Day-time feeding ecology of *Eulemur cinereiceps* in the Agnalazaha Forest, Mahabo-Mananivo, Madagascar

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ABSTRACT

The Agnalazaha Forest, a degraded fragment of littoral forest in southeast Madagascar, contains a small population of the endangered *Eulemur cinereiceps*. To better conserve this species its feeding ecology was described by habituating two groups and recording their activities, the food types and species exploited, and the location of food trees by focal animal sampling. The lemurs' environment was also described by measuring forest structure, and monitoring climate and phenology. In total, the groups were observed for 498 hours over 11 months. Monthly time spent feeding averaged 9.6 % of total observation time. The species was highly frugivorous (93 % of total time spent feeding). 55 different plant species were exploited for food. Time spent feeding and diet were not simply related to rainfall and temperature nor to food type availability. The two groups' home ranges were 54.9 ha and 58.4 ha and showed a 40 % overlap. The overlap occurred in the swamp forest, which is rich in food plants. To improve the conservation of *E. cinereiceps* at the Agnalazaha Forest, it is recommended that: The swamp forest be included within the zone of strict conservation; important lemur food plants used for restoration; and alternative sources of timber and fuel wood provided for the local population, thereby allowing greater forest regeneration.

RÉSUMÉ

La forêt d'Agnalazaha est un bloc de forêt littorale dégradée d'une superficie de 1,500 ha dans le sud est de Madagascar qui abrite une petite population de l'espèce en danger *Eulemur cinereiceps*. L'écologie de ce lémurien n'a jamais été étudiée dans les forêts littorales et pour améliorer la protection de cette espèce prestigieuse, l'écologie de son régime alimentaire a été étudiée en habituant deux groupes et en relevant la nature des activités, le type de nourriture consommé, les espèces consommées et la localisation des arbres source de nourriture par *focal animal sampling*. L'environnement d' *E.cinereiceps* a également été décrit avec des informations portant sur le climat, d'une part, et d'autres portant sur la structure de la forêt, sa composition et la phénologie en utilisant deux parcelles de 1 ha de forêt dans lesquelles tous les arbres dont le tronc avait un diamètre au moins égal à 10 cm ont été relevés, identifiés et suivis quant à leur fructification et floraison mensuelles. La structure et la composition de la forêt d'Agnalazaha se sont révélées typiques des forêts littorales malgaches. Au total, les groupes de lémuriens ont été observés pendant 498 heures au cours d'une période de 11 mois. La durée mensuelle moyenne consacrée à l'alimentation était de 9,6 % de la durée totale des observations. L'espèce s'est montrée nettement frugivore (93 % de la durée totale consacrée à l'alimentation) mais elle consommait également des feuilles, des inflorescences, des fleurs, du nectar, des insectes et des champignons. Les feuilles et les nectars ont pu être des composants importants du régime alimentaire à certaines périodes. Un total de 55 espèces de plante ont été consommées, parmi lesquelles *Noronhia emarginata, Pandanus microcephalus, Garcinia verrucosa* et *Uapaca louvelii* étaient les plus courantes. Le temps consacré à l'alimentation et celui alloué à la consommation des divers aliments n'étaient liés ni au climat ni à la disponibilité de la nourriture. Les superficies des territoires occupés par les deux groupes étaient de 54,9 ha et de 58,4 ha et présentaient un chevauchement de 40 % au niveau de la forêt marécageuse où les plantes consommées à titre de nourriture étaient abondantes. Pour protéger *E. cinereiceps* dans la forêt d'Agnalazaha, nous recommandons que la forêt marécageuse soit incluse dans une zone de conservation stricte ; que les plantes importantes faisant partie du régime alimentaire de ces lémuriens soient considérées dans les activités de restauration de la forêt ; et que des sources alternatives pour l'obtention de bois d'œuvre ou de chauffe soient proposées à la communauté villageoise locale pour permettre à la forêt de se régénérer.

KEYWORDS: Conservation, brown lemur, diet, home range, littoral forest.

MOTS CLEFS : conservation, lémur brun, régime alimentaire, territoires, forêts littorales.

INTRODUCTION

Since 2002 the Missouri Botanical Garden (MBG) has been working with local stakeholders to conserve the Agnalazaha Forest (also known as Mahabo Forest; see Hobinjatovo et al. 2009), a 1,500 ha fragment of littoral forest located in southeastern Madagascar. This site's fauna includes the endangered lemur *Eulemur cinereiceps* (IUCN 2010), whose conservation at

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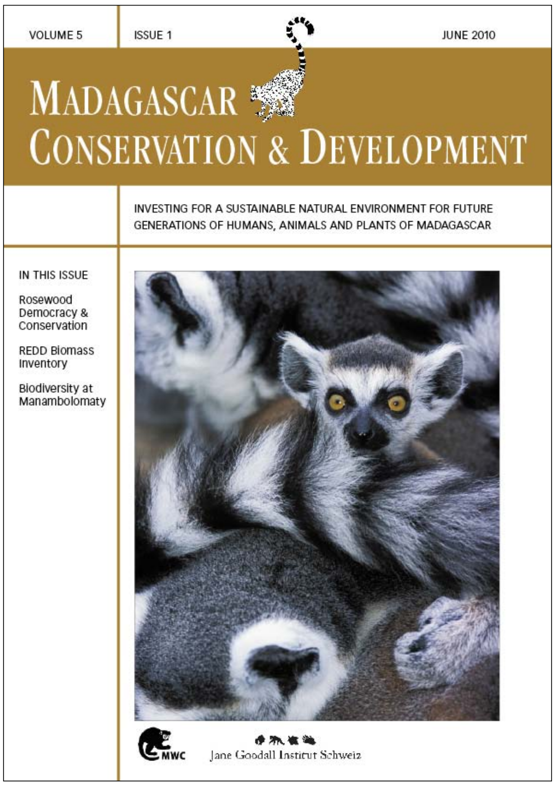

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Agnalazaha is important because it is a threatened part of our natural heritage that likely plays an important role in forest regeneration as a key seed dispersal. To conserve *E. cinereiceps* at this site, information is required to complement earlier studies conducted at Vevembe (Johnson 2002) and Manombo (Ralainasolo et al. 2008), neither of which examined them in littoral forest. The vegetation type comprises humid evergreen forest growing on loose sand close to the sea (Consiglio et al. 2006). The structure, flora and fauna of littoral forest differ significantly from those of humid forest located on other substrates, and it would be reasonable to expect that the ecology of *E. cinereiceps* in this habitat is likewise distinct.

The Agnalazaha Forest (E47°43’07”, S23°11’10”) is located in the Mahabo-Mananivo Commune, 50 km south of Farafangana (Reza et al. 2005) (Figure 1). Within the forest, two major vegetation types can be recognised based on differences in their structure and floristic composition: Swamp forest and well-drained forest. Swamp forest is located within depressions frequently inundated with fresh water in the gently undulating topography of former sand dunes, whereas the well-drained forest is located on the slopes and summits of these dunes. Swamp forest is characterised by a predominance of *Pandanus* and species of Clusiaceae, whereas the well-drained forest is characterised by the predominance of species of Sarcolaenaceae. Agnalazaha is one of the largest fragments of littoral forest remaining in Madagascar (Consiglio et al. 2006).

Around 7,000 people live in the Mahabo-Mananivo Commune and they rely heavily on the Agnalazaha Forest for a range of resources, including timber (for the construction of traditional houses), fuel, foods, medicines and materials for handicrafts (Reza et al. 2005). Fire is widely used as an agricultural tool to reduce the abundance of weeds in rice fields and to encourage young growth of grass in pastureland, and each year these activities typically result in about five wildfires within the Commune (Ludovic Reza, pers. obs.). The Agnalazaha Forest is thus mainly threatened by exploitation of timber, shifting cultivation and wildfires.

In 2007, monitoring of *Eulemur cinereiceps* in Agnalazaha Forest revealed a population of 73 individuals. Until recently, lemurs were hunted at the site by means of traps, but this activity appears to have ceased as a result of a campaign to raise awareness among local people and the implementation of local rules (called *dina*) forbidding the exploitation of lemurs. Missouri Botanical Garden and local stakeholders have formally proposed that Agnalazaha Forest be classified as a New Protected Area as part of the Malagasy Government’s initiative to triple the area of the country managed primarily for nature conservation (Durbin 2006).

The current study aims to provide information on the daytime feeding ecology of *Eulemur cinereiceps* at Agnalazaha to assist the Missouri Botanical Garden and their local partners, who manage this site, so that they can meet their obligations to conserve this rare and threatened lemur and the habitat on which it depends. Although this species is cathemeral (Mittermeier et al. 2006), the study was restricted to daytime observations because local guides were reluctant to work at night in an area where wild pigs are abundant and considered aggressive, a restriction that represents an unavoidable constraint on the utility of this research.

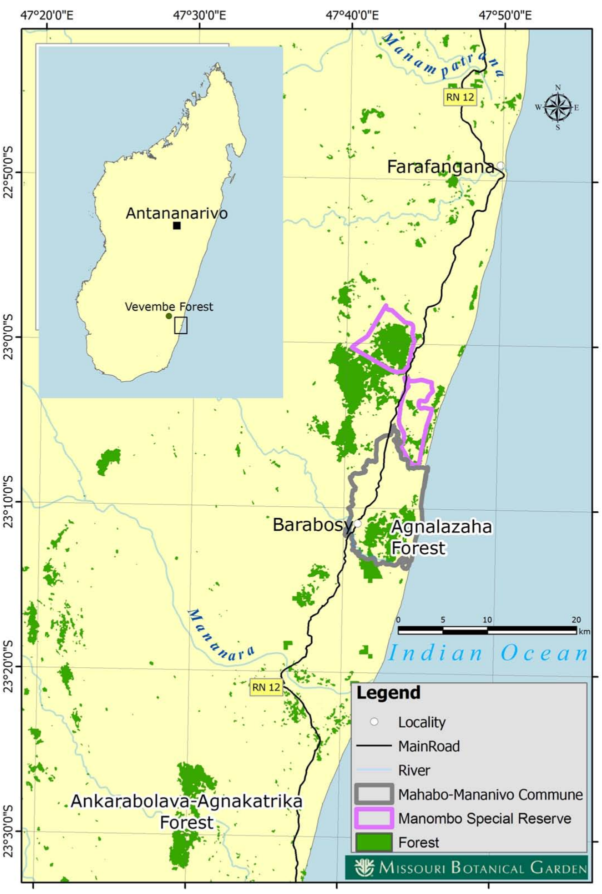

FIGURE 1. Location of the Agnalazaha Forest.

METHODS

STUDY SPECIES. *Eulemur cinereiceps* Grandidier and Milne Edwards 1890 is regarded as synonymous with *Eulemur albocollaris* and *Eulemur fulvus albocollaris* (Rumpler 1975, Johnson et al. 2008), and is classified as Endangered (IUCN 2010). It is a medium-sized, group-living, dichromatic, cathemeral lemur with a body weight of 2-2.5 kg (Tattersall 1982, Mittermeier et al. 2006, Ralainasolo et al. 2008). It is predominantly frugivorous but also eats leaves, flowers, nectar and fungi (Johnson 2002, Ralainasolo et al. 2008). This species is reported to occur in more or less degraded littoral and escarpment humid evergreen forests in a small area in south-east Madagascar, between the Manampatrana and Mananara Rivers (Groves 2001). However, Irwin et al. (2005) report the presence of *E. cinereiceps* north of the Manampatrana River and we have recently located what appears to be a population of this species in the Ankarabolava-Agnakatrika Forest (E48°33’41”, S19°08’24”) just south of the Mananara River. This species is threatened by hunting and loss of habitat due to shifting cultivation, timber exploitation and wild fires (Irwin et al. 2005).

ENVIRONMENTAL DESCRIPTION. To facilitate the interpretation of this lemur’s feeding ecology, their natural environment was described with regard to climate, forest structure, and the composition and phenology of the local flora.

The climate of the Agnalazaha Forest was described using data from MBG’s weather station at Barabosy, a hamlet located 2 km west of the study site, outside the forest, in an anthropogenic landscape of grassland and eucalyptus plantations (see Figure 1). This station measures daily precipitation using a rain gauge and daily maximum and minimum temperature.

The forest structure was described using two one-hectare plots (Plot 1: From E47° 43’ 17.5’’, S23° 11’ 10.1’’, elevation 31 m to E47° 43’ 04.3’’, S23° 11’ 20.2’’, 49 m; Plot 2: From E47° 44’ 02.4’’, S23° 10’ 38.9’’, 22 m to E47° 44’ 00.5’’, S23° 10’ 39.7’’, 13 m), one each placed in the home range of the two lemur groups selected for study. The plots were established and censused using the methodologies described in Birkinshaw et al. (2000). Each of the 500 m × 20 m plots was oriented to include areas of both well-drained and swamp forest. Unfortunately, the significance of these two forest types in the understanding feeding ecology of the study groups was not fully appreciated until the end of the study, and the experimental design precluded analysis of data in these terms. Only trunks of trees included in the plots that had a diameter at breast height (dbh) ≥ 10 cm were considered in this study; their dbh was measured and their height estimated. Because of previous exploitation of timber within the study site, many individual trees had been coppiced and thus exhibited several trunks.

The description of floristic composition was limited to trees with dbh ≥ 10 cm located within the two plots. Each species initially was identified by scientific and vernacular names. Scientific identifications were verified and confirmed by collecting voucher herbarium specimens (following protocols described in Dold et al. 2000), and consulting the literature (e.g., the taxonomic treatments in Adansonia), specialists, and specimens in Madagascar’s main herbaria. Vernacular identifications were made by consulting local people. Floristic composition was assessed by conducting an inventory of tree species, recording their respective abundances and total basal area. The Shannon diversity index (*H*) was used to compare the results of this study with those of Johnson (2002), calculated as follows:

$$H = -\sum_{i=1}^{s} (p_i)(\log p_i)$$

where s = number of species and p_i is the relative abundance of each *i*th species. Relative abundance (p_i) = N_s/N_t, where N_s is the number of trunks of the species and N_t is the number of trunks of all species.

Tree phenology was described by examining each tree in Plot 1 (N = 771) once per month with binoculars and noting the presence or absence of open flowers and/or mature fruit.

LEMUR FEEDING ECOLOGY. With the assistance of three local guides, two lemur groups (Group 1 and Group 2) were habituated to human presence. The size of each group was assessed periodically during the study by counting the total number of individuals. The feeding ecology of each group was described using ‘continuous focal animal sampling’ (Altmann 1974), in which an individual within the group is randomly selected and observed continuously for two hours before switching to another individual. Most observations were made between 1000h and 1600h because of the time required to locate the lemurs in the morning and the necessity of returning home before nightfall. Initially during this study, individual lemurs were identified by differences in their pelage, but in June 2006 they were captured by another group of researchers, who fitted each animal with a coloured collar. To facilitate the weekly collection of information, each lemur group was observed for three days in succession before switching to the other group. We recorded when the focal animal began and stopped each activity. Short lapses (e.g., of less than ten seconds) in an otherwise continuing activity were regarded as a cessation and resumption. Three classes of activity were recognised: Resting (which included socialising), feeding (which included foraging) and travelling. When an individual was seen feeding, the item of food being eaten was classified as ripe fruit, unripe fruit, leaves, flowers, nectar, insects, or fungi. Ripe and unripe fruit were distinguished by examining their physical characteristics and those of their seeds. For plant foods, the species was also initially identified using its vernacular name and by flagging the source plant so that a specimen could be collected to verify the identification. To define the home ranges of the two groups, the locations of the trees exploited by its members were recorded (using a global positioning system unit). These locations were then mapped using Arcview 3.2., and the area of the minimum convex polygon encompassing the locations was calculated.

RESULTS AND DISCUSSION

ENVIRONMENT. Table 1 summarises the climate at the study site. The mean minimum and maximum monthly temperature ranges from 12°C to 20°C and 27°C to 34°C, respectively. The total precipitation for the 11-month period October 2006 to August 2007 (data are missing for September 2006 because of equipment failure) was 3,144 mm. Although temperatures are high and there is some precipitation in every month of the year, the climate was hottest between November and March and wettest between January and May.

The density of trees in the Agnalazaha Forest was estimated as 809 trunks per hectare. A total of 88.2 % of the trunks were in the diameter class 10-20 cm; mean trunk diameter

TABLE 1. Climate at Barabosy and flowering and fruiting phenology of 1,618 trunks included in the two plots (m: missing data point).

Months	Mean temperature (°C)		Precipitation (mm)	Number of trunks in plots	
	Minimum	Maximum		with flowers	with fruit
VI 2006	16.4	31.6	0	0	0
VII 2006	15.6	26.7	223	36	59
VIII 2006	15.6	27.3	173	45	61
IX 2006	13.5	27.8	m	49	52
X 2006	m	m	29	40	28
XI 2006	17.6	34.0	171	61	46
XII 2006	19.7	33.8	48	94	56
I 2007	20.2	33.2	784	103	61
II 2007	19.5	34.0	587	117	60
III 2007	19.5	33.2	589	126	59
IV 2007	18.3	31.1	345	124	64
V 2007	16.0	29.5	319	126	70
VI 2007	12.9	28.0	139	m	m
VII 2007	12.9	29.0	68	m	m
VIII 2007	11.7	30.9	65	m	m
IX 2007	m	m	m	m	m
X 2007	m	m	m	m	m
XI 2007	m	m	m	m	m
XII 2007	m	m	m	m	m
I 2008	19.7	34.0	332	m	m
II 2008	19.0	31.7	492	m	m
III 2008	18.0	33.3	291	m	m
IV 2008	16.8	30.2	314	m	m
V 2008	14.4	27.5	335	m	m

was 14.6 cm and maximum dbh was 48.2 cm. The average tree height was 9.7 m and the total trunk basal area was 30.1 m^2 per hectare. Rabevohitra et al. (1998) described the flora and structure of littoral forest in ten one-hectare plots established at five sites distributed along the east coast of Madagascar. They report that trunk density ranged from 542 to 1,221 trunks per ha, total trunk basal area from 19.03 to 38.9 m^2, and mean tree height from 9.92 to 12.56 m. Thus, the structure of the Agnalazaha Forest can be considered as typical of Malagasy littoral forest in its current state. However, it should be noted that all remaining areas of this vegetation type in Madagascar have been subjected, to a greater or lesser extent, to anthropogenic pressures, and its natural structure was almost certainly different (Consiglio et al. 2006).

Compared to the Vevembe Forest, the evergreen humid forest on basement rock where Johnson (2002) conducted his ecological study of *Eulemur cinereiceps*, Agnalazaha Forest has a lower trunk density, a lower canopy height, a smaller mean trunk size and a lower trunk basal area per unit area (see Table 2). These differences likely reflect the geology of the two sites as well as the higher level of forest degradation at Agnalazaha. Forest structure cannot be compared between the Agnalazaha Forest and the evergreen humid forest on lava at Manombo, the study site for Ralainasolo et al. (2008), because of fundamental differences in the methods used in these studies.

Among the 1,618 trunks included in the plots at Agnalazaha, a total of 145 species were recorded. The most speciose families were: Salicaceae (with 14 species), Clusiaceae (12 species), Euphorbiaceae (11 species), Myrtaceae (10 species), Anacardiaceae (8 species), and Ebenaceae (8 species). The value of the Shannon diversity index is 1.659. The species with the highest trunk abundance and trunk basal area were: *Intsia bijuga* (Fabaceae, 12.5% of total trunks, 12.2% total trunk basal area), *Anthostema madagascariensis* (Gentianaceae, 8.1%, 7.4%); *Uapaca louvelii* (Euphorbiaceae, 7.2%, 9.4%); *Asteropeia multiflora* (Asteropeiaceae, 5.4%, 4.9%); *Brochoneura acuminata* (Myristicaceae, 4.4%, 3.9%); and *Agarista salicifolia* (Ericaceae, 1.9%, 4.8%). At each of the five littoral forest sites studied by Rabevohitra et al. (1998) the number of tree species recorded in the pair of one-hectare plots ranged from 60 to 144. Thus, with 145 tree species per hectare, the Agnalazaha Forest can be considered relatively species rich. Johnson (2002) reports 60 species among the 267 trunks included in the plots established at Vevembe Forest, with a Shannon diversity index ranging from 1.072 to 1.269 (among four plots, each with a size of 0.0625 ha). Because of the different sample sizes used by Johnson (2002) and the current study it is difficult to compare species diversity between the two sites. A comparison of floristic composition between the forests at Agnalazaha and Manombo (Ralainasolo et al. 2008) is also difficult because of the different dbh classes recorded in the two studies.

TABLE 2. Comparison of forest structure between Vevembe Forest (Johnson 2002) and Agnalazaha Forest.

Study Site	Johnson (2002) Vevembe Forest	This study Agnalazaha Forest
Trunk density [per ha]	1,068 (based on area of 0.25 ha)	809 (based on area of 2 ha)
Mean trunk dbh [cm]	18.4 (N = 267)	14.6 (N = 1,618)
Trunk basal area [m²/ha]	35.8 (based on area of 0.25 ha)	30.1 (based on area of 2 ha)
Mean tree height [m]	12.5 (N = 267)	9.7 (N = 1,618)

Table 1 shows the number of trees in the two Agnalazaha plots bearing flowers and fruits during the period July 2006 to May 2007. Approximately three times the number of trees flowered between December 2006 and May 2007 compared to the period July to November 2006. The phase of maximum flowering coincides with the period of highest precipitation. The number of trees with fruit was nearly constant throughout the study period except during October 2006, when few trees carried fruit. October was also the month with lowest precipitation.

FEEDING ECOLOGY. In total, Group 1 was observed for 229 hours distributed over nine months and Group 2 for 269 hours distributed over 11 months. Group 1 could not be located during the months of February and March 2007 and data are therefore lacking from this period. We suspect that this group had left the area where hitherto it had been located and was instead feeding on the nectar of *Ravenala madagascariensis*, which is abundant elsewhere and was flowering at this time. During the study, the size of Group 1 ranged from five to seven individuals, while Group 2 comprised from nine to eleven individuals.

Table 3 shows the percentage of total observation time that Group 1 and Group 2 respectively spent feeding, travelling and resting during each month from June 2006 to May 2007. For both groups, during every month, a majority of their time was spent resting (55-85% total time); time spent feeding ranged from 2% to 22%, and travelling occupied from 7% to 23% of the time. During most months, Group 1 spent more

TABLE 3. Percentage of total observation time that Group 1 and Group 2 spent feeding, travelling and resting during each month of the study (m: missing data point).

Month	Group	Observation time [min]	% total observation time spent on each activity		
			Feeding	Travelling	Resting
VI 2006	1	1,187	14.0	13.5	72.5
	2	1,244	6.6	16.0	77.4
VII 2006	1	2,293	14.4	14.0	71.6
	2	675	10.0	16.7	73.3
VIII 2006	1	0	m	m	m
	2	0	m	m	m
IX 2006	1	2,606	7.4	16.0	76.6
	2	1,031	9.3	7.1	83.6
X 2006	1	1,999	8.8	16.4	74.9
	2	1,106	9.0	17.9	73.1
XI 2006	1	1,641	14.3	14.7	71.0
	2	1,318	5.3	13.9	80.8
XII 2006	1	1,022	15.4	22.0	62.6
	2	1,063	4.9	10.2	85.0
I 2007	1	896	21.5	23.3	55.1
	2	654	6.3	20.3	73.4
II 2007	1	0	m	m	m
	2	2,444	9.9	14.4	75.8
III 2007	1	0	m	m	m
	2	2,626	9.8	15.7	74.5
IV 2007	1	1,460	10.1	23.4	66.5
	2	3,138	6.0	17.3	76.7
V 2007	1	623	7.6	17.1	75.3
	2	893	1.8	17.9	80.3

time feeding than Group 2. For both groups, time spent feeding fluctuates through the year, but the pattern of fluctuation differs between the groups: For Group 1, a relatively large amount of time was spent feeding from November 2006 to January 2007 and from June to July 2006, whereas for Group 2 peaks in time spent feeding occur between July to October 2006 and February to March 2007.

The average monthly time spent feeding by *Eulemur cinereiceps* at Agnalazaha is 9.6 %, lower than the values reported for this species by both Johnson (2002) at Vevembe (12-15 %) and Ralainasolo et al. (2008) at Manombo (12 %). The lower value found at Agnalazaha may result from the fact that most observations of feeding ecology were made between 1000h and 1600h, which could have led to an under-representation of possible early morning and late afternoon feeding periods. However, Johnson (2002) and Ralainasolo et al. (2008) do not mention the distribution of their observations during the day.

Table 4 shows the percentage of total time that Group 1 and Group 2 spent feeding on different types of food. For both groups, during every month of the study, the diet was dominated by ripe fruit, with the percentage of total monthly feeding time allocated to this food type ranging from 63 % to 100 %. Combining the data from the two groups reveals that at Agnalazaha *Eulemur cinereiceps* is strongly frugivorous (93 % of feeding time). A variety of other food types were important secondary dietary constituents at certain times of the year, including unripe fruits for Group 1 in June 2006, leaves for Group 1 for September 2006, and nectar for Group 2 in May 2007. It is possible that nectar was also an important food item for Group 1 during February and March 2007, when the Group could not be found where it was normally located, and on the basis of observations made by local people, is thus suspected to have been feeding on nectar of *Ravenala madagascariensis* elsewhere . Rare foods included insects and fungi.

Eulemur cinereiceps was considerably more frugivorous in the Agnalazaha Forest (93 %) than at Vevembe (66 %) or Manombo (67 %) (Johnson 2002, Ralainasolo et al. 2008), a finding that may reflect the different seasons during which these studies were conducted. The high frugivory observed at Agnalazaha Forest is similar to that reported for the hybrid *E. cinereiceps* × *E. fulvus rufus* (95 % of feeding time) at Andringitra (Johnson 2002). According to Johnson (2002), levels of frugivory reported for brown lemurs range from 67 % to 89 % (with the exception of the mainly folivorous groups of *E. fulvus rufus* studied by Sussman (1974, 1977)). Given the partially degraded state of the Agnalazaha Forest, the high level of frugivory of *E. cinereiceps* was unexpected. Food categories less important for *E. cinereiceps* (i.e., unripe fruit and leaves) also contribute to the diets of brown lemur populations elsewhere (Johnson 2002, Ralainasolo et al. 2008), although typically these items have been found to be of greater importance in these studies than is the case in the current study.

The time spent feeding by the two lemur groups at Agnalazaha Forest was not related in any simple way to availability of broadly defined food type classes or to precipitation. For example, the time spent feeding was relatively high for Group 2 in both September 2006 (a time with low precipitation

TABLE 4. Percentage of total feeding time that Group 1 and Group 2 spent feeding on different food types during each month of the study. (* time spent feeding during observation time).

Month	Time* [min]	Group	% time spent feeding on food type						
			Ripe Fruits	Unripe Fruits	Leaves	Flowers	Insects	Nectar	Fungi
VI 2006	166	1	79.1	18.4	2.5	0.0	0.0	0.0	0.0
	82	2	90.1	2.8	7.0	0.0	0.0	0.0	0.0
VII 2006	330	1	96.8	0.0	1.9	1.0	0.3	0.0	0.0
	75	2	100.0	0.0	0.0	0.0	0.0	0.0	0.0
VIII 2006	0	1	m	m	m	m	m	m	m
	0	2	m	m	m	m	m	m	m
IX 2006	194	1	73.6	0.0	22.3	4.1	0.0	0.0	0.0
	83	2	100.0	0.0	0.0	0.0	0.0	0.0	0.0
X 2006	175	1	86.2	4.6	6.9	2.3	0.0	0.0	0.0
	99	2	98.0	0.0	2.0	0.0	0.0	0.0	0.0
XI 2006	235	1	98.7	0.0	0.4	0.0	0.9	0.0	0.0
	70	2	100.0	0.0	0.0	0.0	0.0	0.0	0.0
XII 2006	157	1	91.0	9.0	0.0	0.0	0.0	0.0	0.0
	53	2	100.0	0.0	0.0	0.0	0.0	0.0	0.0
I 2007	184	1	91.1	4.5	0.0	0.7	2.8	0.0	0.9
	42	2	93.8	3.1	0.0	0.0	3.1	0.0	0.0
II 2007	0	1	m	m	m	m	m	m	m
	234	2	98.3	0.0	0.4	0.9	0.4	0.0	0.0
III 2007	0	1	m	m	m	m	m	m	m
	258	2	86.6	2.8	1.6	1.2	0.4	7.3	0.0
IV 2007	146	1	83.2	3.8	2.3	1.5	0.8	8.4	0.0
	186	2	78.6	0.0	11.9	1.8	2.4	5.4	0.0
V 2007	47	1	89.5	0.0	2.9	3.9	1.9	1.8	0.0
	16	2	62.5	0.0	0.0	6.3	6.3	25.0	0.0

and low fruit availability) and February 2007 (high precipitation and high fruit availability). Also, the diet of the two lemur groups does not seem to be related simply to the availability of fruit or of flowers, nor to the amount of precipitation. In September 2006, when fruit was least available, Group 1 spent more time eating leaves than in any other month, yet during this same month, Group 2 was 100 % frugivorous. Furthermore, when fruit was most available in May 2007, Group 2 spent more time exploiting nectar than in any other month. This observation suggests that nectar should not be regarded as a less preferred food type than fruit. Johnson (2002) also found that his study groups did not track resources in predictable ways.

Table 5 lists the plant species eaten by the two groups. In total, food from 55 different plant species was consumed. Table 6 lists the most important food for the two groups, defined as items consumed for ≥ 10 % of total time spent feeding during a given month. Food that is frequently listed include ripe fruits of *Noronhia emarginata, Pandanus microcephalus, Garcinia verrucosa* and *Uapaca louvelii.* The fruits from two alien species (*Clidemia hirta* and *Psidium cattleianum*) were also exploited by the lemurs.

TABLE 5. Plant species and plant parts exploited by the two study groups of *Eulemur cinereiceps* at Agnalazaha Forest.

Family	Species	Vernacular Name	Part Consumed	Group	
				1	2
Anacardiaceae	*Abrahamia* sp. 1.	Tarata lahy	fruits		X
Annonaceae	*Ambavia gerrardii*	Rombavy	fruits	X	X
Annonaceae	sp. 1.	Fotsivavy	leaves		X
Asclepiadaceae	*Secamone* sp. 1.	Vahisisika	leaves	X	
Arecaceae	*Dypsis linearis*	Vonitra	fruits		X
Arecaceae	*Dypsis mananjariensis*	Varaotra	fruits	X	X
Bignoniaceae	*Colea* sp 1.	Fotsitsoy	fruits	X	X
Bignoniaceae	*Phyllarthron mada-gascariensis*	Retsirika	flowers	X	X
Canellaceae	*Cinnamosma mada-gascariensis*	Fotsignana	fruits	X	X
Clusiaceae	*Calophyllum milvum*	Vitagno	fruits + leaves	X	X
Clusiaceae	*Garcinia verrucosa*	Tsingarahara	fruits	X	X
Clusiaceae	*Psorospermum* sp 1.	Haronganala	fruits	X	
Ebenaceae	*Diospyros ferrea*	Ramagnopaka	fruits		X
Erythroxylaceae	*Erythroxylon* sp. 1.	Sakainala	fruits	X	
Euphorbiaceae	*Uapaca louvelii*	Voapaky	fruits	X	X
Euphorbiaceae	*Uapaca* sp.1.	Voapaky lahy	fruits		X
Fabaceae	*Intsia bijuga*	Hintsy	leaves + fruits	X	X
Icacinaceae	*Cassinopsis* sp. nov.	Hazomafaitra	fruits	X	X
Lamiaceae	*Clerodendrum* sp. 1.	Tarata	fruits	X	X
Lamiaceae	*Vitex chrysomallum*	Sarivatoa beravina	fruits	X	
Lamiaceae	*Vitex oscitans*	Sarivatoa	fruits	X	
Loranthaceae	*Bakerella* sp. 1.	Velomihato	leaves		X
Melastomataceae	*Clidemia hirta*	Voatrotrakala	fruits	X	
Melastomataceae	*Tristemma virusanum*	Voatrotroka	fruits	X	
Meliaceae	*Astrotrichilia* sp. 1	Sagnira	fruits		X
Menispermaceae	*Burasaia australis*	Mafanakelika	fruits	X	
Moraceae	*Ficus lutea*	Amontana	fruits		X
Moraceae	*Ficus rubra*	Laza	fruits	X	X
Moraceae	*Ficus tiliifolia*	Ara	fruits		X
Myrsinaceae	*Embelia incumbens*	Masomazava	fruits		X
Myrsinaceae	*Monoporus spathulatus*	Varikanda	flowers		X
Myrtaceae	*Psidium cattleianum*	Goavy	fruits	X	X
Myrtaceae	*Syzygium* sp. 1	Rotra	fruits		X
Oleaceae	*Jasminum kitchingii*	Vahimavo	fruits	X	X
Oleaceae	*Noronhia emargnata*	Randra	fruits	X	X
Oleaceae	*Noronhia* sp. 1	Randra beravina	fruits	X	
Pandanaceae	*Pandanus* sp. 1	Farafatrala	fruits	X	X
Pandanaceae	*Pandanus microcephalus*	Tsirika	Fruit + flowers	X	X
Pteridaceae	*Pteridium aquilinum*	Tsipang-ampaga	leaves	X	X
Rubiaceae	*Antirhea borbonica*	Hazomalefaka	fruits	X	X
Rubiaceae	*Coffea resinosa*	Sarikafe	fruits	X	
Rubiaceae	*Enterospermum* sp. 1	Apody	fruits	X	X
Rubiaceae	*Gaertnera* sp. 1	Sarikafenala	fruits	X	
Rubiaceae	*Pyrostria* sp. 1	Fotsikahitra	fruits	X	X
Rubiaceae	*Saldinia* sp. 1	Sarikafe manga	fruits	X	X
Salicaceae	*Scolopia erythrocarpa*	Fotsivogny	leaves	X	
Sapindaceae	*Filicium thouarsianum*	Sagnira lahy	fruits	X	
Sapindaceae	*Tinopsis conjugata*	Sagnira	fruits		X
Sarcolaenaceae	*Leptolaena pauciflora*	Fatra	fruits	X	
Sarcolaenaceae	*Sarcolaena multiflora*	Hela	fruits	X	X
Solanaceae	*Solanum* sp. 1	Anamamy	fruits	X	
Streliziaceae	*Ravenala mada-gascariensis*	Ravinala	nectar	X	X
Unknown	Unknown	Hazomaimbo	fruits	X	
Unknown	Unknown	Vatoadambo	fruits	X	
Unknown	Unknown	Hazonoaty Kely	leaves	X	

TABLE 6. Main food items for the two study groups of *Eulemur cinereiceps* at Agnalazaha Forest.

Month	Group 1			Group 2		
	Species	Food Type	% total feeding time	Species	Food Type	% total feeding time
VI 2006	*Ambavia gerrardii*	Ripe fruit	67	*Ambavia gerrardii*	Ripe fruit	65
	Pandanus sp. 1	Unripe fruit	10	*Dypsis linearis*	Ripe fruit	19
VII 2006	*Ficus rubra*	Ripe fruit	37	*Noronhia emarginata*	Ripe fruit	79
	Noronhia emarginata	Ripe fruit	15	*Ficus tiliifolia*	Ripe fruit	10
	Vitex oscitans	Ripe fruit	13			
	Uapaca louvelii	Ripe fruit	13			
	Pandanus sp. 1	Ripe fruit	11			
VIII 2006						
IX 2006	*Noronhia emarginata*	Ripe fruit	37	*Noronhia emarginata*	Ripe fruit	51
	Uapaca louvelii	Ripe fruit	27	*Uapaca louvelii*	Ripe fruit	49
	Secamone sp. 1	Leaves	10			
X 2006	*Noronhia emarginata*	Ripe fruit	11	*Noronhia emarginata*	Ripe fruit	28
	Garcinia verrucosa	Ripe fruit	11	*Uapaca louvelii*	Ripe fruit	25
	Pandanus microcephalus	Ripe fruit	58	*Pandanus microcephalus*	Ripe fruit	19
				Uapaca sp. 1	Ripe fruit	14
				Calophyllum milvum	Ripe fruit	10
XI 2006	*Garcinia verrucosa*	Ripe fruit	37	*Garcinia verrucosa*	Ripe fruit	65
	Pandanus microcephalus	Ripe fruit	23	*Pandanus microcephalus*	Ripe fruit	12
	Tristemma virusanum	Ripe fruit	18	*Calophyllum milvum*	Ripe fruit	12
	Cinnamosma madagascariensis	Ripe fruit	12			
XII 2006	*Abrahamia* sp. 1	Ripe fruit	36	*Pandanus microcephalus*	Ripe fruit	77
	Garcinia verrucosa	Ripe fruit	10	*Garcinia verrucosa*	Ripe fruit	24
I 2007	*Coffea resinosa*	Ripe fruit	57	*Abrahamia* sp. 1	Ripe fruit	71
	Psorospermum sp. 1	Ripe fruit	14	*Pandanus microcephalus*	Ripe fruit	13
				Embelia incumbens	Ripe fruit	10
II 2007				*Pandanus microcephalus*	Ripe fruit	45
				Astrotrichilia sp. 1	Ripe fruit	27
				Abrahamia sp. 1	Ripe fruit	19
III 2007				*Syzygium* sp. 1	Ripe fruit	47
				Dypsis mananjariensis	Ripe fruit	19
IV 2007	*Pyrostria* sp. 1	Ripe fruit	61	*Pyrostria* sp. 1	Ripe fruit	57
	Antirhea borbonica	Ripe fruit	11	*Dypsis mananjariensis*	Ripe fruit	13
				Calophyllum milvum	Young leaves	12
V 2007	*Pyrostria* sp. 1	Ripe fruit	47	*Dypsis mananjariensis*	Ripe fruit	63
	Dypsis mananjariensis	Ripe fruit	21	*Ravenala madagascariensis*	Nectar	27

The estimated dietary diversity of *Eulemur cinereiceps* in the Agnalazaha Forest was considerably less than at Vevembe (55 versus 96 plant species), despite the fact that two groups were studied for nine and 11 months, respectively, at Agnalazaha whereas only one group was studied at Vevembe for five months. However, at Manombo, Ralainasolo et al. (2008) reported similar dietary diversity for *E. cinereiceps* as our findings indicate at Agnalazaha, with 54 plant species being exploited during their nine-month study. It is likely that the comparatively low dietary diversity of *E. cinereiceps* at Agnalazaha compared to Vevembe is related to the higher degree of frugivory shown by this species at the former site. Johnson (2002) also reports lower dietary diversity for highly frugivorous *E. cinereiceps* × *E. fulvus rufus* at Andringitra (69 and 27 species, respectively, for two study groups) than for *E. cinereiceps* at Vevembe. However, this does not explain the lower dietary diversity at Manombo compared to Vevembe, where *E. cinereiceps* showed a similar degree of frugivory. It is also possible that the dietary diversity of *E. cinereiceps* at Agnalazaha is lower now than it once was because some plant species have become increasingly rare or have been extirpated as a result of heavy exploitation by humans. For example, several genera of Sapotaceae (e.g., *Capurodendron*, *Faucherea* and *Sideroxylon*) with large fleshy fruits that are included in the diets of *E. cinereiceps* at Manombo (Ralainasolo et al. 2008) and Vevembe (Johnson 2002) are, according to elderly residents living close to Agnalazaha Forest, much more rare now than in the past because they have been exploited for their valuable timber.

Table 6 shows that during several months the two groups of *Eulemur cinereiceps* at Agnalazaha spent more than 50 % of their time feeding on the fruit of a single species. This contrasted with the situation at Vevembe, where for each month of the study much less time was spent eating the most important food item (the maximum being August 2000, when the group spent 35.6 % of its time eating *Pandanus* flowers). However, the apparent frequent dominance of one food item in monthly diets at Agnalazaha may be due to the relatively short monthly observation times for each group at this site. At both Agnalazaha and Vevembe, *Pandanus* species were identified as being among the most important food items. The fruits of this genus are also reported in the diet of *E. cinereiceps* at Manombo (Ralainasolo et al. 2008).

The home ranges of Group 1 and Group 2 measured during the study period are 54.9 ha and 58.4 ha, respectively. However, as mentioned above, in February and March 2007, Group 1 could not be found in the part of the forest where it was normally located, and we have deduced that it was probably spending long periods outside this area, in which case the home range for this group would be considerably larger than indicated above. Johnson (2002) reports a home range of 33.5 to 64.3 hectares (depending on method of estimation used) for his group at Vevembe, and provides a literature review of home range estimates for brown lemurs that reveals a huge variation, from 0.75 ha to 100 hectares.

There is a 40 % overlap between the home ranges of the two study groups at Agnalazaha, and most of this overlap coincides with the swamp forest, where many of the species most frequently exploited for food are located (including *Calophyllum milvum, Ficus rubra, Garcinia verrucosa, Pandanus* spp, *Ravenala madagascariensis*, and *Uapaca louvelii*). A third group of *Eulemur cincereiceps* was also observed on occasion in the swamp forest. Johnson (2002) similarly reports high home range overlap between groups of *E. cinereiceps* at Vevembe and refers to studies of other brown lemur species in which similar ranging patterns have been found.

RECOMMENDATIONS FOR IMPROVING THE CONSERVATION STATUS OF *EULEMUR CINEREICEPS* AT AGNALAZAHA FOREST. Based on the results presented in this study, we formulate a number of recommendations to improve the conservation status of *Eulemur cinereiceps* at the Agnalazaha Forest, as follows:

1. Further research is required to test the hypothesis that areas of swamp forest are of critical importance for *E. cinereiceps* in the Agnalazaha Forest. In the meantime, further degradation of these areas from ongoing timber extraction should be avoided and their regeneration encouraged. In particular, these areas should be included in the 'zone of strict conservation' of the proposed New Protected Area.
2. Several plants are of particular importance as food for *E.cinereiceps*, including *Noronhia emarginata, Pandanus microcephalus*, *Garcinia verrucosa*,*Uapaca louvelii*, and perhaps also *Ravenala madagascariensis*. We recommend that these species should be included among those chosen for forest restoration at Agnalazaha Forest. Species of Sapotaceae, whose fruits were likely once heavily exploited by lemurs but are now rare due to over-exploitation, should also be considered for inclusion in programmes of forest restoration.
3. In general, it would appear that *E. cinereiceps* is an adaptable species that has been able to survive in Agnalazaha Forest despite its partially fragmented and degraded condition. *Eulemur* species seem to recover rapidly from perturbations to their habitat (Ratsisetraina 2006, Ralainasolo et al. 2008) and it is likely that the current small population of *E. cinereiceps* at Agnalazaha would increase rapidly if the current levels of timber extraction are reduced and the forest is able to regenerate. Such a population increase should be encouraged because the long-term viability of this and other species at this site will remain questionable as long as the population of *E. cinereiceps* remains small.

CONCLUSIONS

Despite the partially degraded condition of the Agnalazaha Forest, its resident populations of *Eulemur cinereiceps* are highly frugivorous. In addition to fruit, other food types consumed include leaves, inflorescences, flowers, nectar, insects and fungi, and of these, leaves and nectar may be important dietary constituents at certain times. Although 55 plant species are exploited for food, the diet of *E. cinereiceps* is dominated by 25 of these species. Although the two groups studied at Agnalazaha had home ranges of at least 55 ha and 58 ha, respectively, most of the plants exploited for food were located in an area of swamp forest where the home range of these groups overlapped. These results suggest that the conservation of *E. cinereiceps* at Agnalazaha can be improved by:

(i) including the swamp forest in the 'zone of strict conservation' of the proposed new protected area so that it can regenerate following years of over-exploitation;

(ii) by incorporating important lemur food plants in efforts to restore very degraded forest; and

(iii) by activities that result in reduced exploitation of the forest for timber and fuel, including, most importantly, the provision of alternative resources.

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