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ABSTRACT

A preliminary study of the ecology and behavior of *Lemur mongoz mongoz* was carried out in the northwestern part of Madagascar during July and August, 1973. The animals were observed for approximately 250 hours. *Lemur mongoz mongoz* had been reported to be diurnal and to live in groups of six to eight individuals. However, we found the animals to be nocturnal and groups to contain an adult male, an adult female, and their offspring (thus numbering from two to four individuals). The animals did not defend territorial boundaries, and the home ranges of groups overlapped extensively.

Lemur mongoz mongoz is thus the only species of the genus *Lemur* studied to date that is active exclusively at night and which lives in "family" groups.

During our study, the diet of *L. m. mongoz* was very specialized. It consisted almost entirely of the nectar, fruit, and possibly pollen of two species of trees. This feeding adaptation is convergent with that of many species of flower and fruit visiting bats. General ecology and inter-group and intragroup interactions are described.

INTRODUCTION

Although *Lemur mongoz* was named as early as 1766 by Linnaeus, and illustrated even earlier (Edwards, 1758), it remains among the least well documented of all Malagasy primates. Most observations of *L. mongoz* in the wild have been little more than anecdotal, and few authors have gone beyond noting, for instance, that *L. mongoz* is "thoroughly arboreal but diurnal" (Hill, 1953, p. 422).

We report here on a preliminary study of the behavior and ecology of *Lemur mongoz mongoz*, undertaken in Madagascar during July and the first week of August, 1973. The study was carried out close to the village of Ampijoroa in the forest reserve of Ankarafantsika, about 100 km. south of Majunga on Route Nationale #4 (fig. 1). Approximately 250 hours of intensive observation were made on the animals.

Although *L. m. mongoz* had previously been reported as diurnal, we quickly discovered that, at least at this season of the year, it is strictly nocturnal. This species is relatively abundant in the region of Ampijoroa and quite vocal during the night. The failure of previous investigators to recognize that *L. m. mongoz* is nocturnal may be because it is easily confused with *Lemur fulvus fulvus* in both appearance and vocalizations. The two species are sympatric at Ankarafantsika, and *L. f. fulvus*, although primarily diurnal, is sometimes active at night.

Acknowledgments

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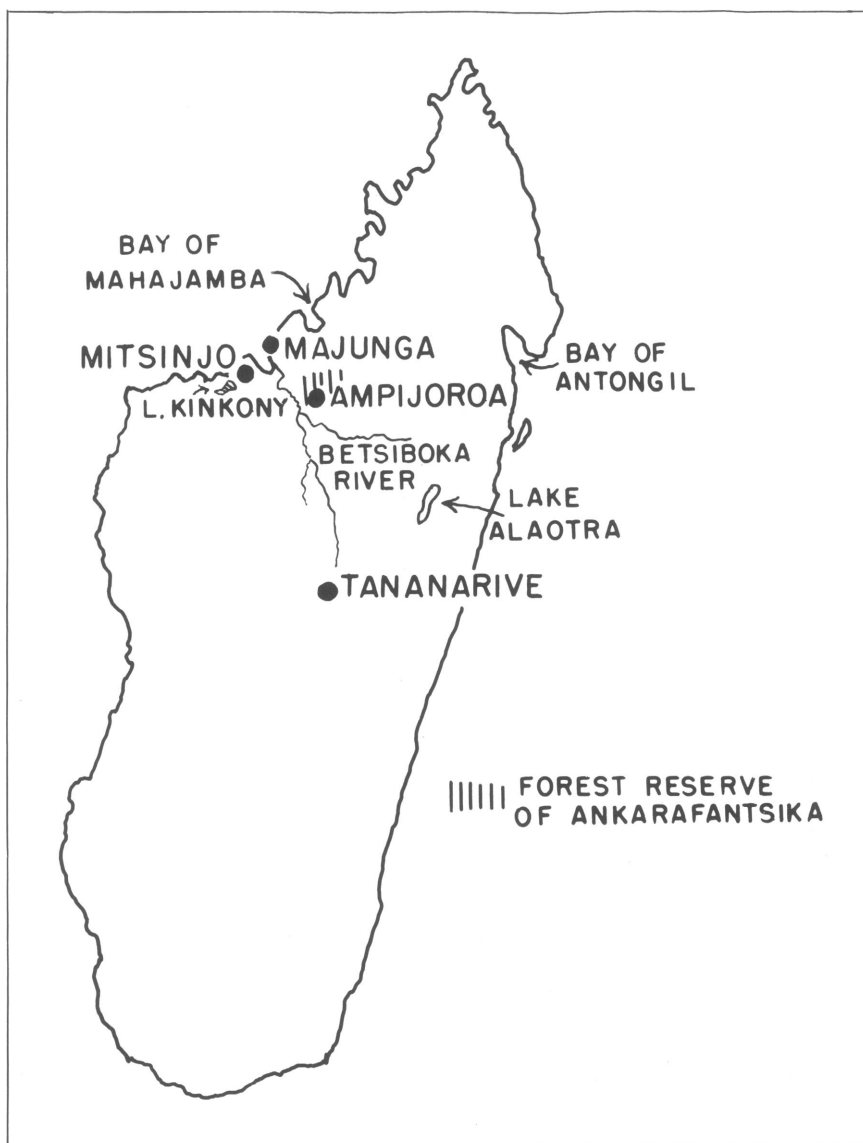


FIG. 1. Map of Madagascar showing location of Ampijoroa and other localities mentioned in text.

TAXONOMY AND DISTRIBUTION

The polytypic species *Lemur mongoz* is divided into two subspecies: *L. m. mongoz* and *L. m. coronatus*. The former is sympatric over much of its range with *Lemur fulvus fulvus* (east

of the Betsiboka River) or *Lemur fulvus rufus* (west of the Betsiboka). *Lemur mongoz mongoz* is only slightly smaller than *L. f. fulvus* and is similar to it in coloration. The two species, we believe, have frequently been confused, as Schwartz (1931) has also noted.

Earlier authors observed two color variants of *L. m. mongoz*: the "red-cheeked" and the "white-cheeked." In fact, in both forms the differences in coloration extend across the throat where they are clearly visible from the ground. According to Schwartz (1931) and Paulian (1955), this dichromatism is sex-linked in specimens from the Comoro Islands: the male possesses the red beard and the female the white. This is not the case in mainland representatives of the subspecies. In our observations on the mainland, we found all females to have white beards, black faces, and brown heads and pelage (fig. 2). We have, however, observed a dichromatism among the males: a red-bearded form with a white muzzle, light face, red head, and gray pelage be-

coming orange around the feet, hands, and tail (fig. 3); and a white-bearded form with a black face and head and charcoal gray pelage becoming darker toward the hands, feet, and tail (fig. 4). The beards of both types of males are quite fluffy. The latter color variant is superficially similar to *L. f. fulvus* and may have served to foster confusion between the two species. Hill (1953) discussed the characteristics of subspecies of *L. mongoz* and *L. fulvus*.

No comprehensive survey has been made of *L. mongoz* populations, and information on the distributions of the subspecies remains sketchy and conflicting. It may well be that *L. m. coronatus* occurs only to the north of an east-west line joining the Bay of Mahajamba to the Bay of Antongil



FIG. 2. Female *Lemur mongoz mongoz*.



FIG. 3. Male *Lemur mongoz mongoz*, red-cheeked variety.

(fig. 1), but this has not been confirmed, and even within this region the precise distribution of the species is unclear. There is even less agreement about *L. m. mongoz*. Schwartz (1931) claims that *L. m. mongoz* is restricted to the "south" (i.e., the west) of the Betsiboka River and that *L. m. coronatus* replaces it immediately to the "north" (i.e., the east). We studied *L. m. mongoz*, however, in a forest east of the Betsiboka. Furthermore, the evidence that *L. m. coronatus* is distributed to the south of the Bay of Mahajamba, about 60 km. north of Ankarafant-

sika, is equivocal. Hill (1953) likewise restricts *L. m. mongoz* to the west bank of the Betsiboka, but only within a narrow strip. We have, however, observed this subspecies on the shores of Lake Kinkony, near Mitsinjo (fig. 1), which lies some distance to the west of the area indicated by Hill. His map, further, extends the range of *L. m. mongoz* in a narrow northwest-southeast belt running from Majunga almost to Tananarive. It is highly unlikely, however, that the distribution of *L. m. mongoz* has ever, or at least within historic times, extended as far to the southeast as Hill's

map suggests. Beyond this, reports of the presence of *L. m. mongoz* in the area south of Lake Alaotra (e.g., Schwartz, 1931) are very probably unreliable.

Lemur mongoz mongoz also occurs on the islands of Moheli and Anjouan [but not on Grand Comoro as Hill's figure (1953, fig. 137) suggests], and *Lemur mongoz* is the only lemur species besides *Lemur fulvus* found on the Comoro Islands. Indeed, it is on specimens from Anjouan that most of the early descriptions of this species were based.

THE STUDY AREA

Vegetation. The animals were studied in the immediate vicinity of the forestry station at

Ampijoroa (fig. 1). The vegetation of the region consists of deciduous forests, often partially degraded, of the type characteristic of the richer soils of the western lowlands of Madagascar. The study area itself, however, is extremely atypical, its vegetation having resulted from replanting experiments carried out by the colonial administration during the 1930s. Small plots, disposed around the perimeter of the station compound, were each reafforested with a different mixture of species; this gave rise to the present vegetal pattern, shown in figure 5. Most of the planted species are not native to Madagascar.

To the east of the compound, in the area designated "A" in the figure, the vegetation is relatively thin and irregular, with no species dominant. For the most part, however, a continuous



FIG. 4. Male *Lemur mongoz mongoz*, black-faced variety.

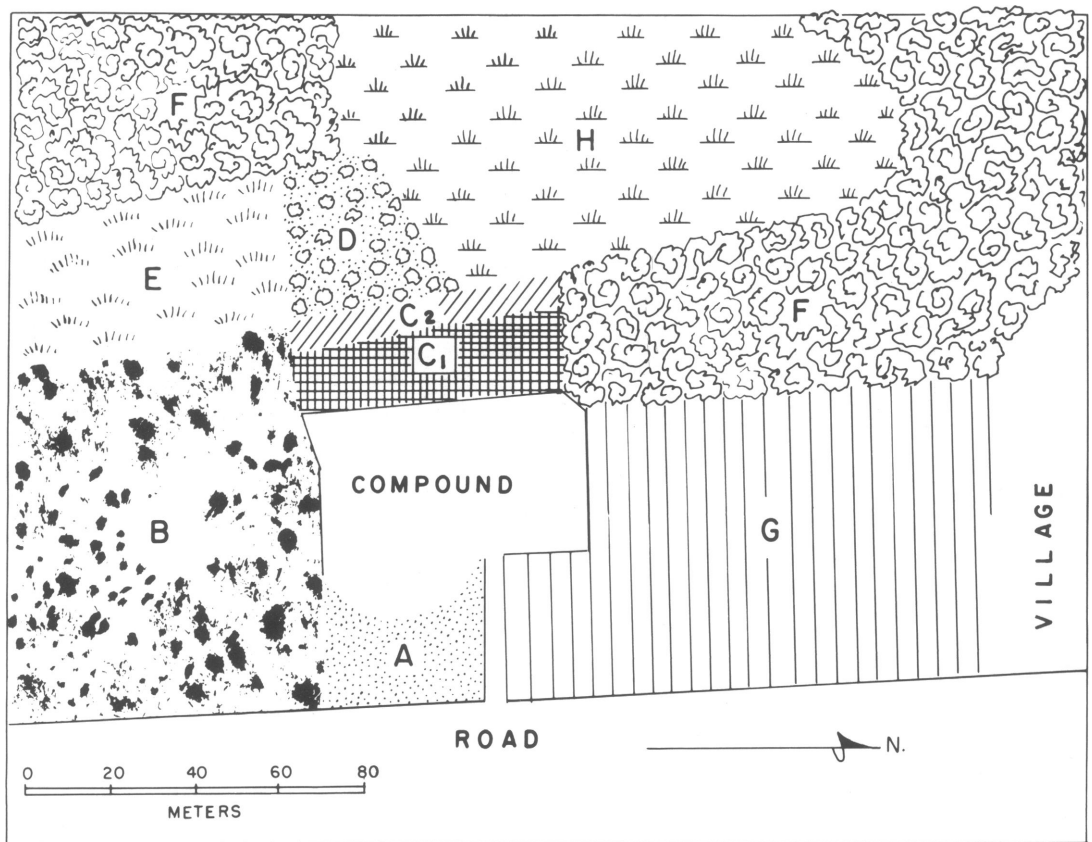


FIG. 5. Pattern of vegetation surrounding forestry compound at Ampijoroa. See text.

canopy is present. The trees composing this include *Tectona grandis* (Verbeceae; local name: teck), virtually leafless at the time of the study; two species of *Albizia*—*A. lebeck* and *A. sp. indet.* (Mimosaceae: bonara); *Hura crepitans* (Euphorbiaceae: hazomboay); and *Mangifera indica* (Anacardiaceae: manga). Two tree species are represented in this area of the compound only by single individuals, but both are exploited for food by *L. m. mongoz*: *Kigelia madagascariensis* (Bignoniaceae: somontsohy) and *Ceiba pentandra* (Bombaceae: pamba). The large pamba tree is on the western periphery of this area and was the dietary staple of *L. m. mongoz* during our study. The vine *Combretum phanopetalum* (lavanana) is also found at canopy level. Ground cover is minimal, consisting of thin brush together with some aloes planted toward the

road; the intermediate vegetal level is chiefly composed of bonara saplings.

Area B, to the south of the compound, represents a much more successful replanting, showing a regular pattern of mature tecks spaced at about 2-m. intervals (fig. 6) except where cutting has taken place. These trees, although leafless during the period of the study, provide a continuous branch stratum between about 8 and 15 m. high (fig. 7). There is virtually no intermediate level, and the ground level is largely bare, although it is covered with a thick leaf litter and supports a few aloes. In the northeastern part of the area is a scattering of bonara, and in the northwest corner is a large pamba of considerable dietary significance to the animals (fig. 8).

Area C₁ similarly shows a regular pattern of mature tecks, these bearing a few dry leaves and

again providing a continuous canopy layer. Within this pattern are found a few bonara, and in the eastern portion of the zone, bordering the compound, there is a strip of intermixed and irregularly spaced hazomboay, pamba, and manga. The ground level is open with a deep leaf litter and very little underbrush. The intermediate level is almost absent, with only a few teck saplings.

Area C₂, along the base of the slope upon which C₁ lies, supports a closely spaced mixture of teck, bonara, and hazomboay, generally less mature than those found higher up the slope. In the western portion the hazomboay become dominant over the teck. The canopy level is dense, with some lianas and vines. There is also a dense subordinate tree layer, composed largely of saplings. The underbrush is quite thick. At the

base of the hill, bordering the open area H, is a stand of *Raphia* palms (Palmaceae).

Area D is characterized by a growth of mature *Eucalyptus*, interspersed with a few bonara saplings. To its south, area E supports a dry, primary brush-and-scrub forest. Area H, an open tract with a lush grass cover that becomes a marsh during the wet season, is surrounded for the most part by autochthonous forest (F) which may approximate the climax condition. Relatively low, and supporting a dense although not specifically varied underbrush, this forest is largely composed of endemic species but contains a number of large hazomboay; most of the trees are covered with lianas, and vines entangle the canopy. There appear to be no dominant tree species.



FIG. 6. Spacing of *Tectona grandis* trees in figure 5, area B.



FIG. 7. Continuous canopy provided by *Tectona grandis* in figure 5, area B.

The largest planted area, G, is dominated by fairly widely spaced, high tecks which at the time of study bore more leaves than those bordering the other sides of the compound. Also present, especially toward the north, are a number of large hazomboay and a substantial scattering of manga, pamba, and kily (*Tamarindus indica*: Caesalpiniaceae). Some cutting has taken place, primarily affecting the tecks. The intermediate layer is open except where it is occupied by some patches of aloe; otherwise there is little underbrush, but a substantial leaf litter. In the extreme north of this area, surrounding the village, is an extensive grove of large pamba trees.

Sympatric species. *Lemur mongoz mongoz* is sympatric at Ankarafantsika with six lemur species and subspecies: the diurnal *Lemur fulvus fulvus* and *Propithecus verreauxi coquereli*; and the nocturnal *Avahi laniger occidentalis*, *Lepilemur mustelinus ruficaudatus*, *Cheirogaleus medius*,

and *Microcebus murinus*. Of these, *P. v. coquereli*, *L. f. fulvus*, *A. l. occidentalis*, and *M. murinus* were observed frequently.

In addition to the lemurs, sympatric mammals include the viverrid carnivorans *Cryptoprocta ferox* and *Eupleres goudoti*; the insectivorans *Tenrec ecaudatus*, *Echinops telfairi*, *Oryzorictes talpoides*, and the ubiquitous *Suncus murinus*; the chiropteran *Pteropus rufus*; and sundry rodents.

Raptorial birds that might conceivably pose a predatory threat to *L. m. mongoz* include *Gymnogenys radiata* and *Buteo brachypterus*.

Climate. Since the study was undertaken during the austral winter, precipitation was minimal; the only rainfall to occur was 2.7 mm. on the night of July 22. A Science Associates maximum-minimum thermometer in a plastic orchard thermo-shelter was used to record daily maximum and minimum temperatures ($n = 13$). The

mean maximum daily temperature was 32.3° C.; the mean minimum was 14.7° C. The highest temperature recorded was 33.5° C.; the lowest, 12.0° C.

METHODS OF OBSERVATION

During the study period the times of activity

of *L. m. mongoz* coincided almost exactly with the hours of darkness, and it was thus necessary to observe the animals with the aid of spotlights and headlamps. Artificial light was used as sparingly as possible, however; except when conditions were such as to preclude location of the animals without their use, lamps were employed only during the actual recording of activity.



FIG. 8. *Ceiba pentandra* in figure 5, area B, a dietary staple of H group during period of study.

The groups we studied were in a protected reserve and accustomed to human activity in the forest station compound around which they live. They appeared to be little disturbed by either our presence or our lights. Habituating the animals to us posed few problems, and we were generally able to approach within a few meters of them without producing any obvious effect on their behavior. Nonetheless, initial location of the groups (when their daytime resting place had not been recorded) or their relocation during the night was often difficult because *L. m. mongoz* has only a partially reflecting tapetum. Light reflected from the eyes, therefore, could not consistently be relied on to reveal the presence of the animals. Once located, however, the animals generally proved relatively easy to follow during travel because of both the open nature of much of the forest floor and the seasonal loss of leaves of many trees.

Four people took part in the study and either worked in rotation on one group of animals, or in pairs, following separate groups simultaneously. Observations were focused on activity cycles, group structure and relationships, foraging behavior and diet, and the general ecology and natural history of the species. Observations were generally written in journal form or recorded on tape. The animals were observed for about 250 hours.

Approximately 100 hours of observation were devoted to latitudinal time-sampling, in which the activity of each animal visible to the observer was recorded at five-minute intervals. Latitudinal sampling was appropriate in this case rather than

longitudinal sampling (during which a single animal is followed throughout the observation period) because it was not possible to keep any given individual in constant view for the entire night. Subsequent analysis of the data thus collected, however, has revealed that over the limited period of the study the data were subject to undue bias arising from the highly differential visibility of the various activities recorded. Our observations are in many cases so heavily weighted in favor of those activities most readily visible to the observer that we believe it would be misleading to present them in quantified form. We have, albeit with regret, limited ourselves in this preliminary note mainly to subjective description.

At one stage of the study, continuous observation for 72 hours was maintained on a single group of *L. m. mongoz*; this was done to verify total nocturnality of activity during this season. To the same end, periodic daytime checks were made on sleeping groups when daytime resting sites were known.

RESULTS

Group Size and Composition. Five groups of *L. m. mongoz* were censused during the study (table 1). The census data indicate that this species lives in "family" groups containing an adult male, female, and their immature offspring. Although discrimination between the sexes is facilitated by the sexual dichromatism mentioned earlier, estimation of the ages of immature individuals is difficult in the absence of knowledge of

TABLE 1
Group Size and Composition

Group	Adult		Juvenile		Infant		Totals
	Males	Females	Males	Females	Males	Females	
Ampijoroa (Reserve)							
H	1	1	—	—	—	—	2
T	1	1	—	1	1	—	4
B	1	1	—	1	—	—	3
Lake Ampijoroa							
L	1	1	—	—	—	—	2
Lake Kinkony							
K	1	1	—	—	—	—	2
Totals	5	5	—	2	1	—	13

the reproductive cycle in wild-living populations. Our observations strongly suggest, however, that as in other lemurs mating is seasonal, since the nonadult animals observed during the study appeared to fall into two distinct age-classes. If the birth season of *L. m. mongoz* accords with that of *L. fulvus* in the same area in being restricted to the middle of October, then the older juveniles observed (J2) were approximately 21 months old, and the younger ones (J1) were about nine months old. On this assumption aging is in agreement with the apparent stages of development of the animals concerned. One female in group T, a J2 subadult, did not consistently remain with the group, leaving and rejoining it throughout the night. She did, however, sleep with the group during the day. The most plausible explanation for this behavior seems to be that individuals, upon approaching maturity, become increasingly independent of the parental group.

Groups of *L. m. mongoz* were very cohesive. Generally, all the animals within the group remained in close proximity to one another during activity, and activities of group members were generally coordinated. While sleeping during the day, the adult male and female in each group remained in almost constant contact. The same was generally true during resting periods at night. The juveniles and infants did not usually sleep in contact with each other or with the adults, but remained about 2 or 3 m. apart. Members of the same group invariably rested in the same tree. Travel from one area to another within the home range was done with close coordination between members of the group. Where individuals could be recognized, the adult males of the groups were observed leading travel 24 times while the adult females led group travel 21 times. After travel was initiated, the animals would keep close, often passing one another. If one group member got too far ahead, it would stop and wait for the other(s). Throughout this activity, the animals exchanged contact vocalizations: grunts and "creaking door" sounds (see below). The animals did not coordinate specific movements while feeding on the flowers of the large pamba trees or on nectaries in the hazomboay trees. While feeding in these trees, individual animals ran rapidly and randomly from one flower or leaf

stem to another without regard to the movement of other individuals. However, group members generally began and ended feeding activity in synchrony and almost always fed in the same tree.

There were only two exceptions to this very cohesive and coordinated behavior. The first was the behavior of the subadult female in group T who, as mentioned above, often left her group during the night. The second occurred when the adult male of group B left his group to join this same subadult female. He remained with her for approximately 15 minutes, during which time the only copulation observed during the study was recorded (see below).

Activity Cycles. During the period of the study, the animals were observed to be active only at night. Groups regularly entered their sleeping trees between 05.55 and 06.02 hrs., corresponding to ambient light intensities between 1.4 and 22.0 Lux. Groups left their sleeping trees and commenced activity between 17.55 and 18.01 hrs. (fig. 9), corresponding to ambient light intensities between 2.8 and 22.0 Lux. Our observations indicate that, at least at this time of year, the groups began and ceased their activity with a temporal regularity which, in turn, corresponded to a narrow range of ambient light intensity. Activity during the night was not obviously influenced by conditions of new moon or full moon. Light intensity (Lux) was estimated using a Gossen Luna Pro light meter. Incident readings were taken from a clearing at a height of 1.5 m. with the sensor pointed toward the zenith.

We can provide here only a very general discussion of patterns of activity of the animals throughout the night, since continuous visual contact with them was very difficult to maintain. Those activities such as travel and feeding on flowers where the animals moved rapidly and vocalized frequently were usually easily observed, but those such as feeding on fruit, grooming, and resting, where movement was minimal, were often invisible to the observer. Any systematic quantification of activity cycles on the basis of our data would thus be subject to undue bias.

The night's activity commenced with a prolonged activity period lasting approximately from 18.00 to 23.00 hours. Activity during this time consisted primarily of feeding and travel re-

lated to feeding. However, the entire period of activity was interspersed with short bouts of resting.

A major rest period of about two to three hours' duration occurred between about 22.00 and 03.00 hours. After this rest period activity was resumed. The general pattern of activity at this time was very similar to that of the earlier period of activity. There was, however, one fairly substantial rest period (half to one and a half

hours) before final travel to the sleeping site, which was usually undertaken in one sustained movement. Figure 9 shows a fairly typical night's travel, and its timing, by group H.

While resting during the day, *L. m. mongoz* slept in very dense foliage and often chose the same trees day after day. It did not, however, use nests of any kind.

Utilization of Forest Strata. Lemur mongoz mongoz was observed almost exclusively in the

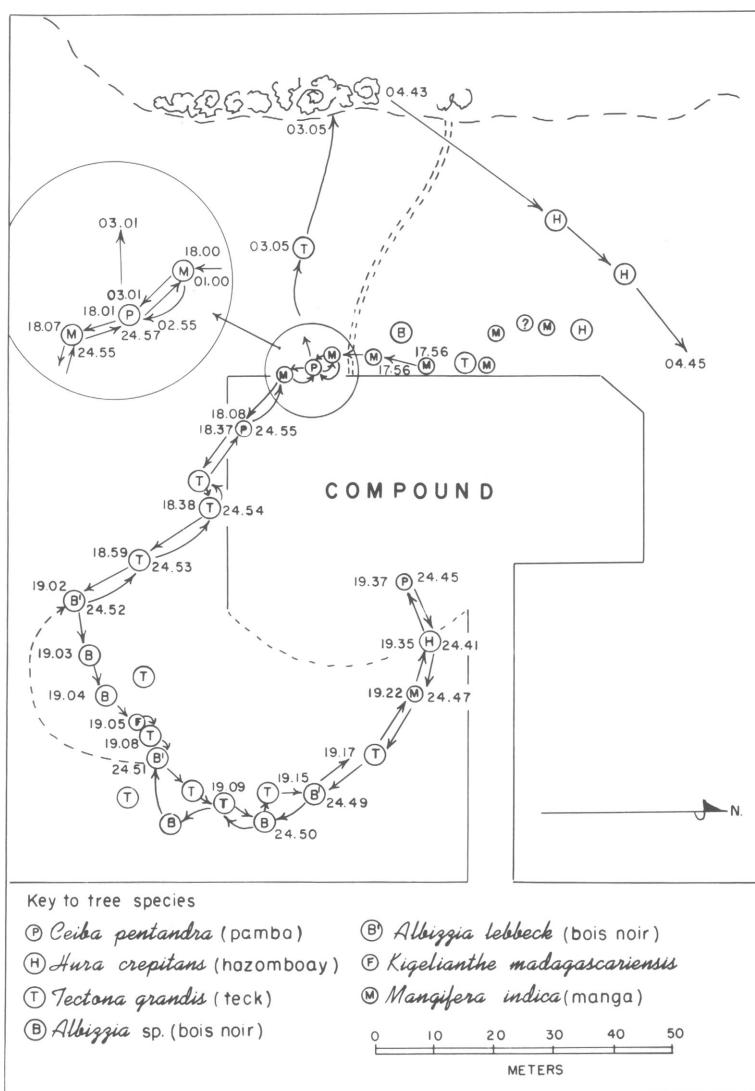


FIG. 9. Movement of group H during night of July 24-25, 1973.

highest strata of the forest, i.e., between about 10 and 15 m. They were seen in the lower levels only while feeding in the lower branches of tall trees or when their continued forward progression necessitated traveling through smaller trees contiguous with the larger ones. Very occasionally the animals would stop briefly to feed in a small tree en route to a regular feeding site. *Lemur mongoz mongoz* was never seen on the ground.

Travel was most easily observed in the largely leafless tecks, which provided a continuous stratum of branches throughout most of the forest at a level above 8 m. (fig. 7). Most travel took place on medium- to small-sized horizontal or, more commonly, oblique branches. Movement along such branches was quadrupedal and usually

rapid. In crossing from one tree to another, the animals almost always jumped, even where the branches of neighboring trees provided a continuous substrate, as was often the case. Although most jumps started from oblique branches, they frequently ended on horizontal or vertical ones, the animals' forefeet in all cases reaching the support first. Travel was most rapid when the animals moved through a succession of oblique branches at the same level.

Lemur mongoz mongoz slept during the day in dense foliage or entangled vines in branches close to the tops of tall trees. In these sites, the animals were extremely difficult to find. Adults generally rested in close physical contact (fig. 10), but juveniles usually slept a few meters away from their parents. Each group tended to sleep



FIG. 10. Adult male and female of group L in typical daytime resting position.

within a specific area of its range (fig. 11); indeed, group H slept in the same tree, a manga, on 11 of the 14 days for which we have records. While resting during the night, however, the animals made no effort to conceal themselves, often resting in trees in which they happened to be feeding or traveling, whether or not they were leafless.

Night and Home Ranges and Group Interactions. The ranges covered by the various groups of *L. m. mongoz* during the period of study corresponded to the specific food resources available at the time. Patterns of group dispersion and movement probably differ radically with seasonal changes in the distribution of these resources. The fact that a single flowering pamba repre-

sented the primary food source for group H during the observation period is thus closely reflected in the observation that a very substantial proportion of the movement of the group took place between the preferred sleeping site (fig. 9) and this tree.

The minimum distance traveled from the sleeping tree to the favored pamba was about 180 m. The minimum distance the animals were observed to travel during one night was approximately 460 m., and the greatest distance the animals were recorded to travel during a single night was about 750 m. At times, travel was very rapid: we observed group H cover more than 150 m. in less than five minutes, despite frequent pauses.

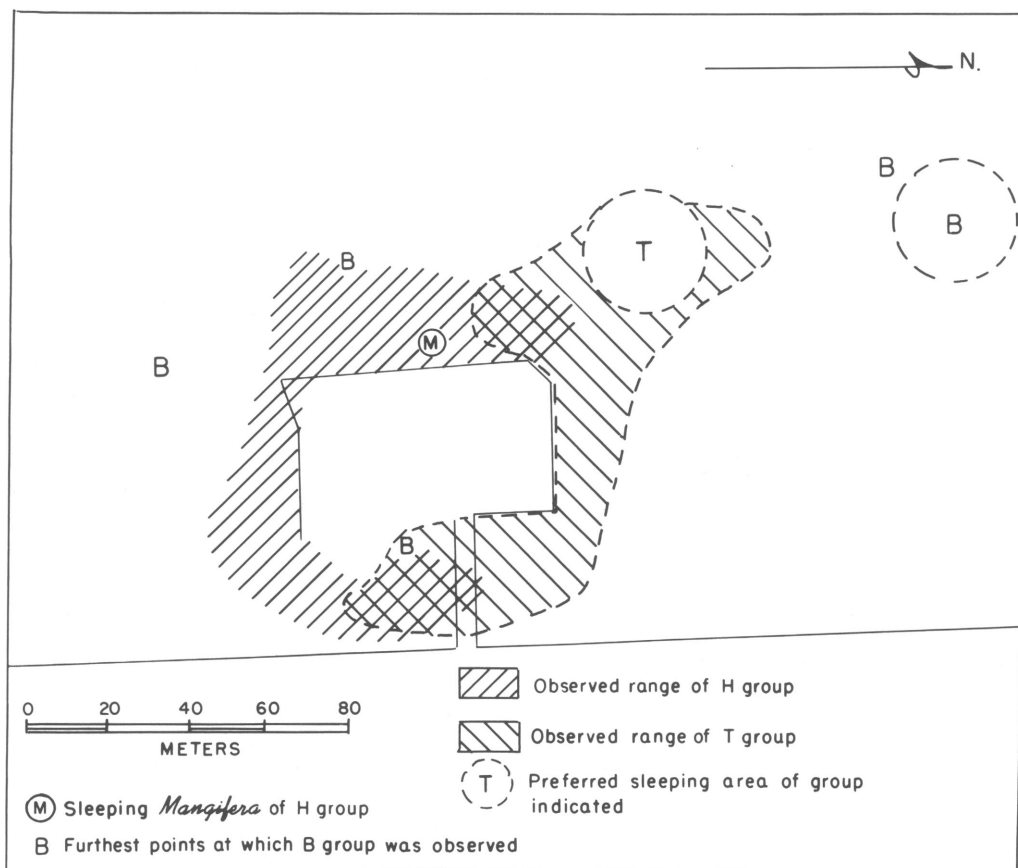


FIG. 11. Observed ranges and preferred sleeping areas of groups H and T; farthest points at which group B was observed.

Over the period of the study, group H was never observed outside an area of about 1.15 hectares (fig. 11); we emphasize, however, that this is very probably a seasonally limited range. From our data we have no way of predicting the definitive range of this group.

Extensive overlap was observed in the ranges of the three groups living in the area of the forestry compound at Ampijoroa (fig. 11). At different times during the night, different groups were observed utilizing many of the same resources. Intergroup encounters were infrequent and very similar to those noted for *Lemur fulvus rufus* (Sussman and Richard, 1974) in that they were never associated with the defense of boundaries: usually, they occurred when one group surprised another by entering the same tree. In no case did any of these encounters appear to be actively instigated by either of the groups involved. The groups usually coordinated their movement by exchanging vocalizations.

During intergroup encounters the animals showed a great deal of agitation. Group members usually remained in close proximity while constantly shifting position in the trees. Individuals would slowly wave their tails from side to side below the branch and might emit "creaking door" vocalizations (see below) or low grunts. Throughout the encounter the males and females of both groups frenetically marked numerous branches, both large and small. Females mark anogenitally and males mark both anogenitally and with glands located on the top of the head. Encounters lasted no longer than four or five minutes and ceased when the two groups moved off in opposite directions. During these encounters, we observed no physical contact between individuals of different groups. Marking continued undiminished for some minutes as the groups moved away from each other.

Diet and Foraging Behavior. *Lemur mongoz mongoz* was observed feeding on five species of plant during the study period. Table 2 shows the percentage of time the animals were observed utilizing each of these resources.

The figures given in the table, however, are almost certainly subject to considerable bias due to differences in the visibility of the various behaviors involved. The animals were highly visible while feeding on flowers, especially those of the

pamba. They would pass quickly from flower to flower, licking nectar from the base of the flower, but for the most part ignoring the petals. The pattern of movement during such feeding appeared to be random, although it was of course confined to the flower-bearing parts of the tree, primarily the terminal branches. In contrast to the movement involved in travel, which was almost exclusively along radiating oblique or horizontal branches, movement during feeding on flowers involved much climbing and leaping between flowering branches at different levels in the periphery of the same tree. The animals assumed an extraordinary variety of postures during such activity.

The preferred method of exploiting flowers above the level of the supporting branch was to reach out with both forelimbs, the hindlimbs fully extended, to pull the flowers within reach of the mouth. When the flowers were below the support, the animal would hang or progress quadrumanally below the branch and feed upside down on nearby flowers. When the flowers required reaching for, it would happily hang upside down from its hind extremities, or even from only one of them, and draw the flowers toward its mouth with its anterior extremities. The flowers were never picked; almost invariably they were released intact after being licked, although occasionally a petal might be consumed. During flower-feeding, the tail was often used in conjunction with the hind limbs. In these instances, the distal portion of the (nonprehensile) tail was wrapped around a branch while the animal hung upside down by one or both hind limbs. When the tail was not used in this manner, it simply hung straight down behind the animal.

Since flower-feeding was done very briskly

TABLE 2
Percentage of Time Animals Were Seen Feeding on
Various Plant Species

<i>Ceiba pentandra</i> (pamba) ^a	81.5
<i>Hura crepitans</i> (hazomboay)	14.0
<i>Kigelia the madagascariensis</i> (hazopanjaka)	2.0
<i>Combretum phaneropetalum</i> (lavanana)	2.0
<i>Tamarindus indica</i> (kily)	0.5

^a All vernacular names are in the Malagasy language.

and noisily in the slender outer branches of the trees, it is highly unlikely that it often went unnoticed by the observers. Feeding on pamba fruit, however, was a much more unobtrusive activity. Again, the animals would not normally detach the long, pendulous fruit, but would eat it in situ, holding it with one or both hands while quietly sitting atop a branch. A part of the green rind was bitten off, and some of the white pulp subsequently consumed, followed by the removal of more of the green outer skin. The process generally took about 10 minutes for a single fruit, but frequently a fruit would be visited several times before the animal, breaking away periodically to explore other sources, was finished with it. We do not have a photograph of *L. m. mongoz* feeding on this fruit, but figure 12 shows a *Propithecus verreauxi coquereli* eating a pamba fruit in much the same fashion. The bias against observation of this process is obviously as great as the bias in favor of flower-feeding; for this reason we consider that table 3 underestimates the time spent feeding on fruit relative to the time spent licking flowers.

A similar observation applies to the exploitation of the hazomboay tree. This also was an activity not easily observed, especially given the dense foliage of the hazomboay at this time of year, although substantial movement around the tree was involved. This movement was, however, slower than the frenetic activity associated with flower-feeding. The leaf itself was generally not eaten; instead, the animals bit off the portion of the stem connecting with the leaf. This ingested portion contained a pair of spherical glands, "nectaries" (fig. 13), that contain nectar. As the animal moved around in the tree, it would either

bring the stem to its mouth and bite off the nectaries or simply snip off the glands with its mouth while passing. After the nectaries had been bitten off, the leaf fell to the ground. Within the space of one minute, an animal might exploit 15 to 20 stems.

Despite the biases we have described, it is clear that nectar provided a major component of the diet of *L. m. mongoz* during the period of study and that pollen may have also been an important constituent. It is interesting to compare this dietary preference to the proclivity of certain bats for feeding on nectar and pollen. Indeed, if competition for this food source existed at Ampijoroa, the most likely competitor of *L. m. mongoz* was the fruit bat, *Pteropus rufus*, although *Microcebus* and certain insects were also seen visiting flowers. In many cases, the large fruit bats and *L. m. mongoz* were seen feeding side by side in the pamba trees, and, in fact, it was sometimes difficult to distinguish between the two at first sight, especially given the propensity of *L. m. mongoz* for feeding upside down.

In many species of bats, nectar and pollen feeding is related to the seasonality of flowers, and most species are frugivorous only during periods of low flower abundance (Heithaus, Fleming, and Opler, In press). Nectar provides the carbohydrate requirement for these animals and may contain some essential amino acids (Baker and Baker, 1973). During nectar feeding, it is possible that *L. m. mongoz* is also ingesting pollen. It has been shown that pollen is a highly valuable foodstuff (Todd and Bretherick, 1942; Pryce-Jones, 1944; Howell, 1974). The most important constituent of pollen is protein, but fats, carbohydrates, vitamins, and minerals are also present. The pollen of many plants, especially those that are "bat-adapted," is very high in total nitrogen and contains all the amino acids regarded to be essential for commonly studied laboratory animals (Howell, 1974). However, the difficulty in breaking down a hard pollen exoderm has led to the evolution of digestive specializations in bats; but in the case of *L. m. mongoz*, knowledge of whether pollen is being utilized must await further study. Further studies will also show if flower feeding in this species is seasonal or locale-specific.

Communication. Visual communication in nocturnal forms is necessarily limited to signals

TABLE 3
Percentage of Time Animals Were Seen Feeding on
Various Plant Parts

Species	Flowers	Nectaries	Fruit	Leaves
Pamba	64.0	—	17.5	—
Hazomboay	—	14.0	—	—
Hazopanjaka	2.0	—	—	—
Lavanana	1.0	—	—	1.0
Kily	—	—	—	0.5
Totals	67.0	14.0	17.5	1.5
	81.0			



FIG. 12. A *Propithecus verreauxi coquereli* consuming fruit of *Ceiba pentandra* in the fashion employed by *Lemur mongoz mongoz*.

given when the animals are in close proximity to each other, and, because of the obvious difficulties attendant upon observing such signals, we

were unable systematically to collect data on communication of this type.

As we have briefly mentioned, both males and

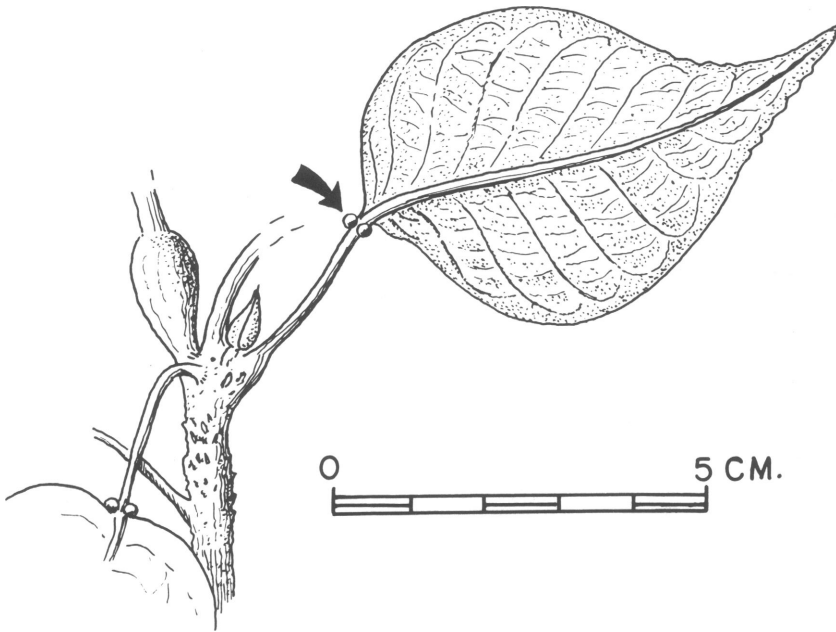


FIG. 13. Leaf of *Hura crepitans*; arrow indicates nectary.

females of *L. m. mongoz* possess glands used in marking. Anogenital glands are shared by both sexes; the males alone possess glands atop the head. Although marking was observed in a variety of contexts, it does not appear to be a dominant component of the behavioral repertoire of the subspecies. Of 26 incidents of marking observed, 10 occurred during or immediately following intergroup encounters. Marking was, indeed, the most prevalent single activity associated with such encounters. Eight incidents of marking occurred during general group movement or travel, while five took place immediately preceding initial travel away from the daytime sleeping tree or before a group entered a feeding tree. In one case, the female marked immediately prior to the only copulation observed, while the male marked the same tree immediately afterward; in another the adult male of group T marked a neighboring tree for several minutes before entering the tree in which the other members of the group had settled for the day's rest.

In all, males marked in 19 of the 26 incidents observed, while females marked only four times.

In three incidents the animal was unidentified. Only four of the male marking incidents involved the head gland; the use of this gland was not consistently associated with any specific activity.

Tactile, like visual, communication can be very subtle and difficult to discern, especially among nocturnal animals. It is, for instance, likely that tactile greeting signals exist in *L. m. mongoz* as in *Aotus* (J. Dahl, personal commun.). We can comment here, however, only on the less subtle tactile communications of grooming and copulation.

Grooming in *L. m. mongoz* was relatively infrequent. Only 18 instances of mutual grooming were observed; in all but two of these cases the grooming partners were the adult male and female of the group concerned. Of the exceptions, one occurred between the adult female and juvenile of group T; the other followed copulation between a male and a female belonging to different groups. Mutual grooming occurred mainly in two contexts: during day resting, usually within the hour before the night's activity commenced; and, less frequently, during short rest periods at night.

A few instances of allogrooming were observed following intergroup encounters or when, for some other reason, the individuals involved were somewhat agitated. More often, however, agitation stimulated autogrooming.

One copulation was observed in the early evening of July 30. This occurred between the black-faced adult male of group B, and a female, probably the J2 subadult, of group T. At about 18.10 hrs. these two animals moved quickly to a remote portion of area B, widely separated from any other group. The details of the behavior sequence accompanying this movement were not observed. The actual copulation sequence was very brief. The female marked, and was then twice mounted by the male. In each case mounting lasted less than 30 seconds and was accompanied by a few quick thrusts; the two episodes were separated by under a minute. Following copulation, the male immediately anogenitally marked the branch on which the mating had occurred. Meanwhile the female had moved a few feet away in the same tree, and was soon joined by the male. An intense bout of mutual grooming, lasting about 10 minutes, followed a short rest. Most of the grooming was done by the female. Just prior to the separation of the animals at 18.25 hrs. the male licked and sniffed the area of the branch where the female had been sitting.

Lemur mongoz mongoz is quite highly vocal, and employed vocalizations in a variety of contexts. Tape recordings of vocalizations were made on a Sony TC-55 tape recorder and analyzed on a Kay Elementrics 6061A Sound Spectrograph, at a frequency response of 4 Hz-4 kHz. Four distinct vocalizations were identified: the grunt (fig. 14C), the explosive grunt (fig. 14B), the rasp (fig. 14A), and the creaking door (fig. 15).

The grunt, a soft guttural sound uttered singly or in series, was emitted in almost all contexts, but most notably prior to or during travel, during feeding, and in association with intergroup encounters. In these contexts grunts may function to maintain group cohesion. Frequently, a single grunt, or even a rapid series, preceded vocalizations of other kinds, but the grunt itself was generally indicative of low emotional intensity.

The explosive grunt, sounding like a loud

grunt combined with a sudden expiration of air, was generally emitted in association with softer grunts, and indicated a state of somewhat higher emotional arousal.

The creaking door vocalization, sounding somewhat like a door moving on rusty hinges, consists of three loud elements, the dominant frequency declining slightly through the series. The two shorter elements contain harmonic overtones at twice the frequency of the fundamental; the longer, initial, element lacks overtones of this nature. Figure 15 shows two creaking doors given in series; the structure of the first, with an initial component of only half the duration, appears to represent a "wind-up" to the second. Primarily emitted during travel, although also associated with intergroup encounters and, to a yet lesser extent, with rest and feeding, the creaking door, which seems to represent an intermediate level of emotional arousal, probably functions primarily to maintain group contact during fast travel, and to maintain distance between groups.

Uttered in yet fewer contexts, the rasp, indicative of the highest level of emotional intensity, was almost always associated with group travel, but occasionally also with group encounters and feeding. Loud and rather hoarse-sounding rasps were often preceded by series of grunts, increasing in tempo and intensity before the utterance of the rasp. Once one member of a group had rasped, the other(s) usually joined in immediately and were often answered in kind by neighboring groups. The rasp, of shorter duration than the creaking door, usually consists of four elements: the first, third, and fourth very brief and the second, main, element more prolonged. Lasting well under a second, and with dominant frequencies at about 1.5 and 1.9 kHz, this element is characterized on sonograms by a series of bands, not strictly identifiable as harmonics, extending over the spectrum from 0.5 to 3.2 kHz (fig. 14).

Interactions with Other Species. At various times, as we have already mentioned, bats, *Microcebus murinus*, and various insects were seen feeding on pamba flowers concurrently with *L. m. mongoz*. Generally, these animals were not seen to interact. In a few instances, however, as *L. m. mongoz* was rapidly running in the pamba tree

while feeding on flowers, it would inadvertently dislodge a fruit bat from a branch. The bat would fly off and alight elsewhere in the same tree.

On two occasions we observed *Propithecus verreauxi coquereli* disturb *L. m. mongoz* groups during the daytime. On one of these, late in the afternoon, a *P. v. coquereli* actively displaced the male of Group L from the sleeping tree and chased him for a short distance. The female followed the male after the *Propithecus* had left,

and the pair commenced activity somewhat earlier than usual. On the other occasion, a group of *P. v. coquereli* entered the regular sleeping tree of group H. There was on this occasion no interaction between the species; the *L. m. mongoz* shifted position in the tree and then resumed sleeping. Similarly, *L. m. mongoz* occasionally disturbed groups of sleeping *P. v. coquereli* during the night.

No definite interactions were observed be-

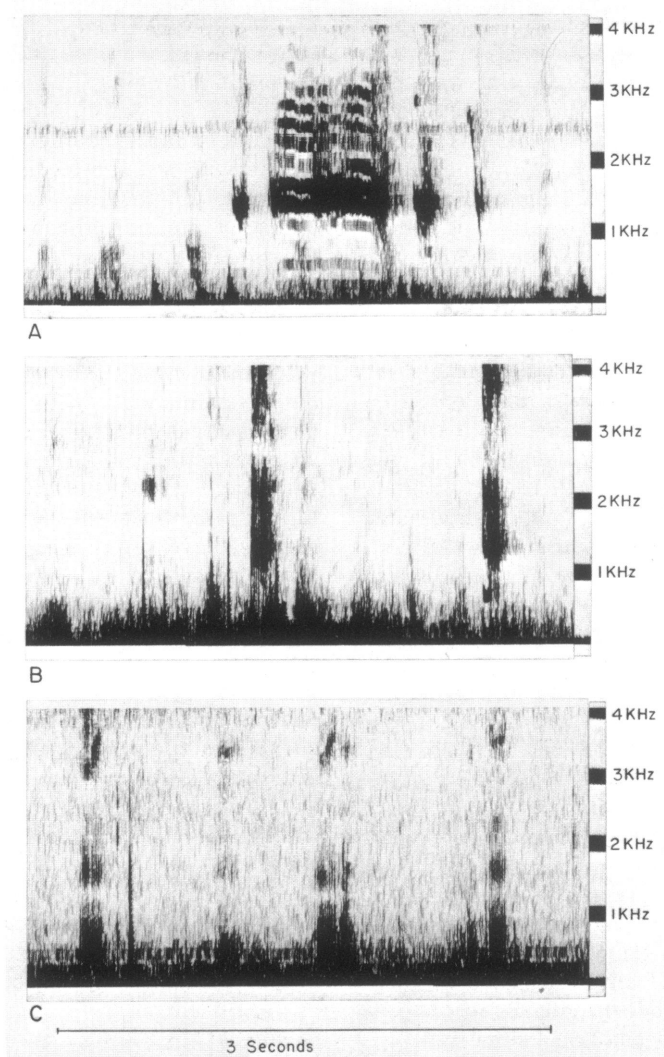


FIG. 14. Sonagrams of tape-recordings of a rasp (A), two explosive grunts (B), a sequence of grunts (C).

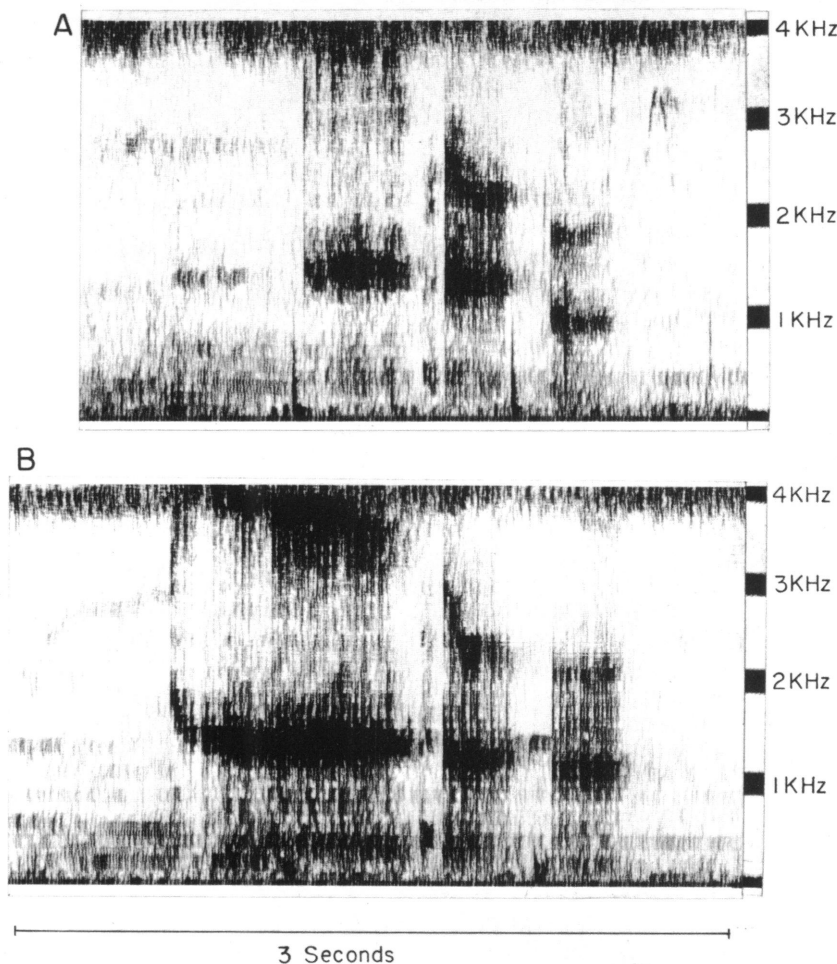


FIG. 15. Sonagrams of two "creaking-door" vocalizations given in sequence. The initial call (A) preceded B by a very short interval.

tween *L. m. mongoz* and *L. f. fulvus*, although groups of both were seen in close proximity. On one occasion, early in the evening, the activity of *L. m. mongoz* may have been stimulated by the passage of *L. f. fulvus*. In another instance, *L. f. fulvus* and *L. m. mongoz* were seen resting during the day close together in the same tree. Despite their similar activity rhythms and size, at no time were *L. m. mongoz* and *Avahi* seen to interact.

SUMMARY AND CONCLUSIONS

On the basis of our preliminary observations,

L. m. mongoz appears to be unique to its genus in a variety of ways. It is active solely at night, at least from July to mid-August, and lives in family groups consisting of a male, a female, and their immature offspring, thus limiting group size to a maximum of four individuals unless twins are born. Unlike other primates living in family groups, groups of *L. m. mongoz* live in home ranges which overlap extensively and, as far as we could determine, do not defend home range boundaries. Marking is associated with intergroup encounters, but apparently is not used to specify range limits.

During the period of the study, *L. m. mongoz* subsisted on a highly specialized diet. This observation accords with the growing evidence (see, for example, Charles-Dominique and Hladik, 1971; Sussman, 1974) that seasonally specialized diets may be more prevalent among the Malagasy prosimians than generally realized. *Lemur mongoz mongoz* ate fruit, but spent most of its feeding time licking flowers, primarily of *Ceiba pentandra* (but also of *Kigelia* *the madagascariensis* and *Combretum phaneropetalum*), and presumably ingesting large quantities of nectar. Group movements at this time of year appeared to be determined largely by the distribution of this food resource. Pollen is a very important component of the diet of numerous species of plant-visiting bats and is of very high nutritional value. It is also possible that *L. m. mongoz* ingests a substantial amount of pollen. Further comparisons between the feeding adaptations of these two mammals may prove informative.

Group composition of *L. m. mongoz* is widely divergent from that of other species of the genus *Lemur*. But it is, on the other hand, similar to that found among other primates (e.g., *Avahi*, *Aotus*) which are almost certainly also secondarily nocturnal. In fact, much of the behavior we have observed in *L. m. mongoz* is reminiscent of behavior reported from preliminary observations on *Aotus*. We believe that further studies of these secondarily nocturnal forms, and in particular of *L. m. mongoz* and *Aotus trivirgatus*, may reveal a wide-ranging spectrum of adaptive similarities.

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