Chapter 4.8
Lemurs in Evergreen Littoral Forest Fragments

Jörg U. Ganzhorn[1], Tolona Andrianasolo[2], Tantely Andrianjazalahatra[2], Giuseppe Donati[3], Joanna Fietz[4], Petra Lahann[1], Ivan Norscia[5], Jacques Rakotondranary[2], Bakoly M. Rakotondratsima[6], José Ralison[6], Roger E.A.F. Ramarokoto[2], Seheno Randriamanga[6], Sandrine Rasarimanana[6], Berthe Rakotosamimanana†, Jean-Baptiste Ramanamanjato[7], Gisèle Randria[2], Mamitiana Tovonanahary Rasolofoharivelo[2,8], Marlène Razanahoera-Rakotomalala[6], Jutta Schmid[4] and Simone Sommer[1,9]

Abstract

The aim of this project was to provide baseline data for long-term monitoring studies to identify the effects of habitat fragmentation and degradation on the population dynamics of lemurs in the littoral forests of southeastern Madagascar. Populations of the various lemur species responded differently to habitat fragmentation and degradation. The larger species, *Eulemur collaris* and *Avahi meridionalis*, showed strong, negative population responses (population decline, reduced group size) in degraded habitats, and eventually disappeared from smaller fragments. *Microcebus* spp. populations fluctuated non-systematically between fragments with localized declines and recoveries.

Résumé

Les lémuriens des fragments de forêt littorale sempervirente. Les objectifs de ce projet consistaient à produire les données de base destinées aux études du suivi à long terme pour identifier les effets de la fragmentation et de la dégradation de l'habitat sur les dynamiques des populations de lémuriens dans la forêt littorale du sud-est de Madagascar. Les populations des diverses espèces de lémuriens ont réagi différemment quant à la fragmentation et à la dégradation de l'habitat. Les plus grandes espèces, *Eulemur collaris* et *Avahi meridionalis* ont montré une forte réaction de leur population (déclin de la population, réduction de la taille des groupes) dans les habitats dégradés pour finir par disparaître dans les plus petits fragments. Les populations de *Microcebus* spp. ont fluctué selon les fragments mais pas de façon systématique. Leur dynamique de population est caractérisée par des déclines et des rétablissements localisés.

Introduction

Lemurs are among the most important target species for conservation in the littoral forest remnants of the region. Even though no other taxon on Madagascar has been studied with similar intensity (e.g. Petter *et al*. 1977, Tattersall 1982, Harcourt and Thornback 1990, Mittermeier *et al*. 2006), it is still not clear how certain species respond to habitat degradation or whether or not some species can use regenerating or replanted forests (e.g., Ganzhorn 1987, Ganzhorn and Abraham 1991, Ganzhorn *et al*. 1997, Colquhoun 1998, Goodman *et al*. 1997, Merenlender *et al*. 1998, Styger *et al*. 1999, Ratsirarson and Ranaivonasy 2002, Holloway 2003).

[1] Department of Animal Ecology and Conservation, Hamburg University, Martin-Luther-King Platz 3, 20146 Hamburg, Germany. Email: Ganzhorn@zoologie.uni-hamburg.de; petra.lahann@gmx.de

[2] Departement de Paléontologie et d'Anthropologie Biologique, Université d'Antananarivo, BP 906, Antananarivo 101, Madagascar. Email: tolona1@yahoo.fr; rsjacques@yahoo.fr; ravolrandria@yahoo.fr

[3] Department of Biology, Institute of Anthropology, University of Pisa, Via S. Maria, 55, 56126 Pisa, Italy. Present address: Anthropology Department, Oxford Brookes University, Gipsy Lane, Oxford, OX3 0BP, UK. Email: gdonati@brookes.ac.uk

[4] Department of Experimental Ecology, Albert Einstein Strasse, Ulm, Germany; Email: joanna.fietz@t-online.de; GuntherSchenkel@aol.com

[5] Museo di Storia Naturale e del Territorio, Centro Interdipartimentale, Université de Pisa, Via Roma, 79, 56011, Calci, Pisa, Italy. Email: rca00012@lunet.it

[6] Département de Biologie Animale, Faculté des Sciences, Université d'Antananarivo, BP 906, Antananarivo 101, Madagascar. Email: jo_ralison@yahoo.fr; marlene@dts.mg;

[7] QIT Madagascar Minerals, BP 225, Tolagnaro 614, Madagascar. Email: jeanbaptiste.ramanamanjato@riotinto.com

[8] Conservation International, BP 5178, Antananarivo 101, Madagascar. Email: loverabe@yahoo.fr

[9] Institute for Zoo and Wildlife Research, Postfach 601103, 10252 Berlin, Germany. Email: sommer@izw-berlin.de

The utilization of short-term lemur inventories as indicators of habitat suitability can be problematic since lemurs are long-lived animals able to persist in habitats that do not allow positive population growth (Ganzhorn and Schmid 1998, Ganzhorn 1999, Ratsimbazafy *et al*. 2002). Thus, long-term studies are needed to document the population dynamics and allow conclusions to be made about the fate of the population over time (e.g., *Propithecus edwardsi* (Pochron *et al*. 2004), *P. verreauxi* (Jolly *et al*. 1982, Richard *et al*. 2002), *Mirza coquereli* (Kappeler 1997), *Lemur catta* (Sussman 1991), *Microcebus murinus* (Hladik *et al*. 1998, Eberle and Kappeler 2002).

The specific aim of this chapter is to document encounter rates of lemurs along transects in forests of different degrees of degradation between 1998 and 2006. These data should provide the basis for long-term monitoring of the population dynamics of the lemur communities in the evergreen littoral forests surrounding Tolagnaro.

Methods

Study sites and dates

The study was initiated in 1998 at least in part to update earlier inventories from 1989 (Lewis Environmental Consultants 1992). Three different littoral forest blocks, Petriky, Mandena, and Sainte Luce, were studied with respect to presence/absence data, but only the sites of Mandena and Sainte Luce were examined in detail for changes in lemur populations and forest cover and structure over time associated with the fragmentation studies.

Surveys were carried-out during times of the year when all primate species were active. These surveys were part of different studies, and therefore, not all forest fragments were covered in any given year. Also, the degradation of the forest fragments varied over the years. The classification of degradation follows the procedure outlined by Vincelette *et al*. (Chapter 2.4), which distinguishes 5 classes of degradation based on the percentage of cover of canopy trees: > 90%, 71 – 90%, 51 – 70%, 21 – 50%, ≤ 20% (Table 1). Fragments in the Mandena region are labeled with 'M,' and those of the Sainte Luce region with 'S'.

Fragment M13 was classified as degraded forest in 1989-1990 (Lewis Environmental Consultants 1992). It had been severely degraded by charcoal makers prior to the onset of the 2000 lemur surveys reported herein. Based on remote sensing data, the size of M13 was estimated at 74 ha in 1998. The estimated increase to 109 ha in 2005 was associated with certain former areas of bare ground being colonized by vegetation in the intervening years. M3 had been exploited for charcoal and devastated by 2002, M4 was destroyed by charcoal makers in August 2005, M5 was severely degraded by 2005, and in 1998, S7 was still connected with S6. The fragment S9 consists of a northern area characterized by a

Table 1. Localities of lemur surveys and the degree of canopy cover at the various study sites. "M" and "S" mark forest fragments of the Mandena and Sainte Luce regions, respectively. Size measurements of forest blocks are based on satellite images.

Year	1998	2000	2005	1998	2000	2005
Site	Size[ha]	Size[ha]	Size[ha]	Canopy cover	Canopy cover	Canopy cover
Petriky			800			0-70%
M3	220		Destroyed	51-90%	51-90%	0
M4		36	Destroyed	51-70%	51-70%	0
M5		18	Degraded	51-70%	51-70%	≤ 20%
M13	74		109	≤ 20%	≤ 20%	≤ 20%
M15	94	95	95	51-70%	51-70%	51-70%
M16	57	53	53	51-70%	21-50%	51-70%
M20	6	6	6	21-50%	21-50%	≤20%
S7	385	198	198	> 90%	> 90%	> 90%
S8	95	61	48	71-90%	21-70%	≤ 20%
S9	275	251+16	252+16	71-90%	71-90%	71-90%
S17	237	237	237	> 90%	> 90%	> 90%

canopy cover of 61 - 80%, and a southern area of 16 ha with a canopy cover of 41 - 60%. The southern part did not change in size or degree of degradation over the study period. The northern part was corroded by large *tavys* along its northeastern corner (G. Donati, pers. obs.). Only the northern part of this parcel is listed in Table 1. In 2000, large active *tavys* were recorded in S17, but this is not reflected in the size estimates for S17 listed in Table 1.

Vegetation descriptions

Several different methods were employed to measure and illustrate the state of the forest's vegetation. The vertical forest structure was described quantitatively with the line-intercept technique (Gautier *et al*. 1994; Fig. 1). For this, contacts of vegetation on a vertical line are recorded from 100 points spaced at 1 m intervals along a transect. At each sampling point, the heights at which plants touched a pole were recorded. Heights of contact above 8 m were estimated. For dense foliage, the lower and upper points of the foliage mass were recorded. For a visual representation of the vertical structure, sketches of a 25 m strip of forest were drawn for 10 forest fragments.

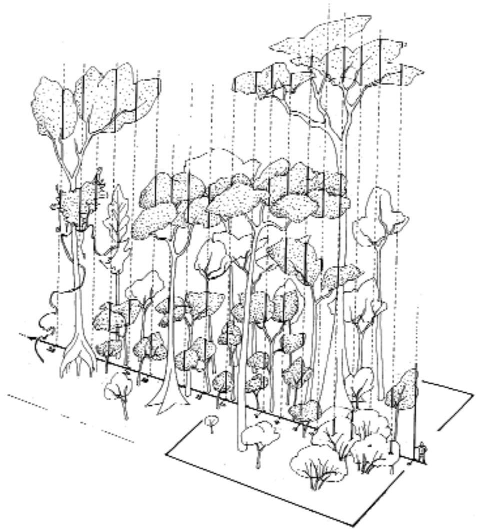

Figure 1. Illustration of vertical forest structure based on a linear sampling design (after Gautier *et al*. 1994; figure drawn by C. Chatelain; reproduction with permission from C. Chatelain; from Ganzhorn 2003).

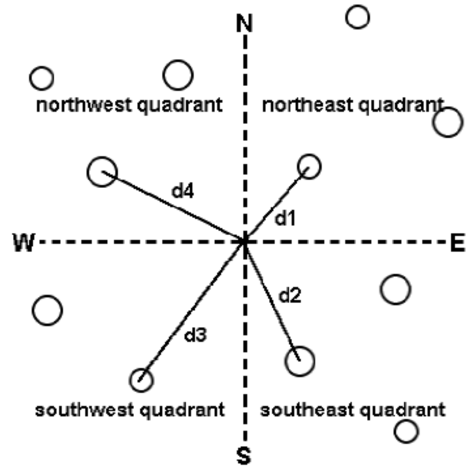

Figure 2. Point-centered quadrants or point-quarter sampling (after Brower *et al*. 1990, from Ganzhorn 2003).

The point-centered, quarter method was used to describe the horizontal structure of the different forests (Brower *et al*. 1990; Fig. 2). For this, each sample point represents the center of four compass directions that divide the sampling plot into four quarters. In each quarter, the distance from the center of the nearest plant to the sampling point is measured (d_1 – d_4). Two size classes of trees were measured separately: trees ≥10 cm DBH (diameter at breast height), and trees 5 – 9.9 cm DBH. Thus, four trees of each size class were recorded per sample point. Based on these distances, the density of trees per unit area (A) can be calculated as: A / d^2 where d equals the mean distance from the trees to the center of the sampling plot. The density of trees is inversely related to the distance between the center of the plot and the trees considered. Representative samples (RS) were measured at all four sites. In S9 the RS were arranged along the same transects used for the lemur surveys. In 2005, 15 points were measured as the RS in the intact portion of S9, and ten points were measured as the RS in the degraded part of S9. In M13 and M16, 50 RS were measured at each site. Sample points were located at 25 m intervals along parallel transects spaced 25 m apart (Schüller 2003, Rüdel 2004).

Lemur surveys

For the lemur surveys, existing trails were marked and measured. Trails measured 1000 m in M13, 700 and 1000 m in M15/M16, 1855 m in the northern, intact part of S9, and 1456 m in the southern, degraded part of S9. One transect in M15 started at the tree nursery at 24°57.2"S, 47°00.2"E and ran south for 700 m. The other transect in M15/M16 also started at the tree nursery, but then ran west for 1300 m. A 300 m section of trail crossing a swamp and a low running river were not considered during the lemur surveys. The transects in S9 started at the field station towards the north (24°45"S / 47°11"E).

Lemur transects were walked at a speed of about 1 km/hour. At night, a headlamp was used to spot lemur eye shine, and once detected, a maglite and binoculars were used as aids in species identification. For each lemur contact, the species, time of contact, number of individuals, height above ground at which the animal was first sighted, general activity, and distance of the animal perpendicular to the trail were noted. Encounter rates were recorded by different observers over the years. Each observer calculated the mean detection distance per species, and the median and quartiles of encounter rates per species and per site.

Population densities were calculated as the number of animals sighted, divided by the length of the transect, times twice the distance perpendicular to the trail at which the animals were seen. To account for observer bias, we provide a range of population densities. For this, we used the lowest and the highest mean distance perpendicular to the trail at which any given species was recorded by the different observers. The highest mean detection distance and the 25% quartile of encounter rates were used to calculate the low estimate of population densities, while the lowest mean detection distance and the 75% quartile were used to calculate the high estimate of population densities. For example, the lowest and the highest mean detection distances recorded for *Microcebus* were 2.8 and 7.8 m, respectively. The median of encounter rates of *Microcebus* in M13 in March 2004 was six animals/km with 25% and 75% quartiles of five and six animals/km, respectively. The low estimate of the population density is then: five animals / (1000 m * 2 * 7.8 m) = 0.00032 animals/m^2; this corresponds to 3.2 animals/ha. The high estimate of the population density is: six animals / (1000 m * 2 * 2.8 m) = 0.00107 animals/m^2, which corresponds to 10.7 animals/ha.

Data were analyzed with SPSS (1999).

Results

Vegetation measures

The different forests differ in their canopy cover, and the height and density of their trees (Table 2, Fig. 3). The sketches of the forest structure along 25 m are illustrated in Figure 4.

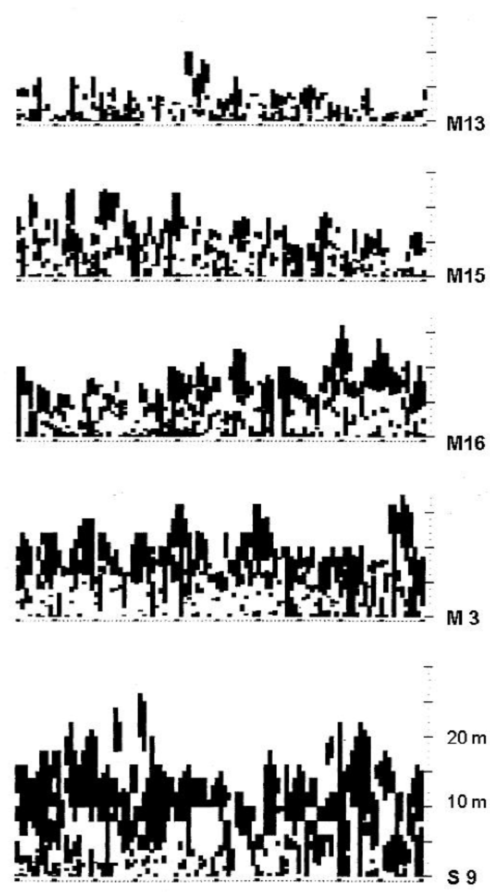

Figure 3. Vertical profile of different forests in Mandena and Sainte Luce measured by the line-intersect technique; measurements were taken in 2000 along a 100 m transect at 1 m intervals (from Rasolofoharivelo 2002).

Table 2. Representative samples of the microhabitats of study sites in Sainte Luce and Mandena based on the point-centered quadrant method. Values are means and standard deviations. N = sample size. Different superscripts indicate differences between sites with $p < 0.05$ according to Scheffé post-hoc tests (from Schüller 2003, Rüdel 2004, Andrianasolo *et al*. 2006).

	S9 north	**S9 south**	**M15/M16**	**M13**	**M5**	**M20**
Year of measurement	2003	2003	2001	2001	2001	2001
N	15	10	50	50	50	40
Distance of large trees ≥ 10 cm DBH [in m]	4.8a ± 1.3	4.7 a ± 1.1	5.3 a ± 2.4	11.1c ± 4.1	4.7 a ± 1.4	8.0 b ± 3.0
Distance of small trees 5 – 9.9 cm DBH [in m]	4.0 a ± 0.8	4.3 a ± 0.8	3.8 a ± 2.0	6.9 b ± 3.5	2.9 a ± 1.1	3.7 a ± 1.2
DBH of large trees ≥ 10 cm DBH [in cm]	19.8 a ± 4.5	18.7 ab ± 3.8	15.9 b ± 3.9	15.8 b ± 5.3	15.3 b ± 3.1	16.9 b ± 5.3

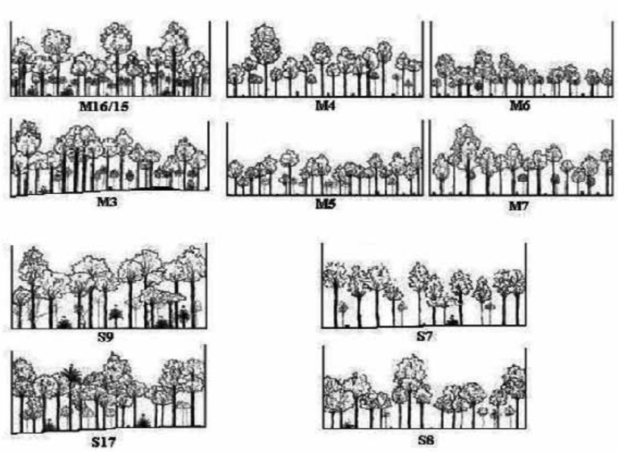

Figure 4. Schematic profiles of Mandena and Sainte Luce littoral forests at different stages of degradation. The length of each profile measures 25 m. Drawings were made in 1999 (from Ralison *et al*. 2006).

Lemur surveys

Encounter rates

The three different regions differ in their lemur species. The species recorded in the different regions and fragments are listed in Table 3. The distributions of the species within each of the three regions are listed in Table 4. *Microcebus* at Petriky may not be *M. murinus*. They resemble *M. griseorufus* in some physical and genetic respects (Hapke 2005). The form listed as *Cheirogaleus medius* is also likely to be distinct, and could be considered a separate species if the current criteria of lemur species descriptions were applied. The form from Mandena and Sainte Luce originally considered *Avahi laniger* has now been described as a new species, *Avahi m. meridionalis* (Zaramody *et al*. 2006). The form of *Hapalemur* occurring in the region had previously been assigned to *H. griseus*, but it is now considered a distinct species, *H. meridionalis*.

Encounter rates of the different species per km transect walks are listed in Table 4. Given the various pitfalls associated with calculating densities based on line transects (e.g., Buckland *et al*. 1993; illustrated for lemurs by Sterling and McFadden 2000), the number of animals seen per km transect walk might represent the most robust data. Rough estimates of lemur densities are listed below.

The population dynamics of the various species differ markedly between fragments. *Microcebus* spp. populations show pronounced fluctuations over the years. The population dynamic in one fragment seems to be completely independent of the dynamic in another fragment (Fig. 5).

Table 3. Lemur species recorded in three different regions of littoral forest near Tolagnaro.

	Petriky	Mandena	Sainte Luce
Microcebus murinus	+	+	
M. cf. *rufus*			+
Cheirogaleus medius	+	+	+
C. major		+	+
Avahi meridionalis	+	+	+
Hapalemur meridionalis		+	
Eulemur collaris		+	+
Lemur catta	+		
Propithecus verreauxi	+ (not resident)		

Table 4. Encounter rates of lemurs (individuals/km transect). Values are medians and quartiles if the number of transects > 3; for N ≤ 3 values are medians and ranges. *Microcebus* spp. are *M. rufus* in fragments of Sainte Luce, and *M. murinus* in fragments of Mandena. Empty cells mean that there are no reports of presence either from surveys, or from reports or other observations. + indicates that the species has been reported at the site, but not recorded during the survey. 0 means that transects were made but no animals were found. * indicates that the species is present. Data for *Eulemur collaris* for 1998 are from Ralison (2001) and Ralison *et al*. (2006). Data for subsequent years are from Rasolofoharivelo (2002) and Donati *et al*. (Chapter 4.9).

	No of transect walks	*Microcebus* spp.	*Cheirogaleus* spp.	*Avahi meridionalis*	*Hapalemur meridionalis*	*Eulemur collaris*
Year round 1998/1999						
Petriky	1	3	+	0		
Mandena						
M3		+	+	+	+	+
M13		+	+	+		
M15/M16	1	3	3	1.3	+	+
M16	2	10/10	2/3	0/3	+	+
M20	1	3	0	3	0	0
Sainte Luce						
S9 intact	7	2	2	2	0	1.4
		1 — 2.5	0 — 6	0 — 5		0 — 2.2
S8	1	2	2	2	0	0
S17	2	2/2	4/5	0/3	0	1.4/3.2
November 2000 – January 2001						
Mandena						
M3		+	+	+	+	+
M13	16	6.5	1.5	1.0		
		3.3 — 9.8	0.3 — 3.5	0.0/1.8		
M15	20	2.9	2.1	0.0	+	+
	0.4 – 6.8	1.4 – 2.9	0.0 – 1.4			
M15/M16	20	5.0	3.0	1.0	+	+
		3.3 – 6.0	1.0 – 4.0	0.0 – 1.0		
Sainte Luce						
S9 intact	22	0.5	1.6	2.4	0	2.2
		0.0 – 0.5	1.1 – 2.2	1.1 – 3.8		1.3 - 2.2
S9 degraded	22	0.0	1.7	1.4	0	0
		0.0 – 0.7	0.7 – 2.1	0.0 – 2.1		

Table 4. Continued

	No of transect walks	*Microcebus* spp.	*Cheirogaleus* spp.	*Avahi meridionalis*	*Hapalemur meridionalis*	*Eulemur collaris*
March 2004						
Mandena						
M13	3	6.0	0.0	0.0		
		5.0 – 6.0	0.0 – 0.0	0.0. – 1.0		
M15	5	5.0	1.0	0.0	+	+
		4.0/6.5	0.0/2.0	0.0/1.0		
April-May 2004						
Mandena						
M13	10	4.0	hibernating	0.0*		
		0.8/5.0	(if present)	0.0/0.0		
M15	10	4.0	hibernating	0.0	+	+
		2.0/6.5	0.0/1.0			
October - December 2004						
Mandena						
M3						
M13	8	+	+	0		
				0/0		
M15	8	4.0	0.0	0.5	+	+
		2.3/9.0	0.0/1.8	0.0/1.0		
M15/M16		+	+	+	+	+
M16	8	1.0	0.0	0.0	+	0.5
		0.0/4.3	0.0/1.5	0.0/1.8	0.0 – 1.5	
M20		+	+			+
Sainte Luce						
S9 intact	8	1.0	7.5	3.0		+
		0.3/1.8	2.5/9.8	2.0/5.5		
S8	8	2.0	5.5	4.0		
		1.0/3.0	4.0/7.5	3.3/5.0		
S17	8	0.0	3.5	3.5		+
		0.0/0.8	1.3/4.0	1.25/4.0		
S7	8	3.5	4.0	0*		
		2/5	4.0/5.0	0/0		
September 2006						
Mandena						
M15/M16	3	2.3	1.0	1.0	+	+
		0 – 5	0 – 2	0 - 2		
M16	3	10	0	0	+	+
		5 – 12	0 – 2	0 - 4		
M20	1	10	0	0		+

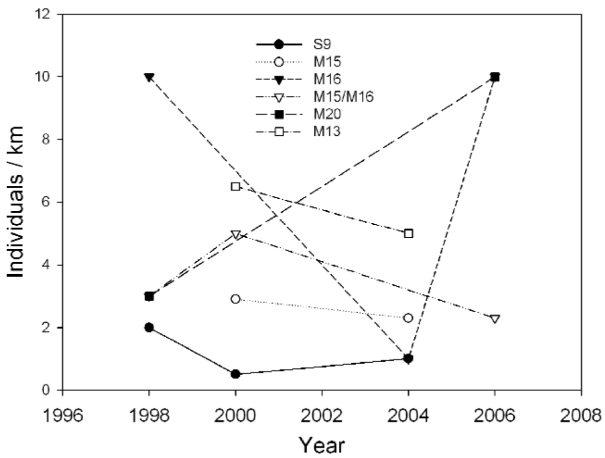

Figure 5. Population dynamics of *Microcebus* spp. in different littoral forest fragments near Tolagnaro. Values are medians of animals seen per 1 km of transect.

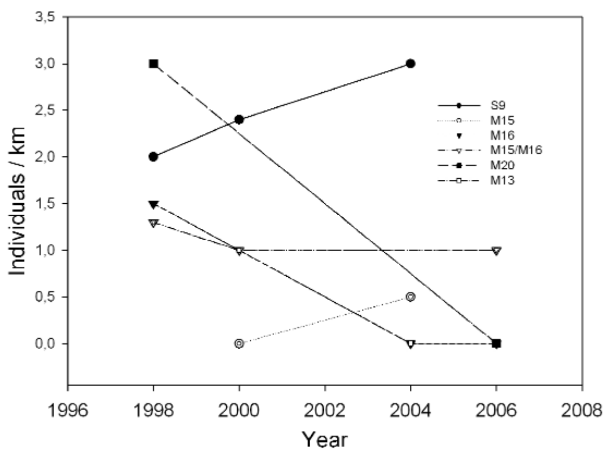

Figure 6. Population dynamics of *Avahi meridionalis* in different littoral forest fragments near Tolagnaro. Values are medians of animals seen per 1 km of transect.

The population dynamics of the two species of *Cheirogaleus* cannot be assessed properly at this time. First, it is unknown whether the species were still in hibernation during the surveys in some years. Second, the two species present in the forests could not be reliably distinguished.

The population dynamics of *Avahi meridionalis* seem more predictable (Fig. 6). Populations of this species declined in the highly degraded fragment M13, and went extinct in the very small fragment M20. Their populations also declined in M16 during the years that this fragment was degraded by uncontrolled extraction of forest resources. However, populations increased in fragments of less degraded forests (S9 and M15), which coincided with the establishment of contracts for forest management (*dina*) with local villagers (see Rarivoson Chapter 6.1), and the reduction of hunting pressure.

The diurnal and cathemeral species, *Hapalemur meridionalis* and *Eulemur collaris*, are confined to fragments larger than 200 ha (Ralison *et al*. 2006, Rasolofoharivelo 2002). *Hapalemur meridionalis* is unknown in Sainte Luce. In Sainte Luce, *Eulemur collaris* populations showed high densities in the two largest fragments, S9 and S17. Furthermore, the *Eulemur* population in S9 seemed to increase from 1999 to 2001. This was probably due to the prevention of lemur hunting in the area and facilitated detection of animals (G. Donati, unpub. data). *Eulemur collaris* was translocated from M3 to M15/M16 after the destruction of M3 by charcoal makers (see Donati *et al*. Chapter 4.9). Prior to the translocation, the *Eulemur collaris* populations of the intact fragment S9 and the more degraded M3 and M15/M16 showed some marked structural differences. Group size declined with the increasing degree of degradation from 7.7 ± 2.1 individuals in S9 (n = 3 groups), to 4 ± 0 individuals in M3 (n=3), and 2 ± 0 individuals in M15 and M16 (n=2) (Rasolofoharivelo 2002).

Population densities and population size

Based on the encounter rates listed above, densities were calculated to provide a rough estimate of the population size of lemur species in different fragments. In previous publications, densities were calculated as the number of animals sighted, divided by the length of the transect, times twice the distance perpendicular to the trail at which the animals were seen (e.g. Norscia *et al*. 2006). This method has its advantages and drawbacks and might yield different results than other methods (Sterling and McFadden 2000).

The distances at which animals were detected varied between observers and sites. The mean detection distances reported by the various observers ranged from 2.8 – 7.8 m for *Microcebus* spp., from 4.8 – 14.2 m for *Cheirogaleus* spp., from 6.6 – 24.3 m for *Avahi meridionalis*, and from 3.5 – 26.2 m for *Eulemur collaris*. The number of sightings of *Hapalemur meridionalis* was too low to allow meaningful calculations of detection distances. The detection distances recorded increased systematically from *Microcebus* spp. to *Cheirogaleus* spp. to *Avahi meridionalis* and to *Eulemur collaris* in the data of all observers. The low and high estimates of population densities are listed in Table 5.

The densities listed in Table 5 were then multiplied by the size of their respective forest fragment to calculate the size of the population in each of the different fragments at the time of the last survey (Table 6). The transect M15/M16 was not considered. The population size and dynamic of *Eulemur collaris* is described in more detail by Donati *et al*. (Chapter 4.9).

Table 5. Lowest and highest density estimates of lemurs (individuals/ha) in different littoral forest fragments near Tolagnaro at the latest survey (in parentheses) reported in Table 4. *Microcebus* spp. is *M. murinus* in Mandena and *M.* cf. *rufus* in Sainte Luce. The *Eulemur collaris* density in Mandena is precise since the number of animals was known.

	Microcebus spp.	*Cheirogaleus* spp.	*Avahi meridionalis*	*Eulemur collaris*
M13	3.2 – 10.7 (March 2004)	Not seen (March 2004)	0.0 – 0.8 (March 2004)	
M15	2.6 – 11.6 (March 2004)	0.0 – 2.1 (March 2004)	0.0 – 0.8 (March 2004)	
M15/M16	0 – 8.9 (2006)	0.0 – 2.1 (2006)	0.0 – 1.5 (2006)	0.16 (2004)
M16	3.2 – 21.4 (2006)	0.0 – 2.1 (2006)	0.0 – 3.0 (2006)	
M20	6.4 – 17.9 (2006)	Not seen (2006)	Not seen	
S9 intact	0.2 – 3.2 (December 2004)	0.9 – 10.2 (December 2004)	0.4 – 4.2 (December 2004)	0.17 – 1.28 (2000)

Table 6. Lowest and highest estimate of the population size of different lemur species in different littoral forest fragments near Tolagnaro in the years indicated in Table 5.

	Fragment size	*Microcebus* spp.	*Cheirogaleus* spp.	*Avahi meridionalis*	*Eulemur collaris*
M13	109 ha	349 – 1166	0	0 – 87	
M15	95 ha	247 – 1264	0 – 200	0 – 76	25
M16	53 ha	170 – 1134	0 - 111	0 – 159	
M20	6 ha	38 – 107	0	0	
S9 intact	252 ha	50 — 806	227 — 2570	111 — 1058	43 — 323

Discussion

The different forest fragments showed pronounced variations in vegetation structure, which could be illustrated in the vertical as well as the horizontal dimensions. In Mandena, populations of *Microcebus murinus* do not seem to be affected by the degradation of the forest. Populations in relatively intact forests (M15, M16) fluctuated as much as those of the most degraded fragments, M13 and M20. The changes in population densities were not synchronized in the different fragments. While this species declined in some fragments (e.g., M15/M16), its density increased in adjacent transects and fragments (M16 and M20). *Microcebus murinus* is known to occur in distinct population nuclei, which are geographically and genetically distinct (Martin 1972, Radespiel *et al*. 2001, Fredsted *et al*. 2004, 2005). These localized populations either shift their range, and thus might not be covered by transects in all years, or they are subject to rapid decline and recovery. In the Kirindy (CFPF) forest north of Morondava, areas with high densities of *M. murinus* one year did not contain any individuals a few years later (Schwab and Ganzhorn 2004, Dammhahn, pers. comm.). Thus, here, their overall population resembles a meta-population structure with uncoupled population dynamics in sub-populations.

In contrast to the lemurs at Mandena, the populations of *Microcebus* cf. *rufus* and *Avahi meridionalis* in the quasi-intact forest of Sainte Luce (S9) remained relatively stable over the years. Similarly, the populations of *Microcebus* in Berenty did not change over several decades (Hladik *et al*. 1998). Even though Sainte Luce and Berenty are heavily frequented by humans (with substantial hunting in Sainte Luce prior to the installation of the protected areas), the impact on the forest is still much lower than at Mandena. Given the large variation in life history traits within the species *Microcebus murinus* (Lahann *et al*. 2006), it is unclear whether these differences in the populations at Mandena and those of Sainte Luce and Berenty are due to environmental effects, human impacts, or differences that might be rooted in phylogenetic history.

Both species of *Cheirogaleus* respond negatively to forest degradation. Together with the food specialist *Hapalemur meridionalis*, they might be the most affected of all local lemur species because they require holes in large trees for hibernation. At Mandena, all sleeping trees of *C. major* had diameters at breast height larger than 47 cm (Lahann 2007b). In addition to the effect of habitat degradation, populations of the larger *C. major* are likely to be below the critical size required to ensure long-term survival. Based on a comparative analysis, lemur populations of 30 to 40 adult individuals do not seem to survive longer than 20 to 40 years (Ganzhorn *et al*. 2000). In studies where both species could be identified, the encounter rates of *C. medius* and *C. major* were 4:1. This ratio is supported by the detailed studies of Lahann (2007a). Both species of *Cheirogaleus* live in pairs or small family units, which occupy exclusive home ranges of about 1 ha and 4-5 ha for *C. medius* and *C. major*, respectively. Thus, if M15 and M16 contain about 200 *Cheirogaleus* spp., no more than 40 of them are *C. major*.

Avahi meridionalis are also affected by forest degradation. Their populations plunged in M20 and M13. Densities of these animals in littoral forest fragments are correlated with the presence of trees with diameters larger than 3.2 cm. This threshold includes trees used by *A. meridionalis* 98% of the time. Their densities also tend to increase with increasing plant species diversity. Moreover, the birth rate seems to be most related to fragment size (Norscia 2006, unpubl. data). In a direct comparison of the intact part of S9 to the highly degraded southern part of S9, the densities of *A. meridionalis* were 1.9 and 1.3 animals/ha, respectively. Thirty-four percent of the groups in the intact part had offspring while only 16% of those in the degraded part had offspring (Rakotondranary 2004).

At the beginning of this study, *Eulemur collaris* only occurred in fragments larger than 200 ha (Ralison *et al*. 2006). While affected by forest degradation, this very mobile species may easily cross anthropogenic habitats, and even open habitat, to move between fragments. Furthermore, *E. collaris* seems able to use degraded parts of forests, such as M20 or portions of M15-M16. In the intact forest of Sainte Luce, they rely on a few food resources during lean times of the year, such as the fruits of *Syzigium* spp., *Dypsis* spp., and *Uapaca* spp. (Donati *et al*. 2007). However, in the degraded areas of Mandena, they show high dietary flexibility by shifting to a low-quality diet (i.e. eating leaves, stems, and flowers) when fruit availability is low (G. Donati, unpubl. data).

Implications for conservation

The results of this long-term study of lemur population shifts in relation to forest fragment size illustrate some well-known principles which need to be considered for conservation activities:

1. Forest degradation and declining size of forest habitat have immediate negative effects on specialized species such as *Cheirogaleus* spp. and *Avahi meridionalis*.
2. Forest size is crucial for *Eulemur collaris*, which were not recorded in isolated fragments smaller than 200 ha (except where translocated).
3. Populations of *Microcebus murinus* show different dynamics in different fragments and population segments within a forest. To account for the possibility that one population goes extinct and the habitat can be re-colonized, the species needs several forest fragments which are linked by corridors.
4. For the more mobile species (*M. murinus* and *E. collaris*), the negative effects of habitat degradation and size reduction are mitigated in fragments linked to other suitable habitats (such as M20, which is linked to M15 and M16).

In Mandena, the conservation zone consisting of the fragments M15 and M16 is unlikely to maintain viable populations of all lemur species without continuous human intervention. The only possible way to guarantee the long-term survival of these lemur populations seems to be the creation of a corridor between these fragments and the natural block of forest to the west of Mandena.

Acknowledgements

We thank the Direction des Eaux et Forêts and the Committee “CAFF-CORE” for authorization of our research. We thank QIT Madagascar Minerals, and in particular, Manon Vincelette and the environmental and conservation team for providing excellent logistics at Tolagnaro and the study sites. The study has been carried-out under the accords de collaboration between QMM, the Département Biologie Animale and the Département de Paléontologie et d’Anthropologie Biologique of the Université d’Antananarivo, and the Zoological Institute of Hamburg University. Funds were provided by DFG, DAAD, Margot Marsh Biodiversity Foundation, and QMM.

References

Andrianasolo, T. H., T. L. Andrianjazalahatra, S. J. Rakotondranary, R. E. A. F. Ramarokoto, G. Randria, N. Rüdel, J. Schüller and J. U. Ganzhorn. 2006. Habitat utilization of nocturnal lemurs in evergreen littoral forests of different degrees of degradation. Pp. 151-159 *in*: C. Schwitzer, S. Brandt, O. Ramilijaona, M. Rakotomalala Razanahoera, D. Ackermand, T. Razakamanana and J. U. Ganzhorn, eds., *Proceedings of the German-Malagasy Research Cooperation in Life and Earth Science*. Concept Verlag, Berlin.

Buckland, S. T., D. R. Anderson, K. P. Burnham and J. L. Laake. 1993. *Distance Sampling*. Chapman & Hall, London.

Brower, J.E., J.H. Zar and C.N. von Ende. 1990. *Field and Laboratory Methods for General Ecology*. Brown Publishers, Dubuque, Iowa.

Colquhoun, I.C. 1998. The lemur community of Ambato Massif: an example of the species richness of Madagascar’s classified forests. *Lemur News* 3:11-14.

Donati G., A. Bollen, S.M. Borgognini Tarli and J.U. Ganzhorn. 2007. Feeding over the 24-hour cycle: dietary flexibility of collared lemur (*Eulemur collaris*). *Behavioural Ecology and Sociobiology*. 61:1237-1251

Eberle, M. and P.M. Kappeler. 2002. Mouse lemurs in space and time: a test of the socioecological model. *Behavioral Ecology and Sociobiology* 51:131-139.

Fredsted, T., C. Pertoldi, J.M. Olesen, M. Eberle and P.M. Kappeler. 2004. Microgeographic heterogeneity in spatial distribution and mtDNA variability of gray mouse lemurs (*Microcebus murinus*, Primates: Cheirogaleidae). *Behavioral Ecology and Sociobiology* 56:393-493.

Fredsted, T., C. Pertoldi, H. Schierup and P.M. Kappeler. 2005. Microsatellite analyses reveal fine-scale genetic structure in grey mouse lemurs (*Microcebus murinus*). *Molecular Ecology* 14:2362-2372.

Ganzhorn, J.U. 1987. A possible role of plantations for primate conservation in Madagascar. *American Journal of Primatology* 12:205-215.

Ganzhorn, J. U. 1999. Lemurs as indicators for assessing biodiversity in forest ecosystems of Madagascar: why it does not work. Pp. 163-174 *in*: Kratochwil, A., ed., *Biodiversity in Ecosystems*. Kluwer Academic Publishers, The Hague.

Ganzhorn, J.U. 2003. Habitat description and phenology. Pp. 40-56 *in*: Curtis, D. and J. Setchell, eds., *Field Methods in Primatology*. Cambridge University Press, Cambridge.

Ganzhorn, J.U. and J.-P. Abraham. 1991. Possible role of plantations for lemur conservation in Madagascar: food for folivorous species. *Folia Primatologica* 56:171-176.

Ganzhorn, J. U. and J. Schmid. 1998. Different population dynamics of *Microcebus murinus* in primary and secondary deciduous dry forests of Madagascar. *International Journal of Primatology* 19:785-796.

Ganzhorn, J.U., S. Malcomber, O. Andrianantoanina and S.M. Goodman. 1997. Habitat characteristics and lemur species richness in Madagascar. *Biotropica* 29:331-343.

Ganzhorn, J.U., S.M. Goodman, J.-B. Ramanamanjato, J. Ralison, D. Rakotondravony and B. Rakotosamimanana. 2000. Effects of fragmentation and assessing minimum viable populations of lemurs in Madagascar. Pp. 265-272 *in*: Rheinwald, G., ed., *Isolated Vertebrate Communities in the Tropics*. Museum Alexander Koenig, Bonn.

Gautier, L., C. Chatelain and R. Spichiger. 1994. Presentation of a relevé method for vegetation studies based on high resolution satellite imagery. Pp. 1339-1350 *in*: Seyani J.H. and A.C. Chikuni, eds., Proceedings of the XIIIth Plenary Meeting AETFAT, Malawi.

Goodman, S.M., D. Rakotondravony, G. Schatz and L. Wilmé. 1997. Richesse spécifique en oiseaux forestiers, mammifères rongeurs et insectivores dans une forêt plantée en arbres autochtones: un cas test de l'Ankaratra, Madagascar. *Akon'ny Ala* 21:37-48.

Hapke, A. 2005. Populationsgenetik und Differenzierung von Arten der Gattungen Mausmaki, *Microcebus* (E. Geoffroy St. Hilaire, 1828) und Katzenmaki, *Cheirogaleus* (E. Geoffroy St. Hilaire, 1812) in Südost-Madagaskar. Dissertation, Universität Hamburg.

Harcourt, C. and J. Thornback. 1990. *Lemurs of Madagascar and the Comoros*. IUCN, Gland.

Hladik, C.M., M. Pinte and B. Simmen. 1998. Les densités de population des prosimiens nocturnes du sud de Madagascar varient-elles à long terme dans les réserves forestières accessibles au public? *Revue d'Ecologie* 53:181-185.

Holloway, L. 2003. Ecosystem restoration and rehabilitation in Madagascar. Pp. 1444-1451 *in*: Goodman, S.M. and J.P. Benstead, eds., *The Natural History of Madagascar*. The University of Chicago Press, Chicago

Jolly, A.H., Gustafson, W.L.R. Oliver and S.M. O'Connor. 1982. *Propithecus verreauxi* population and ranging at Berenty, Madagascar, 1975 and 1980. *Folia Primatologica* 39:124-144.

Kappeler, P. M. 1997. Intrasexual selection in *Mirza coquereli*: evidence for scramble competition polygyny in a solitary primate. *Behavioral Ecology and Sociobiology* 45:115-127.

Lahann, P. 2007a. Feeding ecology and seed dispersal of sympatric cheirogaleid lemurs (*Microcebus murinus*, *Cheirogaleus medius*, *Cheirogaleus major*) in the littoral rainforest of south-east Madagascar. *Journal of Zoology, London* 271:88-98.

Lahann, P. 2007b. Biology of *Cheirogaleus major* in a littoral rainforest in southeast Madagascar. *International Journal of Primatology* 28:895-905.

Lahann, P., J. Schmid and J.U. Ganzhorn. 2006. Geographic variation in life history traits of *Microcebus murinus* in Madagascar. *International Journal of Primatology* 27:983-999.

Lewis Environmental Consultants. 1992. Madagascar Minerals Project. Environmental Impact Assessment Study. Part 1: Natural Environment. In Ilmenite Project. Social and Environmental Impact Assessment. Supporting Document no 5. Presented by QIT Madagascar Minerals S.A. to the Madagascar National Environment Office, May 2001.

Martin, R.D. 1972. A preliminary study of the lesser mouse lemur (*Microcebus murinus* J.F. Miller 1777). *Zeitschrift für Tierpsychologie, Supplement* 9:43-89.

Merenlender, A., C. Kremen, M. Rakotondratsima and A. Weiss. 1998. Monitoring impacts of natural resource extraction on lemurs of the Masoala Peninsula, Madagascar. *Conservation Ecology* 2: Article 5.

Mittermeier, R. A., W. R. Konstant, A. F. A. Hawkins, E. E. Louis, O. Langrand, H. J. Ratsimbazafy, M. R. Rasoloarison, J. U. Ganzhorn, S. Rajaobelina, I. Tattersall and D. Meyers. 2006. *Lemurs of Madagascar*. Conservation International, Washington, D.C.

Norscia, I. 2006. Adaptation strategies of a nocturnal lemur (*Avahi laniger*) in a pluvial littoral forest of southeastern Madagascar: implications for conservation. Dissertation, Dipartimento di Etologia, Ecologia ed Evoluzione. Università di Pisa.

Norscia, I., O.G. Rahanitriniaina, A. Jolly and G.

Donati. 2006. Preliminary survey of lemur density in the semimontane rainforest of Anka, Fort-Dauphin region. *Lemur News* 11:14-17.

Petter, J.J., R. Albignac and Y. Rumpler 1977. *Faune de Madagascar: Mammifères Lémuriens*. ORSTOM-CNRS, Paris.

Pochron, S.T., W.T. Tucker and P.C. Wright. 2004. Demography, life history and social structure in *Propithecus diadema edwardsi* from 1986 to 2000 in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology* 125:61-72.

Radespiel, U., Z. Sarikaya, E. Zimmermann and M.W. Bruford. 2001. Sociogenetic structure in a free-living nocturnal primate population: sex-specific differences in the grey mouse lemur (*Microcebus murinus*). *Behavioral Ecology and Sociobiology* 50:493-502.

Rakotondranary, J. 2004. Effets de la dégradation sur la population de *Avahi laniger* dans la forêt littorale de Sainte-Luce. DEA, Département de Paléontologie et d'Anthropologie Biologique. Université d'Antananarivo.

Ralison, J. 2001. Influence de la qualité de la forêt sur la population de *Eulemur fulvus collaris* dans la formation littorale de Mandena et Ste Luce, Tolagnaro en 1998-99. DEA, Département Biologie Animale. Département Biologie Animale, Université d'Antananarivo, Antananarivo.

Ralison, J., J.-B. Ramanamanjato and M.R. Rakotomalala Razanahoera. 2006. Influence de la qualité de la forêt sur *Eulemur collaris* (E. Geoffroy, 1812) dans les formations littorales de Mandena et de Sainte Luce à Tolagnaro en 1998-1999, Madagascar. Pp. 161-167 *in*: Schwitzer, C., S. Brandt, O. Ramilijaona, M. Rakotomalala Razanahoera, G. Randria, D. Ackermand, T. Razakamanana and J.U. Ganzhorn, eds., *Proceedings of the German-Malagasy Research Cooperation in Life and Earth Sciences*. Concept Verlag, Berlin.

Rasolofoharivelo, T.M. 2002. Impacts anthropiques sur *Eulemur fulvus collaris* E. Geoffroy, 1812 et son habitat naturel dans la forêt littorale de Mandena, Fort Dauphin, Madagascar. DEA, Département Paléontologie. Université d'Antananarivo, Antananarivo.

Ratsimbazafy, J. H., H. V. Ramarosandratana and R. J. Zaonarivola. 2002. How do Black-and-White Ruffed Lemurs still survive in a highly disturbed habitat? *Lemur News* 7:7-10.

Ratsirarson, J. and J. Ranaivonasy. 2002. Ecologie des lémuriens dans la forêt littorale de Tampolo. *Lemur News* 7:26-30.

Richard, A.F., R.E. Dewar, M. Schwartz and J. Ratsirarson. 2002. Life in the slow lane? Demography and life histories of male and female sifaka. *Journal of Zoology*, London 256:421-436.

Rüdel, N. 2004. Auswirkungen von Degradation und Fragmentation madagassischer Küstenregenwälder auf graue Mausmakis (*Microcebus murinus*). Diploma thesis, Department of Animal Ecology and Conservation, University Hamburg.

Schüller, J. 2003. Auswirkungen von Degradation und Fragmentation madagassischer Küstenregenwälder auf endemische Nager *Eliurus webbi* (Nesomyinae). Diploma thesis, Department of Animal Ecology and Conservation, Universität Hamburg.

Schwab, D. and J.U. Ganzhorn. 2004. The distribution and population structure of *Microcebus berthae*, the smallest known primate and its habitat use in relation to other sympatric cheirogaleids. *International Journal of Primatology* 25:307-330.

SPSS. 1999. *SPSS Base 9.0 User's Guide*. SPSS Inc., Chicago.

Sterling, E. and K. McFadden. 2000. Rapid census of lemur populations in the RNI de Marojejy, Madagascar. Pp. 265-274 *in*: Goodman, S.M., ed., A floral and faunal inventory of the Réserve Naturelle Intégrale de Marojejy, Madagascar: with reference to elevational variation. *Fieldiana: Zoology*, new series, 97.

Styger, E., J.E.M. Rakotoarimanana, R. Rabevohitra and E.C.M. Fernandes. 1999. Indigenous fruit trees of Madagascar: potential components of agroforestry systems to improve human nutrition and restore biological diversity. *Agroforestry Systems* 46:289-310.

Sussman, R.W. 1991. Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *American Journal of Physical Anthropology* 84:43-58.

Tattersall, I. 1982. *The Primates of Madagascar*. Columbia University Press, New York.

Zaramody, A., J.-L. Fausser, C. Roos, D. Zinner, N. Andriaholinirina, C. Rabarivola, I. Norscia, I. Tattersall and Y. Rumpler 2006. Molecular phylogeny and taxonomic revision of the eastern woolly lemurs (*Avahi laniger*). *Primate Report* 74:9–22.