

DISTRIBUTION OF THE MALAGASY LEMURS
PART 2: *LEMUR CATT*A AND *LEMUR FULVUS*
IN SOUTHERN AND WESTERN MADAGASCAR*

Robert W. Sussman

Department of Anthropology
Washington University
St. Louis, Missouri 63130

This report is the result of surveys conducted in southern and western Madagascar during an 18-month field study (September 1969–November 1970) and two 3-month studies (June–August, 1973 and 1974). Thirty-three separate forests were surveyed in which *Lemur catta* and/or *Lemur fulvus* were found. The surveys were conducted to determine (1) the northern and southern limits of the distribution of the two species, (2) precisely where the ranges of the two species overlap, and (3) whether the dispersion of populations within the area of overlap revealed any difference in habitat preferences between the species. The forests surveyed extend from Berenty in the south to the area near Majunga in the northwest (TABLE 1; FIGURES 1–3). Sixteen of these forests are in the area in which the ranges of *L. catta* and *L. f. rufus* overlap. All of the forests listed in TABLE 1 were extensively surveyed, and the list of the diurnal species is inclusive.

GEOGRAPHICAL DISTRIBUTION

Populations of *Lemur fulvus rufus* and *Lemur catta* are found in the western and southern regions of Madagascar. *L. f. rufus* occurs in the west and southwest and *L. catta* in the southwest and south (FIGURE 1). Previously, knowledge of the distribution of these species was based mainly on early reports (summarized by Hill¹). I have tried to enhance this knowledge through the use of literature not available to Hill and by conducting extensive surveys of certain regions within the total range of the two species. A Malagasy guide who spoke English or French accompanied me on all of the surveys. A general area to survey was chosen and then the inhabitants of villages within this area were asked if lemurs (“maki”) were found in any of the nearby forests. If so, we hired a local guide to take us into the forest. He usually told us which diurnal lemurs were found in the forest and, in most cases, because of his knowledge of the forest and the animals, he could lead us directly to the animals he named. We camped for more than one day in many of the forests, especially where the animals were difficult to find. Approximately one-fourth of the forests surveyed were studied for a week or more. All of the forests listed in TABLE 1 were extensively surveyed, and the list of the diurnal species is inclusive.

Further information on the ranges of the two species was obtained through discussions with local inhabitants whose observations were considered reliable and with researchers who were in Madagascar during my study. Extensive sur-

*This study was supported in part by NIMH Research Fellowship MH 4628-01; NSF Research Grant BG-41109; Biomedical Research Support Grant RR-07054 from the Biomedical Research Support Program, Division of Research Resources, NIH; and by Duke University and Washington University.

veys were carried out in the areas where *L. catta* and *L. f. rufus* coexist. These surveys were done mainly to collect ecological data, but they also enabled me to determine the precise northern and southern limits of the ranges of *L. catta* and *L. f. rufus*, respectively.

The northern limit of populations of *Lemur fulvus rufus* has been reported to extend at least to the Bay of Bonbetoka and the Betsiboka River.¹ Schwartz² reported a black-headed form north of this region between the Bay of Bombe-

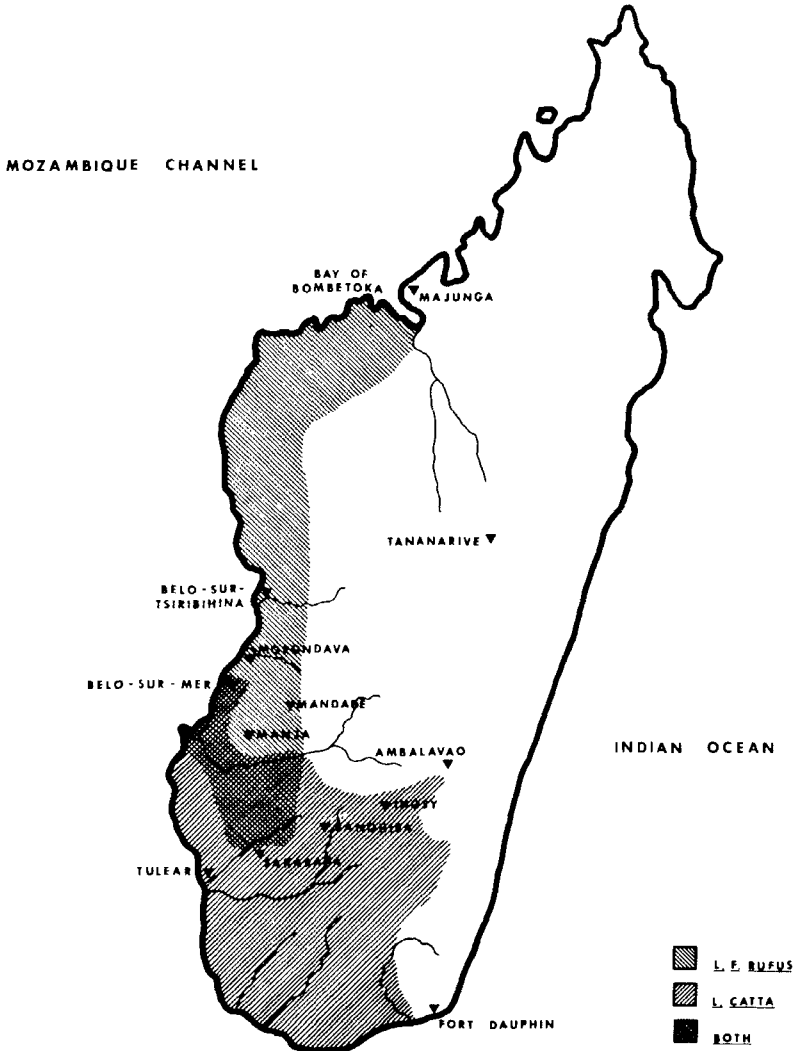


FIGURE 1. Distribution of *Lemur fulvus rufus* and *Lemur catta* in western Madagascar. Populations are not continuous within these areas but are only found where suitable primary vegetation exists.

TABLE 1
SURVEY DATA SHEET
(SEE FIGURES 2 AND 3)

Forest	Continuous Canopy	Brush & Scrub	Mixed	River Edge	Cliff Edge, Hillly	Plat	Species of Lemna* & Propithecus*
<i>Non-overlap (South)</i>							
1. Beomby, 24° 15' S. Lat., 44° 15' E. Long.	X		X	X X		X X X	Lc Puv Lc Puv Lc Puv
2. Berenty, 25° S. Lat., 46° 20' E. Long.			X	X X		X X X	
3. Ejeda, 24° 20' S. Lat., 44° 30' E. Long.			X	X X		X X X	
<i>Overlap Area</i>							
Near Tulear							
4. Fiherenana I., 23° 10' S. Lat., 43° 55' E. Long.		X	X	X X X	X X X		Lc Lc Lfr Lc Lfr Puv
5. Fiherenana II., 23° 10' S. Lat., 43° 55' E. Long.			X	X X	X X X		
6. Lambomakandro, 22° 45' S. Lat., 44° 40' E. Long.			X	X X	X X X		
Near Ankiliabo							
7. Antanimangotroky, 21° 40' S. Lat., 43° 55' E. Long.	X			X		X	Lfr
Near Manja							
8. Ankerandriere, 21° 41' S. Lat., 44° 7' E. Long.		X X		X X	X X		Lc Lc Lc Lfr Puv
9. Ambohy Menafify, 21° 42' S. Lat., 44° 6' E. Long.		X X		X X	X X	X X X	Lc Lfr Puv Lc Lfr Puv Lc Lfr Puv
10. Antserananomby, 21° 42' S. Lat., 44° 8' E. Long.			X X	X X	X X	X X X	Lfr Puv Lfr Puv Lc Lfr Puv
11. Ianadranto I., 21° 43' S. Lat., 44° 7' E. Long.			X	X	X	X	Lfr Puv Lfr Puv Lc Lfr Puv
12. Ianadranto II., 21° 43' S. Lat., 44° 7' E. Long.			X	X	X	X	Lc Lfr Puv Lc Lfr Puv Lc Lfr Puv
13. Malindira, 21° 38' S. Lat., 44° 15' E. Long.	X		X	X	X	X	Lc Lfr Puv Lc Lfr Puv Lc Lfr Puv
14. Mangoky, 21° 50' S. Lat., 44° 8' E. Long.	X		X	X	X	X	Lc Lfr Puv Lc Lfr Puv Lc Lfr Puv
15. North Bengily, 21° 42' S. Lat., 44° 8' E. Long.		X		X	X X	X	Lc

16. Tarata, 21° 20' S. Lat., 44° 29' E. Long.	X		X						<i>Lfr Pvv</i>
17. Tongobato, 21° 46' S. Lat., 44° 8' E. Long. Manja to Morondava	X			X					<i>Lfr Pvv</i>
18. Belo-sur-Mer, 20° 44' S. Lat., 44° 0' E. Long.		X							<i>Lc Lfr Pvv</i>
19. Soaserana, 21° 5' S. Lat., 44° 13' E. Long. <i>Non-overlap (North)</i>			X						<i>Lc</i>
Manja to Mahabo (via Mandabe)									
20. Ambatovoamba, 20° 35' S. Lat., 44° 42' E. Long.	X			X					<i>Lfr Pvv</i>
21. Andranomena, 20° 10' S. Lat., 44° 26' E. Long.				X					<i>Lfr Pvv</i>
22. Angansiva, 20° 27' S. Lat., 44° 23' E. Long.				X		X			<i>Lfr Pvv</i>
23. Ankilimare, 21° 0' S. Lat., 44° 54' E. Long.				X			X		<i>Lfr Pvv</i>
24. Befasy, 20° 35' S. Lat., 44° 21' E. Long.				X					<i>Lfr Pvv</i>
25. Beroboka, 19° 58' S. Lat., 44° 36' E. Long.				X			X		<i>Lfr Pvv</i>
26. Manamby, 20° 25' S. Lat., 44° 48' E. Long.				X					<i>Lfr Pvv</i>
27. Maroary, 20° 26' S. Lat., 44° 21' E. Long.	X								<i>Lfr Pvv</i>
28. Tanambao, 20° 7' S. Lat., 44° 33' E. Long. Near Majunga				X					<i>Lfr Pvv</i>
29. Ampijoroa, 16° 19' S. Lat., 46° 50' E. Long.					X		X		<i>Lff Pccoq Lm</i>
30. Kasepy, 15° 43' S. Lat., 46° 13' E. Long.	X			X			X		<i>Lfr Pvd</i>
31. Lac Kinkony, 16° 6' S. Lat., 45° 50' E. Long.				X			X		<i>Lm</i>
32. Madirovalo, 16° 33' S. Lat., 46° 24' E. Long.	X				X				<i>Lfr Pvcor Lm</i>
33. Marohogo, 15° 43' S. Lat., 46° 28' E. Long.	X								<i>Lff</i>
34. Mitsinjo, 16° 2' S. Lat., 45° 54' E. Long.	X			X					<i>Lfr Pvd</i>

**Lc* = *Lemur catta*
Lfr = *Lemur fulvus rufus*
Lff = *Lemur fulvus fulvus*
Lm = *Lemur mongoz*
Pvv = *Propithecus verreauxi verreauxi*
Pccoq = *Propithecus verreauxi coquereli*
Pvcor = *Propithecus verreauxi coronatus*
Pvd = *Propithecus verreauxi deckeni*

toka and the Bay of Narinda. He assumed that this was a population that represented a mixture between *Lemur fulvus albifrons* and *L. f. rufus* (but see accompanying report by Tattersall).

Our observations did not confirm these earlier reports. In surveys conducted in the northwest of Madagascar in 1973 and 1974, *Lemur fulvus rufus* was found in forests to the west of the Betsiboka River (TABLE 1, FIGURE 2). In the forests to the east of this river we only found populations of *L. f. fulvus*, *L. f. rufus* was not found in any forests east of the Betsiboka River. *Lemur mongoz* (= *L. m. mongoz*), however, inhabited forests on both sides of this river.

Moving northeast from the Betsiboka there are two subspecies of *Lemur fulvus* (*L. f. fulvus* and *L. f. sanfordi*). Distributions of these forms are discussed by Tattersall in the accompanying article.

To the west and east, the range of *Lemur fulvus rufus* is necessarily limited by the availability of suitable primary forests. In the western part of the range of *L. f. rufus*, the boundaries of the forest approach the shores of the Mozambique Channel. In the eastern part, the forests are bounded by the mountains bordering the Central Plateau. From west to east, the primary forests become less frequent and are replaced by savannah and prairie. The primary vegetation extends furthest east along the large rivers.

South of the Betsiboka River until populations of *Lemur fulvus rufus* meet

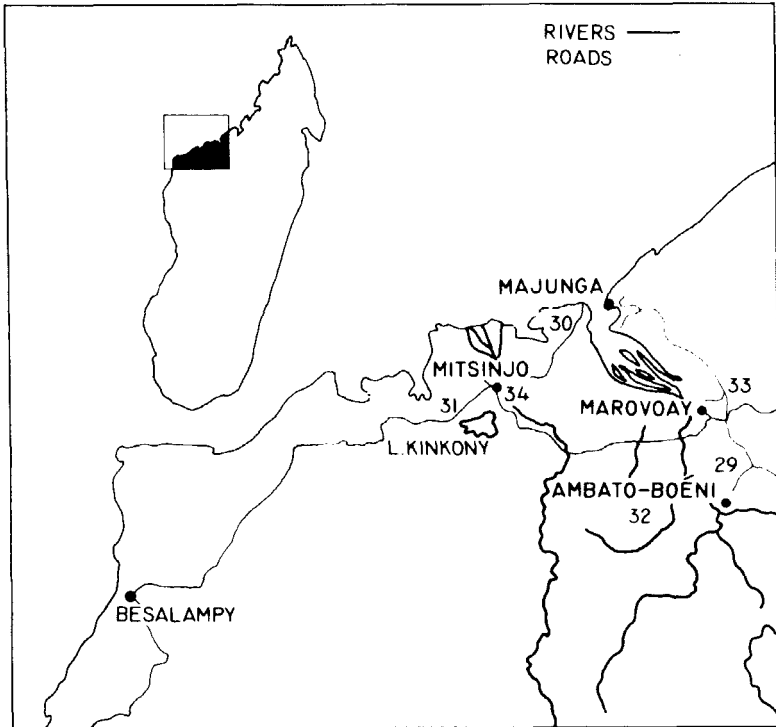


FIGURE 2. Locations of forests surveyed in the northwest. Numbers correspond to those in TABLE 1.

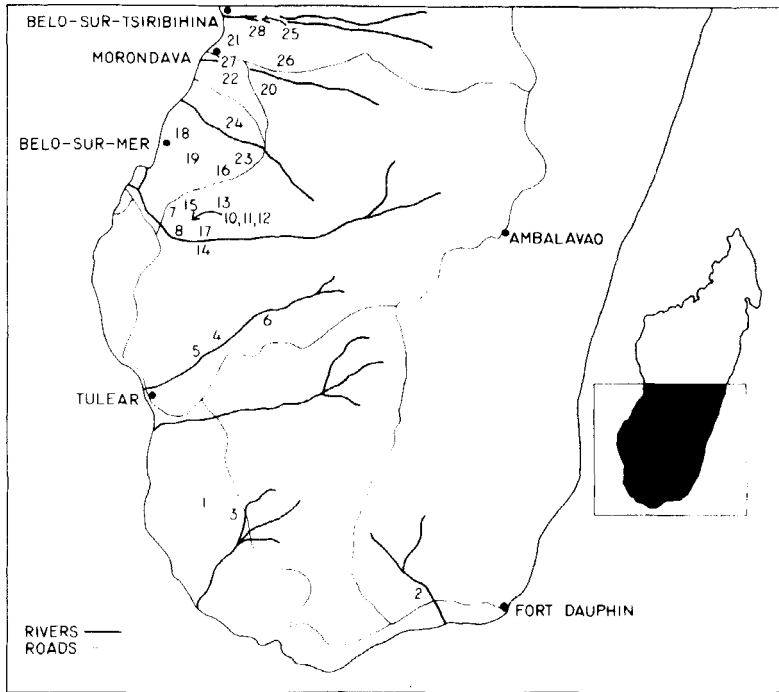


FIGURE 3. Locations of forests surveyed in the southwest. Numbers correspond to those in TABLE 1.

those of *Lemur catta*, there are no other species or subspecies of *Lemur*. *Propithecus verreauxi* ssp. are found in this western region (FIGURE 4).

P. v. coquereli is found in forests east of the Betsiboka River; *P. v. deckeni* and *P. v. coronatus* are found in forests immediately to the west of this river (TABLE 1, FIGURE 2), but the precise distribution of these two subspecies in this region is not known. *P. v. deckeni* has been reported as far south as Belo-sur-Tsiribihina ($19^{\circ} 42' S. lat., 44^{\circ} 30' E. long.$). Populations of *Propithecus verreauxi verreauxi* extend from around Belo-sur-Tsiribihina south to the forested areas near Fort Dauphin.¹ They are coincidental with populations of *L. f. rufus* and/or *L. catta* in many forests of the southwest and south.

The southern limit of the range of *L. f. rufus* is listed by Hill¹ as the Fiherenana River. His species distribution map is most likely based on museum specimen lists of Schlegel³ and Jentink.⁴ The findings from our surveys concur with these earlier reports. We did not find any populations of *L. f. rufus* south of the Fiherenana River, although they could be found on the banks of this river and in the forest of Lambomakandro just north of Sakaraha (TABLE 1; FIGURE 3). *L. f. rufus* was also seen at Lambomakandro by Boggess and Smith,⁵ Jolly,⁶ and Buettner-Janusch.⁷

Lemur catta and *Propithecus verreauxi verreauxi* are the only diurnal lemur species found south of the Fiherenana River. Populations of *L. catta* have been reported to extend northeast into the borders of the Central Plateau in the

following locations: north of the village of Ranohira ($22^{\circ} 33' \text{ S. lat.}, 45^{\circ} 25' \text{ E. long.}$) in the national reserve of Isalo (Georges Randrianasolo, Personal Commun.); 45 km west of Ihosy along Route Nationale No. 7 (approximately $22^{\circ} 35' \text{ S. lat.}, 46^{\circ} 29' \text{ E. long.}$)⁸; in the forests southeast of Ihosy—near the village of Anosibe ($22^{\circ} 35' \text{ S. lat.}, 46^{\circ} 29' \text{ E. long.}$) (R. Huntington, personal commun.); and south of Ambalavao along Route Nationale No. 7 (approximately $22^{\circ} 51' \text{ S. lat.}, 46^{\circ} 56' \text{ E. long.}$) (Georges Randrianasolo, personal commun.). Thus, *L. catta* ranges quite extensively to the north into the regions bordering the Central Plateau and is probably to be found in scattered populations throughout the entire south of Madagascar. In the survey I was only able to study the southern sector of the range of *L. catta* (along Route Nationale No. 10, from Tulear to Fort Dauphin). There is no published information on the populations that exist between this southern sector and the Central Plateau.

In eastern Madagascar, populations of *Lemur catta* are not found past the boundaries of the wet Oriental forest. The furthest east they have been observed is south of Manamboro ($25^{\circ} 2' \text{ S. lat.}, 46^{\circ} 48' \text{ E. long.}$), in dry forests off the road between Manamboro and Italy (A. Jolly, personal commun.). The Oriental rain forest extends most of the length of the island on the east coast, and most of the fauna, as well as the flora, in this forest is distinct from that of the dry Occidental forests. To the extreme south and west, *L. catta* ranges to the coasts of the Indian Ocean and the Mozambique Channel.

The geographical distribution of *Propithecus verreauxi verreauxi* in the southern region of the island is very similar to that of *Lemur catta*, although these species are not always found in the same type of forest (see below). The limits of the range of *P. v. verreauxi* towards the Central Plateau are not known. In 1929, Archbold⁸ reported seeing a troop of *P. v. verreauxi* close to where he had found *L. catta*—45 km west of Ihosy. Huntington, however, during his field work on the Bara near Ihosy, did not see any populations of *P. v. verreauxi*, although he saw *L. catta* in this area.

In the west, above the Fiherenana River, the ranges of *Lemur catta* and *Lemur fulvus rufus* overlap. (TABLE 1; FIGURES 3 and 5; see also Appert⁹). North of the Mangoky River, however, although we found populations of *L. f. rufus* near Mandabe ($23^{\circ} 3' \text{ S. lat.}, 44^{\circ} 56' \text{ E. long.}$) and along Route Nationale No. 9, the range of *L. catta* did not extend this far east. Populations of *L. catta* do, however, exist all along the Mangoky River, to the coast. We found no *L. catta* in the forests to the east of Manja ($21^{\circ} 26' \text{ S. lat.}, 44^{\circ} 20' \text{ E. long.}$) above the Mangoky River, but there were many populations of this species in the forests located to the west of this village.

The northern limit of the range of *Lemur catta* is reported to be the Morondava River.^{1,10} We could find no *L. catta* in the forests bordering this river, and the local inhabitants told us that *L. catta* could not be found this far north. The northernmost forest in which we found *L. catta* was the forest of Mahabokoy in the reserve of Kirindy just east of Belo-sur-Mer ($20^{\circ} 44' \text{ S. lat.}, 44^{\circ} 0' \text{ E. long.}$). This forest reserve is approximately 45 km south of the Morondava River, just below the Maharivo River.

Thus, on the west coast of Madagascar, populations of both *Lemur catta* and *Lemur fulvus rufus* can be found in forests between the Kirindy forest reserve and the Fiherenana River. In the extreme south of the range of *L. f. rufus* and in the extreme north of the range of *L. catta*, there is a large area (approximately 250 km from north to south) in which the ranges of the two species overlap. However, the ecology of this area is by no means uniform, and it offers these two forms a number of alternative possibilities for different modes of adaptation.

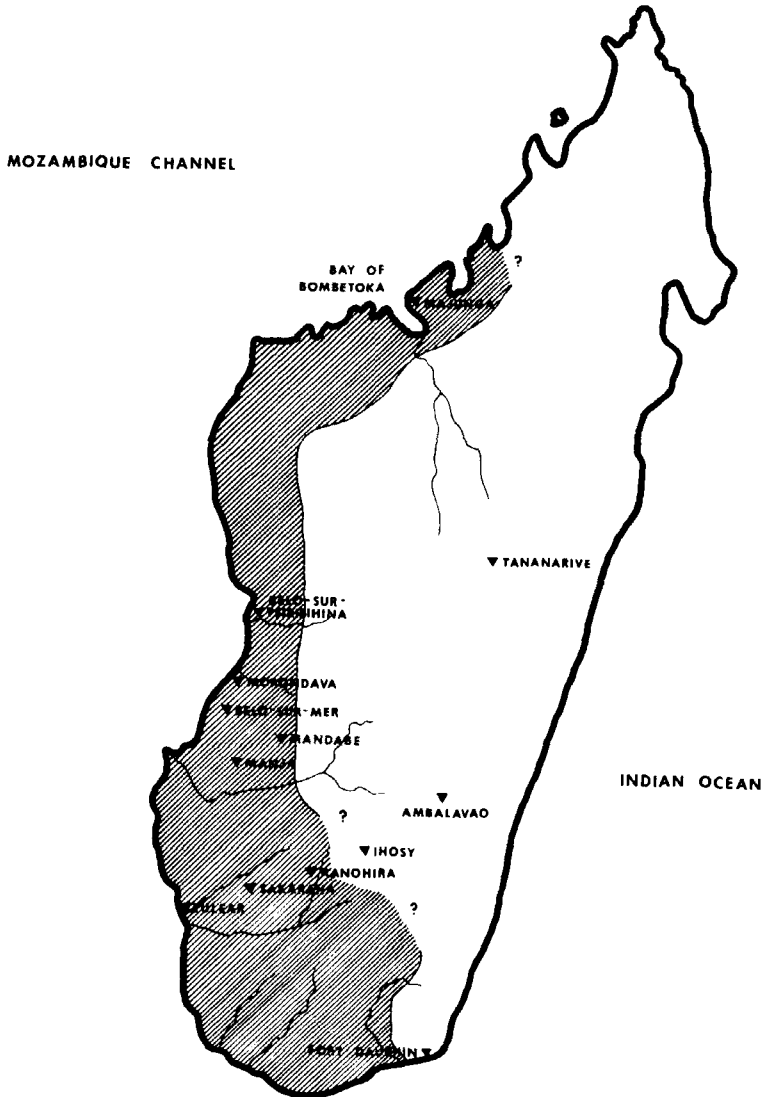


FIGURE 4. Distribution of *Propithecus verreauxi*. Populations are not continuous within these areas but are only found where suitable primary vegetation exists.

VEGETATION OF THE WEST AND SOUTH OF MADAGASCAR

The vegetation of Madagascar has been described by Perrier de la Bathie^{11,12} Humbert,¹³ Humbert and Cours-Darne,¹⁴ and Koechlin.¹⁵ The primary forests of Madagascar can be divided into two principal zones (FIGURE 6): the wet, evergreen vegetation zone ("Région Orientale") found in the east, the extreme

north, the Central Plateau, and the high mountains; and the dry zone ("Région Occidentale") of the western and southern regions of the island.

The Occidental zone is subdivided into two sectors: the western and the southern. Both of these regions are below 800 meters in altitude and are characterized by the presence of a marked dry season. In the northwest (near Majunga) the rains total about 1350 mm in the rainy season (November–March) and about 80 mm in the dry season. The amount of rainfall diminishes from northwest to south: at Morondava it is about 700 mm in the rainy season and hardly a tenth of this during the dry season. At Tulear the mean rainfall in the hot season is about 340 mm.

In the southern section, there is not a well-marked difference between the seasons. Rain falls irregularly in the course of the year and may be absent locally for as many as 12 to 18 months. The semiarid climate of the south supports a xerophytic vegetation rich in many genera and species peculiar to this region.

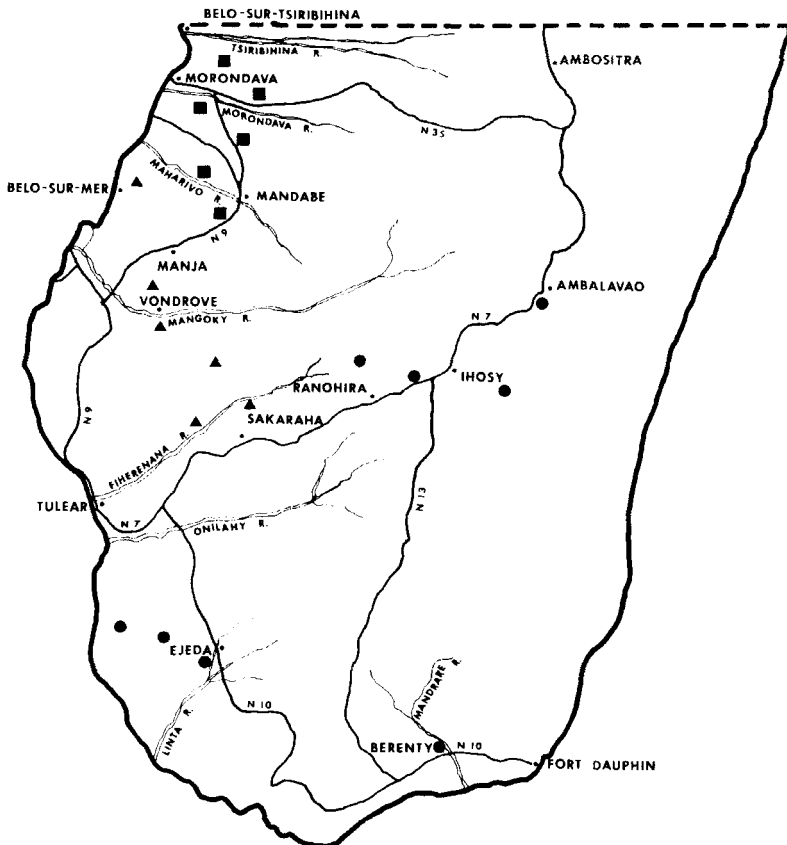


FIGURE 5. Areas in which *Lemur catta* and/or *Lemur fulvus rufus* have been sighted south of Belo-sur-Tsiribihina. In the region where the ranges of the two species overlap, only sites at which the species coexist are included. (circle=*Lemur catta*; square=*Lemur fulvus rufus*; triangle=*Lemur catta* and *Lemur fulvus rufus*).

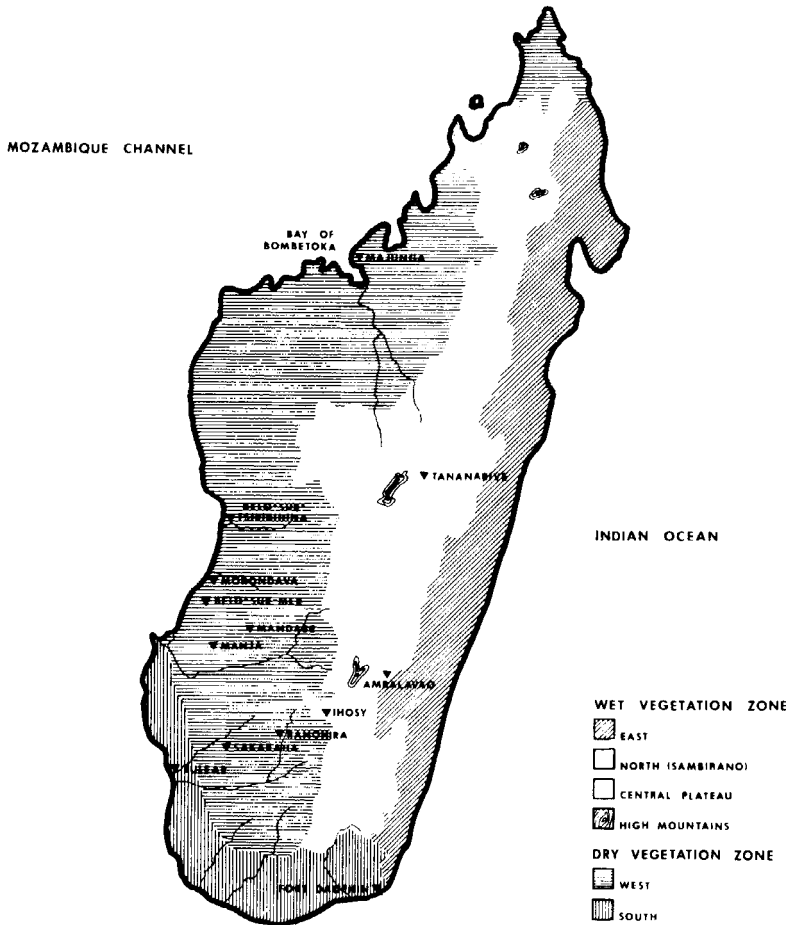


FIGURE 6. Vegetation zones of Madagascar as defined by Humbert.¹³

The primary vegetation of the west consists of deciduous forests which contrast with the perennial, evergreen forests of the Oriental zone. Three types of forest have been distinguished by Perrier de la Bathie¹¹ in the west, their distribution depending largely on soil type (siliceous, calcareous, or rocky).

The deciduous forests, which flourish on siliceous soil, are found in the river valleys and in certain basins in which the ground retains some moisture (FIGURE Tupper). The forests are characterized by a continuous canopy, about 7 to 15 meters in height, formed, in most cases, by a *Tamarindus indica* consociation. The annual cycle of leaf growth is very uniform. The young leaves begin to form at the first rains of the hot season. However, the fruits of various plant species ripen at different intervals throughout the year. Continuous canopy forests of this sort present essentially the same characters from the northwest to the southwest. Similar forests are also found along the larger rivers in the south. *Tamarindus indica* is usually dominant in these forests, but some of the other species of plant differ between different areas.

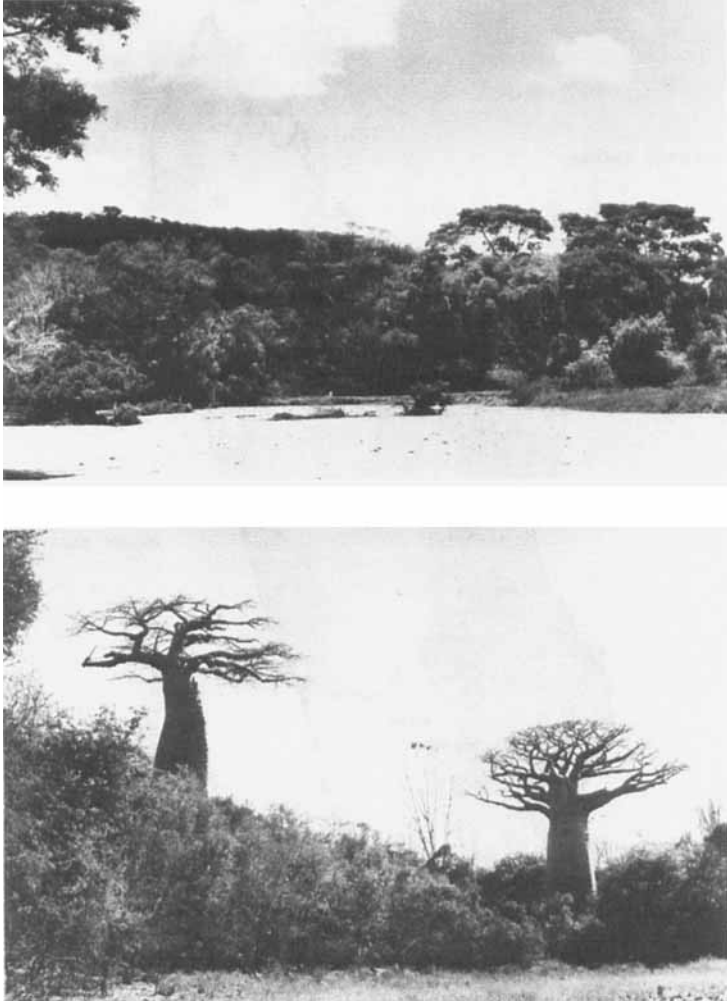


FIGURE 7. *Upper*, Continuous canopy forest at Antserananomby. *Lower*, A brush and scrub forest near the Mangoky River.

The forests on calcareous soils are much drier. The xerophytic character is accentuated. In these forests there is no continuous canopy, and the forest only reaches the height of what would be the subordinate tree layer in the continuous canopy forest (FIGURE 7*lower*). There is no dominant tree species. Forests of this type are found throughout the west on soils with little moisture. I refer to forests of this type as brush and scrub forests. Where a brush and scrub forest merges directly into a continuous canopy forest, I use the term "mixed" forest.

Finally, xerophytic thickets are found in the driest areas—usually on tops of hills or where rocky outcrops exist. This type of forest or thicket is very dense and almost impassable. There is no tree layer and the dominant species are those of the shrub layer.

In many areas of the west these three types of primary forest are contiguous and merge into one another. Generally, continuous canopy forests are smaller than mixed forests. They are usually in circumscribed areas where remnants of a *Tamarindus indica*-dominated forest are surrounded by cultivated fields and/or degraded savannahs or prairies. Brush and scrub forests, in some cases, include areas with rocky outcrops. In these forests thickets are found within the brush and scrub forest.

Besides the three principal types of primary forests of the west and a few more localized formations (e.g., the bamboo forest of the Bay of Baly), towards the interior there is a discontinuous prairie, and toward the sea, a mangrove forest that shows little species variation but is often quite widespread. Furthermore, a degraded formation of wooded savannah results from fires that are set to obtain and rejuvenate grazing pastures. Savannah replaces the primary forest after trees are cut down and burned. Under the repeated action of fires, trees become spaced further apart and finally disappear, leaving a monotonous prairie.^{14,16} The little varied vegetation of these degraded formations supports a very poor fauna, in sharp contrast to the rich savannah fauna of Africa. Since this slash-and-burn technique is common in the west of Madagascar, much of the area is covered with degraded savannahs and prairies. Indeed, these secondary formations are now far more widespread than the primary forests.

In the south of Madagascar the primary vegetation is desert-like and rich in endemic species. Two genera of Didiereaceae characterize it: *Didierea* and *Alluaudia*. Co-dominant with Didiereaceae is the genus *Euphorbia* with several arborescent species. These rather short trees, 8 to 10 meters high, have pulpy and thorny branches. The trees, shrubs, and lianas are in part aphyllic (of reduced foliage), in part deciduous, and in part evergreen, depending on the species. There is a large proportion of thorny plants, as well as species with thick succulent leaves.

These desert-like forests are found throughout the south of the island up to the border of the eastern rain forest. However, in the whole region, there are continuous canopy, gallery forests along the rivers and streams. These forests differ little from the continuous canopy forests of the West.

The border between the south and the southwest is the Onilahy River. To the north of this river, up to the Mangoky River, plant formations characteristic of both the west and the south are found—continuous canopy forests, brush and scrub forests, thickets, and the desert-like *Didierea* forests, as well as the degraded savannahs and prairies. This region between the Mangoky and the Onilahy Rivers has been referred to by many authors as the transition zone between the west and the south.^{12,14,17}

ECOLOGICAL DISPERSION

During the surveys, the following data were collected: the diurnal species observed (nocturnal species sighted were also noted); the type of forests in which the animals were found; the presence of a river or lake bordering the forest; and the presence of hilly or flat terrain. These data are summarized in TABLE 2. Only data from the 16 forests in the area in which the ranges of *Lemur catta* and *Lemur fulvus rufus* overlap are included.

Populations of *Lemur catta* and *Lemur fulvus rufus* were observed in three types of primary vegetation habitat: continuous canopy forests, brush and scrub forests, and mixed forests. TABLE 2 clearly illustrates that, in the area where the ranges of *Lemur fulvus rufus* and *Lemur catta* overlap, populations of *L. f. rufus* are found alone only in the small, circumscribed, continuous

canopy forests. On the other hand, *L. catta*, in this area, exists alone only in brush and scrub forests. Brush and scrub forests, as I have described earlier, are very dense, with a subordinate tree layer and no continuous canopy. *Propithecus verreauxi verreauxi* is not found in brush and scrub forests. This is probably because the density and stratigraphy of these forests necessitate terrestrial locomotion.

Populations of *Lemur fulvus rufus* and *Lemur catta* coexist only in mixed forests. We found two variations of the mixed forests: gallery forests bordering rivers which flow at the foot of dry hills (e.g., Fiherenana II, Sakaraha, and Mangoky); and large mosaic areas with a canopy forest bordered and/or broken up by areas of primary brush and scrub forest (e.g., Antserananomby, Iana-dranto I., and Belo-sur-Mer). Within the mixed forests, both in the area in which the ranges of *L. f. rufus* and *L. catta* overlap and in areas in which the species are allopatric, *L. f. rufus* was found only in sections of the forests with a continuous canopy. *L. catta* was observed in all parts of the mixed forests.

TABLE 2
THE FREQUENCY AT WHICH *L. F. RUFUS*, *L. CATT*A, AND
P. V. VERREAUXI WERE FOUND IN VARIOUS TYPES OF FORESTS*

	Continuous Canopy	Brush and Scrub	Mixed	River Edge	Not on River Edge	Cliff Edge, Hilly	Flat
<i>Lemur fulvus rufus</i> only	5	0	0	3	2	0	5
<i>Lemur catta</i> only	0	5	0	2	3	5	1
<i>L. f. rufus</i> and <i>L. catta</i>	0	0	6	4	2	3	3
<i>Propithecus verreauxi verreauxi</i>	4	0	5	4	5	2	7

*Data are from the survey within the area in which the ranges of *L. f. rufus* and *L. catta* overlap.

The table further indicates that: (1) the presence or absence of a river does not seem to be significant; (2) the continuous canopy forests are flat, while most of the brush and scrub forests are in hilly regions; and (3) mixed forests are evenly distributed in hilly and flat areas.

Data collected during the survey suggest that *Lemur fulvus rufus* and *Lemur catta* have different habitat preferences. While *L. f. rufus* is limited to areas with a continuous closed canopy, *L. catta*, because much of its travel is done on the ground^{18,19} can exploit a number of regions that differ in ecological structure.

SUMMARY

The southern and northern limits of the distribution of *Lemur catta* and *Lemur fulvus rufus* are described. The range of *L. catta* extends in the north from the forest of Mahababoky, east of Belo-sur-Mer, to near the border of the eastern rain forest south of Manamboro in the south. The northern limit of the range of *L. f. rufus* is the western banks of the Betsiboka River. To the south, this species ranges to the northern banks of the Fiherenana River. Thus, the ranges of *L. catta* and *L. fulvus rufus* overlap in a large area (approximately 250 km north-south) of western Madagascar.

Within the area of overlap, *Lemur catta* and *Lemur fulvus rufus* are sympatric only in large areas in which continuous canopy forests merge into primary brush and scrub vegetation. In these areas, *L. catta* is found in both the canopy and scrub vegetation, whereas *L. f. rufus* is limited to the continuous canopy portion of the forest. *L. f. rufus* was never found in regions where there is only brush and scrub vegetation. These preferences for different types of forest are related to locomotor differences, and also to other extensive differences in habitat preference between the two species. These differences are discussed in detail elsewhere.

ACKNOWLEDGMENTS

Research in Madagascar would not have been possible without the assistance of M. Etienne Rakotomaria, Directeur de la Recherche Scientifique et Technique, Tananarive; Georges Randrianasolo, Directeur de la Parc de Tsimbazaza, Tananarive; Mm. Ramanantsoavina, Andriamampianina, and Finoana, respectively Directeur, Ingénieur en Chef, and Ingénieur, Service des Eaux et Forêts, Tananarive. During various phases of this project, field assistance was provided by Folo Emmanuel, Linda Sussman, Ian Tattersall, and Bernard Tsiefatao. Ian Tattersall commented upon the manuscript.

REFERENCES

1. HILL, W. C. O. 1953. Primates: comparative anatomy and taxonomy. Vol. 1: Strepsirhini. Edinburgh Univ. Press. Edinburgh, Scotland.
2. SCHWARTZ, E. 1931. A revision of the genera and species of Madagascar Lemuridae. Proc. Zool. Soc. London 339-428.
3. SCHLEGEL, H. 1876. Les faux-singes. Muséum d'Histoire Naturelle des Pays-bas 7: 279-356.
4. JENTINK, F. A. 1892. Catalogue systématique des mammifères. Muséum d'Histoire Naturelle des Pays-Bas. 11: 1-219.
5. BOGGESS, P. & J. SMITH. 1963. Unpublished field notes.
6. JOLLY, A. 1966. Lemur behavior. University of Chicago Press. Chicago, Ill.
7. BUETTNER-JANUSCH, J. The lemurs of Madagascar (ms.).
8. ARCHBOLD, R. 1930. Madagascar Journal (mission zoologique franco-anglo-américaine 4 April 1929-14 May 1930). Unpublished manuscript. Am. Mus. Nat. Hist. Archives. New York.
9. APPERT, O. 1966. La distribution géographique des lémuriers diurnes de la région du Mangoky au sud-ouest de Madagascar. Bull. Acad. Malgache, N. S. 44(2): 43-45.
10. WALKER, A. C. 1967. Locomotor adaptations in recent and subfossil Madagascan lemurs. Ph.D. Thesis. University of London.
11. PERRIER DE LA BATHIE, H. 1921. La végétation malgache. Ann. Mus. Colon. Marseille, 3^o sér. 9: 1-268.
12. PERRIER DE LA BATHIE, H. 1936. Biogéographie des plantes de Madagascar Soc. Edit. Géogr. Marit. et Colon. Paris.
13. HUMBERT, H. 1954. Les territoires phytogéographiques de Madagascar. Leur cartographie. In LIX^o Colloque International du Centre National de la Recherche Scientifique. 439-448.
14. HUMBERT, H. & G. COURTS-DARNE. 1965. Notice de la carte Madagascar. Institut de la Carte Internationale du Tapis Végétal, Toulouse.

15. KOEHLIN, J. 1973. Flora and vegetation of Madagascar. *In* Biogeography and Ecology of Madagascar. R. Battistini & G. Richard-Vindard, Eds. 145-190. W. Junk. The Hague, Netherlands.
16. HUMBERT, H. 1927. La destruction d'une flore insulaire par le feu. Principaux aspects de la végétation à Madagascar. *Mém. Acad. Malgache (Tananarive)*. 1-80.
17. PETER, J. -J. 1962. Recherches sur l'écologie et l'éthologie des Lémuriens malgaches. *Mém. Muséum Nat. Hist. Nat. (Paris), Sér. A 27*: 1-146.
18. SUSSMAN, R. W. 1972. An ecological study of two Madagascan primates: *Lemur fulvus rufus* Audebert and *Lemur catta* Linnaeus. Ph.D. Thesis, Duke University. Durham, N.C.
19. SUSSMAN, R. W. 1974. Ecological distinctions in sympatric species of *Lemur*. *In* Prosimian Biology. R. D. Martin, G. A. Doyle & A. C. Walker, Eds. 75-108. Duckworth. London.