

ECOLOGY AND BEHAVIOR OF  
*LEMUR FULVUS MAYOTTENSIS*  
(PRIMATES, LEMURIFORMES)

IAN TATTERSALL

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## CONTENTS

Abstract . . . . .	425
Résumé . . . . .	425
Introduction . . . . .	426
Acknowledgments . . . . .	426
Taxonomy and Distribution . . . . .	428
The Study Area . . . . .	429
Vegetation . . . . .	432
Climate . . . . .	440
Sympatric Species . . . . .	441
Methods of Observation . . . . .	441
Observational Bias . . . . .	444
Preparation of the Forest . . . . .	445
Censusing . . . . .	445
The Social Unit . . . . .	445
Day Ranges and Population Density . . . . .	451
Diet and Feeding Behavior . . . . .	452
Feeding Techniques . . . . .	458
Patterns of Activity . . . . .	460
Daily Activity Cycle . . . . .	462
Preferential Use of Forest Strata and Substrate Types . . . . .	466
Locomotion and Substrate Preferences . . . . .	469
Social Behavior . . . . .	471
Discussion . . . . .	477
Literature Cited . . . . .	481







## ABSTRACT

*Lemur fulvus mayottensis* is unique to the island of Mayotte, one of the Comoro group. It quite closely resembles *L. f. fulvus*, from which it is probably derived, but is characterized by an enormous variability in pelage coloration. Between January and May 1975, more than 500 hours of quantifiable (time-sampled) field observations were accumulated on this island subspecies.

*Lemur fulvus mayottensis* does not live in stable groupings, but rather in fluid "associations" of regularly changing composition. Whether or not these form part of larger, exclusive groupings is not known. Mean size of 100 associations censused all over Mayotte was 9.1 individuals; the observed range was from two to 29 individuals. The socionomic sex ratio was ca. 1:1. Population density was high: approximately 10 individuals/hectare. Day ranges varied from 450 to 1150 meters, with a mean of ca. 800 meters.

The lemurs fed on the leaves, fruit, flowers, and buds of 32 identified plant species, to a total of 48 species/parts. However, 29 species/parts were only very infrequently exploited, to a total of only 3.7% of time spent feeding. Conversely, the fruit of three plant species accounted for 61.3% of feeding time. Overall, fruit formed 67.4% of the diet, leaves 27.3%, and flowers/buds 5.0%. These figures were accumulated during the wet season; the dry season diet is presumably somewhat different.

*Lemur fulvus mayottensis* is active at night as well as during the day. This may account, at least partly, for a very low diurnal activity:rest ratio of 0.52. During the day, resting occupied 65.7% of time; moving, 12.8%; feeding, 11.3%; traveling, 4.7%; and grooming, 4.3%. Activity was greatest in the early morning and late afternoon; there was a major rest period during the middle of the day. Daily schedules varied somewhat, however.

The upper levels of the forest were preferred by *L. f. mayottensis*; the ground was rarely visited. A preference was also shown for movement along horizontal or gently sloping supports of medium to large diameter, although locomotor behavior was extremely flexible and no part of the forest was inaccessible to the lemurs because of locomotor restrictions. Leaping was agile, but was far from a preferred means of displacement.

No discernible social dominance relationships existed among *L. f. mayottensis*, and agonistic interactions were quite rare. These lemurs are highly social; about half of the resting time of individuals was spent in physical contact with other lemurs, and autogrooming was less common than allogrooming. Correspondingly, the dispersion of individuals within an association was usually rather restricted. Marking (anogenital) was of low frequency and was most commonly associated with encounter behavior and travel.

Comparison of *L. f. mayottensis* with *L. f. rufus* of southwest Madagascar shows that a great deal of ecological/behavioral flexibility exists within the species *Lemur fulvus*.

## RÉSUMÉ

*Lemur fulvus mayottensis* est unique à Mayotte, l'une des îles de l'archipel des Comores. Il ressemble d'assez près à *L. f. fulvus* dont il est probablement issu, mais dont il se distingue par une plus grande diversité dans la coloration du pelage. Voici les résultats de plus de 500 heures d'observation quantifiées, effectuées sur le terrain entre janvier et mai 1975.

*Lemur fulvus mayottensis* ne vit pas en groupes stables, mais plutôt en "associations" fluides de composition constamment changeante. Peut-être celles-ci font-elles partie d'un groupe exclusif plus vaste, cela reste à vérifier. La taille des associations recensées était en moyenne de 9,1 individus, variant entre 2 et 29. Le rapport mâles-femelles ("sex ratio") était d'environ 1 pour 1. La densité de population sur les lieux de l'étude atteignait approximativement 10 individus à l'hectare, chiffre comparable aux plus fortes densités enregistrées à Madagascar. La distance quotidienne parcourue par les lémuriens variait de 450 à 1150 mètres, avec une moyenne de 800 mètres environ.

La nourriture des lémuriens se composait de feuilles, de fruits, de fleurs et de boutons de 32 espèces de plantes identifiées; soit un total de 48 aliments distincts parmi lesquels 29 n'étaient exploités qu'à 3,7% du temps d'alimentation alors que 3 espèces de fruits en occupaient 61,3%. En tout, les fruits formaient 67,4% du régime alimentaire des animaux, les feuilles 27,3% et les fleurs et boutons 5,0%. L'étude ayant eu lieu



pendant la saison humide, il faut sans doute s'attendre à une certaine variation de ces chiffres pour la saison sèche.

*Lemur fulvus mayottensis* est actif la nuit comme le jour. Cette activité nocturne peut-être expliquer le fait que le rapport diurne activité/repos est très faible, soit 0,52. Pendant le jour, le repos constituait 65,7% du temps, le déplacement (12,8% "moving" + 4,7% "travel") 17,5%, l'alimentation 11,7%, et la toilette (léchage) 4,3%. L'activité était plus importante tôt le matin et en fin d'après-midi, et aux alentours de midi on pouvait observer un long repos. Cet emploi du temps quotidien variait cependant quelque peu.

On a pu remarquer une nette préférence de *L. f. mayottensis* pour les niveaux supérieurs de la forêt, à l'exclusion presque totale du sol. Lors de ses déplacements dans les arbres, bien que son comportement locomoteur soit si flexible qu'il n'existe pas de coins de forêt où il n'ait accès, *L.*

*f. mayottensis* affectionne plus particulièrement les supports horizontaux ou modérément inclinés, de diamètre moyen ou grand. S'il lui arrive de sauter agilement d'une branche à l'autre le saut n'est certes pas son moyen de locomotion favori.

Il n'existe aucune relation de dominance sociale notoire chez *L. f. mayottensis*, et les interactions agressives sont rares. Les animaux étant très sociables, le contact physique entre individus occupe la moitié du temps de repos. *L. f. mayottensis* procède moins fréquemment à sa propre toilette qu'à la toilette mutuelle. La dispersion des membres de l'association est normalement assez restreinte. Le marquage (génito-anal) est peu fréquent et plus communément associé au déplacement et aux rencontres entre associations.

Une comparaison entre *L. f. mayottensis* et *L. f. rufus* de Madagascar montre qu'il existe une grande flexibilité écologique et comportementale dans l'espèce *Lemur fulvus*.

## INTRODUCTION

Outside Madagascar, wild-living natural populations of lemurs are confined to three of the four islands of the Comoro group, an archipelago lying in the northern entrance to the Mozambique Channel, between Madagascar and the African mainland (fig. 1). Of such populations, the only subspecies to be found uniquely outside Madagascar is *Lemur fulvus mayottensis* (Schlegel, 1866). As its name implies, this lemur is limited to Mayotte, the most southerly (fig. 1) of the Comoros and the second smallest, with an area of only 375 km<sup>2</sup>.

Neither the time nor the means of arrival of the lemurs on Mayotte will ever certainly be known, but as I have noted elsewhere (Tattersall, 1976, 1977a), the most likely mechanism of introduction is human activity. This would in turn indicate a recent date of arrival: probably within the past millennium. *Lemur fulvus mayottensis* is closely reminiscent in its external characters and pelage of *Lemur fulvus fulvus*, the primary area of distribution of which is in north-west Madagascar (see Tattersall, 1977b), and is most probably derived from individuals of this subspecies. The problem of the origin of *L. f. mayottensis* raises several intriguing questions, however, which will be discussed elsewhere.

In the present report, the results are presented of a field study of *L. f. mayottensis*

undertaken from January through May 1975. Most of the data were collected in such a manner as to be as directly as possible comparable to the observations made by Sussman (1972, 1974, 1975) on *Lemur fulvus rufus* in seasonal forests in southwest Madagascar. *Lemur fulvus fulvus* has also been the subject of field observation (Harrington, 1975), but that study, aimed at the recording of social interactions, involved a level of recognition of individual animals impossible to attain under the conditions of the work reported here. During this study, in addition to time devoted to habituation and subjective observation, some 570 hours of quantifiable (time-sampled) observations were accumulated.

This study was carried out during the rainy season, and it is hoped in the near future to supplement its results with similar observations made during the dry season (June-October). The present report is thus of a preliminary nature, and the data summarized here will be more extensively analyzed in conjunction with such further observations.

## ACKNOWLEDGMENTS

This study could not have been begun without the active assistance of the Comorian authorities, or completed without that of the Institut de



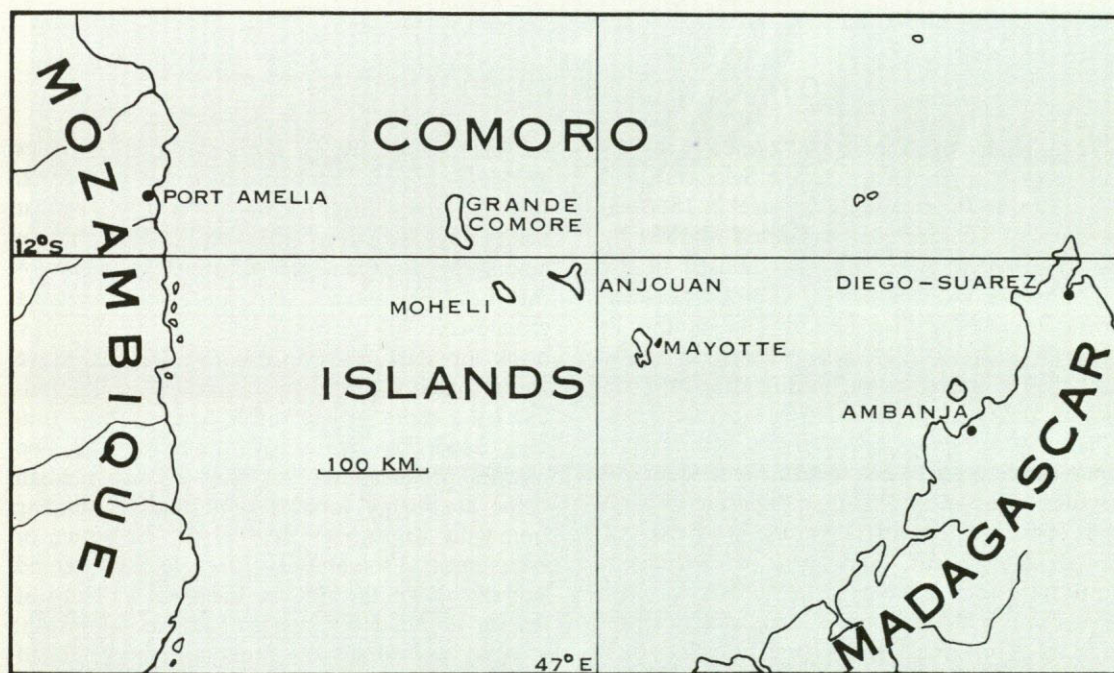


FIG. 1. Location and disposition of the Comoro Islands in the Mozambique Channel.

Recherches Agronomiques Tropicales (IRAT). Among the central officials of the former Comorian government, I should particularly like to thank Mm. Omar Tamou, Ministre du Développement Rural; Mouhtar Rachide, Directeur de la Production, Service des Eaux et Forêts; Francis Debuissy, Vétérinaire; and Robert Tapia, Conseiller Technique. Among local officials in Mayotte I am especially grateful to M. Ahmed Abdallah, former Chef de la Circonscription Agricole, Mamutzu, and to members of his staff and that of the office of M. le Préfet, Mamutzu. I owe a deep debt of thanks to M. Jacques Larcher, Directeur de l'IRAT Comores, who placed IRAT facilities at my disposal, and to Mme. Larcher; equal thanks are due M. Henri Reneaud, Chef de la Station IRAT de Coconi, and to Mme. Reneaud, for their hospitality and extensive assistance during the study. M. and Mme. Christian Gaiani, of Pamanzi, M. Patrice "Shetwane" Segonne, of Mamutzu, M. P. Garczynski, of Dzaoudzi, and M. and Mme. Marc Lauret, of Combani, also provided invaluable hospitality and help, as did M. and Mme. J.-C. Favetto, of Moroni.

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## TAXONOMY AND DISTRIBUTION

The lemur of Mayotte, "komba" to the Mahorais (as is *L. macaco* to the Sakalava), was first scientifically named by Schlegel in 1866, on the basis of 10 specimens collected in 1864 by Van Dam and Pollen and now housed in the Rijksmuseum van Natuurlijke Historie, Leiden. Having lumped together the forms now known as *L. fulvus collaris*, *L. f. fulvus*, *L. f. rufus*, and (partially) *L. mongoz*, but having effectively described only *L. f. fulvus*, Schlegel remarked: "C'est à cette espèce, à laquelle on peut réserver l'épithète de *collaris*, que se rattache le Lemur de Mayotte." However, "Sans insister sur la différence spécifique de notre Lemur d'avec le *L. collaris* de Madagascar, nous nous permettons de l'introduire sous le nom de Lemur mayottensis, dans le seul but d'indiquer . . . son origine et les variations, soit locales, soit individuelles, qu'il présente, en comparaison de celles de Lemur *collaris* de Madagascar" (p. 76).

As far as I am able to ascertain, the first worker formally to make the assignment, already implicit in Schlegel's discussion, of the Mayotte lemur to a subspecies of *L. fulvus*, was Schwarz (1931). Writing on the basis of four skins scattered among the natural history museums of London, Paris, and Berlin, Schwarz had apparently not seen the material in Leiden described by Schlegel. This may account for the fact that although Schlegel claimed that *L. f. mayottensis* "offre la même distribution de teintes de la tête [as in *L. f. fulvus*], mais ces teintes sont en général beaucoup plus prononcées et plus tranchées" (p. 76), Schwarz remarked that "in the specimens I have seen the supraorbital marks are very indistinct and the general colour . . . paler . . . than in *L. f. fulvus*" (p. 44).

In fact, both of these assertions are substantiable on the basis of available specimens. For among the most striking characteristics of the Mayotte lemur is its remarkable chromatic variability: a variability which in nature far exceeds that to be seen in the meager total of 14 existing museum specimens. This variation, which apparently provides a classical example of character release, centers around a mean closer to that of *L. f. fulvus* than to that of any other *L. fulvus*

subspecies (figs. 2, 3). Both males and females generally possess black muzzles and periorbital regions; where black is not present, gray most commonly is. Gray faces are more common among females than among males. The crown of the head is almost always darker than the ground-color of the body, and is most frequently black or dark brown; this variably extensive darker patch is joined to the muzzle in the midline by a more or less visible narrow stripe running down the center of the brow. The two patches produced on the brow by this median stripe are highly variable in coloration, ranging from gray through cream to beige to brown or even russet. Sometimes these patches extend laterally down the side of the head in front of the ear to join cheek pelage of similar coloration; in other individuals the brow and cheeks are of different color. The ears are visible; hairy, but not tufted, they are generally of the same color as the dorsum. The beard is usually the color of the cheeks; where not, it is in most cases the color of the ventrum. In large males, light flashes may be present slightly below the eyes. White fur may appear on the cheeks, beard, or brow, or on all three.

Body coloration is generally brown, with varying influences of gray, russet, and other colors. The dorsum is always darker than the ventrum and the tail is generally darker than the dorsum, at least distally. A dark spot is invariably present at the dorsal base of the tail. Both sexes possess extensive perianal areas of naked, wrinkled, glandular skin. In general, males tend to be darker than females in body coloration, as in that of the head. The lightest colored individual seen, a female, was of a very light golden-brown; the darkest, a male, was as dark as *L. rubriventer*, although lacking the reddish tincture of the latter. Considerable practice is needed to distinguish between males and females when the genital area is not directly visible; in general, males possess a bushier pelage in the region of the cheeks and beard, and thus appear rounder-faced. There is no reliable chromatic criterion, although no females were observed to possess the light patches below the eyes characteristic of some males.





FIG. 2. *Lemur fulvus mayottensis*, adult male.

The exact degree of distinction between *L. f. mayottensis* and *L. f. fulvus* is at present problematical. As I have noted, the Mayotte lemur most closely resembles the latter among the various mainland subspecies of *L. fulvus*; but it is not certain, for instance, that no hybridization between *fulvus* subspecies occurred in the establishment of the lemur population of Mayotte. Chromosome studies planned for the near future will, it is hoped, throw more light on the precise affinities of the Mayotte lemur; in the interim, it is clearly most helpful to maintain a separate subspecific designation for the island form. Simpson

(1961) has propounded the appealingly pragmatic dictum that subspecies may be recognized if they are useful to the taxonomist; and subspecific separation for the isolated lemur of Mayotte is useful from a variety of points of view.

The Mayotte lemur is found in all parts of its island, or, at least, wherever there is forest (Tattersall, 1977a, In press). Population density is low at altitudes above about 400 meters, and is higher in the north than in the drier south. It is unclear whether or not this latter is entirely due to the greater extent of devastation of the vegetation in the south than in the north.

### THE STUDY AREA

Except in a few limited areas of high altitude in the north of the island, and in the regions of Dapani and Choungui in the south, the vegetation of Mayotte is entirely secondary. Traditional

agricultural practices demand the constant abandonment of existing plots and the clearance of new ground with the result that, particularly in the south, large tracts of land are denuded of





FIG. 3. *Lemur fulvus mayottensis*, adult female.

vegetation except for stunted grass cover. The situation is less critical in the somewhat more humid north, perhaps largely because of the presence of the "avocat marron" (*Litsea tersa*: Lauraceae), a tree originally introduced to Mayotte from Réunion to provide fuel for sugar refining and, more recently, for the distillation of perfume essences. This fast-growing tree possesses a complex and extensive root system and is difficult to extirpate even using modern methods; traditional agricultural practices, which involve the cutting and burning of existing vegetation but not the removal of roots, very rarely succeed in killing it. The blackened stumps are left in the ground where they act to retard the loss of soil from the slopes, and the green shoots which they send up are cut off as long as the field is under cultivation. When the cultivator (the French term "gratter" describes his activities to perfection) moves elsewhere, the regeneration

of the avocat marron proceeds apace. The avocat marron does, however, require a considerable depth of soil to flourish, and those areas where the tree is unable to establish itself are often subject to deterioration. Moreover, the rapid dispersal of its seeds (probably primarily by lemurs), together with human clearing practices, is leading to the spread of the avocat marron at the expense of other tree species. It is notable, and predictable from local agricultural practices, that most avocat marron forests on Mayotte are young; large mature trees are comparatively rare.

The study area consisted of some 3.2+ hectares of forest, bordering a stream (nameless to the locals, but indicated on the 1:50,000 map of Mayotte [Inst. Géog. National Paris, 1955/6] as the River Adembini) adjoining the village of Mavingoni Nambaragoa (fig. 4). The largest of three villages called Mavingoni in the region of that name, Mavingoni Nambaragoa is on the



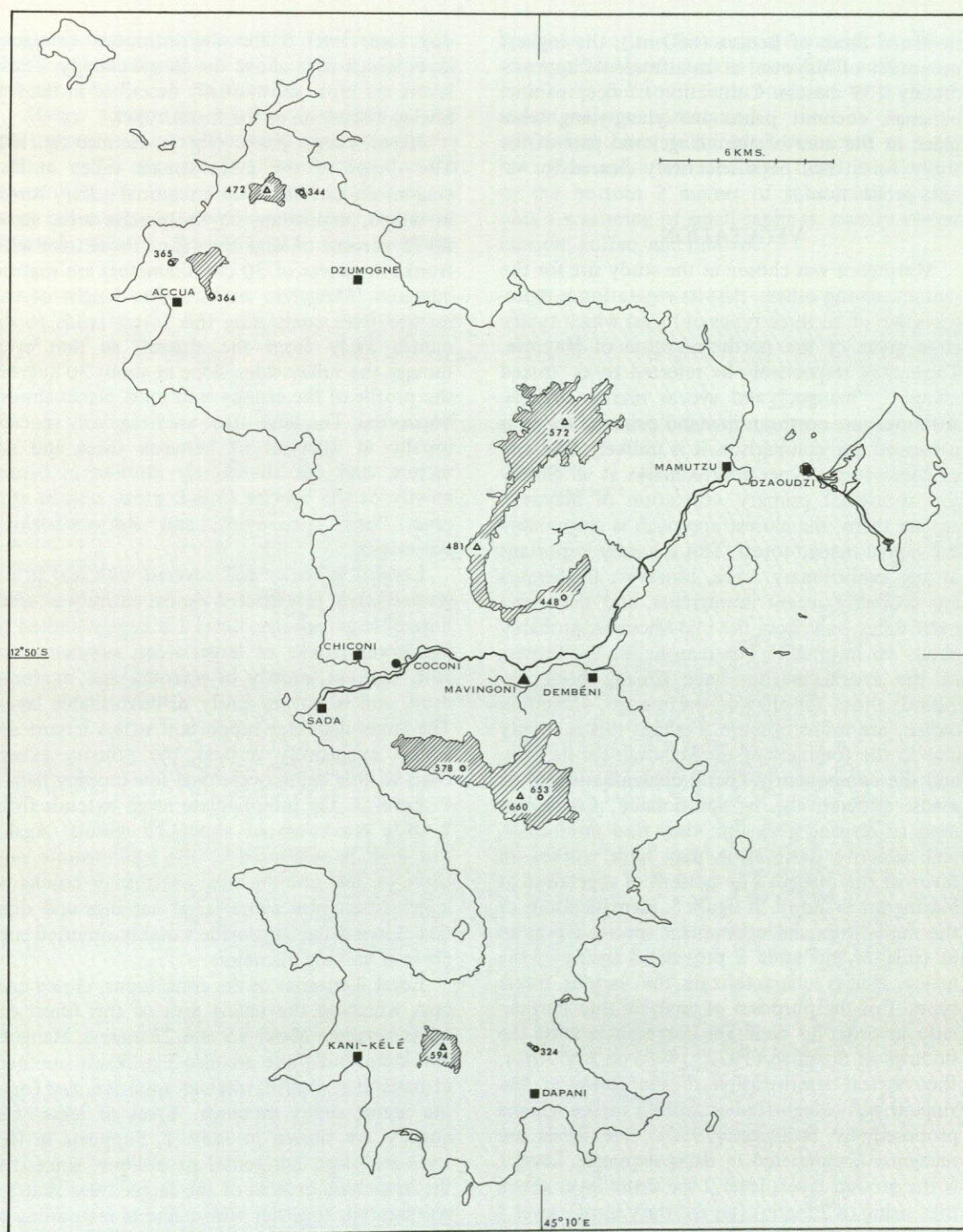


FIG. 4. Map of Mayotte showing the locations of Mavingoni, Coconi, and other localities. Hatched areas are those lying above the 300 meter contour; elevations of high points are given in meters.



northern flank of Benara (660 m.), the highest mountain of Mayotte, at an altitude of approximately 100 meters. Cultivation of rice, manioc, bananas, coconut palms and ylang-ylang takes place in the area of the village, and part of the study forest had been selectively cleared for vanilla production.

### VEGETATION

Mavingoni was chosen as the study site for the reason, among others, that its vegetation is representative of all three types of forest which typify large areas of the northern region of Mayotte. These may respectively be referred to as "mixed mango," "mango," and avocat marron forests. Although no northern lowland primary forest is preserved for comparison it is unlikely that any of these forest types approximates at all closely the aboriginal primary vegetation of Mayotte; among them, the closest approach is presumably the mixed mango forest. This is hardly important in any evolutionary sense, however: the lemurs are probably recent immigrants, and the island itself dates only from the mid-Miocene, probably about 16 m.yr. B.P. The reasons for the success of the avocat marron have already been discussed; those for that of the mango, *Mangifera indica*, are more obscure. Perhaps this is simply due to the fondness of the Mahorais for its fruit, and the consequently liberal dissemination of its seeds; alternatively, or additionally, Comorians tend to respect trees that they find productive, and selective destruction may have worked in favor of the mango. The pattern of vegetation at Mavingoni is shown in figure 5, identifications of the major tree and other plant species are given in table 1, and table 2 provides a listing of the major species characterizing the various forest types. For the purposes of analysis, and particularly in order to facilitate comparison with the findings of Sussman (1972, 1975) on *L. f. rufus*, the vertical stratification of the forest at Mavingoni was categorized according to the scheme proposed by Richards (1952): five levels are recognized, numbered in rising sequence. Level 1 is the ground layer; level 2 the shrub layer above this, rising to 2 meters (an arbitrary limit); level 3 the intermediate layer between the shrub layer and canopy; level 4 the continuous forest canopy;

and level 5 the discontinuous emergent layer which rises above the closed canopy. These layers are more substantially described in the following discussion of the forest types.

*Mixed mango forest* (fig. 6; see also fig. 10). The slopes of the main stream valley at Mavingoni are covered with a seasonal gallery forest in which, depending on the precise area, some 60-75 percent of large trees (i.e., those trees with trunks in excess of 30 cm. diameter) are mature mangoes (*Mangifera indica*). The height of the mature trees composing this forest tends to diminish away from the stream, so that even though the valley sides slope at about 30 degrees the profile of the canopy is in most places almost horizontal. The large trees are irregularly spaced, usually at intervals of between three and six meters, and are abundantly clothed in lianas, mostly of the species *Entada gigas*, *Entada africana*, *Saba comorensis*, and *Ancyclobothrys petersiana*.

Level 1 is rocky and covered with leaf litter; ground cover is restricted almost entirely to seedlings of larger species. Level 2 is largely limited to the lower trunks of larger trees, supplemented with saplings, mostly of *mrandra* and *nyafoundrou*, and is not an easily distinguishable layer. The larger-diameter supports it offers lemurs are almost exclusively vertical, the primary exceptions to this being occasional low-looping lianas.

Level 3, the intermediate level, extends from 2 to a maximum of about 15 meters. Again, this level is composed of the intermediate portions of the unbranching or forking trunks of larger trees, plus some larger saplings and *dououa*. Lianas (fig. 7) provide variably oriented supports of varying diameters.

Level 4 consists of the continuous, closed canopy, which in the tallest area of this forest extends between about 15 and 22 meters. Mangoes dominate, but there are also significant numbers of badamier, msafiri, mselani, mouriyé, and (near the water only) mouinga. Trees of lesser frequency are shown in table 2. Supports in this level are often horizontal or oblique, since it is the branching crowns of the larger trees that are represented, together with a liberal festooning of lianas of all diameters and orientations.

Only the crown of the occasional badamier



pokes above the continuous layer to form level 5. The maximum height of such trees is around 25 meters.

*Mango forest* (fig. 8). This is limited to the northwestern part of the study area, close to the village, and is almost isolated from the rest of the forest (fig. 5). It consists almost exclusively of very tall mango trees well-spaced apart and interspersed with a few badamier and mouinga.

Peripheral to it in the north are stands of trees of economic interest, such as breadfruit, coffee, and kapok; in the south it is bordered by a mixed avocat marron consociation.

Ground cover is minimal, restricted to bamboo grass and a few seedlings. Level 2 is limited to the bottom 2 meters of substantial trunks, plus a scattering of small saplings, mostly avocat marron, coffee, and mbovo.

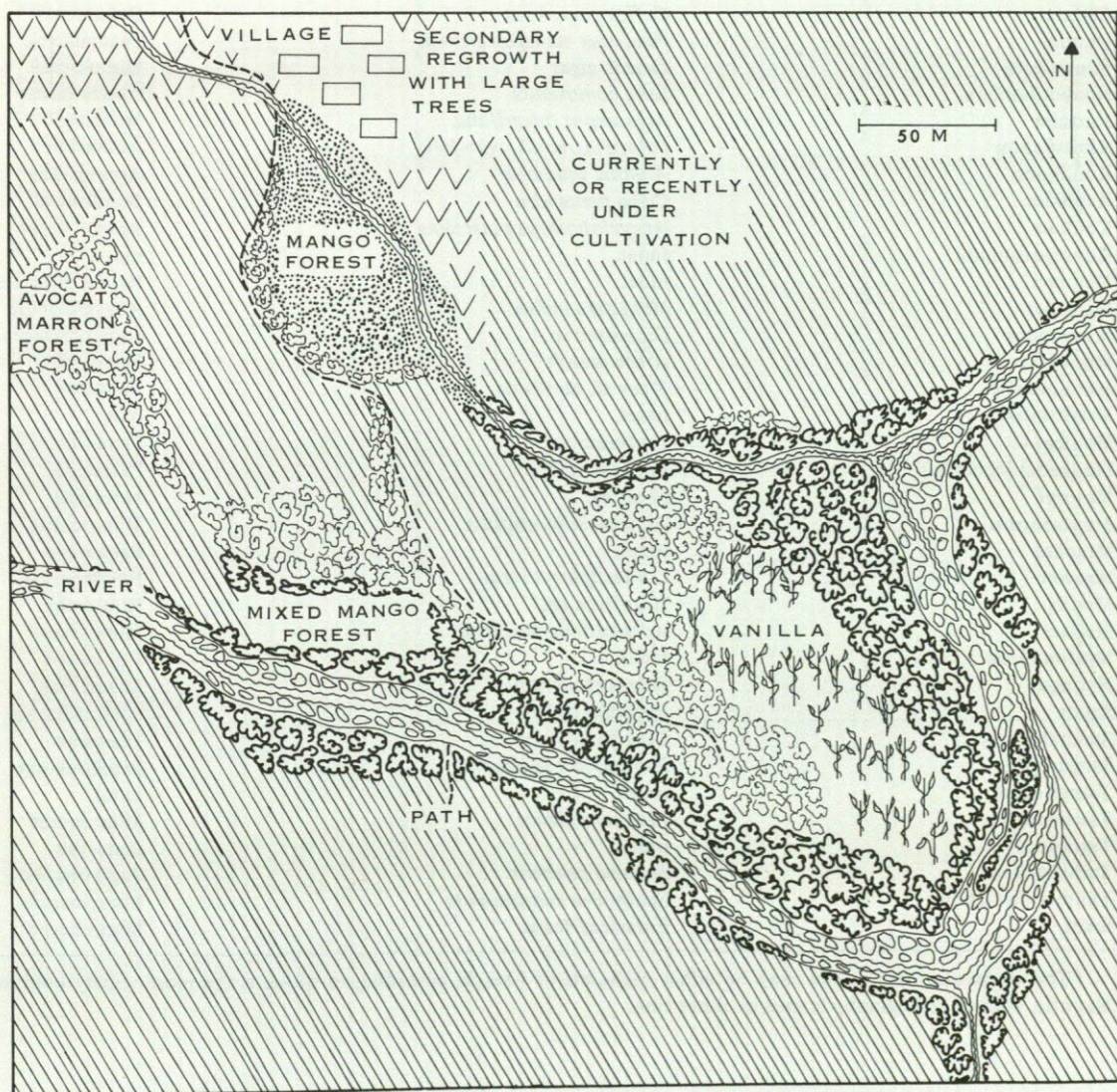


FIG. 5. Vegetation of the study area.



TABLE 1  
Major Tree and Other Plant Species Occurring at Mavingoni

Vernacular name <sup>a</sup>	Species	Family
Arbreá Pain	<i>Artocarpus incisa</i>	Moraceae
Avocat marron	<i>Litsea tersa</i>	Lauraceae
Badamier	<i>Terminalia catappa</i>	Combretaceae
Bahibahi	<i>Dioscorea</i> sp.	Dioscoriaceae
Barabahi	indet.	Myrsinaceae
Bois noir	<i>Albizzia lebbeck</i>	Mimosaceae
Caffeier	<i>Coffea canephora</i>	Rubiaceae
Dououa	<i>Pandanus madagascariensis</i>	Pandanaceae
Fourefoure	<i>Entada gigas</i>	Mimosaceae
Houbouhoubou	<i>Saba comorensis</i>	Apocynaceae
Jacquier	<i>Artocarpus integrifolia</i>	Moraceae
Kibitsoukou	<i>Polysphaeria</i> aff. <i>parvifolia</i>	Rubiaceae
Konokono	<i>Annona squamosa</i>	Annonaceae
Kapokier	<i>Ceiba pentandra</i>	Bombaceae
Koukou	<i>Ancyclobothrys petersiana</i>	Apocynaceae
Koureyatsoumbi	indet.	indet.
Maloravi	indet.	(Order Malvales)
Manguier	<i>Mangifera indica</i>	Anacardiaceae
Mavoundro	<i>Dioscorea</i> sp.	Dioscoriaceae
Mbovo	<i>Areca catech</i>	Palmaceae
Mhoumambé	<i>Ficus</i> cf. <i>racemosa</i>	Moraceae
Mouhamba	indet.	indet.
Mouinga	<i>Erythrina</i> sp.	Papilionaceae
Mounadzi (cocotier)	<i>Cocos nucifera</i>	Palmaceae
Mouriyé	<i>Ficus</i> sp.	Moraceae
Moutsoutsou	<i>Albizzia adionthifolia</i>	Mimosaceae
Mrandra	indet.	Palmaceae
Mrovou	<i>Cordia</i> ? <i>platythyrsa</i>	Boraginaceae
Msafiri	? <i>Gardenia</i> sp.	Rubiaceae
Msélani	<i>Adenanthera pavonina</i>	Mimosaceae
Nyafoundrou	indet.	Rubiaceae
Nyongo	<i>Solanum nigrum</i>	Solanaceae
Sakoa	<i>Spondias dulcis</i>	Anacardiaceae
Sandrakidraki	<i>Leea guineensis</i>	Leeaceae
Sangdragon	<i>Pterocarpus indicus</i>	Papilionaceae
Tsangitsangé	indet.	indet.
Tsarimougou	<i>Leucaena glauca</i>	Mimosaceae
Tsarintsoa	indet.	Rutaceae
Tschitsangou	<i>Mucuna pruriens</i>	Papilionaceae
Tulipier du Gabon	<i>Spathodea campanulata</i>	Boraginaceae
indet.	<i>Entada africana</i>	Mimosaceae

<sup>a</sup>The vernacular name given may be either Mahorais or French, according to which is the more widely used in Mayotte. French orthography is used in either case.



TABLE 2  
Distribution of Major Tree and Other Plant Species in the  
Various Forest Types at Mavingoni

Species (Vernacular name)	Mixed mango	Mango	Avocat marron	Peripheral
Arbre à Pain	—	X	—	X
Avocat marron	—	—	X	—
Badamier	X	X	—	—
Barabahi	X	—	—	—
Bois noir	X	—	X	—
Caffeier	—	—	—	X
Dououa	X	—	—	—
<i>Entada africana</i>	—	—	X	—
Fourefoure	X	—	X	—
Houbouhoubou	X	X	X	—
Jacquier	X	—	—	X
Konokono	—	—	—	X
Kapokier	—	—	—	X
Koukou	X	—	X	—
Maloravi	X	—	—	—
Manguier	X	X	X	X
Mavoundro	X	—	X	—
Mbovo	—	X	—	—
Mhoumambé	—	—	X	—
Mouinga	X	—	—	—
Mounadzi	—	—	X	X
Moutsoutsou	X	—	—	—
Mrandra	X	—	—	—
Msafiri	X	—	—	—
Msélani	X	—	X	—
Nyafoundrou	X	—	—	—
Sakoa	—	—	—	X
Sandrakidraki	—	—	—	X
Sangdragon	—	—	—	X
Tschitsangou	—	—	X	X
Tulipier du Gabon	X	—	—	—





FIG. 6. View of mixed mango forest from the river. Conversion from color transparency.





FIG. 7. Typical pattern of lianas in the mixed mango forest. Conversion from color transparency.





FIG. 8. View within mango forest. Conversion from color transparency.

Apart from the trunks supporting the canopy, level 3 consists only of the crowns of a few smaller mangoes which branch off before the canopy level. In the northern extremity of the area this level, which extends from 2 to approximately 17 meters, is represented by the lower branches, horizontal in orientation, of some breadfruit trees.

Level 4 runs in vertical extent between 17 and

22 meters. About 85 percent of the canopy consists of mango crowns: the rest, of the crowns of badamier, breadfruit, and mouinga. Level 5 is represented by the topmost branches of a single badamier.

*Avocat marron forest* (fig. 9). Occupying the flatter land away from the river, this forest type consists of an avocat marron consociation at a relatively early stage of development, into which



the mixed mango forest grades toward the top of the stream valley. In terms of the number of trees, this forest contains over 95 percent avocat marron. Most of these, however, are saplings of small stature; only about 60 percent of trees with diameters at waist height of over 14 cm. are avocat marron, and of those with a diameter in excess of 30 cm., none is. The remaining trees in this forest are mostly mangoes and bois noir.

As would be expected of what is mainly a young secondary succession, the avocat marron forest is of relatively short stature; level 5 is absent, and the structural equivalent of level 4 in the other forest types is (a) lower, extending from about 8 to about 15 meters, and (b) discontinuous, consisting almost entirely of the crowns of the scattering of long-established mango and bois noir. These larger trees, particularly,



FIG. 9. View within avocat marron forest. Conversion from color transparency.



are behung with lianas. The dominant level here is level 3, between 2 and 8 meters, which consists of the branching portions and upper trunks of the slender *avocat marron*. In terms of supports, in its upper reaches it offers the lemurs an intricate interweaving pattern of fine and small horizontal and oblique branches together with, below, an array of closely spaced vertical trunks, mostly of medium diameter. Thin lianas are abundant. Level 2 is only arbitrarily distinguishable from level 3; ground cover consists mostly of *avocat marron* and *nyafoundrou* seedlings, with a few ferns.

In one area (see figs. 5 and 10), the forest has been selectively cleared for the cultivation of vanilla. In the northwestern portion of this area the vanilla has replaced *avocat marron* forest and no trees survive; in the southeast mixed mango forest was cleared and several large trees (principally mango, *bois noir*, and *msélani*) were left to provide shade for the vanilla and, incidentally, sources of sustenance for the lemurs.

The approximate spatial extent of the various forest types is (or was) as follows: mixed mango, 1.6 hectares (or, if the area of the river bed, overhung and in some places roofed by the forest, is included, 2.1 ha.); mango forest, 0.4 ha.; *avocat marron* forest, 1.2 ha. The area cleared for the cultivation of vanilla measures 0.5 ha.; almost exactly half of this was formerly occupied by mixed mango forest, of which remnants persist. The total forest area is thus, depending on how it is calculated, between about 3.2 and 4.4 ha. Neither figure, of course, includes contiguous areas of planting or young regrowth exploited by the lemurs.

#### CLIMATE

Climatic figures do not exist for Mavingoni, but it is unlikely that they would differ substantially from those reported from the pluviometric station at Coconi, some 4 km. distant as the crow flies. If there is any difference, it is



FIG. 10. View across vanilla clearing toward the mixed mango forest lining the river.



probably that Mavingoni, on the flank of the highest massif in Mayotte, is marginally wetter. As the figures for Coconi show (fig. 11) daily variation in temperature considerably exceeds annual variation; in fact, mean daily temperature varies only about 4°C throughout the year. In terms of rainfall, on the other hand, the climate is very distinctly seasonal (fig. 12), precipitation peaking at a high level during the austral summer, when the study was undertaken, and declining very considerably between May and October.

In figures 13 and 14 temperatures and rainfall are compared over the period of the study with the means for the corresponding period from 1969-1974. Two-week intervals are used as a basis for comparison. Although in temperature January-May 1975 was a relatively average period it is clear that precipitation during these months was substantially lower than usual, although rainfall was nonetheless considerable and apparently normal phenological patterns were exhibited by the vegetation.

### SYMPATRIC SPECIES

The mammalian fauna of Mayotte is rather impoverished. Besides the lemurs and the obvious imported livestock there exist wild pigs; a "wild cat," probably a viverrid; *Tenrec ecaudatus*; various rodents; and at least one species of the large, fruit-eating bat *Pteropus*. Among these, only man and *Pteropus* appear to offer *L. f. mayottensis* any substantial competition for resources, and in any direct encounter between lemur and bat, it was invariably the latter that was dislodged from its feeding-place. In general, my impression is that the fruit bats provide less competition for food resources for *L. fulvus* on Mayotte than they do for *L. mongoz* on Anjouan and Mohéli.

Although sizable raptorial birds—buzzards and owls—are found on Mayotte, it is unlikely that they, or any reptile, pose a significant threat of predation to the lemurs. Certainly if they do, only the very smallest infant/juvenile lemurs are at risk.

### METHODS OF OBSERVATION

Lemurs are hunted and eaten in Mayotte, but not yet on a large scale; around Mavingoni they are largely left alone by man. Habituation of the

animals to the observer was therefore relatively easy, at least in terms of physical effort; lacking a marked flight response to the passage of humans

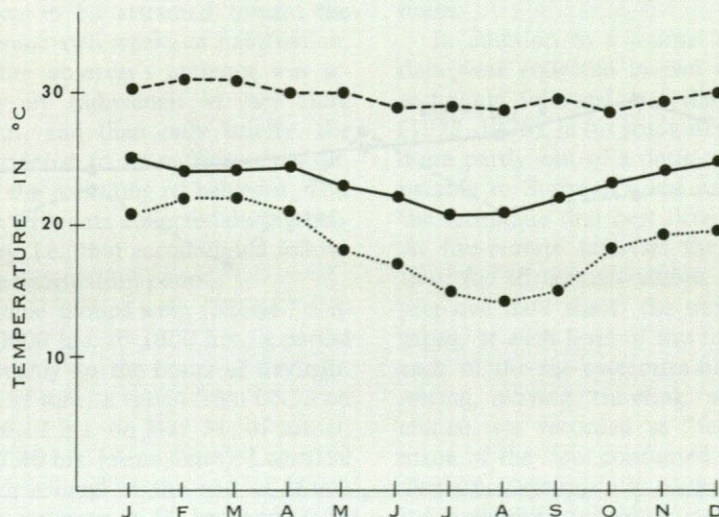


FIG. 11. Average daily maximum, mean, and minimum temperatures, by month, recorded at Coconi for the period 1961-1970 (in °C.).



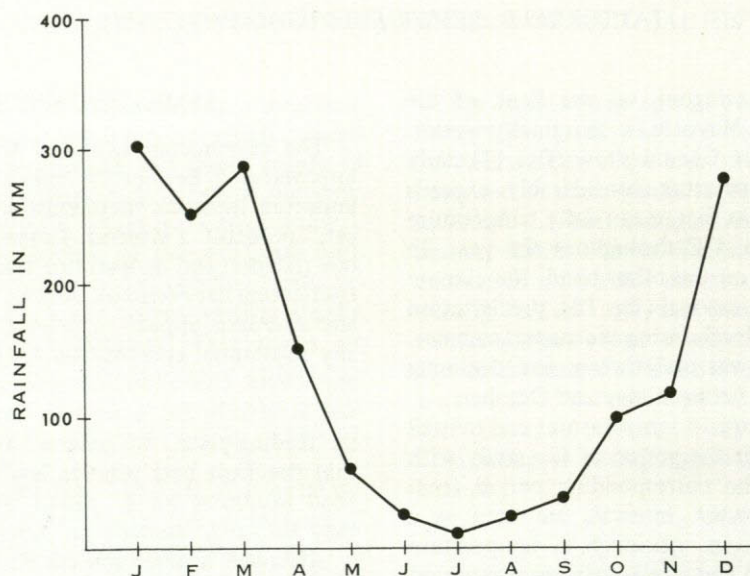


FIG. 12. Average monthly rainfall (in millimeters) recorded at Coconi for the period 1961-1970.

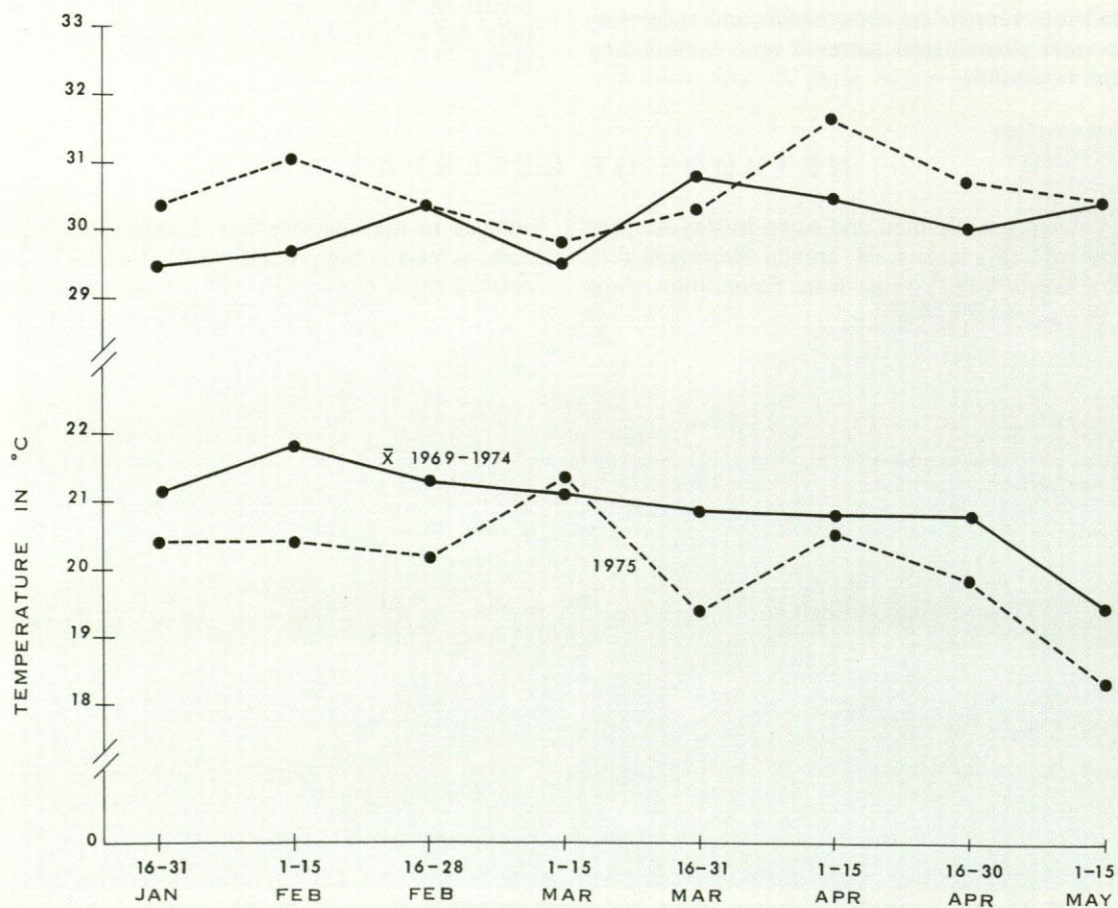


FIG. 13. Average daily maximum and minimum temperatures (over two-week periods) recorded at Coconi during the period of the study (broken lines), compared with the corresponding means for the previous five years (solid lines).



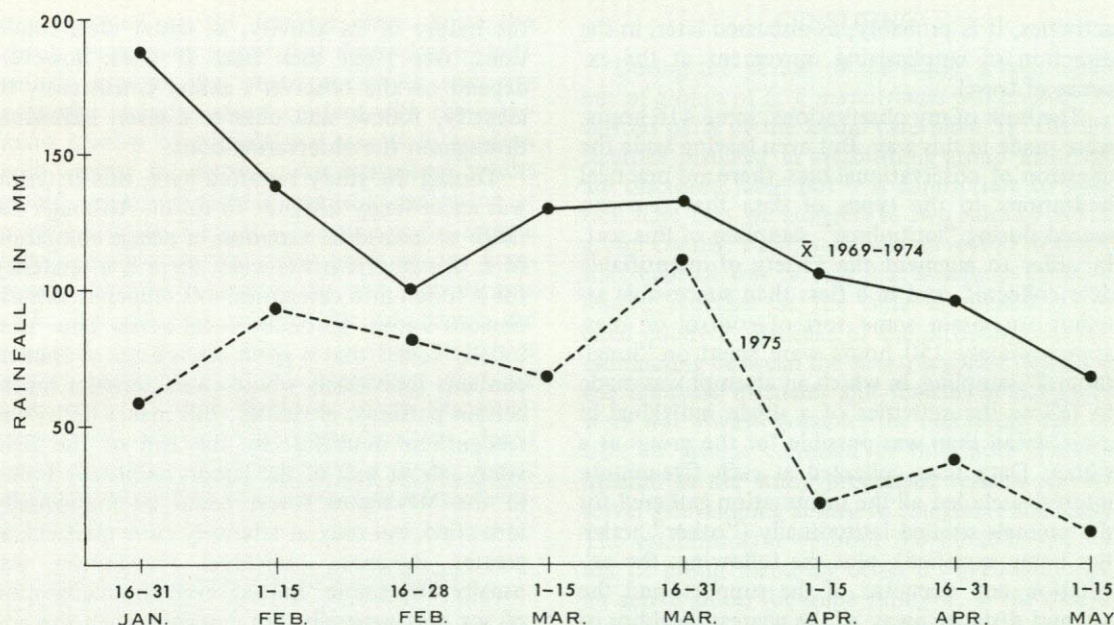


FIG. 14. Rainfall (over two-week periods) recorded at Coconi during the study (broken line), compared with the corresponding means for the five preceding years (solid line).

unless the intruders were noisy, the lemurs rarely tried to escape from the observer. In terms of eliminating any reaction by the animals to the observer's presence, the problem was the precise reverse: they displayed a great deal of curiosity, indeed a tendency to be attracted toward the observer. After some two weeks of habituation, by which time the observer's presence was acknowledged only by individuals in very close proximity to him, and then only briefly, the lemurs were considered to be sufficiently indifferent to permit the recording of behavior. This report deals only with data collected during February through May, i.e., that accumulated following the end of the habituation period.

As far as possible groups were followed continuously from 0600 hrs. to 1800 hrs., a period corresponding roughly to the hours of daylight. The official time of sunrise varied from 05.53 on February 1 to 06.12 hrs. on May 31; of sunset, from 18.32 to 17.40 hrs. (same dates). Logistical difficulties that developed at the end of March made observation between 06.00 hrs. and 06.30 hrs. only irregularly possible during April and May (although the shortening day length might have necessitated this anyway), whilst during

May, because of advancing nightfall, observation ceased at 17.30 hrs. Only on rare occasions was it not possible to maintain contact with the animals throughout the day; the observations are thus quite evenly distributed throughout the daylight hours.

In addition to a journal record, quantifiable data were collected in two ways. Primarily, the technique followed was that used by Sussman (1972, 1975), in his study of *L. f. rufus*. This was done partly out of a desire to collect data comparable to Sussman's and partly because it was the technique that best fitted the field situation. At five-minute intervals the following information, for all animals visible, was entered upon a prepared data sheet: the number of animals engaged, at each level of the forest, in activities in each of the six categories of feeding, grooming, resting, moving, traveling, and other. When an animal was recorded as "feeding," a note was made of the item consumed. "Movements" were displacements made in conjunction with individual activities; animals moved to groom, or to feed, and so forth. "Travel" refers to movements affecting the position of the group as a whole. If there is any bias in discrimination between these



activities, it is probably, as discussed later, in the direction of emphasizing movement at the expense of travel.

The bulk of my observations, some 416 hours, were made in this way. But even leaving aside the question of observational bias, there are practical limitations to the types of data that one can record during "latitudinal" sampling of this sort. In order to augment the variety of quantifiable data collected, and in a (less than successful) attempt to obtain some sort of control on bias, approximately 150 hours were spent on "longitudinal" sampling, in which an attempt was made to follow the activities of a single individual in more detail than was possible for the group as a whole. Data thus collected at each five-minute interval included all the information gathered for the animals studied latitudinally ("other" activities being specified), plus the following: the orientation and diameter of the support, and the sex and distance away of the nearest neighbor of the subject animal.

In the analysis, the unit used is the time-sample: "percent of time" spent in any particular activity refers to the proportion of observations, over a given period, in which a given behavior was recorded. Obviously, using the latitudinal technique, a number of observations were made for every five-minute interval. As has already been implied, quantitative analysis is restricted in this report to summarizing of the data; more extensive comparative analysis is reserved until projected studies have provided data relating to other seasons of the year.

#### OBSERVATIONAL BIAS

By their very nature, quantitative approaches to data collection depend heavily on the assumption that the information accumulated is free from observer bias, i.e., that greater weight is not given to those activities most easily visible to the observer. Of the two methods of sampling employed in this study, the latitudinal approach, while maximizing the sample size and providing information on synchrony in group activities, is theoretically the weaker from this point of view. Longitudinal sampling, where observation is concentrated upon a single individual regardless of

the nature of its activity, is, under ideal conditions, free from such bias. It does, however, depend on the observer's ability consistently to identify, follow, and observe a given individual throughout the observation bout.

During the study reported here, this criterion was exceedingly difficult to fulfill. Although the range of individual variation in pelage coloration of *L. f. mayottensis* is wide, there is a tendency for it to fall into categories; this tendency is most obvious within particular local areas. Thus it is usually found that a given assemblage of animals contains individuals whose characteristics repeat certain patterns; obviously, this makes individual recognition doubtful. By the end of the field study, about half of the lemurs habitually found in the Mavingoni forest could be individually identified, but only at relatively close quarters; at greater distances individual recognition was usually impossible. Indeed, even the recognition of sex was generally not possible when the animals were in the high canopy or when an animal was partially hidden from, or unfavorably oriented toward, the observer.

Longitudinal sampling at Mavingoni was thus fraught with problems. Most importantly, because of the difficulties of individual recognition, unceasing visual contact normally had to be maintained with the subject animal; if such contact was lost, as not infrequently occurred, a lemur of the same sex was chosen anew in the area in which its predecessor had disappeared.

Because of the shortcomings of this approach, reference is made in this report to the longitudinal data only in the cases of substrate preference and individual spacing; in the remaining categories of activity, where latitudinal and longitudinal data are duplicated, the former is preferred.

A rough field check was run on the degree of bias involved in the latitudinal observations. On several occasions throughout the study two observers were deployed, observing the same agglomeration of animals from separate positions. Comparison of these independent results, combined over half-hour periods, revealed close similarities between the records, and suggested that under the conditions of this study, the primary bias was one of horizontal distance, i.e., that those activities least visible to the observer were



those carried on the farthest away. Since the check results also imply that dispersion of individuals around the observer (whose aim was normally to retain visual contact with the maximum number of animals) was essentially random with regard to activity, the latitudinal results would appear to provide a reliable indication of overall activity. Certainly the substantial sample sizes recorded during those times of day commonly devoted to resting do not support as a valid generalization, at least for this forest, the frequent contention that it is those activities which entail little or no movement that are necessarily the most likely to escape the attention of the observer. Obviously, however, this is highly variable with conditions; a resting lemur high in a breadfruit tree is likely to be an invisible lemur.

#### PREPARATION OF THE FOREST

At the start of the study, the forest at Mavingoni was gridded by the marking of north-south and east-west lines spaced at 50-meter intervals. Where necessary, narrow paths were cleared along these lines. The original intention was to use this grid system in quantifying the utilization of different parts of their home range by *L. f. mayottensis* groups; but because of the heterogeneity of the forest, and for reasons of group structure, which will become obvious, this hope turned out to be impractical. The grid did, however, permit more accurate mapping of the study area than would otherwise have been possible, and enabled precise records to be made of the movements of lemurs through the forest.

#### THE SOCIAL UNIT

Although the popularity of the endeavor demonstrates the facility with which types of primate social unit may, rightly or wrongly, be categorized, the concept of the "group" eludes ready characterization. In most cases the observer in the field has no difficulty in recognizing "groups" of individual animals that tend to associate over longer or shorter periods of time, but since such association may vary substantially

#### CENSUSING

During the period of the study, a large number of groups of *L. f. mayottensis* was counted in various parts of the island (see table 3). The difficulties involved in establishing group identities are discussed later, but it is appropriate to mention here that we adhered to two rules to obtain group counts. First, we made no record of group size unless it was certain that all lemurs active or resting together at the time of censusing had been counted. Because of the difficulties of discriminating between the sexes, separate counts of the numbers of males and females in the group were not always possible; the increasing proportion of groups censused in this more detailed manner as the study progressed reflects the observer's developing ability to categorize the sexes. The establishment of both the number and the sex of group members often involved following an active group for some time, or, in the case of resting groups, waiting for activity to begin and concealed individuals to become visible. Second, each area of forest was visited only once, even if it was known to contain lemurs not censused. This was done in order to minimize double-counting, although it was realized that in the absence of recognizable individuals no safeguard against this could be infallible.

Where a reliable count of the number of individuals together at the time of censusing was not possible, no count was recorded. Although no record was kept of the number of groups seen but not successfully counted, my impression is that the ratio of groups located to groups censused was under 2:1.

in degree of exclusivity, in structure, in duration and in ecological role, it is difficult to propound any general definition of this term. Even more specific designations such as "social group," "foraging group," and "sleeping group" have their difficulties. It seems unnecessary to amplify here the discussions of these problems provided by Struhsaker (1969) and Richard (In press); these remarks are merely made as preamble to



the observation that, however liberally the term group is interpreted, it seems better, because of its general connotations of exclusivity, not to apply it to the aggregations of *L. f. mayottensis* seen in the field. Instead, I shall apply the term association to such aggregations.

On the basis of field studies of the red-fronted lemur, *Lemur fulvus rufus* (Sussman, 1972, 1975), and of the brown lemur, *Lemur fulvus fulvus* (Harrington, 1975), the Mayotte lemur had been expected to live in recognizable groups of at least relatively stable composition. It was rapidly realized, however, that although the animals studied at Mavingoni were highly gregarious, the associations observed were fluid and temporary. During the course of a single day, the numbers of individuals in the association under observation varied considerably, as animals left or joined those being followed. It was rare for a lone animal to leave or to join an association, although this may have occurred more often than I was aware of it; usually a number of individuals would arrive or depart together, or at least in succession. Such departing associations appeared generally to remain as separate units for some time, although occasionally they would break off from the association under observation and almost immediately join another; this was usually in response to vocalization by the latter. On different occasions associations passed close to one another without exchanging individuals, or even overtly noticing the passage of the other.

As a general rule, an association with a small number of individuals could expect to be augmented within a period of several hours; conversely, one with a high number could be expected to split during the course of the day. Association size was thus in a constant state of flux.

The number of individuals in associations followed at Mavingoni was not often below six or in excess of 16; the mean number was around nine or 10. Although it was never possible to identify individually all the lemurs inhabiting the study area, by the end of the fieldwork about half could be recognized under favorable conditions. Observation of identifiable animals did not suggest that there was a pronounced tendency for particular adults to associate consistently over

prolonged periods of time; whether or not this is so, however, will require intensive further investigation to discover.

If *L. f. mayottensis* resembles other members of its genus studied in this respect, it breeds seasonally, and infants are produced during a short and well-defined birth season. In *L. f. fulvus* of northwest Madagascar this takes place during October (Harrington, 1975); in the case of *L. f. mayottensis* one is restricted to drawing inferences from the stages of development of the young individuals observed, and then only if extrapolation is permissible from the data given for *L. f. rufus* by Sussman (In press a). According to Sussman, the infant *L. f. rufus* begins to leave its mother's back and move around independently at about the age of four weeks; complete independence from the mother in this respect (achievement of juvenile status) is, however, not reached until the age of 16 weeks. At about 11 or 12 weeks, the infant *L. f. rufus* still spends only about 30 percent of its time away from the mother.

Only during surveys made in other areas of Mayotte at the beginning of this study, and never at Mavingoni, did we observe infants riding on the mother's back. After January we did not see one instance of this. If, then, the end of January represents the end of the transition period from infant to juvenile status, the extrapolation from Sussman's figures is permissible, the birth season on Mayotte occurs around the beginning of October, and the infant-juveniles observed at the beginning of the study were aged around 14 to 16 weeks. By the end of the study, individuals in this category were approaching eight months and were sufficiently large to be mistaken, in conditions of poor visibility, for small adults. Individuals in the second sub-adult category, i.e., those born at the beginning of October 1973, were already of adult size, and under most conditions indistinguishable from the latter.

It should be noted that one group (MA88), censused at the beginning of May, contained, in addition to six adult-sized males and six adult-sized females, three very small immature individuals. These were all moving independently of their mothers at the time of censusing, but their size suggested an age of only *ca.* 12 weeks, at a



time when all other J1 juveniles we saw were approximately seven months old. This is the only evidence we observed of any lack of synchrony in the birth season.

In order to augment the information available on the range in size of associations of *L. f. mayottensis*, as well as to obtain distributional data, surveys were undertaken throughout Mayotte. During these surveys 102 associations were counted (table 3, fig. 15); in 32 cases association members were identified by sex.

Considerable variation in association size was revealed by the surveys; the smallest (MA68) numbered two (both males), whereas the largest (MA64) contained 29 individuals. This latter, located at approximately 0600 hrs., had, by 0630 hrs., broken up into three unequally-sized units. Mean association size was 9.1 individuals, the mode six (although in a non-normally distributed sample such as this, it is probably more useful to say that we saw associations of every size between six and 10 on at least 10 occasions).

In associations in which all adult or adult-sized individuals could be identified by sex, the sex ratio was almost exactly 1:1 (139 males to 135 females), a figure closely comparable with the exact 1:1 ratio given for *L. f. fulvus* by Harrington (1975), on the basis of a sample of two groups. More extensive sampling in southwest Madagascar of *L. f. rufus* by Sussman (1974, 1975) revealed a small preponderance of females (male:female ratio 1:1.22). It is interesting that the mean group size recorded by Sussman for *L. f. rufus* was 9.4 individuals, a figure very close to the mean size found in this study for associations of *L. f. mayottensis*.

Since, as time progressed, the identification of juveniles became less reliable, and because the accurate identification of adults by sex was not invariably possible, we did not consider it worthwhile to calculate juvenile/adult female ratios from the survey results, although limited data of this kind do exist from Mavingoni. At the end of April, by which time it had become apparent that the animals left the study area only infrequently (at least during the daytime), and when a fair degree of familiarity had been acquired with individual lemurs, the forest at Mavingoni was censused and yielded the following count: 38

individuals, of which 19 were adult-sized males, 16 were adult-sized females, one was a juvenile male, and two were juvenile females. At the time of censusing these animals were grouped into four associations, of which the compositions are given in table 4. The sex ratio of adult-sized individuals was 1.2 males to 1.0 females, and the overall sex ratio 1:1.1. A slight preponderance of males over females was thus found at Mavingoni, as in the overall census, but neither figure departs significantly from the 1:1 ratio. The ratio of juveniles to adult-sized females was 1:5.33.

Klein and Klein (1975) found *Ateles belzebuth* to associate in temporary "subgroups" which formed part of larger, apparently exclusive, "social networks." Similarly, Nishida (1968) proposed that independently associating chimpanzees nonetheless belong to discrete "regional populations." It is tempting to speculate that the fluid associations of *L. f. mayottensis* likewise correspond to subunits of larger and better-defined (i.e., exclusive) social groupings; but whether this is indeed the case or, if so, the size and spatial extent of such groupings, cannot be determined on the basis of available information. It was rare that an association being followed would leave the forest area shown in figure 5, except occasionally to forage in the semi-planted areas immediately adjacent to the village; conversely, animals that could definitely be established as unfamiliar were very infrequently observed within the study area. But we are not certain that no individuals were exchanged between the nucleus of animals inhabiting the study area and those from surrounding forests, although no known individual disappeared from the forest during the period of study.

Interactions observed between associations do not help to clarify the question. On one occasion (April 4), a resting association of seven individuals was joined, over a period of approximately 12 minutes, by the sequentially arriving members of another, until the resulting large association numbered 13. Shortly thereafter the augmented association began to travel; it was followed outside the study area, through some secondary vegetation on the southeastern outskirts of the village, and into a long-established patch of avocet marron forest on the slopes of a low hill. After



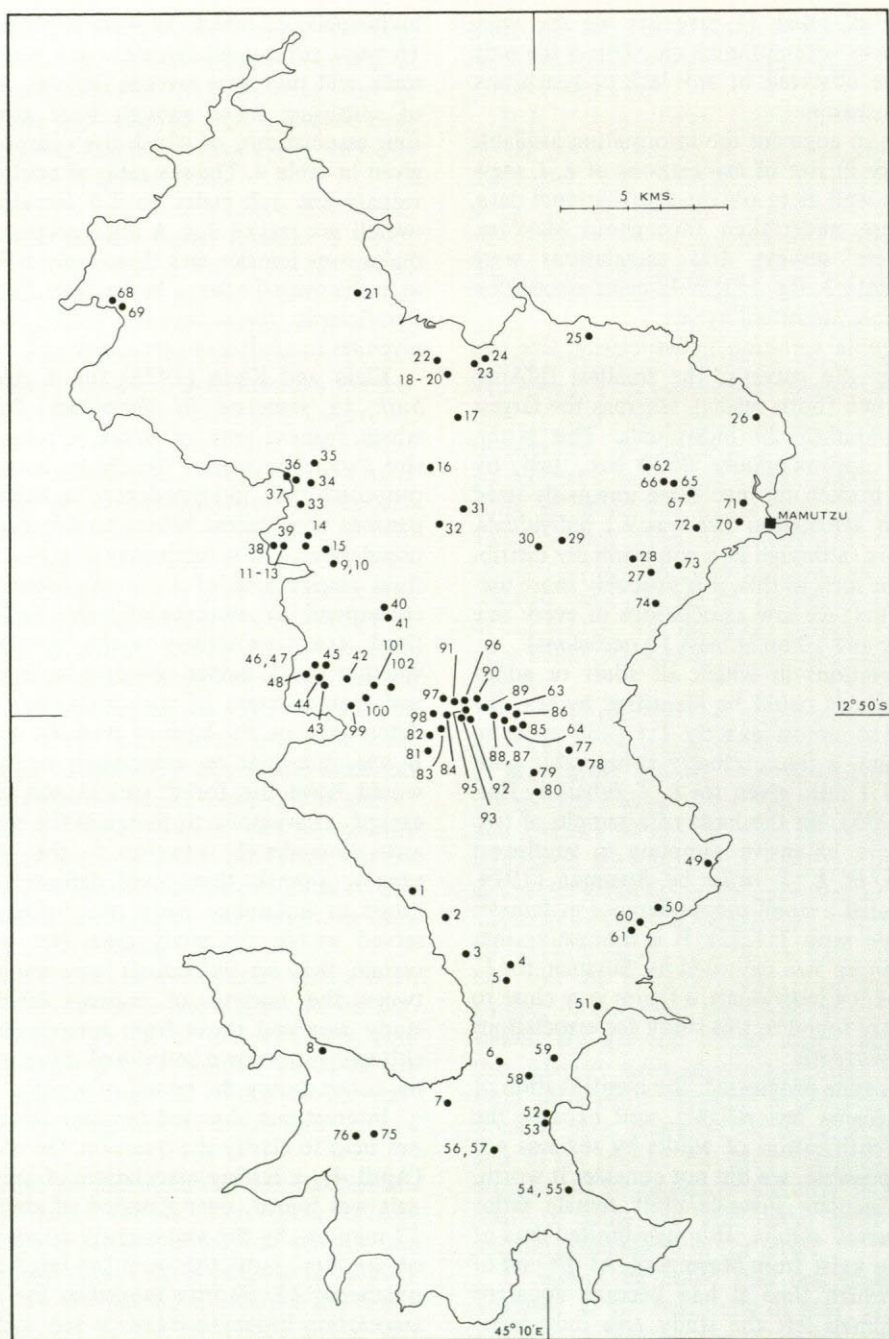


FIG. 15. Localities at which associations of *Lemur fulvus mayottensis* were censused. Numbers correspond to the association numbers given in table 3.



TABLE 3  
Census Results

Association number <sup>a</sup>	Location	Number of individuals	Notes
MA 1	M'Tsangatchei	12	—
MA 2	Magnassini	7	incl. 1 inf. on mother
MA 3	Kavani	7	—
MA 4	Miréréni I	7	incl. 1 inf. on mother
MA 5	Miréréni II	8	—
MA 6	Galidjou	6	—
MA 7	Tsimkoura	20	—
MA 8	Magiméouni	6	incl. 1 inf. on mother
MA 9	Karihani	13	incl. 2 juv.
MA 10	Karihani	16	incl. 3 juv.
MA 11	Chingoni	14	—
MA 12	Chingoni	14	—
MA 13	Chingoni	11	—
MA 14	Badajou	10	incl. 1 juv.
MA 15	Hamarabou	5	—
MA 16	Gounasaha	6	incl. 1 juv.
MA 17	Badamagi	9	—
MA 18	La Carrière	5	incl. 1 juv.
MA 19	La Carrière	6	—
MA 20	La Carrière	8	—
MA 21	Dzumogné	6	incl. 2 inf./juv. <sup>b</sup>
MA 22	Hanziwi	4	—
MA 23	Lakourou	10	—
MA 24	Gounalahé	6	—
MA 25	Kisambi	8	incl. 1 juv.
MA 26	Magikhavo I	6	—
MA 27	Mbolimadirou	10	—
MA 28	Karosidi	10	—
MA 29	Bouelandrouna	8	—
MA 30	Chofel	9	incl. 1 juv.
MA 31	Kamboni	8	incl. 1 juv.
MA 32	Ngounasaha	9	incl. 1 juv.
MA 33	Hamdallabouana	7	—
MA 34	Chirini	12	incl. 1 juv.
MA 35	Bandazia	12	incl. 1 juv.
MA 36	Maboungani	9	—
MA 37	Chirini	7	—
MA 38	Zidakani	6	incl. 1 juv.
MA 39	Zidakani	10	—
MA 40	Haoufoungou	6	—
MA 41	Haoufoungou	14	incl. 1 juv.
MA 42	Jitroni	12	—
MA 43	Mavadzanisohoa	17	incl. 1 juv.
MA 44	Roaka	8	—
MA 45	M'Roni Kélé	10	incl. 2 juv.
MA 46	Sohoa	9	incl. 2 juv.
MA 47	Bangashahé	4	—
MA 48	Adaboujou	6	—



TABLE 3 - (Continued)

Association number <sup>a</sup>	Location	Number of individuals	Notes
MA 49	Masimoni	3	2♂, 1♀
MA 50	Bouéni	5	3♂, 2♀
MA 51	Msatoundrou	4	2♂, 2♀
MA 52	Miambani	5	—
MA 53	Miambani	6	—
MA 54	M'Roni Andaza	4	—
MA 55	M'Roni Andaza	5	—
MA 56	Mgoubili	10	incl. 1 juv.
MA 57	Mgoubili	7	incl. 1 juv.
MA 58	Barakani	8	incl. 1 juv.
MA 59	Bambo Est	7	4♂, 3♀
MA 60	M'Ro Mouhou	11	—
MA 61	M'Ro Mouhou	6	—
MA 62	Namhako	10	—
MA 63	Bassan	10	—
MA 64	Bassan	29	—
MA 65	Namhako	20	incl. 1 juv.
MA 66	Namhako	5	3♂, 2♀
MA 67	Mrambouni	9	—
MA 68	Antsiraka Bora	2	2♂
MA 69	Antsiraka Bora	7	—
MA 70	Mahabou	5	2♂, 3♀
MA 71	Mariaz	8	5♂, 3♀
MA 72	Kavani	21	12♂, 9♀
MA 73	Doujani	3	1♂, 2♀
MA 74	Hanandji	9	5♂, 4♀
MA 75	Kani-Kélé	n.d.	—
MA 76	Kani-Kélé	n.d.	—
MA 77	Iloni	11	5♂, 6♀
MA 78	Iloni	6	2♂, 4♀
MA 79	Voundzé	6	2♂, 4♀
MA 80	Voundzé	13	7♂, 6♀
MA 81	Ouangani	7	—
MA 82	Poujourou	14	6♂, 8♀
MA 83	Poujourou	16	9♂, 7♀
MA 84	Ongojou	12	—
MA 85	Dembeney-Sada	7	2♂, 5♀
MA 86	Bassan	10	5♂, 5♀
MA 87	Bassan	12	—
MA 88	Bassan	15	6♂, 6♀, 3 juv.
MA 89	Hamshindra	11	7♂, 4♀
MA 90	Hafaki	8	4♂, 4♀
MA 91	Ongojou	7	3♂, 4♀
MA 92	Mabandran	8	4♂, 4♀
MA 93	Mabandran	10	4♂, 6♀
MA 94	Mabandran	8	4♂, 4♀
MA 95	Mabandran	5	2♂, 3♀
MA 96	La Renaissance	6	3♂, 3♀
MA 97	Ongojou	8	5♂, 3♀
MA 98	Savegnan	16	7♂, 9♀



TABLE 3 - (Continued)

Association number <sup>a</sup>	Location	Number of individuals	Notes
MA 99	Ourini	9	4♂, 5♀
MA 100	Ourini	13	—
MA 101	Ourini	9	—
MA 102	Ourini	9	4♂, 5♀

<sup>a</sup>Association numbers given here correspond to those used in figure 14.

<sup>b</sup>Probably twins; one was riding on its mother's back, while the other followed the same female very closely.

TABLE 4  
Compositions of Associations  
Censused at Mavingoni

Number of individuals	Males	Females
9	6	3
11	5	6
11	6	5
7	3	4
Totals 38	20	18

the animals had progressed some distance, they encountered another association composed of individuals unfamiliar to me and which had not been seen in the study area. The animals in the vanguard of each association, males and females alike, rushed toward and past each other; two males briefly fought. The lemurs, now spatially mixed, remained quiet for a moment; then a period of frenzied chasing and fighting ensued. Individuals of both sexes were involved in this activity, although males predominated. Not all individuals were involved in the excitement; some of each association remained on the periphery, calmly resting or grooming. A period of relative quiescence followed, during which some individuals moved around slightly, others groomed or rested, some males anogenitally

marked branches, and many individuals grunted softly. The sequence of frenzied activity followed by a lull was repeated, then the original association began to drift back down the hill, some of the departing individuals lagging behind to feed near the others, many of which, of both sexes, were energetically marking anogenitally. It was 18 minutes after the beginning of the encounter before the associations were clearly separated once more. Over the next 20 minutes or so the invaders gradually moved back to more familiar territory. It is probable that no individuals were exchanged between the associations, although it is impossible to be absolutely sure of this; certainly, no known individuals were lost from the original association.

This incident cannot, however, be used as the basis for any statement to the effect that the animals that habitually occupied the study area formed some kind of closed group. In particular, the encounter described differed only in scale from several incidents observed within the study area between associations which subsequently coalesced, and/or which contained identifiable individuals seen in association at other times. I was unable to determine under what circumstances the type of encounter behavior described here was elicited between associations composed of individuals who normally came together without event.

## DAY RANGES AND POPULATION DENSITY

For reasons stated in the preceding discussion, it will be apparent that "home range" is not a concept easily applicable to the ranging behavior

of the Mayotte lemur. As far as could be ascertained, the lemur population at Mavingoni remained stable throughout the study period; as



noted, associations were only very infrequently observed to leave the area of forest delimited in figure 5, and no known individual is recorded to have left this area definitively. On the other hand, all recognizable individuals were seen at one time or another in all areas of the study forest. It is clear that the forest (and hence the distribution of resources within it) was well known to all the lemurs exploiting it; travel between distant feeding sites was almost invariably rapid, direct, and purposeful.

In any event, in the absence of stable identifiable groupings it is clearly more useful to speak of population density than of home range. As noted, the census of the Mavingoni forest yielded a count of 38 individuals in an area variably calculable as from 3.2 to 4.4 ha. in extent (mean: 3.8 ha.). Population density in this forest is thus approximately 10 individuals/hectare (1000/km<sup>2</sup>). This compares closely with the densities of *L. f. rufus* observed by Sussman (1975) at Tongobato (900/km<sup>2</sup>) and Antserananomby (1200/km<sup>2</sup>) in southwestern Madagascar, although *L. fulvus* in Mayotte apparently ranged over a considerably larger area (average home range of *L. f. rufus* at Tongobato was 1.0 ha., and at Antserananomby, 0.75 ha.). This latter difference may well be due to the greater dietary specialization recorded for *L. f. rufus* (see next section).

Daily ranging patterns are difficult to assess in the absence of stable identifiable groups. On one day each month, however, the progress of the "center of gravity" of the association being followed was mapped throughout the day. Where an association divided while under observation, the larger number of animals was followed. Obviously, the distances covered by individuals lemurs were considerably greater than those shown in figure 16, which charts the movements made by the approximate centers of dispersion of the associations followed.

The greatest daily travel distance recorded (in February), was approximately 1150 m.; the least (in May), approximately 450 m. The mean of the four observations was around 800 m.; if anything, this figure is probably on the low side. The strikingly short travel distance recorded in May fairly accurately reflects the rather atypical patterns (relative to February-April) of association movement seen in that month, at a time when the exploitation of fruit dropped quite abruptly with the waning of the rainy season and the apparent fall in abundance of this resource. During this month, the peripheral regions of the forest, with their secondary regrowth, often of domesticated species, were much more frequently visited.

Even the shortest distance recorded, however, contrasts strongly with the average of 135 m. to 150 m. daily travel recorded for *L. f. rufus* in Madagascar. Long travel distances were noted by Sussman only in the cases of unhabituated groups which were fleeing from the observer. Again, this divergence between the two subspecies is most plausibly attributed to the differences observed in their strategies of exploitation of the forest resources.

Data were also collected on the amounts of time spent in the various activities in the contrasting forest types, but for a variety of reasons it is likely that they are too greatly subject to bias to justify analysis. Overall, approximately 47 percent of time was spent in mixed mango forest, 43 percent in avocet marron forest, and 10 percent in mango forest; but quite considerable monthly variation was recorded. As noted, however, it is probable that these figures are somewhat biased, and it seems preferable to wait until better data are available before any detailed attempt is made to analyze patterns of dispersion of the lemurs in relation to the distribution of forest resources.

## DIET AND FEEDING BEHAVIOR

Feeding in *L. f. mayottensis* is normally a highly visible activity, and the data presented here on the proportions of time spent feeding on the various food sources are probably the least

subject to bias of all the data obtained. Only in the cases of a very few plant species, in particular the breadfruit (*Artocarpus incisa*), were the conditions of visibility during feeding such as greatly



TABLE 5  
Percentage of Feeding Time Spent in Exploiting Different Plant Species/Parts<sup>a</sup>

Species/part	Percentage of time	Species/part	Percentage of time
1. <i>Saba comorensis</i> (FR)	22.2	26. <i>Saba comorensis</i> (FL)	0.1
2. <i>Adenanthera pavonina</i> (FR)	20.3	27. <i>Annona squamosa</i> (FL)	0.1
3. <i>Litsea tersa</i> (FR)	18.7	28. indet. (Tsangitsangé) (L)	0.1
4. <i>Entada africana</i> (L)	5.2	29. <i>Ancyclobothrys petersiana</i> (L)	0.1
5. <i>Terminalia catappa</i> (L)	4.8	30. <i>Coffea canephora</i> (FR)	0.1
6. <i>Mangifera indica</i> (L)	4.2	31. <i>Leea guineensis</i> (FR)	0.1
7. <i>Saba comorensis</i> (L)	3.9	32. <i>Dioscorea</i> sp. (Bahibahi) (L)	0.1
8. <i>Entada gigas</i> (L)	2.5	33. indet. (Maloravi) (FL)	0.1
9. <i>Adenanthera pavonina</i> (L)	2.4	34. <i>Leucaena glauca</i> (L)	0.1
10. <i>Albizzia lebbbeck</i> (FL)	2.0	35. <i>Litsea tersa</i> (L)	0.1
11. <i>Ficus</i> cf. <i>racemosa</i> (FR)	1.8	36. <i>Artocarpus integrifolia</i> (L)	0.1
12. <i>Artocarpus incisa</i> (FR)	1.8	37. indet. (Barabahi) (L)	0.05
13. <i>Terminalia catappa</i> (FR)	1.5	38. <i>Polysphaeria</i> aff. <i>parvifolia</i> (L)	0.05
14. <i>Litsea tersa</i> (FL)	1.2	39. <i>Ancyclobothrys petersiana</i> (FR)	0.05
15. <i>Mucuna pruriens</i> (FL)	1.0	40. indet. (Maloravi) (L)	0.05
16. <i>Albizzia lebbbeck</i> (L)	0.9	41. indet. (Koureyatsoumbi) (FR)	0.05
17. <i>Ceiba pentandra</i> (FL)	0.8	42. <i>Adenanthera pavonina</i> (FL)	0.05
18. <i>Ceiba pentandra</i> (L)	0.7	43. <i>Mangifera indica</i> (FR)	0.02
19. <i>Spondias dulcis</i> (L)	0.7	44. <i>Dioscorea</i> sp. (Mavoundro) (L)	0.02
20. <i>Annona squamosa</i> (L)	0.4	45. indet. (Tsarintsoa) (L)	0.02
21. <i>Pterocarpus indicus</i> (L)	0.3	46. <i>Solanum nigrum</i> (L)	0.02
22. <i>Ficus</i> sp. (Mouriyé) (L)	0.3	47. indet. (Mouhamba) (FR)	0.02
23. <i>Ficus</i> cf. <i>racemosa</i> (L)	0.3	48. indet. (Maloravi) (FR)	0.02
24. <i>Erythrina</i> sp. (FR)	0.2	OTHER	0.30
25. <i>Albizzia lebbbeck</i>	0.2		

<sup>a</sup>FR = fruit; FL = flowers; L = leaves.

to limit the accuracy of the data recorded. Such cases, however, represent only a minor proportion of the total time spent feeding.

The latitudinal method of data collecting made it impractical to distinguish between feeding (when the individual was actually chewing) and foraging (hand or nose in contact with the food source). Nor was it possible to distinguish a more subtle aspect of foraging, i.e., when the individual was scanning the tree for further sources of food; such activity was subsumed under the category of "resting." It seems clear, however, that there is a close relationship between the amounts of time spent feeding and foraging (in the restricted sense), and that the lumping together of the two is unlikely to introduce any significant distortion into the information collected. Certainly, except in the occasional special case relating to houbouhoubou fruit (see below),

the lapse of time between the individual's making contact with the food source and its consuming (or rejecting) it was minimal. Movements by individuals between one food source and another during a feeding bout were classified as "moving" rather than as "foraging."

The plant species listed in table 5 provided virtually all the food consumed by the lemurs during the study; "other" resources accounted for only 0.3 percent of time spent feeding. "Percentage of feeding time" as used here is based on a total of 4391 feeding observations.

Over the period of the study *L. f. mayottensis* was observed to exploit more than 48 different food resources, involving the leaves, flowers, and fruit of at least 32 plant species (table 5). Of these resources, however, as many as 29 each accounted for less than 0.5 percent of time spent feeding, to a total of only 3.7 percent; clearly



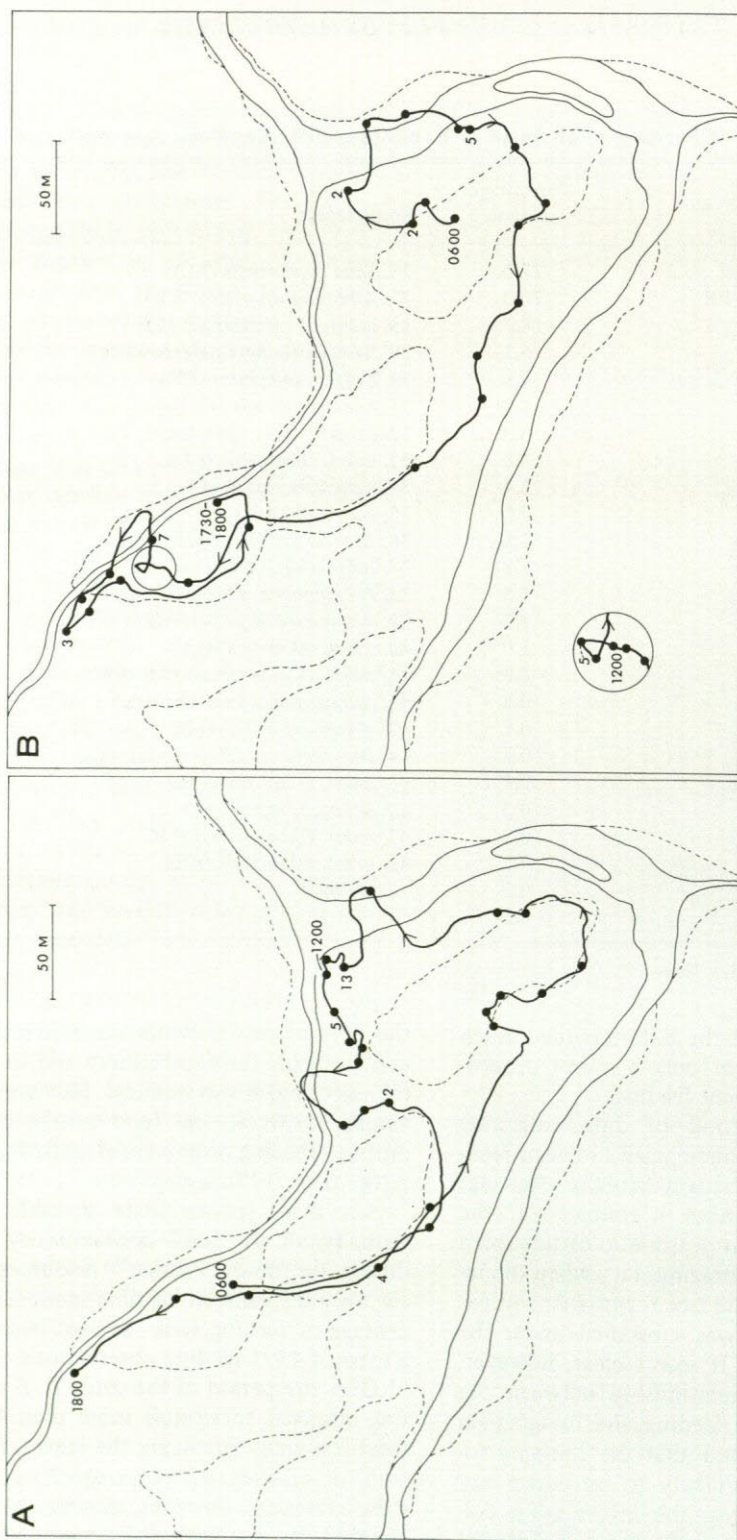
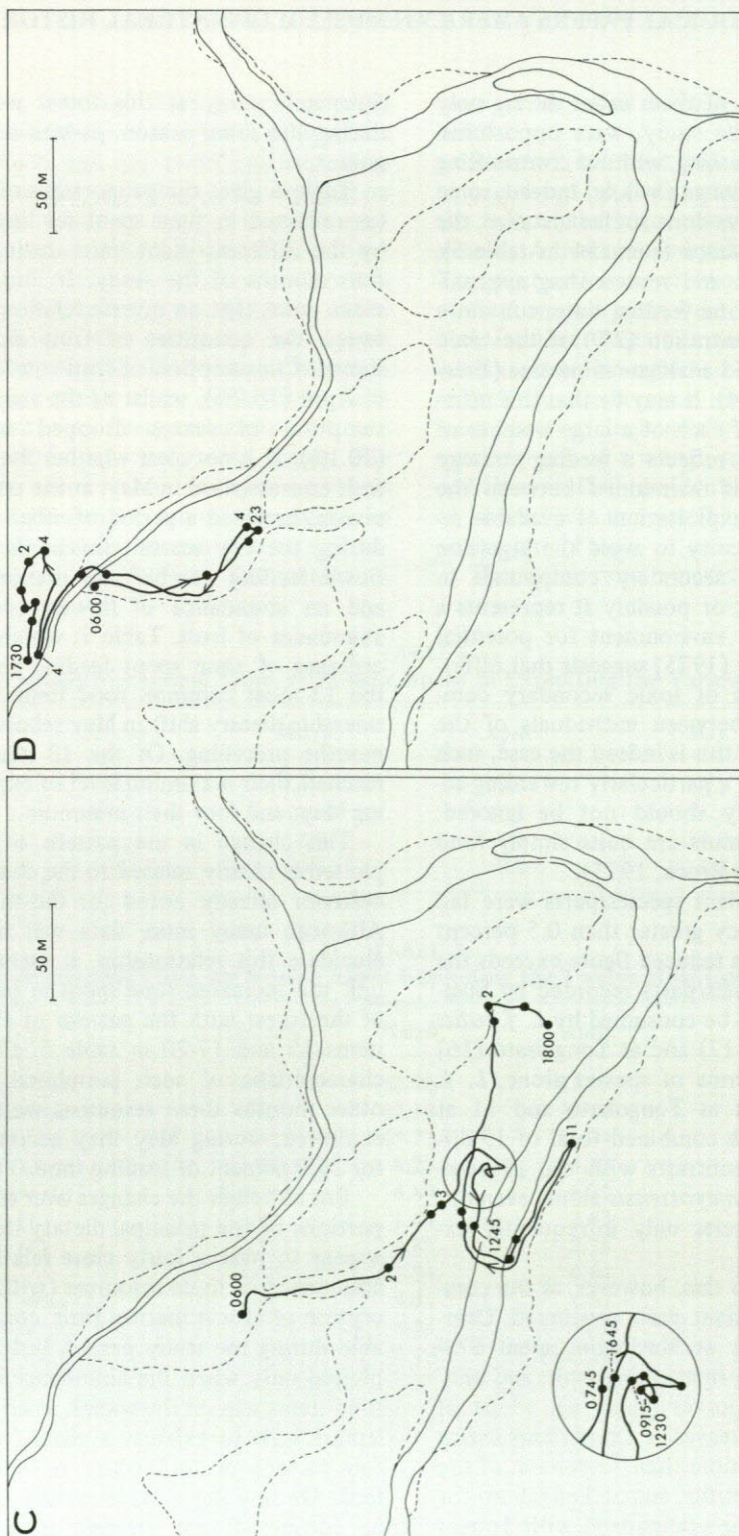


FIG. 16 A, B. Day ranges of the associations followed (A) on February 24, 1975 (total travel over 12 hours ca. 1150 m.), and (B) on March 14, 1975 (travel over 12 hours ca. 900 m.). Arrows show direction of travel; solid circles represent locations of associations at 15-minute intervals. Figures next to circles (apart from those showing the hour) represent the number of sampling intervals at which the association was recorded to be in that location.







such resources, many of them eaten during only a single month of the study, were opportunistically exploited in passing, without contributing significantly to the diet as a whole. Indeed, some of them could not have done so; for instance, the leaves of *Leucaena glauca* (item 34 in table 5), eaten only in March and representing approximately 0.1 percent total feeding time, contain a relatively high concentration (2%) of the toxic uncommon amino acid analogue mimosine (Free-land and Janzen, 1974). It may be that this infrequent exploitation of each of a large number of different food items reflects a feeding strategy whereby a balance is maintained between the maximally efficient exploitation of available resources, and the necessity to avoid the ingestion of potentially toxic secondary compounds in dangerous quantities; or possibly it represents a "monitoring" of the environment for potential food sources. Glander (1975) suggests that differences in the content of toxic secondary compounds may differ between individuals of the same plant species; if this is indeed the case, such monitoring would be a particularly rewarding activity. The possibility should not be ignored, however, that the lemurs are quite simply fond of variety (cf. Clutton-Brock, 1975).

Nonetheless, 19 plant species/parts were fed upon with a frequency greater than 0.5 percent of time, and even this reduced figure exceeds the total number of species/parts recorded by Sussman (1972, 1975) to be consumed by *L. f. rufus* at Antserananomby (17) and at Tongobato (16) in Madagascar. In terms of species alone, *L. f. rufus* exploited eight at Tongobato and 11 at Antserananomby, to a combined total of 13 different species; this contrasts with the 13 commonly eaten by *L. f. mayottensis* alone, even disregarding the 19 species only infrequently exploited.

More striking than this, however, is the comparison in terms of plant parts consumed. Overall, *L. f. mayottensis* at Mavingoni spent 67.4 percent of its feeding time eating fruit, and only 27.3 percent eating leaves (table 6); whilst at Antserananomby the leaves of *Tamarindus indica* alone accounted for more than 75 percent of the feeding time of *L. f. rufus*, and at Tongobato for about 50 percent. The comparison with Tongobato appears the more appropriate here, since

Sussman's study at this forest was undertaken during the rainy season, as was mine at Mavingoni.

Table 6 gives the proportions of the total diet (as reflected in time spent feeding) contributed by the different plant parts during each of the four months of the study. It illustrates the obvious point that an inverse relationship exists between the quantities of fruit and leaves consumed. Consumption of fruit rose to a maximum in April (78.7%), whilst in the same month consumption of leaves dropped to its lowest (20.1%). It is not clear whether the sharp drop in fruit consumption in May, at the end of the rainy season, heralded a period of reliance upon leaves during the dry season; for in the same month flower-feeding reached its maximum (14.2%), and an abundance of flowers presages a later abundance of fruit. Table 7, which gives the percentages of time spent feeding each month on the 12 most common food items, shows a considerable dietary shift in May relative to the three months preceding. Of the 12 items listed, five reached their maximum level of exploitation during May, and four their minimum.

This change in the pattern of resources exploited is clearly related to the change in ranging behavior already noted for the month of May. Although many more data will be required to elucidate this relationship, it seems plausible to link the increased time spent in peripheral areas of the forest with the pattern of exploitation of items 15 and 17-20 in table 5, all of which are characteristic of such peripheral areas. During other months these resources were virtually unexploited; during May they accounted together for 26.0 percent of feeding time.

But although the changes over time in the proportions of the principal dietary items consumed appear to bear a fairly close relationship to the abundance of these resources (with the major exception of avocet marron fruit, consistently available during the study period, but maximally exploited only when the abundance of other major food items was on the wane), at no time were the lemurs seen to exhaust a given food source before moving on to another, or before ceasing to feed. On any day a wide variety of foods might be consumed, but changes from one item to another never appeared to be dictated by neces-



sity. Moreover, although during most feeding bouts all the animals in view were exploiting the same resource, it was not at all uncommon to find members of the same association feeding on several different foods at the same sampling interval. For instance, of the nine individuals visible at 0620 hrs. on April 15, three were eating *Adenanthera pavonina* fruit; two *Mangifera indica* leaves, three, *Litsea tersa* fruit; and one, a *Saba comorensis* fruit. And at 0815 hrs. on March 1, of 13 individuals visible three were eating *Saba comorensis* fruit; one, *Leea guineensis* fruit; and a fifth, *Ancyclobothrys petersiana* leaves. The remaining eight were resting. On such occasions the vertical dispersion of individuals might be considerable; thus at the time of the second example just quoted, members of the association

were to be found in each of forest levels, 2, 3, and 4.

Sussman recorded the consumption of both bark and sap by *L. f. rufus*, with a frequency in the case of the latter resource of 0.3 percent of time at Antserananomby and of 0.6 percent at Tongobato. On one or two occasions individuals of *L. f. mayottensis* were observed to chew on bark or dead twigs, but such instances were too infrequent to be reflected as separate entries in table 5. On one occasion several *L. f. mayottensis* were observed sequentially to approach a point on the trunk of a mango tree and to scrape and/or lick at it. Definite identification of this source of interest was not possible, but it was probably an exudate of sap.

The water requirements of *L. f. mayottensis*

TABLE 6  
Percentage of Feeding Time, by Month, Spent in Exploiting the Various Plant Parts

Part	February	March	April	May	Overall
Fruit	55.3	66.1	78.7	48.2	67.4
Leaves	38.3	28.0	20.1	36.1	27.3
Flowers	5.9	5.8	1.2	14.2	5.0
Other	0.5	0.1	0.0	1.5	0.3

TABLE 7  
Percentage of Feeding Time, by Month, Spent Exploiting the Twelve Most Common Food Items

Species/part <sup>a</sup>	February	March	April	May	Overall
<i>Saba comorensis</i> (FR)	37.94	32.70	12.99	1.55	22.23
<i>Adenanthera pavonina</i> (FR)	0.18	12.18	39.10	7.57	20.34
<i>Litsea tersa</i> (FR)	9.04	15.71	21.74	29.13	18.72
<i>Entada africana</i> (L)	1.77	6.27	4.13	9.32	5.24
<i>Terminalia catappa</i> (L)	0.00	4.69	5.21	8.74	4.76
<i>Mangifera indica</i> (L)	11.70	1.64	3.83	5.44	4.21
<i>Saba comorensis</i> (L)	9.75	4.81	2.28	0.19	3.94
<i>Entada gigas</i> (L)	5.67	3.96	0.66	0.00	2.46
<i>Adenanthera pavonina</i> (L)	2.84	4.45	1.02	0.00	2.41
<i>Albizia lebeck</i> (FL)	4.79	2.74	1.02	0.00	2.03
<i>Ficus</i> cf. <i>racemosa</i> (FR)	0.00	2.56	2.10	0.78	1.84
<i>Artocarpus incisa</i> (FR)	1.42	0.67	1.68	5.83	1.75
TOTAL	85.11	92.39	95.75	68.54	89.93
TOP 3	47.16	60.59	73.89	38.25	61.29
TOP 6	60.63	73.19	87.00	61.75	75.50

<sup>a</sup>FR = fruit; FL = flowers; L = leaves.



are apparently largely satisfied by the water content of the fruit and leaves ingested. On occasion individuals were seen to lap water from natural reservoirs in the trees (particularly in the crowns of coconut palms, where water collects at the base of the fronds). Very rarely, and at only one location, lemurs were observed to lap water directly from a small pool on the ground.

### FEEDING TECHNIQUES

The great variety of postures adopted by the Mayotte lemur during feeding permitted the exploitation of food resources in all parts of the forest. Although they clearly preferred to use the larger horizontal branches (see section on habitat utilization), the lemurs would, for example, quite blithely suspend themselves from clusters of fine terminal branches by both hindlimbs, or even by only one, when the occasion demanded it. No potential source of sustenance was thus beyond their reach, although of course the amounts of effort required to obtain different types of resource varied widely.

Similarly, the lemurs exhibited an impressive variety in feeding technique. Leaves were usually cropped directly from a branch pulled by hand to within reach of the mouth, as were many fruit (fig. 17A). In the case of the mango tree (*Mangifera indica*) only new leaves were selected, whereas the leaves of other plant species appeared to be eaten irrespective of their stage of maturity. Normally leaf blades were consumed; the leaves of the badamier, *Terminalia catappa*, however, represented a special case. The large leaf (up to 30 cm. + long) was not itself eaten; only its petiole (stem) was. A lemur would take a leaf in its fist (fig. 17B), and, using its premolar teeth, scissor the petiole flush with the branch. Then, still holding the liberated leaf in its hand, it would chew on the petiole until nothing was left, whereupon the leaf would be dropped and another selected for similar treatment. The badamier leaf is tough and leathery and, at least to the human eye, exceedingly unattractive as an item of food; the same, however, applies to its petiole. It may be that the leaf blade contains noxious secondary compounds, whereas its petiole, potentially a source of a wide variety of nutrients and trace elements, does not. I know of

no nutrient analysis of this food item, but its content is likely to vary according to the season, and it will be interesting to see whether it is exploited in this fashion year-round, or only seasonally.

Flowers were generally licked, rather than consumed whole, and were thus presumably exploited for their nectar (and pollen?) content. Sussman and Tattersall (In press) and Sussman (In press b) discuss the possible significance of nectar feeding in the closely related *Lemur mongoz*. In Madagascar, the flowers of the kapok tree, *Ceiba pentandra*, were extensively exploited for their nectar content by this species. *C. pentandra* occurred at Mavingoni, and began floral budding at the beginning of May, when its exploitation by *L. f. mayottensis* commenced. As in the case of the toxic-seeded *Mucuna pruriens*, however, the lemurs generally consumed the kapok buds whole, before they blossomed; this destructive bud-feeding may have eliminated much of what might later have become a substantial source of sustenance.

Fruits were usually consumed *in situ*; as noted, they were normally pulled by hand toward the mouth and cropped with the teeth. When the lemurs were feeding on the long immature green pods of *Adenanthera pavonina* (fig. 17C), the pod was grasped in the fist while the seeds, serially arranged along the pod, were bitten out. The white husk of each seed was rejected, and the green inner portion was consumed. When most or all the seeds in the pod had been eaten, the remnants of the fruit, usually still hanging on the tree, were abandoned.

The large (up to 8 cm. in diameter), round fruit of the houbouhoubou vine (*Saba comorensis*) was treated in a rather different manner. The premolar teeth were used to scissor the tough short stem connecting the fruit to the vine; the fruit was held in one or, more commonly, two hands (fig. 17D); a hole was made in the outer husk; and the contents were excavated with the procumbent lower incisors. Very often an individual, having detached a fruit, would retreat before commencing to feed to a larger branch providing a more stable base for squatting on the hind limbs.

It was only in the consumption of houbouhoubou fruit that foodsharing was observed in *L.*

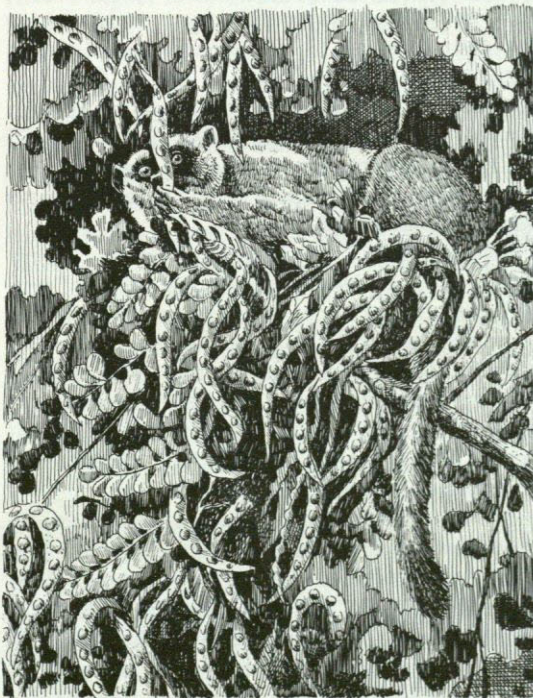




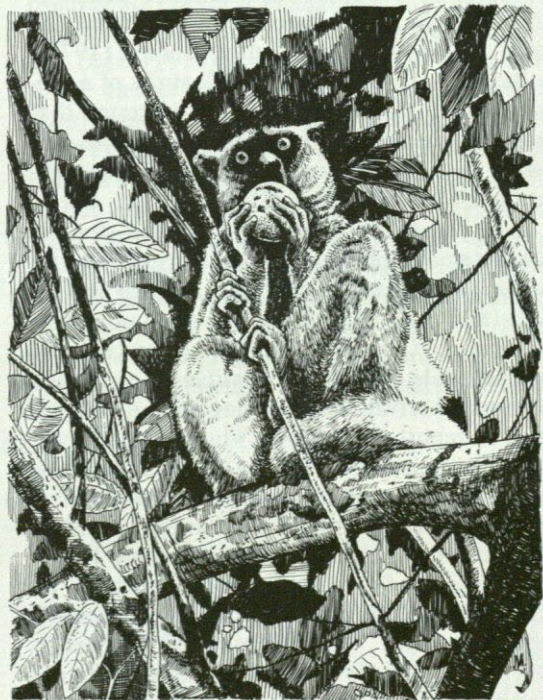
A



B



C



D

FIG. 17. Typical feeding postures of *L. f. mayottensis* when exploiting: (A) *Litsea tersa* fruit. (B) *Terminalia catappa* leaf petioles. (C) *Adenanthera pavonina* fruit. (D) *Saba comorensis* fruit. All drawings made directly from color transparencies.



*f. mayottensis*. Cases were, of course, noted of two or more individuals simultaneously exploiting the same large resource *in situ* in the same tree; not infrequently several individuals might feed together on the same large breadfruit (*Artocarpus incisa*), or on the same cluster of *Adenanthera pavonina* pods. But only in the case of hou-

bouhoubou fruit were individuals in definite proprietorship of a food item (in the sense that the individual had detached the fruit from the vine and retired to eat it elsewhere) seen to share it with other individuals. Such sharing is further discussed under the rubric of social behavior.

## PATTERNS OF ACTIVITY

*Lemur fulvus* has generally been regarded as diurnal in its activity rhythm, and there is of course no question that this lemur is active during the day. Recent observations have, however, begun to cast doubt on the strict diurnality of its activity pattern. Thus, although Sussman (1972) observed a distinct commencement of activity by *L. f. rufus* at around 0600 hrs., and the selection of sleeping sites some time after nightfall, he nonetheless noted that "it is possible that *L. f. rufus* is active with some regularity during the night" (p. 161). More recently, Conley (1975), on the basis of a round-the-clock study of a captive group of *L. f. albifrons*, has suggested that "it may be reasonable to assume that some subspecies of *L. fulvus* are regularly active throughout the 24 hours of the day" (p. 715).

A very real limitation of the present study is that systematic observation was carried out only during the hours of daylight (approximately 0600-1800 hrs.), for there can be no doubt whatever that *L. f. mayottensis* was active on a 24-hour schedule. It was not feasible to undertake nocturnal observations at Mavingoni, but villagers asked to report the times at which lemur vocalizations were heard during the hours of darkness provided a composite picture of vocalization at irregular intervals throughout the night. Lemurs occupying the vicinity of Coconi, where I lived during the study, were frequently seen to be active—feeding, moving, traveling and so forth—during the night. The difficulty of the terrain prevented my following these animals for extended periods, but it was evident that peaks of activity, interspersed with resting, occurred throughout the hours of darkness.

*Lemur fulvus mayottensis* was commonly active both when located at dawn and when left at

nightfall. Indeed, the highest activity levels recorded occurred in the first half-hour (0600-0625) and the last hour (1700-1800) of observation. This corresponds closely to Conley's findings on his captive *L. f. albifrons*; and the rather high proportion of resting observed during the remainder of the day may be related to the existence of substantial levels of nocturnal activity. It seems quite possible that *L. f. mayottensis* is more active during the night than is *L. f. rufus*, since the latter is apparently more active during the day. Sussman (1972) recorded an activity: rest ratio during the day of 50:50 (1.00) at Tongobato (this figure may be artificially high due to habituation difficulties), and of 44:56 (0.79) at Antserananomby; in the case of *L. f. mayottensis* at Mavingoni, the equivalent ratio was a low 34:66 (0.52).

The category "rest" is not, however, a very precise one. An individual was recorded as "resting" when it was not engaged in any activity. Discriminating brief pauses between activities from prolonged periods of inactivity was possible only by hindsight, and it was thus impractical to attempt to make the distinction during data collection. The "quality" of "resting" observations is hence not necessarily uniform.

A somewhat similar problem arose in discriminating between "movement" and "travel." The former term refers to changes in position made in conjunction with individual activities: feeding, grooming, and so forth; the latter to those displacements involving the position of the association as a whole. However, individual lemurs were extremely active, for instance, during feeding; and movements of individuals in search of food might cumulatively result in an appreciable movement of the association as a whole. Since



such movements were categorized as "moving to feed," rather than as "travel," movement was thus presumably emphasized at the expense of travel.

Table 8 summarizes the proportions of total time devoted to the various activities by *L. f. mayottensis*, and compares them to equivalent figures for *L. f. rufus* at two sites in Madagascar. In view of the difficulties of habituation experienced by Sussman (1974) at Tongobato, the more appropriate comparison appears to be between Mavingoni and Antserananomby.

Perhaps the most striking subspecific (or population) difference resides in the proportion of total time devoted to feeding: 11.7 percent in the case of *L. f. mayottensis*, compared with 32.7 percent for *L. f. rufus*. It is as well to note, however, that two potential sources of bias exist in the comparison. First, as noted, it is possible that the greater proportion of time devoted by *L. f. mayottensis* to resting during the day may reflect a higher level of nocturnal activity, including feeding. If this is so, the proportion of total feeding recorded for *L. f. rufus* may not be greater than that recorded for *L. f. mayottensis*.

Second, feeding on leaves is a much more sedentary occupation than is feeding on fruit. A result of this may be that small foraging movements made by *L. f. rufus* during feeding may have been reported as "feeding," rather than as "movement" as were equivalent but larger shifts in *L. f. mayottensis*. There is, unfortunately, no way of determining from available evidence how important (or otherwise) either potential source of bias is.

These reservations notwithstanding, it is clear that substantial subspecific differences do exist in the proportions of time devoted to the various activities. These differences are most reasonably ascribed, at least in part, to the different dietary preferences already noted. At Antserananomby, *L. f. rufus* spent more than 75 percent of its feeding time exploiting the leaves of a single plant species which was, moreover, the dominant tree of the forest. The Mayotte lemur, on the other hand, exploited a greater range of resources, mostly fruit, which were more widely scattered not only within the forest (affecting travel), but also within the individual tree (affecting movement). It may well be, then, that the greater propensity of *L. f. mayottensis* to move is largely a reflection of the distribution of its preferred food sources. Similar correlations between diet and mobility have been observed among related species of colobine monkeys: Feagle (In press), for instance, found that the primarily frugivorous *Presbytis melalophos* is more mobile than the folivorous *P. obscura*, whilst Struhsaker and Oates (1975) suggested that "the more diversified diet of badius [*Colobus badius tephrosceles*] may require that species to feed and move more than guereza [*Colobus guereza occidentalis*], with its more monotonous diet" (p. 112).

But although the difference in ranging patterns (as reflected in distance traveled daily, in size of habitual range, and in the percentages of time spent moving and traveling) between the red-fronted and Mayotte lemurs bears a fairly obvious relationship to the distributions of the food resources exploited by each, the relationship be-

TABLE 8  
Percentage of Time Devoted to Each Activity by *Lemur fulvus mayottensis*,  
Compared with *Lemur fulvus rufus*<sup>a</sup> at Two Sites in Madagascar

Activity	<i>Lemur fulvus mayottensis</i>	<i>Lemur fulvus rufus</i>	
	Mavingoni	Antserananomby	Tongobato
Resting	65.73	51.79	49.55
Moving	12.78	3.15	7.60
Feeding	11.69	32.72	19.03
Traveling	4.75	2.44	10.26
Grooming	4.30	5.03	10.91
Other	0.75	4.87	2.66

<sup>a</sup>Calculated from data provided by Sussman (1972).



tween diet and time spent feeding is less clear. Without knowledge of the nutritive content of the various food items, of the relation between time spent and quantity ingested, and of the efficiency of digestion and energetic expenditures by each subspecies, it is impossible to specify a precise relation between overall feeding activity and the satisfaction of nutritional, digestive, or energetic requirements. In general, leaf-eaters are considered to be less active and to feed less than frugivores. The data at present available on *Lemur fulvus* appear at least partly to contradict this as a generalization; but until the question of possible subspecific differences in nocturnal activity levels is resolved, we cannot be certain.

#### DAILY ACTIVITY CYCLE

To provide a general picture of the pattern of activity throughout the day, the five-minute samples were combined into 24 half-hour periods (0600-0625, 0630-0655 . . . 0730-0800 hrs.). Figure 18 shows the mean percentages of time devoted to each activity (except "other," which accounted for only 0.75 percent of total time) during each half-hour period over the duration of the study.

Although the presentation of mean frequencies permits the appreciation of general regularities in activity, it should be borne in mind that two major variables affect such frequencies. First, there are variations in the timing of activities from one day to the next: differences in schedule. Second, there is the inevitable lack of coordination in association activity: not all individuals do the same thing at the same time. In a simple attempt to disentangle these variables, the latitudinally time-sampled data were converted to the basis of "predominant group activity," in which the entire association is in effect treated as a single individual: at each sampling interval the association is recorded as engaging in that activity occupying the majority of individuals. When these data are consolidated into half-hour periods, frequencies are as shown in figure 19.

A glance is sufficient to reveal that frequencies shown in figures 18 and 19 are exceedingly similar. If there is a discernible pattern, it is for the frequencies based on predominant group activity to accentuate both the peaks and the

troughs on the histogram, but only very slightly. The greatest difference lies in the relatively low frequencies of grooming shown in figure 19; but these merely reflect the fact that grooming, although not an uncommon activity, is rarely one that occupies a majority of individuals visible at any one time. The major implication of the comparison, then, is that although certain general tendencies are apparent, considerable variation exists from one day to the next in activity schedules.

Over most of the study period such differences apparently reflected essentially random variations in daily activity, rather than a consistent shift in activity pattern over time: individual monthly patterns were generally rather similar. Figure 20 gives the half-hourly frequencies of resting (and by extension, of course, of all other activities combined) for each month of the study. Only in May, with a considerable increase in resting during the first two-thirds of the day, is there any notable change from the overall pattern shown in figure 18. As we have seen, May was an unusual month in other respects also, but whether this difference presaged a change in activity pattern during the dry season, only further observation will tell.

Since this study was undertaken during the wettest period of the year, it is worth noting that the Mayotte lemur appeared to be largely impervious to rain. Even heavy rain did not bring activity to a halt; activities in all six categories were observed during torrential downpours. Indeed, precipitation tended, if anything, to trigger activity: rain starting toward the end of a major rest period, or during a minor one, often provoked sustained activity. On the other hand, if rain started in the middle of a major rest period, activity might be stimulated but would last no more than a few minutes, after which the lemurs would resume resting. Given that rain has this effect, it will be interesting, when data are available, to see whether or not *L. f. mayottensis* tends toward a greater regularity in recorded daily schedule during the dry season.

Despite such daily variations, one may in general terms speak of a "typical" day, characterized by early morning and late afternoon activity peaks, with a prolonged rest period between about 1100 and 1300-1400 hrs. Between



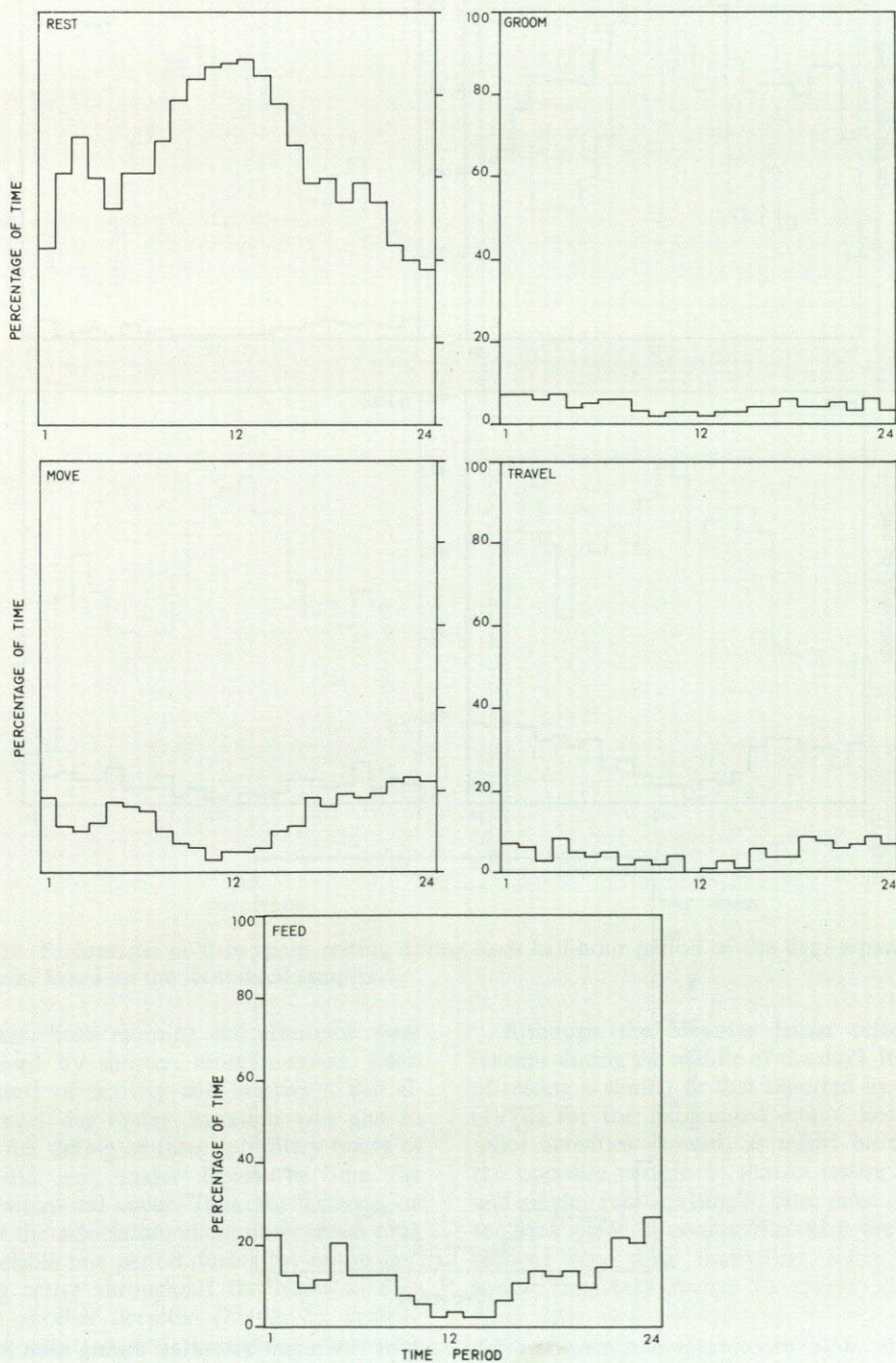


FIG. 18. Mean percentages of time devoted to each of the major activities, during each half-hour period of the day, over the duration of the study. Based directly on the latitudinal samples.



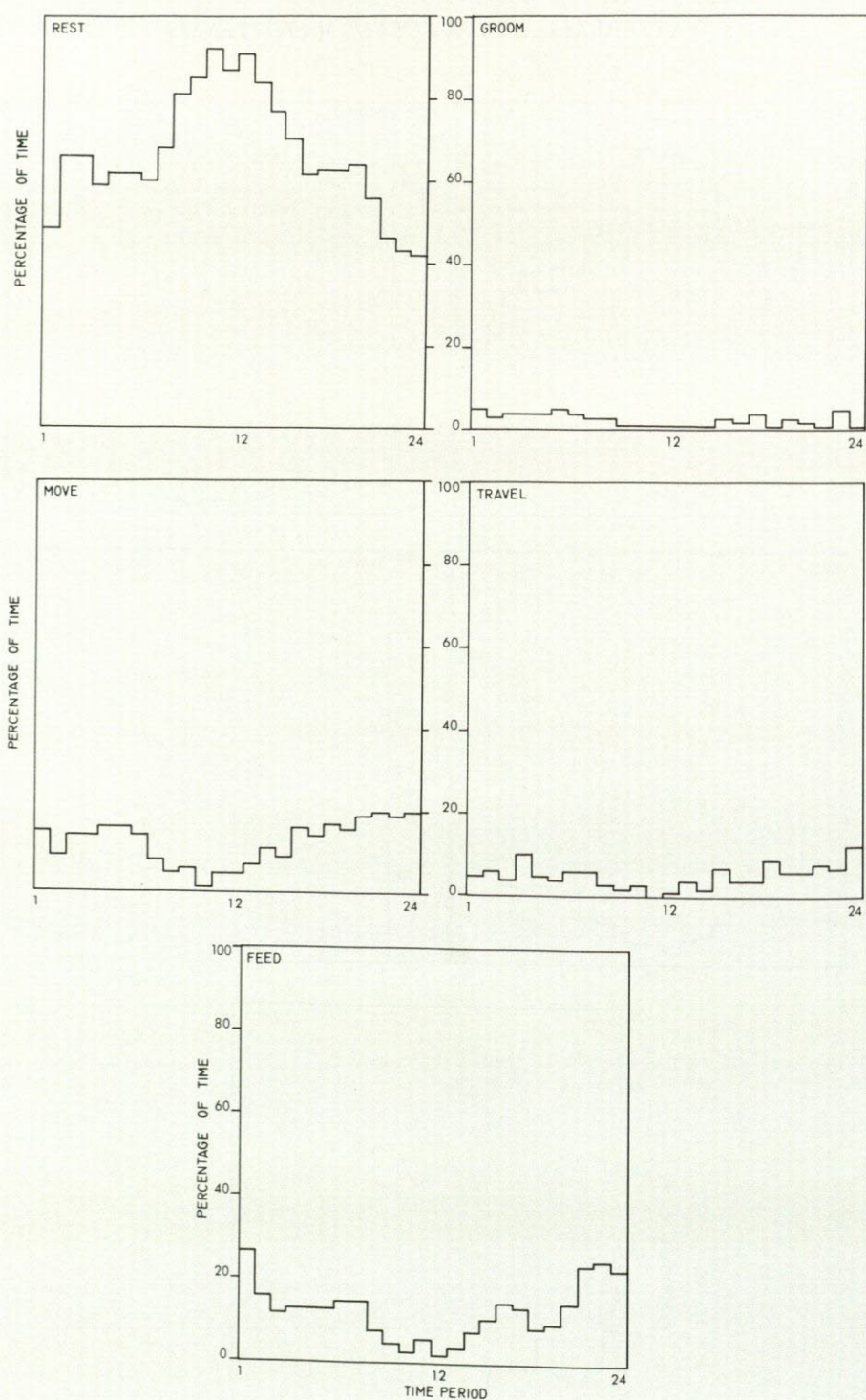


FIG. 19. Mean percentages of time devoted to each of the major activities, during each half-hour period of the day, over the duration of the study. From figures converted to the basis of "predominant group activity."



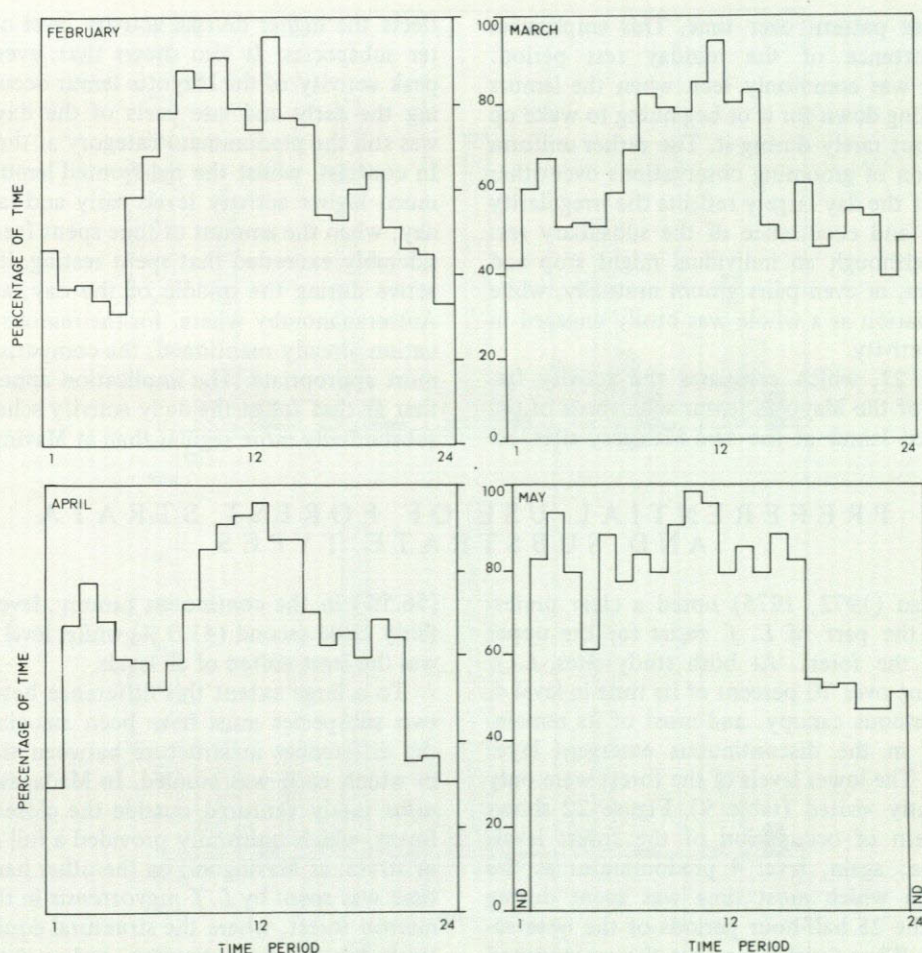


FIG. 20. Percentages of time spent resting during each half-hour period of the day, separately for each month. Based on the latitudinal samples.

these peaks, both morning and afternoon were characterized by shorter, more irregular, alternating bouts of activity and inactivity. But although most day-to-day variation was due to shifts in the timing of these subsidiary bouts of activity and rest, major departures from the general pattern did occur. Thus, for instance, on March 19 the association under observation took no appreciable rest period during the entire day, remaining active throughout the hours of daylight. On another occasion (March 8), activity continued uninterrupted throughout the morning, ceasing only with the commencement of the major rest period at around midday.

Although the Mayotte lemur rested more (except during the middle of the day), its pattern of resting is similar to that reported by Sussman (1972) for the red-fronted lemur. Each of the other activities showed, as might be expected, the opposite pattern to that of resting. Feeding and moving (unsurprisingly, since most of the latter took place in conjunction with the former), showed very close similarities, falling to their lowest frequency during the middle of the day, from early- and mid-morning and late afternoon peaks. Even grooming, an activity normally associated with resting, fell to a minimum during the middle of the day, although otherwise it showed



no distinct pattern over time. This emphasizes the importance of the midday rest period: grooming was commonly seen when the lemurs were settling down for it or beginning to wake up from it, but rarely during it. The rather uniform distribution of grooming observations over other periods of the day largely reflects the irregularity in length and occurrence of the subsidiary rest periods, although an individual might stop and autogroom, or even pairs groom mutually, while the association as a whole was busily engaged in another activity.

Figure 21, which compares the activity frequencies of the Mayotte lemur with those of the red-fronted lemur at the two Malagasy sites, re-

flects the higher diurnal activity level of the latter subspecies. It also shows that, even though peak activity of the Mayotte lemur occurred during the early and late parts of the day, resting was still the predominant category at these times. In contrast, whilst the red-fronted lemur showed much higher activity levels early and late in the day, when the amount of time spent feeding considerably exceeded that spent resting, it was less active during the middle of the day, at least at Antserananomby where, for the reasons of habituation already mentioned, the comparison seems most appropriate. The implication appears to be that at that forest the daily activity schedule was substantially more regular than at Mavingoni.

#### PREFERENTIAL USE OF FOREST STRATA AND SUBSTRATE TYPES

Sussman (1972, 1975) noted a clear preference on the part of *L. f. rufus* for the upper strata of the forest. At both study sites, *L. f. rufus* spent over 70 percent of its time in level 4, the continuous canopy, and most of its remaining time in the discontinuous emergent layer (level 5). The lower levels of the forest were only infrequently visited (table 9). Figure 22 shows the pattern of occupation of the forest levels over time: again, level 4 predominates as the stratum in which most time was spent during each of the 25 half-hour periods of the observation day. When level 4 was not the most-visited layer, level 5 was.

The Mayotte lemur, on the other hand, displayed a rather different pattern. Although it, too, showed a preference for the continuous canopy, level 3, rather than level 5, was favored during those periods when another level was more commonly visited<sup>1</sup> (fig. 22). This pattern is also evident from table 9, which indicates that although the animals spent most of their time

(56.5%) in the continuous canopy, level 3 ran a fairly close second (41.0 %) whilst level 5 (0.5%) was the least visited of all levels.

To a large extent this difference between the two subspecies must have been associated with the differences in structure between the forests in which each was studied. In Madagascar, *L. f. rufus* rarely ventured outside the closed canopy forest, which uniformly provided a full spectrum of strata; at Mavingoni, on the other hand, much time was spent by *L. f. mayottensis* in the avocat marron forest, where the structural equivalent of level 4 was discontinuous and rather poorly represented. Many of the resources on which the Mavingoni lemurs fed were scattered throughout the avocat marron forest; and the avocat marron itself provided close to 20 percent of the lemurs' diet.

Similarly, at Mavingoni level 5 was represented only by the crown of the occasional *Terminalia catappa*, and the occupation by lemurs of level 5 was very closely tied to feeding on the fruit and leaves (particularly the latter) of this species (only one observation was ever made of feeding on another resource at level 5). Very little activity other than feeding was ever performed in the emergent level (table 10), and since the leaves and fruit of *T. catappa* together accounted only for 6.3 percent of diet, rather little time overall was spent in this stratum. Con-

<sup>1</sup>It should be noted that the preference shown in figure 22 for level 2 during the first half-hour of observation may be the result of a biasing factor: the first association to be located in the morning was followed for the day, and the forest was almost always entered through an area where level 3 predominated. Additionally, the lower the animals were in the forest, the less likely were they to escape the attention of the observer.



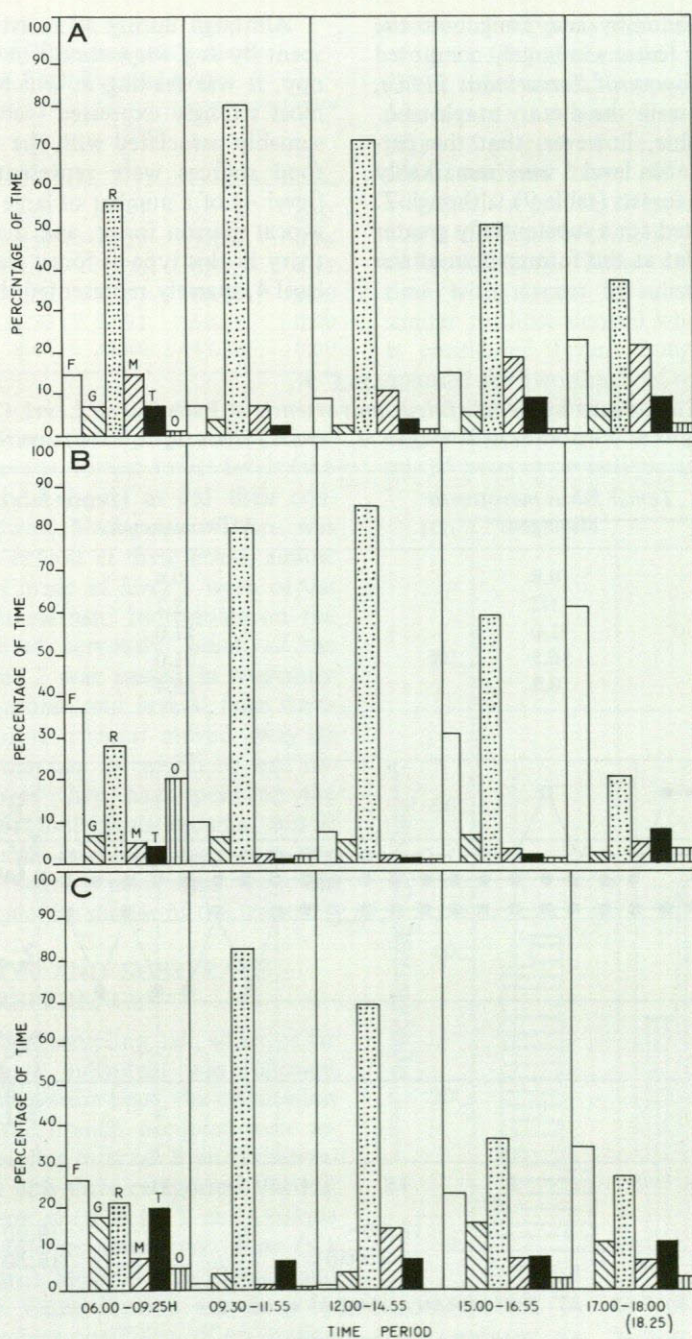


FIG. 21. Mean percentage of animals engaged in each recorded activity during five major periods of the day. (A) *L. f. mayottensis* at Mavingoni (B) *L. f. rufus* at Antserananomby. (C) *L. f. rufus* at Tongobato. B and C after Sussman (1972, 1975). F: feeding; G: grooming; R: resting; M: moving; T: traveling; O: other.



versely, at Antserananomby and Tongobato the topmost layer of the forest was largely composed of the emergent crowns of *Tamarindus indica*, the leaves of which were the dietary staple of *L. f. rufus*. It is notable, however, that the percentages of time spent in level 5 were remarkably similar at these two forests (table 9), although *T. indica* leaves accounted for a substantially greater proportion of the diet at the former than at the latter.

Although during all activities most time was spent by *L. f. mayottensis* in the continuous canopy, it was feeding in which this tendency was most strongly expressed (table 10). This is presumably associated with the fact that important food sources were represented by the crowns (level 4) of a number of large trees located in the avocat marron forest, and that much feeding activity in this type of forest was thus carried on at level 4, sparsely represented though it was.

TABLE 9  
Percentage of Time Spent by *Lemur fulvus mayottensis* at Each Forest Level, Compared with *Lemur fulvus rufus* at Two Sites in Madagascar. *Lemur fulvus rufus* Data from Sussman (1972)

Level	<i>Lemur fulvus mayottensis</i> Mavingoni	<i>Lemur fulvus rufus</i>	
		Antserananomby	Tongobato
1	0.8	0.4	1.6
2	1.2	2.2	3.8
3	41.0	11.0	8.0
4	56.5	71.0	70.4
5	0.5	15.4	16.2

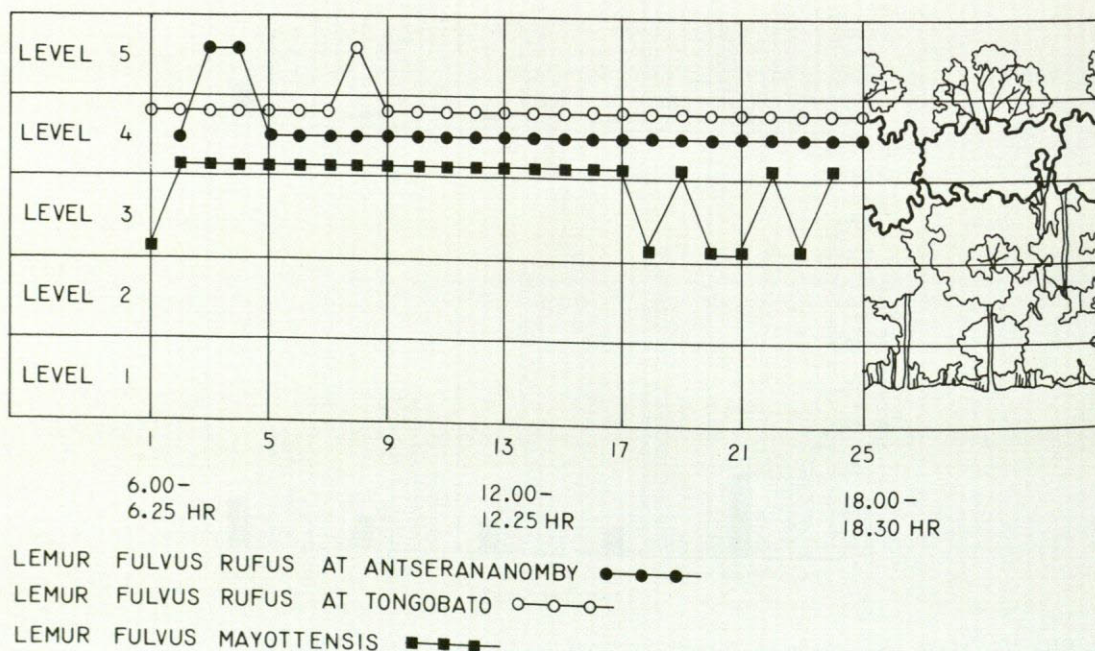


FIG. 22. The forest level at which the highest percentage of animals was observed during each half-hour period of the day: *L. f. mayottensis* at Mavingoni compared with *L. f. rufus* at Antserananomby and Tongobato. Modified from Sussman (1972, 1974).



TABLE 10  
Percentage of Time in Each Activity  
Spent at Each Forest Level

Activity	Level				
	1	2	3	4	5
Rest	0.27	1.05	43.57	55.10	0.01
Move	3.98	2.57	36.20	57.09	0.16
Feed	0.47	0.31	32.30	62.75	4.17
Travel	0.30	1.56	37.51	60.63	0.00
Groom	0.00	1.33	39.91	58.76	0.00
Other	3.00	8.64	39.48	48.88	0.00

The Mayotte lemurs showed the same lack of enthusiasm for the two lowest forest levels (the ground and the shrub layer) as did their conspecifics in southwest Madagascar. There was little for them to exploit at these levels; almost all feeding records made at level 1 were of the eating of fallen breadfruit. Individuals on the ground usually acted nervously; much of the time spent at level 2 was passed in hesitantly approaching the ground, and several false starts might be made before a lemur moved away on the ground from the tree by which he had descended. The longer they had spent on the ground, the bolder individuals became; but if alarmed they would invariably leap into the closest tree. The lemurs never fled over the ground except to gain the shelter of the trees.

#### LOCOMOTION AND SUBSTRATE PREFERENCES

During longitudinal sampling, i.e., when, as far as possible, a single individual was followed throughout the observation bout, the orientation and diameter of the branch occupied were recorded at each sampling interval. Branch orientations were divided into three categories: Vertical ( $90^\circ \pm 15^\circ$ ), Horizontal ( $0^\circ \pm 15^\circ$ ), and Oblique (intermediate); diameters into four: Fine ( $<1$  cm.), Small (1-2 cm.), Medium (2.5-10 cm.), and Large ( $>10$  cm.). Categorization was done by eye, with the attendant possibility of estimation error. When this possibility is added to the problems already noted of following single individuals, it becomes clear that the figures given here can be regarded only as approximations.

When all activities are considered together,

horizontal supports were clearly preferred (61% of time). Oblique branches were also frequented (33%), but vertical supports were used only 6 percent of the time. Fine branches were employed 5 percent of the time, small ones 33 percent, medium ones 48 percent, and large branches, 14 percent. Figure 23 provides a breakdown of diameter preferences within each orientation category. These distributions of overall time with respect to substrate are remarkably similar to those derived when resting time alone is considered (even though, since resting accounted for two-thirds of total time, the amount of possible difference was limited). During resting, 61 percent of the time was spent on horizontal, 35 percent on oblique and 4 percent on verti-

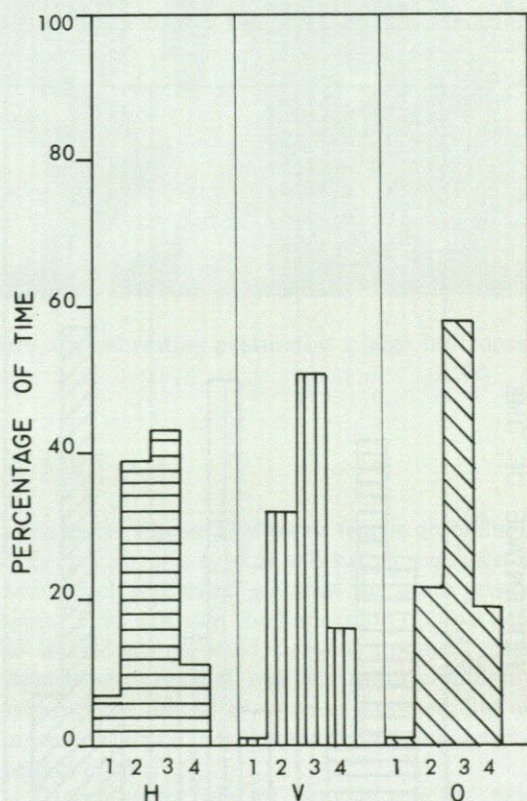


FIG. 23. Percentages of time, within each orientation category, spent on branches of different diameter. H, horizontal (61% of time overall); V, vertical (6%); O, oblique (33%). 1, fine branches; 2, small branches; 3, medium branches; 4, large branches.



cal supports. Fine branches, unsurprisingly, were never used during resting, of which time 28 percent was passed on small, 58 percent on medium, and 14 percent on large branches. Figure 24 shows the distribution, during resting time alone, of diameter preferences within each orientation class.

Individuals were only ever recorded as resting on vertical supports either because they were momentarily still at the time of sampling, or because the branch noted was that grasped by the most extremities; where a vertical support was used during a rest period, individuals supported most or all of their weight on branches forking beneath them. Animals resting on small branches often distributed their weight over several such supports, as did individuals active on (or under) fine ones. Figure 25 shows a male in a favorite

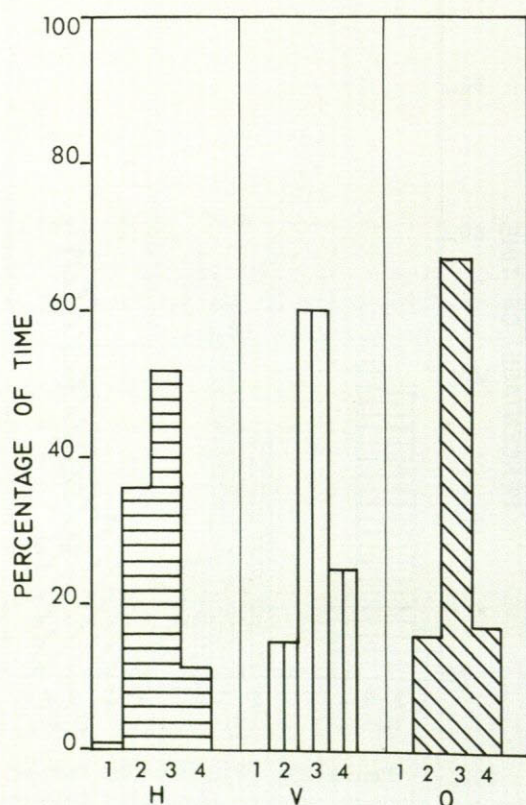


FIG. 24. Percentages of time spent resting, within each orientation category, passed on branches of different diameter. Abbreviations as for figure 23.

resting posture on a large horizontal branch; the rather low figures for both moving and resting on large branches reflect the fact that the majority of supports in this category were vertical or toward the vertical side of oblique.

Although the lemurs tended to shun vertical supports for resting, they showed no aversion to moving through the avocat marron forest by leaping between vertical trunks. Such vertical clinging and leaping was performed with great alacrity and agility, but in contrast to the similar locomotion practiced by the indriids, the forelimbs most often made contact with the arrival support at the same time as, or only just after, the hindlimbs.

Even in the avocat marron forest, however, *L. f. mayottensis* preferred to make use of horizontal supports where available. Normally, all members of the association would successively follow the same or closely similar path(s) of travel through the forest; these tended both to be as horizontal as possible, and to involve the minimum amount of leaping. When necessary, the lemurs would leap without hesitation between supports of any size or orientation; but generally, where an alternative to leaping existed, it was followed. Most travel thus took the form of walking or running along horizontal or relatively gently sloping supports; lianas, unstable though these often were, were frequently favored, especially when they bridged the crowns of neighboring trees. Orientation appears in general to have been a more critical factor than diameter in determining the choice of support during travel and resting.

During feeding, moving to feed, play, and other such activities, however, the lemurs were totally opportunistic in choice of support. That is, there appeared to be no limitation imposed by their postural or locomotor preferences upon the lemurs' exploitation of the forest. Individuals would do whatever was necessary to reach a chosen food source; an awkward location in the tree did not seem to be a deterrent, even when identical but more easily accessible foods were available not far away.

This general pattern of locomotor preference accords well with that described for *L. f. rufus* by Sussman (1974), and with my own observations on *L. f. fulvus* and *L. f. albifrons* in Madagascar.





FIG. 25. *Lemur fulvus mayottensis*, adult male, in a typical resting posture on a large horizontal branch.

## SOCIAL BEHAVIOR

The problems encountered in focal-animal sampling have been noted, and because reliable interpretation of social interactions depends so heavily on the ability consistently to follow and observe identifiable individuals, it will be evident that detailed discussion of social behavior is beyond the scope of this report. It is possible, however, to make a few preliminary comments.

The type of social interaction most commonly observed was grooming, which occupied 4.3 percent of total time. Of the time spent in grooming, 35 percent was devoted to autogrooming, compared with 65 percent to allogrooming or mutual grooming. It was rare that one individual groomed another consistently throughout a grooming bout; usually, individuals groomed each other at the same time or, more commonly,

alternately. Figure 27 shows a female grooming a male as part of a typical alternating sequence in which each individual groomed the other several times. I did not gain the impression that particular individuals groomed, or were groomed, more than others, or that one sex more commonly assumed the role of groomer or groomee. But on present evidence it is, of course, impossible to be certain of this.

Grooming in pairs of animals was generally associated with periods of resting; it occurred sporadically during minor rest periods, but only rarely at the height of the major midday rest. Autogrooming, on the other hand, was more likely to be observed in conjunction with all the various types of activity. Available data suggest that the frequencies of grooming bouts involving





FIG. 26. *Lemur fulvus mayottensis*, in a typical midleap posture.

two males, two females, or one male and one female, did not differ greatly, although heterosexual grooming couples formed the largest single category.

Most allo/mutual grooming was concentrated on the head, shoulders, and back (e.g., fig. 27): those areas of the body inaccessible to an auto-grooming individual. Other body regions did receive attention, however: figure 28 shows, for instance, a male grooming the hand of a female who had a few moments previously been grooming his hand.

In addition to the contact necessarily involved in allo- or mutual-grooming, some 48 percent of the time spent resting by focal animals was passed in physical contact with other individuals. Most commonly, such contact was within pairs; but it was not unusual to observe clusters of three resting lemurs, or of four, or occasionally

of even more. The percentages of total resting time spent in contact differed slightly between the sexes: 44 percent in the case of females, 50 percent among males. On the other hand, where individuals rested alone, the nearest neighbor was less than 2 meters away during 36 percent of resting time when the focal animal was a female, compared with only 30 percent when males were observed (mean: 32%). Percentages were identical regardless of sex when the nearest neighbor of the focal individual was between 2 and 6 meters away (17%), or over 6 meters away (3%).

The figures given above can be regarded only as approximations, and it does not seem advisable at this point to break down the nearest-neighbour data into finer categories. Nonetheless it is fairly clear that, its ephemeral nature notwithstanding, the Mayotte lemur association is spatially a rather cohesive grouping, in which the



dispersion of individuals seems to be essentially random with regard to sex. Certainly, no evidence whatever exists to suggest an organization based on dominance, linear or otherwise. It should be added, however, that it is also difficult at this stage to identify "roles" of the kind proposed by Gartlan (1968) in his critique of the concept of social dominance. For instance, as far as I was able to ascertain, any individual, even a juvenile, might initiate and/or lead association travel. But why associations broke up and coalesced in the ways and in the combinations of individuals, in which they did, must remain a mystery until all individuals can consistently be recognized.

Apart from the type of behavior involved in the "interassociation encounters" described earlier, agonistic interactions were only infrequently seen. "Play" was the most common "other" ac-

tivity observed, but it was occasionally distinguishable only with difficulty from aggressive behavior. Bouts of wrestling or chasing involving two individuals were usually clearly identifiable as "play," although the intensity of such activities sometimes escalated to the point where "fighting" appeared to be a more appropriate descriptive term. Similarly, chasing bouts involving several individuals were often distinguishable only by their lower intensity (and occasionally not at all) from the kind of behavior sometimes elicited by encounters between associations. Obviously, where consistently identifiable social units do not exist it is impossible to draw a distinction between "intergroup" and "intragroup" interactions; and when this is added to an inability to identify individuals, interpretation of behavior of this kind becomes impossible. It may be noted, however, that the frequency of "play"



FIG. 27. *Lemur fulvus mayottensis*, adult female, grooming an adult male during a typical reciprocal grooming bout.





FIG. 28. *Lemur fulvus mayottensis*, adult male, grooming the hand of an adult female during a bout of reciprocal grooming.

declined over time. Sussman (1972) observed a similar phenomenon in the red-fronted lemur, and ascribed it to the maturation of juvenile group members. A similar explanation may hold here, at least in part.

*Food Sharing.* Perhaps the most interesting aspect of social behavior observed was the sharing of food to which brief allusion has already been made. As noted, such behavior was only seen in conjunction with the consumption of the fruit of the houbouhoubou vine, *Saba comorensis*. Sharing is very easily distinguished in the case of the houbouhoubou because the fruit is detached from the vine and, in many cases, carried elsewhere to be eaten. The willingness of the possessor of the fruit to share varied greatly with the occasion, as the following extracts from my field notes show:

March 10, 1320 hrs. A female detaches a hou-

bouhoubou fruit and descends to a large horizontal branch to eat it. Another female joins her, and takes half the fruit while its original possessor offers no objection. The two sit side-by-side on the branch, and eat.

March 12, 0615 hrs. A female carrying a houbouhoubou fruit is being followed by two other individuals. After much dodging around by the one with the fruit one of the others, a female, catches up with her. The two sit together for a minute or two; then, the original possessor holding the fruit in both hands, both animals feed from it.

March 12, 1420 hrs. A female holding a houbouhoubou fruit is joined by another female. The fruit-holder moves. The other follows her and tries to eat from the fruit. She is chased off. After a couple of minutes the second female again approaches the first, and this time is allowed to share.

Persistence was not always rewarded, however:



March 5, 1455 hrs. A female picks a houbouhou fruit and carries it in her mouth to a thick horizontal liana. A male approaches and tries to share the fruit. The female moves away. The male follows. The female moves again. The male abandons his attempt.

Sometimes proprietorial jealousy extended even to unpicked fruit:

February 26, 0655 hrs. A male is eating a houbouhou fruit, one of a cluster still attached to the vine. He holds it in both hands. A female approaches and tries to grasp another fruit in the same cluster. The male turns to her and chases her off. The female tries again, with a similar result: he holds his fruit with one hand, and cuffs her with the other. She moves off to forage elsewhere.

Those exceedingly rare incidents of the kind just described provided the only examples observed of aggressive interactions associated with access to a feeding station. Not uncommonly, sharing or attempted sharing ended in the loss of fruit to both individuals, thus:

February 26, 1450 hrs. A female carrying a houbouhou fruit approaches a male and sits next to him. He turns to the female and sniffs the fruit. The female squeals and drops the fruit.

Almost all successful sharing was between females. On only one occasion was successful fruit-sharing seen between a male (who held the fruit) and a female; male-male sharing was not observed. Sharing of this sort, as opposed to the common exploitation by several individuals of a large single food source, has not been reported previously among lemurs. I have, however, observed an apparently comparable behavior in *Lemur mongoz* on the island of Mohéli. At dusk on November 24, 1974, a male-female pair of *L. mongoz* was sighted in the crown of a coconut palm (*Cocos nucifera*). They were engaged in feeding on a coconut in which a hole had freshly been made. The female put her hand through the hole, and withdrew it dripping with coconut milk. She licked the hand a few times, then passed it to the male, who licked it several times more. She then dipped again into the coconut, and the sequence was repeated.

The process of making the hole in the tough, fibrous husk of the coconut was not observed, but it seems likely that it was the work of rats,

which regularly ravage the Comorian coconut crop. The procumbent anterior lower teeth of lemurs are certainly capable of heavier duty than they have generally been given credit for on the basis of their fragile appearance, but it is nonetheless unlikely that the lemurs could have produced the hole themselves. When the coconut in question was obtained and examined, the hole appeared to be typical of those inflicted by rats. It seems unlikely, however, in view of the fact that the coconut had only freshly been opened and was still full of milk, that the rats had fully exploited it before being replaced by the lemurs. If they had not, this incident provides an example of a kind of parasitism by primates on rodents, although admittedly the evidence to distinguish it from commensalism is conjectural.

**Copulation.** It is probable that the study ended not long before the start of the breeding season, and indeed, one copulation was seen in mid-May. Unfortunately, the initiation of this act was not observed; when the male and female involved were first spotted they were already copulating, on a medium diameter horizontal branch about 4 meters above ground level. Other members of the association were at the time moving around much higher in the forest. Except, that is, for an immature female, aged probably around eight months, who displayed a vigorous interest in the proceedings and attempted to mount the male. The copulating couple, initially locked together, fled to a higher branch, only to be followed by the young female. Whereupon they retreated to the original branch and the male remounted the female, only to be thwarted yet again by the arrival of the adolescent. The male abandoned his attempt to copulate and ran off, followed closely by the female. The young female stayed on the branch for a few seconds, then left.

Throughout this entire sequence, taking almost 90 seconds, no marking whatever was observed. Even though (one hopes) the copulation reported here was not entirely typical, this is perhaps rather surprising since Harrington (1975) noted a good deal of marking and sniffing in conjunction with the copulations of *L. f. fulvus* he saw. Harrington also reported that male *L. f. fulvus* began to show distinct sexual responses to the females some time before the beginning of the short mating period. No such response was



seen in *L. f. mayottensis*, although of course it is not known exactly when the mating period started after the study was completed. The copulation described above was carried out in total silence; I heard no vocalizations before first seeing the copulating pair, and no sounds were emitted at any time during the sequence of events, despite the annoyances inflicted by the young female.

**Marking.** The only form of marking specifically noted during the study was anogenital (fig. 29). Both males and females of *L. f. mayottensis* possess an extensive area of wrinkled, glandular perianal skin, but whether the males possess scrotal glands such as those described for *L. f. fulvus* by Montagna (1962) I do not know. If their subspecies is descended without hybridization from *L. f. fulvus* they presumably do. Anogenital marking is considerably more difficult to observe than is marking performed with glands on the head, throat, antebrachium, and so forth, since it is often so much more unobtrusive, merely requiring slight movements while sitting. The recorded frequency of marking thus doubt-

less severely underestimates the actual occurrence of this behavior, but it is nonetheless probable that the actual frequency is rather low.

Marking was most commonly observed during interassociation encounters, as already described; it is, unfortunately, difficult to provide precise contexts for the other instances of marking observed, some of which were quite elaborate, as in the following example:

March 28, 1735 hrs. The association is on the ground, in an area of scrub near the edge of the forest. A male marks the boulder on which he is sitting, then marks it again before leaving it. A female approaches the rock, sniffs at it, then anogenitally marks it herself. After sitting on it for some minutes, she leaves the boulder. The male, who has meanwhile marked another rock, returns to the original boulder, sniffs at it, then marks it once more. At the same time, the female goes over to the rock the male has just marked, sniffs at it, and marks it. The association moves back to the trees and recommences feeding.

Most marking sequences observed were less complex than the foregoing. On most occasions when



FIG. 29. *Lemur fulvus mayottensis*, a captive adult female, anogenitally marking a horizontal support.



marking was observed the mark was subsequently approached by another individual who would sniff at it, but might or might not also mark the same spot. The information at present available is not sufficient to reveal whether males were most often attracted by the marks of females, or vice versa, or whether marks were equally attractive irrespective of the sex (or of the identity?) of the marker. Sometimes resting sites were marked before departure, and occasionally individuals would pause briefly during travel and mark. Vague though it still is, the pattern of marking observed in *L. f. mayottensis* appears broadly similar to that noted for *L. f. fulvus* by Harrington (1975, 1976), who found that most scent marking and sniffing occurred during sexual behavior (the absence of marking during the copulation described above was almost certainly rather unusual, and in any event, the observation was incomplete), alarm, encounters between groups, and during undisturbed moving around in the trees. It is unlikely that the urination and/or defecation often performed in concert by most or all members of an association at the end of a resting period was at all related to any marking function.

**Vocalization.** *Lemur fulvus mayottensis* is moderately vocal, and has a variety of distinct vocalizations. Broadly, these fall into two categories: those based on the "grunt," and those which correspond in an approximate way to the "rasp" and "creaking door" vocalizations reported for *Lemur mongoz* by Tattersall and Sussman (1974). As in the case of this latter species the grunt is a low, guttural sound of very short duration, emitted either singly or, much more commonly, in series. Soft grunts given at well-spaced intervals (of a second or more) indicate a relatively low level of emotional intensity; louder grunts at shorter intervals express a higher level of arousal and may grade upward into "explosive grunts," in which the sound is combined with a sudden expiration, or into sharper "clicks," or

into "rattles," where the grunts are emitted in such rapid succession as to be almost indistinguishable one from another. Sonographically, individual grunts closely resemble those of *Lemur mongoz* illustrated by Tattersall and Sussman (1974, fig. 14). Grunts were most commonly given during travel, during play, during investigative behavior, and in the periods of relative quiescence during interassociation encounters.

Of the other group of vocalizations, the rasp was the most common; one is shown in figure 30, analyzed on a Kay Elemetrics 6061A sound spectrograph. The average duration of such calls was around two seconds, and they were often preceded by series of grunts. Precise context is difficult to provide for this and related vocalizations, since there were apparently no situations in which they were consistently emitted. When one individual began a rasp, it was frequently joined in vocalizing by other members of its association. Sometimes the call was answered in kind by other associations; as often, however, it was not, even when other associations were nearby. Nonetheless, the rasp is best regarded as a contact vocalization; it was most commonly emitted during travel, or during pauses in travel, and it may have been given more frequently during the night than during the day.

The creaking door call was rarer, and was apparently indicative of a higher state of arousal. It consisted of a sustained fundamental unit at a frequency of about 1.5 kHz, with a minor harmonic at around 3.0 kHz, and its mean duration was similar to that of the rasp. The main note thus closely resembled the major, introductory, note of the three-part creaking door of *Lemur mongoz*; the rasp of *L. f. mayottensis*, on the other hand, was sonographically quite dissimilar to that of the latter species. It is noteworthy that none of the vocalizations of *L. f. mayottensis* analyzed resembled any of those published for *Lemur fulvus* (subspecies unspecified) by Andrew (1962).

## DISCUSSION

It will be amply evident that the behavior of *L. f. mayottensis* differs substantially in some ways from that reported by Sussman (1972, 1974, 1975) for *L. f. rufus* in Madagascar. Many

of these differences appear to be related to the divergent dietary preferences shown by the two subspecies.

Perhaps unexpectedly in view of these dietary



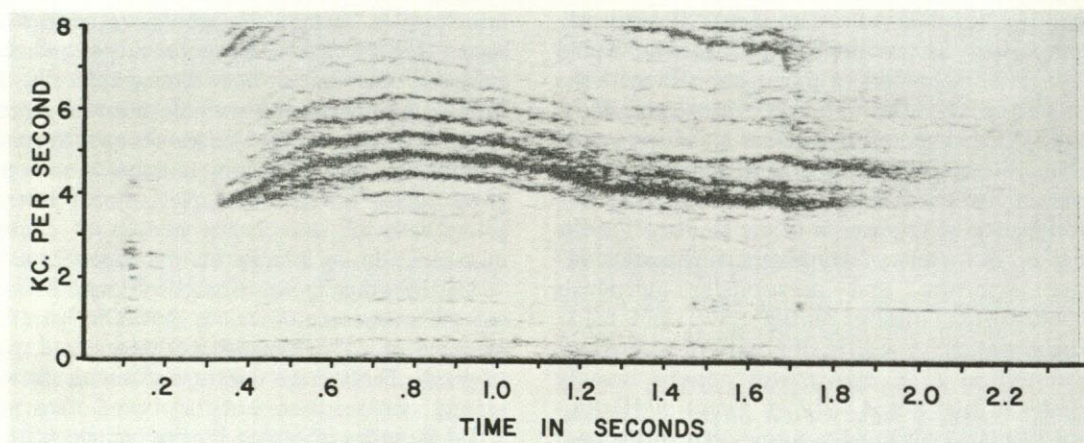


FIG. 30. Sound spectrogram of a "rasp" vocalization of *Lemur fulvus mayottensis*.

differences, density of population appeared to be roughly comparable between the Malagasy and Mayotte study areas; but the ranging behavior displayed by members of the two subspecies differed considerably. Not only were the total ranges covered by individual *L. f. mayottensis* a great deal larger than those inhabited by *L. f. rufus* groups, but daily travel by the former was between three and eight times that recorded for the latter. The diet of *L. f. rufus* was a relatively restricted one, consisting in large part of the leaves of the dominant tree species of the forest in which it lived. On the other hand, the diet of *L. f. mayottensis* was much more varied, and the resources on which it fed were irregularly scattered, both within the forest as a whole and within the individual trees. These differences in distribution of the food resources exploited by the two subspecies apparently correspond to the considerable differences between them in mobility.

This correlation gains emphasis from consideration of the pattern exhibited by *Lemur catta*, also studied in a comparable manner by Sussman (1972, 1974), and which fed on a much more varied diet than did *L. f. rufus*. On the basis of available information *L. f. rufus* is justifiably described as a dietary specialist and a folivore; in contrast, *L. catta*, like *L. f. mayottensis*, could be characterized as a dietary generalist and a frugivore. In keeping with these dietary proclivities *L. catta*, again like the Mayotte lemur, was observed

to devote much more of its time to travel and movement than did *L. f. rufus*; similarly, its home range was vastly larger. Indeed, at Antserananomby the home ranges of 12 groups of *L. f. rufus* ( $\bar{x}$  = 9.2 individuals) were included within the range of a single group of *L. catta* (19 individuals). Average day-range of *L. catta* was 920 meters, close to that of *L. f. mayottensis* and far in excess of the 135-150 meters recorded for *L. f. rufus*.

In its utilization of time the Mayotte lemur differed from both *L. f. rufus* and *L. catta*. If *L. f. mayottensis* was unlike the former in its activity/rest ratio, it differed yet more from *L. catta* (a/r ratio 1.5). Thus, although the Mayotte lemur traveled as far as did *L. catta*, it accomplished this displacement in much less time. *Lemur catta* moved and foraged more slowly and consistently; *L. f. mayottensis* traveled rapidly and directly between distant and obviously well-known feeding sites. Until we know how much nocturnal activity is characteristic of *L. f. mayottensis* (and the others), it will be impossible accurately to interpret currently available data on diurnal patterns of activity and rest; clearly, however, there exists a dismayingly complex relationship between diet, resource distribution, time budget, ranging pattern, size and stability of social units, and kindred variables.

As might be expected, the closest similarities between the two subspecies of *L. fulvus* were shown in those behavioral characteristics most in-



timately related to the anatomy of the animals: locomotion and choice of substrate. Quantitative data are not available for *L. f. rufus*, but Sussman's (1972, 1974) qualitative description, and my own observations of that and other *L. fulvus* subspecies in Madagascar, suggest that patterns of substrate preference and locomotion are substantially the same throughout the species. Although *L. f. rufus* and *L. f. mayottensis* are both sufficiently flexible in their locomotor behavior to exploit virtually any part of the forest or individual tree, these lemurs are clearly happiest moving on top of medium to large horizontal or gently sloping supports. They are agile leapers but, with the leisure to make a choice, will usually leap only when no option other than descending to the ground is available. The composition of the forest at Mavingoni was such that the lemurs inhabiting it were regularly obliged to spend much time in level 3, but it was nonetheless evident that *L. f. mayottensis* preferred to occupy the canopy, as did *L. f. rufus*. Neither subspecies spent more than a tiny fraction of its time on the ground, whereas *L. catta* spent a great deal there, including most of its moving and traveling time.

Although it seems reasonable to assume that the fluid social organization of *L. f. mayottensis* is related to its ranging/foraging strategy, itself in turn related to factors in the external environment such as resource abundance and distribution, the exact nature of such relationships remains obscure. In the case of *Ateles belzebuth*, Klein and Klein (1975) have suggested that the "fission-fusion" social grouping pattern corresponds to "a restricted range of food substances available each day" (p. 82), a suggestion that appears plausible in the light of what is known of the spider monkey, but which runs totally counter to what is known of the Mayotte lemur. This illustrates quite clearly the difficulties inherent in the formulation of general ecological hypotheses of behavior or social organization. Klein and Klein remark that the fact that such "fission-fusion" grouping have evolved separately in Ceboidea and in Hominoidea [and, as this study shows, in Lemuroidea], "suggests that the factors responsible are more likely to be ecological than phylogenetic" (p. 84).<sup>1</sup> But it is

nonetheless evident that a host of factors, many of them adventitious with regard to pure "ecology," must be involved. Thus the Mayotte lemur displays a relatively high level of gregariousness and mutual tolerance compared with the spider monkey, in which the maintenance of individual spacing during feeding appears to be a significant component of social organization. Yet despite the fact that sociability is so different in the two forms it is nonetheless likely that in each case sociability has played a role as important as those of resource distribution or other "ecological" factors in producing grouping patterns which, in some ways at least, appear to be similar.

Speculations of this kind inevitably call into question the value of attempts to categorize different types of primate social structure as functions of unit composition. Apparently similar structures may have come into being through the operation of greatly disparate forces; and to classify groups on the basis, for instance, of the numbers of males they contain may do more to conceal than to reveal the factors underlying group structure.

In comparing the social organization and behavior of several species of African cercopithecines, Gartlan (1973) was led to a similar conclusion, as, for different reasons, was Sussman (1975). At the same time, Gartlan identified three distinct types of variation in social structure and other behavioral characteristics: density-dependent, environmental and phylogenetic. *Cercopithecus aethiops*, for example, shows strong differences in group cohesion, home range, social behavior, and so forth according to the density of its population. This is not unex-

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genetic" behavioral characters one must be bound by the same conditions that govern the phylogenetic analysis of morphological characters even where, as is implicit here, presumed affinity is used to "explain" characters, rather than characters used to determine affinity. Thus there is no logical reason why, for instance, a particular grouping pattern should be regarded as "ecologically-determined" simply because it occurs in three distinct superfamilies within Primates; it might have arisen independently in each and subsequently have been transmitted as a "phylogenetic" characteristic. This is not to say, however, that within the limits of the terminology (see later discussion) the Kleins' suggestion is not borne out by other lines of reasoning.

<sup>1</sup>It should be recognized that in speaking of "phylo-



pected; what is, is to find so close a correspondence in population density between *L. f. rufus* and *L. f. mayottensis* when at the same time they display such substantial differences in diet, ranging behavior, and social organization. It may also be worth noting that the apparent communality of feeding strategy in *L. catta* and *L. f. mayottensis* existed independently of population density; that of the former is only a quarter (Sussman 1972, 1974) or less (Budnitz and Dainis, 1975) of the latter's.

The dichotomy between "phylogenetic" and "environmental" influences on behavior is often seen, if only implicitly, as an absolute one; and it may in fact be self-fulfilling: if a characteristic is not revealed to be "phylogenetic" by its presence in closely related species or by its dependence upon a specialized anatomical structure, it is "environmental"; differences between different species living sympatrically are said to be "phylogenetic." But to propound such generalizations is often to obscure the more complex realities of the situation. Indeed, the use of these terms often implies an understanding which is only apparent. For to know (if in fact one can) that a characteristic is "phylogenetic" (even "genetically determined") or "environmental" (even "ecological") is not really to know very much about it; nothing, certainly, about its functional significance.

As Gartlan (1973) has pointed out, neither phylogenetic affinity nor ecological similarity has much predictive value about behavior. Genetic predisposition must, it is true, establish the limits within which behavior can develop in response to environmental pressures or even to totally random factors; but the breadth of these limits is obviously highly variable, both within and between species. In its locomotion *L. fulvus* shows great flexibility but a clear and consistent preference when a choice is available; this preference is presumably fairly tightly controlled by anatomical, hence relatively directly genetic, factors. In the case of group structure, however, it is not even possible to rule out random influences in the determination of the variety known to exist in *L. fulvus*. More than one solution to most problems of survival will probably lie within the potential of any primate species; and the final choice between viable alternatives might well be due as much as anything to chance. This appears

particularly likely in the case of an introduced isolate such as *L. f. mayottensis*.

In any event, perhaps the most interesting and instructive result of this study is what it adds to our knowledge of the variation in behavior that exists within the genus *Lemur*: a variability which is all the more remarkable when one considers how little we know about the natural history of members of this polytypic genus. *Lemur catta* has now been subjected to a number of detailed field studies (Jolly, 1966; Sussman, 1972, 1974; Budnitz and Dainis, 1975); but almost all of these were carried out at a single location, Berenty. *Lemur mongoz* has been studied in a variety of areas (Tattersall and Sussman, 1975; Sussman and Tattersall, 1976; Tattersall, 1976); but never over an extended period of time. Only two of some seven subspecies of *Lemur fulvus* have been observed in any ecological detail (Sussman, 1972, 1974, 1975; this study); one other has been the subject of a short study of social behavior (Harrington, 1975). Petter's observations on *Lemur macaco* (1962) are brief and preliminary. Four of the subspecies of *Lemur fulvus* have never been studied in the field; neither has *Lemur coronatus*, nor *Lemur rubriventer*.

Not many years ago the behavior and social organization of the lemurs were assumed to be as stereotyped as the supposedly unimpressive performance of these animals in laboratory tests<sup>1</sup> appeared to suggest. Yet within a single poorly studied lemur genus, and indeed within single species of this genus, we have already encountered an extraordinary variety in behavior which surpasses that observed in many higher primate genera. For instance, species of *Lemur* run almost the gamut of types of primate social grouping as conventionally defined: *L. catta* lives in large, multi-male troops with (perhaps) an established pattern of social dominance; uni-male troops are not unknown, however. *Lemur fulvus* and *L. f. rufus* live in smaller heterosexual groupings, the organization of which is apparently not based on dominance relationships. *Lemur mon-*

<sup>1</sup>But a recent review of the literature on discrimination and learning in strepsirrhine primates (Ehrlich, Fobes and King, 1976) has shown that, for example, these animals reach "in the area of complex learning . . . a final level of performance that is at or near the level of the anthropoids" (p. 599).



goz usually, but not everywhere, forms "family" groups consisting of an adult male, an adult female and any immature offspring; and *L. f. mayottensis* forms unstable groupings which are in a constant state of flux. Diet, ranging patterns, activity rhythm, and a host of other types of behavior show similarly impressive ranges of variation.

The lemurs thus offer an almost unparalleled opportunity for the study of an even wider range of behavioral, ecological, and evolutionary problems than has generally been realized. But even in the cases of the best-studied species this fertile ground has hardly yet been scratched. Let us hope that the opportunity may be taken before it vanishes.

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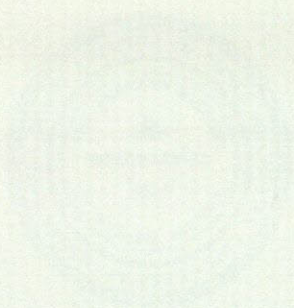
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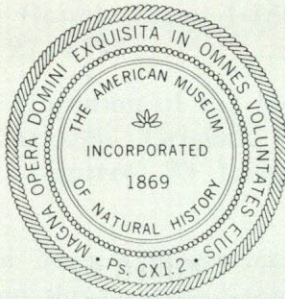
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## ANALYSIS OF THE DATA

The data were analyzed using a series of statistical tests. First, a t-test was performed to compare the means of the two groups. The results showed that the difference between the two groups was statistically significant at the 0.05 level. Next, a chi-square test was used to examine the relationship between the two variables. The results indicated a significant association between the two variables. Finally, a regression analysis was conducted to determine the strength and direction of the relationship between the two variables. The results showed a positive correlation between the two variables, with a coefficient of determination of 0.75.



