceae	Zagna	0.01
Fabaceae	Zagna malotra	1.05
Fabaceae	Zagna mena	1.43
Lauraceae	Antaivaritra	8.00
Lauraceae	Antaivaritra beravina	0.13
Lauraceae	Antaivaritra madinidravina	0.12
Lauraceae	Tapiky	5.78
Lauraceae	Tavia	0.04
Lauraceae	Tavolo	5.55
Lauraceae	Tavolo beravina (Tavolo be)	0.26
Lauraceae	Tavolo madinidravina	0.96

Family	Vernacular names	Stand basal area for each species in all transects DBH>10 cm, in m²
Lauraceae	Tavononana	0.03
Lauraceae or Ebenaceae	Antafanonana	3.57
Loganiaceae	Dindemona	0.01
Malvaceae	Afipotsy	0.03
Malvaceae	Afotra beravina	0.02
Malvaceae	Alampona	3.17
Malvaceae	Fanondamba	1.54
Malvaceae	Hafoankora	0.04
Malvaceae	Hafomena	0.68
Malvaceae	Hafopotsy	0.37
Malvaceae	Magna	4.13
Malvaceae	Magna beravina	0.02
Malvaceae	Vagnana	2.82
Melastomataceae	Tomenja (Tsimahamasantsoky)	0.27
Melastomataceae	Trotroka	0.23
Menispermaceae	Amborasaha	0.15
Menispermaceae	Telotritry	0.03
Monimiaceae	Ambora	2.48
Monimiaceae	Ambora be	0.31
Monimiaceae	Ambora beravina	0.09
Monimiaceae	Ambora madinidravina	2.53
Moraceae	Amotana	0.01
Moraceae	Fotsidity	0.61
Moraceae	Hodipaso	0.35
Moraceae	Voara	0.59
Myristicaceae	Rara	0.80
Myristicaceae	Rara beravina	0.89
Myristicaceae	Rarafotsy	0.01
Myrtaceae	Ompa	0.18
Myrtaceae	Ompa savoka	0.02
Myrtaceae	Ompagavo	0.29
Myrtaceae	Rakotomotro	0.15
Myrtaceae	Rotro	5.41
Myrtaceae	Rotro beravina	2.94
Myrtaceae	Rotro madinidravina	2.23
Myrtaceae	Vaseva	0.01

Family	Vernacular names	Stand basal area for each species in all transects DBH>10 cm, in m²
Ochnaceae	Menavogny	0.32
Oleaceae	Amaninombilahy; Tsiletry	0.54
Oleaceae	Tsilaitry	0.47
Pandanaceae	Rambo	0.27
Pandanaceae	Rambo Be	0.14
Pittosporaceae	Maimbovitsky	0.01
Pittosporaceae	Unkonwn Pittosporaceae	0.02
Rubiaceae	Bitsifo	0.01
Rubiaceae	Kafeala	0.04
Rubiaceae	Mantalagnina	0.21
Rubiaceae	Mantalagnina beravina	0.01
Rubiaceae	Noftrakoho	0.05
Rubiaceae	Tsifo	1.20
Rubiaceae	Tsifo beravina (Tsifo be)	0.28
Rubiaceae	Tsifo madinidravina	0.18
Rubiaceae	Vantriangilandy	0.01
Ruscaceae	Hasimbola	0.01
Rutaceae	Fahavalontrazo	0.21
Salicaceae	Hazombato	0.06
Salicaceae	Kirandrambiavy	0.03
Salicaceae	Maroankoditra	0.25
Salicaceae	Tanantanapotsy	1.69
Salicaceae	Unknown Salicaceae	0.11
Salicaceae or Rhamnaceae	Ravinavetro	0.02
Sapindaceae	Fagnonahoana	0.06
Sapindaceae	Fandifihana	0.59
Sapindaceae	Lavavy	0.06
Sapindaceae	Mampay beravina	0.61
Sapindaceae	Mampay madinidravina	0.27
Sapindaceae	Mandratokina	0.08
Sapindaceae	Menavoafamaky	0.02
Sapindaceae	Soretry	0.84
Sapindaceae	Unknown Sapindaceae	0.04
Sapindaceae or Meliaceae	Somotrorana	0.27
Sapotaceae	Famelona	2.62
Sapotaceae	Nanto	2.61

Family	Vernacular names	Stand basal area for each species in all transects DBH>10 cm, in m²
Sapotaceae	Nanto Beravina	0.17
Sapotaceae	Nanto madinidravina	0.97
Sapotaceae	Nantoboraka	0.28
Sapotaceae	Nantodinga	0.82
Sapotaceae	Nantomena	0.05
Sapotaceae	Nantomendolava	0.26
Sapotaceae	Nantonengitry	0.02
Sapotaceae	Unknown Sapotaceae	0.17
Sarcoleaceae	Unknown Sarcoleaceae	0.25
Strelitziaceae	Ravinala	2.90
Tiliaceae	Unknown Tiliaceae	0.02
Ulmaceae	Angezoka	0.15
Unknown	Aibiliza	0.03
Unknown	Fagnontanpotsy	0.01
Unknown	Fanavilohavato	0.04
Unknown	Fandrinlandry	0.01
Unknown	Favalondrazo	0.08
Unknown	Mahimbovitsika	0.04
Unknown	Mahitsiagnala	0.06
Unknown	Maimbolahiala	0.01
Unknown	Maintimbotora (Maintimpototra, Mahintropotra)	0.32
Unknown	Mankavia	0.01
Unknown	Mantadity	0.46
Unknown	Maroafotitra	0.02
Unknown	Sambala	0.01
Unknown	Tamenaka	0.02
Unknown	Trotroka be	0.08
Unknown	Trotroka madinidravina	0.02
Unknown	Tsinoronoro be	0.13
Unknown	Tsinoronoro fotsy	0.04
Unknown	Vahintrafon'omby	0.02
Unknown	Vapaka matika	0.23
Unknown	Vapaza	0.03
Unknown	Voandrozona	0.19
Various families	Unknown	1.43
Various families	Unknown liana	0.01

Family	Vernacular names	Stand basal area for each species in all transects DBH>10 cm, in m²
Verbenaceae	Ompa malotra	0.13
Violaceae	Hazondramokany	0.93
Total basal area		169.33

Appendix 5. Phenology of fruits and flowers at Ambatoladama of the top food taxa of *Varecia rubra*. FRR = ripe fruit, FUR = unripe fruit, FL = flowers.

Food Taxa	Vernacular name	Basal area, m²	Part fed on	Percent basal area	Nov-06	Dec-06	Jan-07	Aug-07	Sep-07	Oct-07	Nov-07
<i>Garcinia verrucosa</i>	Vongobe	5.28	FRR	3.13%	FRR	FRR	FRR				
<i>Cryptocarya</i> spp.	Tapiky	5.78	FRR	3.42%	FRR			FUR			FRR
<i>Cryptocarya</i> spp.	Tavolo (beravina, madinidravina)	6.77	FRR	4.01%	FRR	FRR		FRR	FRR		FRR
<i>Uapaca</i> spp.	Vapakafotsy	2.09	FRR	1.24%	FRR	FRR		FRR		FRR	
<i>Potameia</i> spp.	Antaivaritra	8.24	FRR, FUR	4.88%	FRR, FUR	FRR, FUR	FRR	FUR	FR	FRR, FL, FUR	FL
<i>Callophyllum milvum</i>	Vintanona	3.5	FRR	2.07%	FRR			FRR	FUR, FRR	FRR	FRR
<i>Ficus</i> spp.	Voara	0.59	FRR	0.35%	FRR	FRR, FUR	FUR		FRR	FRR	FUR, FRR
<i>Ficus</i> spp.	Amotana	0.01	FRR	0.01%				FRR		FRR	FRR
<i>Ficus</i> spp.	Hodipaso	0.19	FRR	0.11%	FRR	FRR					FRR
<i>Symphonia fasciculata</i>	Azinina	3.13	FL	1.85%							FL

Total basal area, m², all trees DBH ≥ 10cm:
168.91

Appendix 6. Interview questions.

Questions are in English and Malagasy along with notes to direct the conversation:

1. When did you arrive on this land? (Answer will be in form of the year or how many years ago or which generation first inhabited the land.)

1. Oviana andre no tonga taketo?

2. Did you buy the land from someone else or from your parents?

2. Tany novidiana-dre tamini'olo hafa na lova avy tamin-dray amam-dreninan-dre?

2.1 Is the land just for you and your immediate family or do you share it with your extended family?

2.1 Anao araiky no tompany sa mbola mizara amina fianakaviana?

3. Was the land already cut for agriculture (as young secondary forest or fallow land) or did you cut the forest?

3. Tany efa vita (savoka, tanin-jirofo, café, vanilla, etc.) sa andre nitevy azy?

4. How do you know this is your land?

4. Inona ahafantarana fo andre ity tany ity?

4.1 If the answer is they were punished by forest service, ask if they have a piece of paper, like a land claim, from the Forest Service (Eaux et Forêts)?

4.1. Raha toa ka olo nitevy ka voasazy tamin'ny Ben'ny Ala, misy taratasy mazava ve?

5. How many hectares or how many rice paddies do you own? (In Malagasy, a “vala” is a rice paddy of approximately 4m².) How much *savoka* do you have? (“*Savoka*” is typically secondary forest growing on an incline. It is not irrigatable, it must be cleared and burned to farm. Size of land is measured in quantity of dry rice produced by land, a “*daba*.” One *daba* is about 15 kilos of dry rice. One person eats a little less than 1 kilo of rice per day.)

5. Firy hectare ny orakanao na firy vala (4m x 4m)? Firy savokanao (mahalany vary firy daba)?

5. 1 Do you rent any of your land to non-family members?

5.1 Mampamondro oraka na tany amin'olo hafa indre?

6. How many children do you have? Grandchildren? How many other people live with you?

6. *Firy zanakanao? Firy zafinao? Misy olo hafa mipetraka aminao?*

6.1 How many “vala” for yourself and for your children?

6.1 *Firy vala ny oraka hiasainao? Firy vala ny oraka hiasain’ny zanakanao? Firy vala ny oraka zafinao? Firy vala ny oraka hiasain’ny olo hafa?*

6.2 How much *savoka* for yourself and for your children?

6.2 *Firy savokanao? Firy savoka zanakanao? Zafinao? Olo hafa?*

7. Does your land produce enough for you and your family all year?

7. *Mahavelona andre ny taminan-dre anin’izao sa tsia?*

7.1. If they answer if NO: What is your suggestion or solution if you cannot grow enough rice for your family?

(Perhaps they talk about the need to develop and a project instead of using more land for cultivation. There are potentially two directions: need land and need development. We will continue with the questions about the land but note their suggestions about development.)

7.1. *Inona no soso-kevitra na vaha-olana hitanan-dre?*

8. Do you need more land? How do you obtain enough land to feed your family for one year?

8. *Mila tany fanampiny andre? Manakory atao mbo ahazoana tany hamokarana hameloman-tegna?*

8.1 Do you know where the park boundary is?

8.1. *Fantan-dre aiza misy ny limite ny Park?*

8.2 Does your land border the Park limit?

8.2M. *Marikitra ny limite Park ve ny taninan-dre?*

[*Mamboly (malaka)*- to own the land; *Mampiasa*- to use the land. We ask the question using both verbs because there are different meanings]

9. Can you own the land in the park?

9M. *Azonan-dre atao malaka tny ao anatany Park?*

9.1 Can you use the land in the park?

9.1M. *Azonan-dre atao mampiasa ny tany ao anatany Park?*

9.2 Who gives you permission to use the land in the park?

9.2M. Izovy no manome ny fahazoan-dalana hiasa na halaka tany anatany Park?

10. What do you think of the law of the Park? OR Do you know the procedure for making your land official, with a title?

10M. Manakory ny lalana mifehy ny Park?

11. Final thoughts about the park, or asked: Is there space/land outside the park boundary to work?

11M. Mbola malalaka ny tany ivetany limite Park? Azo hangatahina amin'ny tompon'andraikitra hiasana?

Appendix 7. Funding History of Masoala National Park adapted from the draft Masoala National Park Business Plan, 2003

http://www.conservationfinance.org/Workshops_Conferences/WPC/WPC_documents/Tools_BusinessPlan_MasoalaNP.pdf. Accessed on 9 March, 2010.

1989-1992: The Masoala Project was operated by Missouri Botanical Gardens (MBG) and a Malagasy NGO (SAFAFI), with the Malagasy Ministry of Water and Forests (MEF) through a grant from the United States Agency for International Development (USAID).

1992-2000: A second group consisting of CARE International, the Wildlife Conservation Society (WCS), the Peregrine Fund, the newly-created national parks service (ANGAP) and MEF joined together to submit a proposal to USAID for an Integrated Conservation and Development Project (ICDP) at Masoala. The ICDP was funded by USAID under its SAVEM program (1993-97), with matching funds provided by CARE and WCS. While CARE addressed the development needs of the people living on the peninsula and WCS worked with ANGAP and MEF to create a new national park, with technical support from The Peregrine Fund for bird inventories and ecological monitoring.

2000: ANGAP and WCS took over park management, which continued to be funded by the Dutch government via a sub-contract with CARE. WWF (Switzerland and Finland) contributed funds to support the marine parks.

2002: 87% of all park funding came from the international community.

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