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ABSTRACT

A previous study in Madagascar revealed *Lemur mongoz* to be nocturnal and to exhibit pair-bonding. Subsequent work in the Comoro Islands has shown that, whereas in the warm, seasonal lowland areas of Mohéli and Anjouan *L. mongoz* is likewise nocturnal, in the humid highlands of Anjouan these animals are active during

the day. This difference appears to be environmentally linked. Further, on Anjouan *L. mongoz* exhibits pair-bonding and the formation of "family" groups, but on Mohéli there is variation in group structure. It is possible that group composition of *L. mongoz* on Mohéli undergoes seasonal change.

RÉSUMÉ

Une première étude de *Lemur mongoz* de Madagascar a révélé que celui-ci est nocturne et qu'il vit par couples de deux adultes avec ou sans enfants de moins de deux ans. Une étude suivante faite aux Comores a montré que dans les basses terres chaudes et saisonnières de Mohéli et d'Anjouan *Lemur mongoz* est également nocturne, alors que dans les hauteurs humides d'Anjouan ces animaux sont actifs pendant le

jour. Cette différence semble être liée à l'environnement. De plus, à Anjouan *Lemur mongoz* se montre en couples de deux adultes avec ou sans enfants, alors qu'à Mohéli on rencontre une certaine variété dans la structure du groupe. Il est possible que la composition de groupe de *Lemur mongoz* à Mohéli soit sujette à des changements saisonniers.

INTRODUCTION

With the exception of *Lemur fulvus*, the only lemur species represented by wild-living populations outside Madagascar is *Lemur mongoz* (= *Lemur mongoz mongoz* of most authors).¹ Such populations are restricted to the Comoro Islands, an archipelago of volcanic origin lying in the northern part of the Mozambique Channel, between Madagascar and Africa (fig. 1). Of the four islands comprising the archipelago, *L. mongoz* is found on two: Anjouan (424 km²) and Mohéli (290 km²). Although the means of introduction of lemurs to the Comoros remains obscure, as does its timing, this seems most likely to have occurred as a result of human activities (Tattersall, In press).

The only previously published study of *L. mongoz* was carried out during July and August of 1973 at Ampijoroa, Madagascar, by the present author in collaboration with Dr. R. W. Sussman (Tattersall and Sussman, 1975; Sussman and

Tattersall, In press). Among the more unexpected results of that study were that, at least seasonally, *L. mongoz* a) lives in "family" groups, containing an adult male and an adult female with or without immature offspring, and b) is nocturnal in its activity pattern. In both of these characteristics *L. mongoz* is unique among those members of its genus studied to date.

From mid-November, 1974, to early January, 1975, a survey was undertaken of the *L. mongoz* populations of Mohéli and Anjouan, during which attention was particularly directed toward group composition and activity rhythm. This was done largely in order to test the possibility that nocturnality and the formation of "family" groups were seasonal or locale-specific in the Malagasy animals studied in 1973, and to augment the rather narrow data-base of that study.

ACKNOWLEDGMENTS

This study could not have been undertaken without the active co-operation of the Comorian authorities. In particular, thanks are due the following officials: in Moroni, M. Omar Tamou, Ministre du Développement Rural; M. Ahmed

¹The species *L. mongoz* is generally considered to contain two subspecies: *L. m. mongoz* and *L. m. coronatus*. However, for a variety of reasons, which will be discussed elsewhere, it is clear that *coronatus* deserves separate specific status.

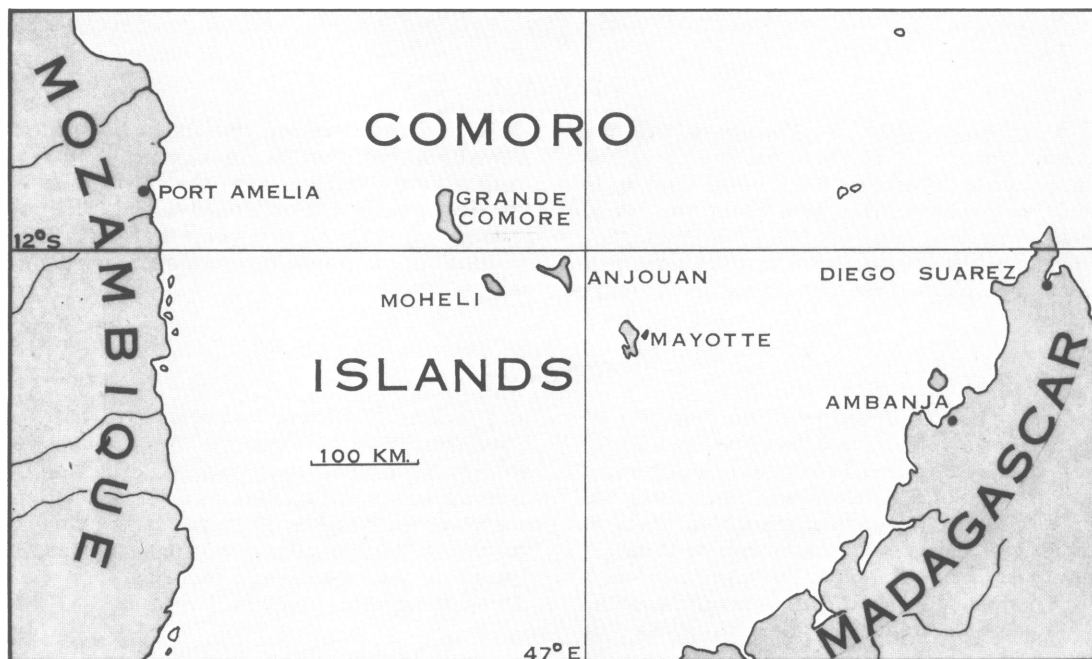


FIG. 1. Location and disposition of the Comoro Islands in the Mozambique Channel.

Djabir, Directeur de l'Agriculture; M. Mouhtar Rachide, Directeur de la Production, Eaux et Forêts; Dr. Francis Debuissy, Vétérinaire; and M. Robert Tapia, Conseiller Technique. In Anjouan: Mm. Swabahaddine Ben Said Mohamed, Ibrahim Mohamed and Nadjib Ahmed, all of the Circonscriptions Agricole or Forestière, Mutsamudu; and the Préfet, M. Abdul Karim Said Omar; also M. Affane Mohamed, of Domoni. In Mohéli: M. le Préfet and M. le Chef de la Circonscription Agricole, Fomboni; M. Mohamed Chararoumane, Chef de l'Elevage; and M. Baco Mari, Surveillant des Forêts; also Mm. Halidi Combo and Ali M'Lindri. Among private individuals, I especially thank M. and Mme. J.-C. Favetto of Moroni; M. and Mme. Soubreville, M. and Mme. Lavarec, and M. and Mme. Fréville of Mutsamudu; and M. and Mme. Latrille and M. and Mme. Ecrepont of Fomboni. The study was made possible by a grant (no. 1305) from the National Geographic Society of Washington, D.C.; I am most grateful for the Society's generous support. The line drawings are the work of Ms. Marjorie Shepatin; I am grateful to Ms. Debra Anne Dobbs for her help with the manuscript, and to Drs. Alison

Richard and Robert W. Sussman for reading and commenting on it. Finally, my thanks above all to Mlle. Christine Lémery, who suffered through it all.

PELAGE AND AGING CRITERIA

In conditions of good visibility, discrimination between the sexes of Comorian *L. mongoz* posed no problem because of a marked sexual dichromatism in the region of the head. Most usefully, the cheeks and beard of the females (fig. 2) are invariably white, whereas those of the males (fig. 3) are a reddish brown. Additionally, the males possess gray faces and white muzzles, in contrast to the black faces of the females, whose muzzles usually possess a much less pronounced whitish spot toward the tip. No evidence at all was found of the two color variants observed among males from the Madagascar mainland (Tattersall and Sussman, 1975).

The sexual distinction is less marked in terms of body coloration, which is predominantly of a mid- to light-gray, usually with reddish brown elements. It was found, however, particularly in

individuals from Anjouan, that whereas the variably extensive reddish brown fur of the male tends to be restricted to the foreparts of the animal, that of the females is generally concentrated posteriorly, leaving the shoulders, forelimbs, neck, and top of the head a pure gray. Resemblance to Malagasy *L. mongoz* is greatest in animals from Mohéli, where the mixture of colors on the body is often somewhat more diffuse. *Lemur mongoz* from Anjouan, particularly from the highlands, appears to be slightly larger than that from Mohéli, and possesses a highly characteristic physiognomy.

Infants and younger juveniles display the white cheeks and beard, and usually the dark face, characteristic of the adult female (fig. 4). Only toward the very end of the survey were some reddish elements beginning to appear on the cheeks (but not yet on the throats) of some juvenile males. No attempt was made during the

study to distinguish between male and female juveniles and infants.

No direct information exists on the timing of the breeding and birth seasons in Comorian, or, indeed, in Malagasy *L. mongoz*. Tattersall and Sussman (1975) found that the stages of development of young *L. mongoz* in northwest Madagascar agreed with the assumption that the birth season of this form coincides with that of *L. f. fulvus* in the same area; this would place the birth season in mid-October. Extension of this assumption to the Comoros suggests that the infant/juveniles observed in Mohéli in mid-November were approximately four weeks of age, and that those observed in Anjouan at the end of the study in early January were aged around 11 weeks. At the beginning of the study the most precocious infants were beginning to leave their mothers' backs and move around independently (transition from infant to juvenile



FIG. 2. Adult female *Lemur mongoz* from Anjouan.



FIG. 3. Adult male *Lemur mongoz* from Anjouan.

status) for part of the time; again, if analogy with *L. fulvus* is permissible, this would suggest an age of four to five weeks since Sussman (In press) recorded that at about four weeks of age the young *L. f. rufus* begins to leave the mother's back. The transition to fully independent status is a lengthy one, however; according to Sussman the infant *L. f. rufus* spends only 30 percent of its time away from the mother at 11-12 weeks, and becomes fully independent only at about 16 weeks. The margin of error on age-estimations based on the degree of contact with the mother is thus large.

Subadult *L. mongoz* aged 14 to 16 months have usually attained both adult size, or very close to it, and adult coloration, but are still sexually immature. Under prevailing observational conditions they were thus difficult to distinguish with certainty on more than a small por-

portion of occasions such as when the genital immaturity of males was observable. The category has not, therefore, been formally recognized in the census tables presented here.

THE ENVIRONMENT

Mohéli, the smallest of the Comoros, is not complex topographically. Roughly oval in shape, it consists of a central longitudinal ridge, 790 meters in altitude at its highest point, which descends fairly sharply to the sea on either side. Coastal plain is very narrow or nonexistent except in the low-lying eastern extremity of the island. Apart from certain limited areas of the central crest at altitudes in excess of 550 meters, Mohéli's vegetation consists entirely of secondary regrowth and plantations. These latter, while including ylang-ylang, bananas, manioc, and rice,

are primarily of coconut palms (*Cocos nucifera*), the dominant floral element of the island. Owing to the low density of human population (approximately 40/km²), few regions of Mohéli are entirely denuded of vegetation, and *L. mongoz* is found throughout the island in relative abundance; the species is apparently at least as successful here in secondary vegetation as in primary forest.

The much greater human population density of Anjouan (over 250/km²), in contrast, has led to the removal of vegetal cover over large areas of the island. Anjouan may be visualized as three peninsulas arranged in a T-formation, striking north, west and south, and each with a more or less well-defined central ridge dropping sharply to the sea. In the central portion of the island, at the junction of the peninsulas, a complex of

massifs rises to 1575 meters, and it is in this area, and in certain limited portions of the southern peninsula, that the surviving rain forest typical of the Anjouan highlands (above about 700 meters) is concentrated. Such forest is disappearing at an ever increasing rate, but still supports *L. mongoz* in what is probably the highest density anywhere. In lower-lying areas of secondary vegetation, however, the abundance of the species is lower than in comparable regions of Mohéli, and in the areas of most intensive ground-cover clearance *L. mongoz* is absent.

METHODS

We followed two rules in censusing *L. mongoz*: first, groups were not included in the census results unless and until the observer was



FIG. 4. Juvenile female (left) and male *Lemur mongoz* from Mohéli. Both are approximately six weeks old; note that both possess the white cheeks and beard characteristic of the adult female.

certain of both the total number of animals active or resting together, and of the sex of each noninfant or nonjuvenile. This normally involved following an active group for as long as was practicable, and the careful searching of adjacent areas. In both Mohéli and Anjouan the ratio of groups located to groups censused was more than 2:1. Second, in order to minimize the possibility of double-counting, no area of forest was visited more than once unless no groups had been censused on the first visit, even where it was known that other groups were present. In the one case where an exception was made to this rule, the census results of the first visit were discarded.

Search time varied considerably according both to the terrain and to the density of lemurs in the area being surveyed. Once a group was located, it was relatively rare that a marked flight response was elicited. Resting groups often moved slightly when the observers approached, which in fact aided exact counting; animals already active were variably easy to census depending on their activity. Feeding animals were easiest to census; traveling ones the most difficult, as their movement was relatively rapid and the terrain and vegetation often considerably impeded observer movement. Few moving groups were considered reliably censused if they had not been followed for at least 15 minutes; counts of resting groups were not recorded where the foliage was dense except where movement, often awaited for a considerable period, confirmed that all individuals had been counted. On the basis of a second study (Sussman and Tattersall, In press) it now seems reasonable to conclude that the *L. mongoz* groups studied in Madagascar are stable over time; in the case of the data presented here there is more emphasis on the observer's inferences as to the stability of the groupings seen.

Light levels were measured using a Gossen Luna Pro light meter with incident light screen. Readings were taken at shoulder-level in areas clear of vegetation with the sensor of the meter oriented to the zenith.

GROUP COMPOSITION

The results of censusing of *L. mongoz* on Anjouan are given in table 1, and the localities of

groups censused are plotted in figure 5. Of a total of 26 groups, eight consisted of one adult male and one adult female. Aside from groups A 10 and A 16, which probably represent special cases and which are discussed below, the remaining groups possessed either three (33%) or four (38%) individuals. The third or fourth individual was an infant/juvenile in 50 percent of cases, and an animal of adult size in the same percentage. Of these latter, 13 in total, six (46%) were males and seven (54%) were females. Mean group size (excluding groups A 10 and A 16) was 3.1 individuals.

The only plausible interpretation of these

TABLE 1
Localities and Compositions of Groups
of *Lemur mongoz* Censused on Anjouan
(Orthography of locality names is French, and
follows where possible that of the 1959
1:50,000 map, Institut
Géographique National, Paris.)

Group	Locality	Male	Female	Infant/ Juvenile
A 1	Hayco	1	2	1
A 2	Hayco	1	1	—
A 3	Daouéjou	1	1	1
A 4	Daouéjou	1	1	1
A 5	Dzialandzé	1	2	1
A 6	Dzialandzé	2	1	—
A 7	Dzialandzé	1	2	—
A 8	M'trouni	2	1	1
A 9	M'trouni	1	2	—
A 10	Jimilimé	—	2	—
A 11	Pomoni	1	2	1
A 12	Changani	1	1	—
A 13	Hombo	1	1	1
A 14	Moujimouvia	1	1	—
A 15	Hagora Iamrogogo	2	1	1
A 16	Bandankoa	2	2	1
A 17	Bandankoa	1	2	1
A 18	Chamninga	2	1	—
A 19	Bouéni	1	2	1
A 20	Dzialandzé	2	1	1
A 21	Daouéjou	1	1	—
A 22	Daouéjou	1	1	—
A 23	Daouéjou	1	1	—
A 24	Daouéjou	1	1	1
A 25	Hamnamgoum	2	1	1
A 26	Maroheni	1	1	—

figures is that, on Anjouan, *L. mongoz* forms "family" groups similar to those observed during the study in northwest Madagascar. Although definite identification of subadults aged 14 to 16 months (the approximate equivalent of the "J2 juveniles" of Tattersall and Sussman, 1975) was possible in only a limited number of cases, the conclusion that the third adult-sized member of any group was in fact subadult is strongly supported by the observation that the proportion of groups containing such members was identical with that of groups containing infant/juveniles. The implication of zero infant mortality may be due to sampling error, but it may well be that such mortality tends to be low in an environment

where predation, even by man, is minimal. It may be significant in this connection that the observations reported here of a mean group size of 3.1 individuals and of no infant mortality are identical with those reported by Pollock (1975) for *Indri indri* which, likewise, forms "family" groups and was studied in an area where it was not hunted.

The interpretation of Anjouan *L. mongoz* groups as "families" is yet further strengthened by the fact that the sex ratio of "third," presumed subadult, animals is approximately 1:1. This is what would be expected in a pair-bonding species where, as here, there is no reason to suspect any marked departure from a 1:1 sex ratio

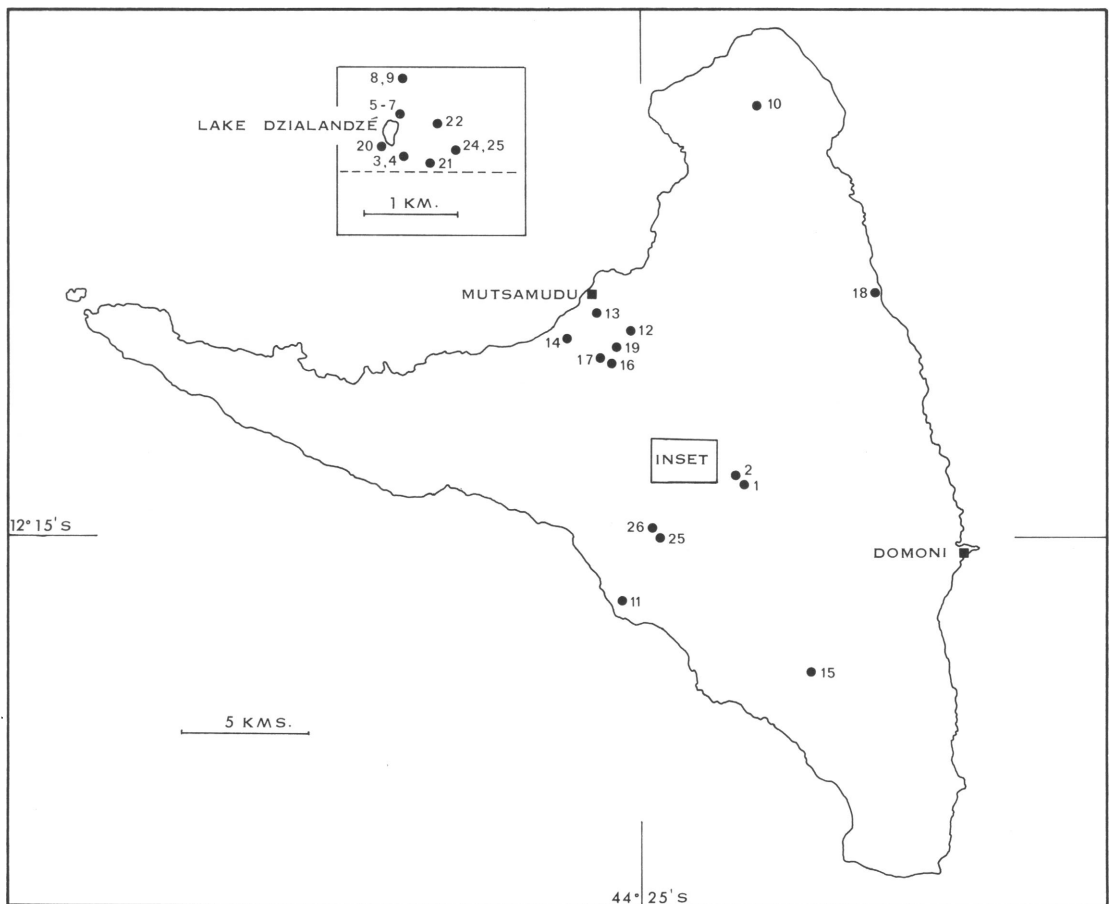


FIG. 5. Outline of Anjouan, to show localities of groups censused.

at birth, or differential viability between immature males and females.

The two groups representing departures from the pattern generally observed in Anjouan may, as suggested earlier, best be regarded as special cases. Group A 10, consisting of two females, one slightly smaller than the other, and living on the outskirts of a large village, represents, according to the testimony of villagers, a "family" group of which the male had recently been lost through human intervention. The composition of group A 16, consisting of two adult-sized males, two adult-sized females and a juvenile, may most plausibly be explained by twinning in 1973. This would represent one birth in the 30 giving rise to the immature individuals censused on Anjouan, or 3.3 percent of births. Multiple births are not rare in the genus *Lemur*; for *L. mongoz* Hill (1973) listed nine sets of twins out of 119 offspring recorded, a rate of 8.2 percent twin births. The assumption in this case of twinning would not, then, appear unreasonable.

During the Madagascar study, counts of five groups of *L. mongoz* yielded a mean of 2.6 individuals per group: three of the five groups were adult pairs without offspring, one possessed four individuals, including a nonadult in each age-category, and the last contained two adults and a subadult. In 1974, three of these groups were recensused by Sussman (Sussman and Tattersall, In press). The subadult female belonging to one group in 1973 had disappeared, as expected, whereas the juvenile male of 1973, now subadult, was still present. The other two groups recensused each contained a new juvenile. Thus the census data from Anjouan, which suggest that each pair produces, on average, two surviving infants every three years, are in agreement with the reproduction/early survival rates observed in the protected reserve at Ampijoroa. It seems likely, however, that survival rates in other, non-protected, areas of Madagascar are considerably lower.

The Mohéli census data (table 2), on the other hand, provide a rather different picture. Of the 22 groups censused, only 10 (45%) appear to have been normally constituted "family" groups, i.e., to have contained an adult pair, with or without a maximum of two offspring, one in each age-category. Even if one adds to these the

six groups in which one twin birth (all, on this reckoning, in 1973; none in 1974) would explain the observed composition, only 73 percent conform to a "family" structure. To explain all such groups thus would, however, involve invoking an abnormally high rate of twinning. Moreover, among these 16 groups the ratio of presumed subadults (i.e., those that would have to be interpreted as subadults to permit the inference of a "family" group structure) to infant/juveniles is 1:1.45; this would represent an unexpectedly large annual variation in either the birthrate or in the pattern of late juvenile mortality.

Of the remaining six groups, two contained three adult-sized males and two females; two contained three adult-sized males, two adult-sized females, and one infant each. The fifth contained four males, two females, and an infant;

TABLE 2
Localities and Composition of Groups of
Lemur mongoz Censused on Mohéli
(Orthography of locality names is French, and
follows where possible that of the 1958
1:50,000 map, Institut
Géographique National, Paris.)

Group	Locality	Male	Female	Infant/ Juvenile
M 1	M'ro Ouamaji	1	1	—
M 2	Mibani	1	2	1
M 3	Ouallah	1	1	—
M 4	Moihani	1	1	—
M 5	Cariela	3	2	1
M 6	Cariela	1	1	1
M 7	Comodjou	1	1	—
M 8	Comodjou	4	2	1
M 9	Djoiezi	3	2	—
M 10	Domoni	2	2	1
M 11	Domoni	2	2	—
M 12	Hoani	2	2	—
M 13	Singani	3	2	1
M 14	Kangani	2	2	—
M 15	M'Babani	1	1	—
M 16	M'Babani	—	4	—
M 17	Djoumadounia	3	2	—
M 18	Mahoudjani	1	2	1
M 19	Mdronisiri	2	2	—
M 20	Bandaharisiri	1	1	1
M 21	Darine	1	1	—
M 22	Combani	1	1	1

this was the largest agglomeration observed. The most oddly constituted of all, however, was group M 16, which contained four females. Such a grouping is unlikely to have been other than ephemeral and, taken in conjunction with the observation of a high proportion of pairs together with groups of more complex composition, leads to the speculation that seasonal variations in group structure may occur, and that censusing was undertaken during the transitional period.

There are a few indications, albeit somewhat indefinite, in support of the hypothesis of seasonal change, at least as far as Mohéli is concerned. First, if the observations reported here were, in fact, being made during a seasonal transition, the transition was occurring at a logical time of year. There is a fairly sharp seasonal variation in rainfall in the Comoros,

although local microclimatic variation (but least of all on Mohéli) may be substantial. In both Mohéli and Anjouan, November represents the tail end of the dry season; the generally rather sudden onset of the rains at the beginning of December has profound effects on the vegetation. Not much rain fell during censusing on Mohéli, but heavy rain began to fall immediately thereafter. If seasonal variation in group structure does occur, a season of climatic and phenological change is a reasonable period in which to expect social change to take place.

Secondly, there is some observational evidence that might be viewed as supporting the fission and/or coalescence of groups. Thus, when groups M 5 and M 6 were censused on November 23, the two were initially thought to constitute a single unit: they were found resting very close to each other as dusk approached, without showing

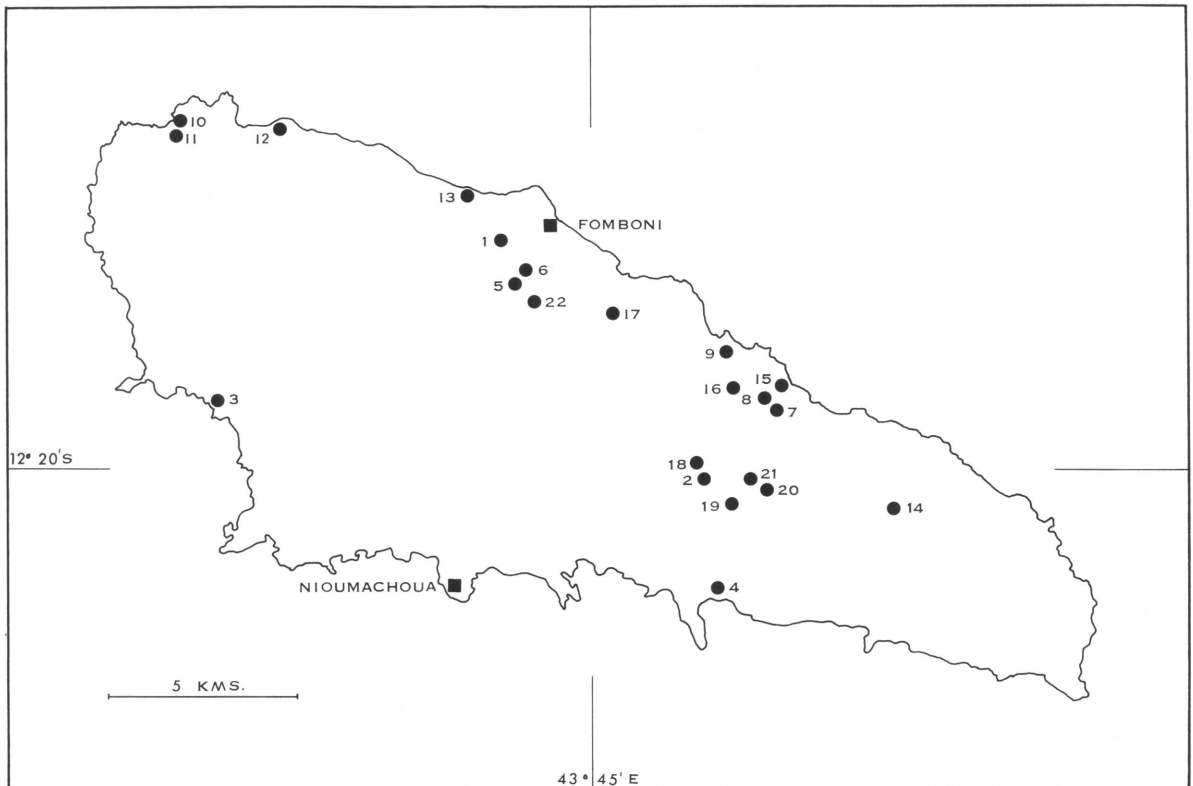


FIG. 6. Outline of Mohéli, to show localities of groups censused.

any signs of unease. Finally, however, the animals of group M 5 moved off by a route which took them closely by group M 6; the latter stayed where it was and showed no reaction whatever, leaving its resting place some 12 minutes later, in almost the opposite direction. Although in Madagascar home ranges of *L. mongoz* groups were observed to overlap extensively, there and in Anjouan group encounters involved a great deal of agitation. It thus appears unlikely that in either place totally discrete groups would rest in such close proximity yet remain apparently indifferent to each other's presence. The most plausible explanation may be that this incident (or nonincident) represented either a large group in the process of fission, or a stage in the coming-together of smaller units.

But if this explanation is far from firm, determination of the polarity of such change is yet more so. Inference from *L. mongoz* elsewhere is hazardous in itself, and, beyond this, data from Anjouan and Madagascar, even if admissible, point in diametrically opposite directions. In Madagascar, pair-bonding was observed in *L. mongoz* during the dry season; in Anjouan not only was it found at the beginning of the wet season in environments apparently comparable with those surveyed in Mohéli, but it was also found to be characteristic of groups living in the more or less permanently humid highlands of the interior. If such seasonal shifts do occur, it would seem more reasonable to expect the larger groupings to characterize the wet season, the period of the greatest abundance of resources. On the basis of currently available data, however, the hypothesis of seasonal change is far from certain; the possibility that we are observing geographical variations due to factors such as habitat or population density cannot be ignored.

The overall sex ratios of adult-sized animals were virtually identical between Mohéli and Anjouan: 37 males to 37 females (1:1) in the former, and 32 males to 33 females (1:1.03) (ignoring group A 10) in the latter. In Madagascar, with a much smaller sample size, and including the single J1 juvenile, whose sex was ascertainable, the ratio was similar: six males to seven females (1:1.17).

It is, then, impossible at present to make any definite statement as to group composition, and its variability, in *L. mongoz*. It seems most likely,

however, that group structure shows geographical differences, i.e., that pair-bonding is typical of both Anjouan and Madagascar, but that in Mohéli the composition of social units is more variable, possibly, but not certainly, on a seasonal basis. What does clearly emerge is that studies of entire annual cycles in different environments in all three areas will be needed before we can confidently speak of group structure in the species as a whole.

ACTIVITY RHYTHM

During the Madagascar study *L. mongoz* was observed to be active solely at night, between approximately 1800 and 0600 hrs. Ambient light intensities when activity commenced were in the narrow range of 2.8 to 22.0 Lux, and when it ceased, of 1.4 to 22.0 Lux.

In Madagascar, observations were made on groups of *L. mongoz* that had become fully habituated to the observers. In the Comoros, on the other hand, no intensive study preceded by an habituation period was made, and it was thus not possible to be completely certain that activity observed before nightfall was not stimulated by the arrival of the observers, usually in the company of local people. It seems probable that the lemurs were normally aware of the presence of the observers well before we located them. Observational bias, therefore, is likely to have been toward the early commencement of activity, although in general Comorian *L. mongoz* is quite well habituated to human presence and, since hunting is rare, not unduly disturbed by it.

Surveying in the early morning was more difficult, and generally less successful, than in the afternoon and early evening. No *L. mongoz* were seen on Mohéli to be active in the hours following sunrise, but sampling was unsatisfactory during this period, and attention will be paid here only to observations made on that island between noon and 2230. The official time of sunset during surveying on Mohéli ranged between 1807 hrs. and 1819, and on Anjouan between 1822 and 1832.

On Mohéli, *L. mongoz* groups censused during the hours of daylight were virtually always sleeping, or, since they were generally aroused by the approach of the observers, resting. During the

late afternoon juveniles were occasionally observed moving around a little while the adults of their groups rested. On only two occasions was *L. mongoz* observed to be active at light levels higher than those which triggered activity in the Malagasy animals. On November 24, at Comodjou, group M 7, consisting of an adult male and female, was observed feeding at 1815, at a light level of 115 Lux. On November 28, group M 15, another adult pair, was observed traveling, although not rapidly, at 1746, when the light level was around 6300 Lux. On two occasions *L. mongoz* groups were observed during the late afternoon in postures and dispositions which did not suggest resting, although the animals were not moving when located.

All *L. mongoz* observed in Mohéli after the official hour of sunset were active at the time of censusing, generally either traveling or feeding. No observations were made after 2230, and the activity invariably recorded between nightfall and this time accords well with the observation of a prolonged activity period at Ampijoroa, Madagascar, between approximately 1800 and 2300. Further, observations on Mohéli suggest that the pattern observed at Ampijoroa, where initial activity consisted of a period of travel away from the sleeping site followed by a long feeding bout, held equally there.

Results from Mohéli thus suggest that the pattern of activity on this island does not differ substantially from that recorded in Madagascar. This corroborative observation allays the suspicion that the nocturnal activity of the animals observed at Ampijoroa may have been related solely to the night-flowering of the kapok tree, *Ceiba pentandra*, whose flowers provided their principal dietary resource during the period of the study (Tattersall and Sussman, 1975).

The data from Anjouan, however, provide a less clear-cut picture. In areas of low-lying secondary vegetation, which offer an environment comparable with those surveyed on Mohéli, an essentially similar pattern was found to that observed on the smaller island. Only on one occasion was a group (A 16) of *L. mongoz* seen to be active earlier than 30 minutes before the official hour of sunset; this was at Bandankoa at approximately 1715 on December 27, at a light level of ca. 1800 Lux. Since the locality at which

this observation was made was close to a well-traveled path, it is possible that this early activity was due to disturbance by earlier passersby; certainly, the later the hour at which sleeping *L. mongoz* groups are disturbed during daylight, the more likely they are immediately to commence sustained activity.

In the highland rain forest, however, at altitudes above ca. 600-700 meters, the survey suggested a radically different activity pattern. The difficulties of access to these areas precluded the observation of *L. mongoz* later than about 1930 hrs., but observations at other times indicated that activity continued throughout the hours of daylight and beyond. Of the 15 groups censused in these highland areas between 0850 and 1930, only two were resting; a further two may have been moving as a result of our approach. All the others were moving, traveling or feeding and, indeed, group encounters were observed on two occasions. One of these, between groups A 8 and A 9, took place at M'trouni, at approximately 1230 on December 14, when the two groups, approaching from opposite directions, surprised each other in the same patch of vegetation. In form it was very similar to the encounter witnessed at Ampijoroa (Tattersall and Sussman, 1975), with the major exception that vocalization, which at Ampijoroa included "creaking door" vocalizations as well, was limited to grunting, of which there was a great deal. The other occurred toward dusk on December 30, at Daouéjou, between groups A 23 and A 24, and included the entire vocal repertoire heard at Ampijoroa. This was a more long-drawn-out confrontation than the earlier one, lasting over a quarter of an hour as opposed to about two minutes, and commenced when the light was already failing; it continued, in bouts, until the light level had sunk below 2.8 Lux, and it was followed by feeding sessions on the part of both groups.

Ambient temperatures and light-levels are considerably lower in the humid central highlands than in the lower-lying coastal areas; at 1030 on December 14, for instance, a light reading of only ca. 3400 Lux was recorded, this on an average day for the time of year, and mist frequently descends over the rain forest. Since diurnality was observed only under these environmental conditions, whereas in the drier,

warmer, brighter and more seasonal lowland environments of both Anjouan and Mohéli (and, for that matter, of Madagascar), a relatively strict nocturnality was seen, variation in activity pattern appears to be environmentally linked. Possibly the diurnality of the lemurs of the Anjouan interior is due to limitations of thermoregulation

during the cold nights they experience. Again, as in the case of group structure, longer-term studies in all three areas and in a variety of environments will be necessary before the full complexity and significance of activity patterns in *L. mongoz* can be appreciated.

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