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Claude Marcel Hladik, Pierre Charles-Dominique

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C. M. HLADIK and
P. CHARLES-DOMINIQUE

*The behaviour and ecology of the sportive lemur
(Lepilemur mustelinus) in relation to its
dietary peculiarities*

Introduction

In the course of a field-visit to the south of Madagascar (September/October 1970), *Lepilemur mustelinus leucopus* (F. Major 1894) was intensively observed in order to define the ecological characteristics of this nocturnal folivorous species (Fig. 1a), which is adapted to particularly arid conditions in this region. Study of one population provided us with an understanding of the social structure, permitting comparison with other prosimian species. Subsequently, a laboratory investigation was conducted on various samples from a digestive tract collected in Madagascar. This permitted more detailed examination of the phenomenon of *caecotrophy*, which had previously been observed in the field.

Field conditions

The sportive lemur,* which is still the subject of taxonomic debate, is found in almost all Malagasy forest areas. Most of the observations made during the present study were carried out in South Madagascar in a quite distinctive forest zone — Didiereaceae bush. This spiny bush forest is characterised by dense undergrowth composed of bushes, lianes and shrubs, dominated by species belonging to the Didiereaceae (a primitive endemic family intermediate between the Cactaceae and the Euphorbiaceae). *Alluaudia procera* and *A. ascendens*, which are the principal representatives of the family in

* The name 'sportive lemur' does not refer to the animal's motor activity, but to the defensive attitude which it adopts when threatened. The hands are used in the manner of a boxer to strike at the aggressor.



Figure 1 (a). The Sportive Lemur *Lepilemur mustelinus leucopus* (F. Major), photographed whilst active at night.



Figure 1 (b). The Didiereaceae bush occupied by the Sportive Lemur in the main study area (Berenty region; South Madagascar). The predominant plant representatives are the tall, taper-like *Alluaudia procera* and *A. ascendens*.

the Berenty region (S. Madagascar), constitute 65 per cent of the vegetation (Fig. 1b). These species resemble large, more-or-less ramifying tapers, about 12 m. in height, with a covering of fleshy leaves set at the bases of hard, sharp spines. Here and there, baobabs and some arborescent leguminous species project above the bush, which lacks a true canopy.

A different plant formation — *alluvial forest* or *gallery forest* — lines the rivers in the same area as a band 100-800 m. in width. This classical forest type is dominated by tamarind trees, which form the closed canopy at a height of 25-30 m., above a relatively scanty under-growth. Observations were conducted in this second type of forest purely for comparative reasons. The transition from gallery forest to Didiereaceae bush is very abrupt.

There is a long dry season, and rainfall (500 mm./year) occurs mainly during the austral summer (December/January/February). The monthly average of the maximum daily temperatures fluctuates between 37°C (austral summer) and 28°C (austral winter), and the monthly average minimum temperature fluctuates between 26°C (austral summer) and 16°C (austral winter).

In this xerophile forest formation, most of the plant species store reserves of water for the austral winter, which is particularly dry. In fact, our observations were conducted during part of the austral

winter, and in that particular year (1970) there was an exceptional drought more pronounced than any experienced over the last ten years, at least.

Diet

In the Didiereaceae bush, the sportive lemur feeds primarily on the tough foliage of the two *Alluaudia* species, and on their inflorescences when the latter are available. *Alluaudia* flowers appear at the end of the dryest period, at a time when almost all of the leaves have fallen. Thus, the sportive lemur survives for some time on the basis of these flowers, which disappear when the first leaves begin to appear. The leaves of certain shrubs and lianes (*Salvadora augustifolia*, *Xerosicyos perrieri*, *Marsdenia cordifolia*, *Boscia longifolia*) are eaten in far smaller quantities. In addition, there may be a large number of other species whose leaves are utilised occasionally, along with certain fruits, since the present list is entirely derived from the end of the austral winter.

The sportive lemur is distinguished from other prosimians by its restricted motor activity during the night, which may obviously be correlated with the poor calorific value of the diet. As soon as the sun sets, the animal — which spends the entire day hidden in a tree-hollow, a fork of *Alluaudia ascendens*, or (more rarely) in a bundle of lianes or *Euphorbia* foliage — makes a number of rapid leaps to arrive at a leafy ramus, where it will 'browse' for short periods of 1-10 minutes (about 10 sessions per night). Apart from these feeding periods, the sportive lemur remains immobile almost continuously, rarely changing its place. When the animal does move, it makes a few rapid leaps and then remains immobile 10-20 m. away.

In the section on 'social life', it will be seen how we were able to study an entire population by capture, marking and release. The individual animals, which were exceptionally lacking in timidity, could be followed continuously with the light of a head-lamp. After a few days, we were able to observe the animals continuously from 3-6 m. without disturbing their activities. Such favourable conditions permitted us to observe the animals clearly and continuously. We were able to identify all of the food items taken, and vegetation samples taken back to the laboratory in France allowed us to conduct detailed analyses. In addition, continuous observation of individual animals and examination of digestive tracts collected at different times permitted us to determine the average dietary intake.*

* We are indebted to the Service des Eaux et Forêts de Madagascar for a special authorisation to capture a small number of specimens for subsequent laboratory analysis.

In collaboration with the Institut National de la Recherche Agronomique (Laboratoire d'Analyse et d'Essai des Aliments), we have analysed and described the average composition of the diet,¹ which is essentially composed of crassulescent leaves. This represents the 'poorest' diet hitherto observed in a primate: 13.6% vegetal proteins; 1.8% lipids; 4.9% reducing sugars; 15.1% cellulose and a 'complementary fraction' representing 64.6% (Fig. 2). The latter fraction is essentially composed of long-chain sugars (ligno-celluloses and hemicelluloses), which cannot be digested by most mammals, together with a large mineral component.

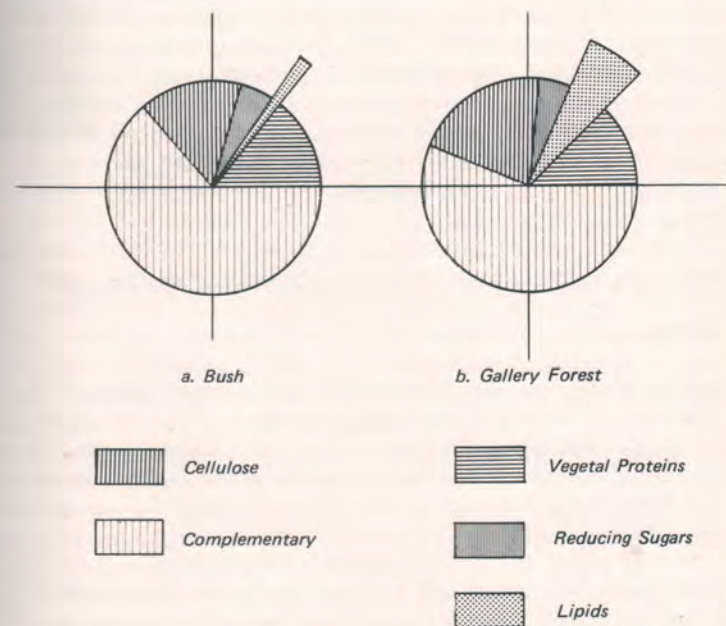


Figure 2. Diagrammatic representation of the dietary components of the Sportive Lemur in Didiereaceae bush and in gallery forest of South Madagascar.

In the gallery forest lining the river Mandrare, other individuals belonging to the same sportive lemur subspecies were, during the same period, feeding primarily on the leaves of *Tamarindus indica*, which contain 12.5% proteins, 6.0% lipids, 4.8% reducing sugars, 20.5% cellulose and a 'complementary fraction' of 56.2%. This composition is little different from that available to the animals feeding in the dryest areas of the bush (Fig. 2).

If this diet is compared with that of other known folivorous primate species, there is a considerable difference. In particular, the

howler monkey (*Alouatta palliata*), which is the most folivorous of the South American monkeys, has a diet under natural conditions which includes a large proportion of fruits (60%), and thus has a relatively higher proportion of reducing sugars (21.7%), which are easily assimilable.² Similarly, among the Colobinae of the Old World the proportion of fruits included in the diet is quite high: 28% in *Presbytis senex* and 45% in *P. entellus*.³ It is therefore certain that conditioning to soluble components of the diet, which plays an important part in the feeding behaviour of the 'higher' primates, is of negligible importance for *Lepilemur*. An immediate response to certain soluble components (principally short-chain sugars) can lead to rapid conditioning, which increases the efficiency of the animal in its natural environment, where it must detect its food with maximum yield. This constitutes motivation of the hedonic type. By contrast, conditioning through factors independent of the 'olfactory-gustatory' sense (physiological factors corresponding to an increased feeling of 'well-being' arising after the animal has taken its food) may play an important part in determining the sportive lemur's activity rhythm.

Dietary utilisation (caecotrophy) and the energy budget

Calculation of the energetic value of the dietary intake (about 60 gm. of fresh food per night), which was determined as part of the study already mentioned, shows that those nutritive elements which are readily assimilable (proteins, lipids and reducing sugars) represent only a weak energy source (13.5 Kcal. per day) for an animal weighing 600 gm. on average.

In fact, the cellulose fraction of the diet is degraded in the course of its sojourn in the caecum and colon of *Lepilemur*. The products of the components thus degraded are at least partially resorbed by the animal during a second passage of the food through the intestinal tract, which is achieved through *caecotrophy* (ingestion of certain faeces).

The behaviour pattern of re-ingesting certain faeces is reminiscent in several respects of similar behaviour in the rabbit, which is now well documented.⁴ At about the mid-point of its diurnal resting period, the sportive lemur exhibits a phase of hyper-excitability. The animal begins by licking its fur and then concentrates on licking the anogenital region. When doing this, the thighs are spread apart and the tail is curled upwards, such that the pelvic area forms a kind of basin. The animal licks its anus and raises its head from time to time in order to swallow. This behaviour was observed directly on several occasions, always at the hottest time of the day (14.00-15.00 hrs.); but it would seem that it can also occur in the morning, as soon as

the animal has returned to its daytime retreat. In fact, in the stomach contents of an animal captured at 7.00 hrs. we found fatty acids of bacterial origin, which could have originated from contamination by material re-ingested the day before, but which were more probably produced in the caecum and re-ingested as soon as the animal returned to its diurnal resting-place.

Analysis of the digestive tract contents of animals captured at different times of the day and night permitted us to follow the actual transformations which take place. In order to conduct this analysis, we profited from the period when the animals were feeding essentially on the leaves and flowers of the two *Althaudia* species (which are very similar in composition), in order to have a 'basic diet' formed of a homogeneous mixture of these dietary samples. The differences in composition along the digestive tract are very marked, and there is no possibility of confusion. Although the basic diet only contained long-chain fatty acids, gas chromatography demonstrated that ramifying short-chain fatty acids ($C \leq 16$) with uneven numbers of carbon atoms were present in the digestive tract (analysis carried out at INRA).⁵ The bacterial origin of these latter acids, and their abundance in the caecum, is not surprising. Electron micrographs of the caecal mucous membrane showed a dozen species of small-sized bacteria in contact with the microvilli. The structure of the caecum itself, which is lined with long villi supported by prolongations of the muscularis mucosae, shows that there must be mixing movements allowing rapid fermentation. The caecal contents become more and more fluid as the transformations progress.

The ingested food initially undergoes rapid absorption of the soluble fractions, which results in an apparent augmentation of the proportions of ligno-cellulose (rising from 21.4% to 43.0%). In the caecum, there is first of all hydrolysis of the cellulose fraction, which brings about a reduction in the ligno-cellulose level (17.5% in the caecal contents by the beginning of the night). The hemicelluloses are subjected to much slower degradation; their concentration amounts to 51.8% of the dry weight of the caecal contents, drops to 34.5% in the colon by the beginning of the night and reaches 20.6% in the faeces. Thus there is a progressive inversion of the hemicellulose/ligno-cellulose ratio, which changes from 3.9 in the caecum to 0.45 in the faeces.

The caecal contents are enriched with proteins (up to 36.0%, whereas the basic diet contents incorporate only 15.1%). The surplus protein is derived from desquamation of the mucous membrane and proliferation of bacteria. The importance of caecotrophy thus lies in limitation of nitrogen-loss. In the rabbit, the caecal matter which is re-ingested similarly contains a much higher concentration of proteins than the ingested food, and there is a marked difference in appearance between the caecotrophe (re-ingested caecal material) and the true faeces. In *Lepilemur*, however, we did not find any

clear-cut morphological difference between the 'true' faeces and the caecotrophe.

In order to calculate an approximate energetic balance for *Lepilemur*, we selected an average example provided by an adult male which was continuously followed from the onset of activity until its return to rest. This individual ingested 61.5 gm. of leaves and flowers, corresponding to 8.0 Kcal. of proteins, 2.7 Kcal. of lipids and 2.8 Kcal. of carbohydrates, and thus to a total of 13.5 Kcal. of directly assimilable elements. The energetic contribution based on bacterial degradation of celluloses can be estimated at 10-15 Kcal. Thus, the overall energetic product is less than 30 Kcal/24 hr.

In the example studied (Fig. 3), the animal which was followed covered 270 m. in the course of the night, making 180 leaps of about 1.5 m. Standard calculation of the energy expenditure indicates a minimum muscular expenditure of 2.16 Kcal.⁶

According to standard calculations of the basal metabolism, an animal of 600 gm. would require 40-60 Kcal. per day. In fact, it is known that many tropical and equatorial animals have imperfect thermoregulation and a basal metabolism inferior to the norm calculated for palaearctic animals adapted to cold climates. As has been demonstrated by Kayser (see also Bourlière and Petter-Rousseau)^{7,8} the metabolic level of homoeothermic animals increases, with increasing perfection of thermoregulation, whilst some primitive homoeotherms in regions with a uniform climate have a basal metabolism at half the standard level. Research in progress in Gabon has confirmed this marked difference at the physiological level between primitive species derived from tropical and equatorial areas and species derived from temperate regions, on which the standard values have been based. For example, Hildwein⁹ has shown that the basal metabolism of certain lorises is inferior to that of 'true' homoeotherms, amounting to a deficit of 20-30% in *Arctocebus calabarensis*, and of 50% in *Perodicticus potto*.

Thus, one can expect that *Lepilemur* has a basal metabolism requiring in the order of 20-30 Kcal.

This crude calculation is not intended as an exact indication of the energetic balance. It simply demonstrates, for an animal living under natural conditions, a system permitting it to survive with a minimal energy-input.

During the night, movement is fragmented into brief, regularly spaced periods (approximately twenty per night, see Fig. 3). Thus, chemical thermoregulation is augmented by the production of muscular heat energy at the time when it is most necessary. By contrast, during the diurnal resting phase, when the external temperature remains in the region of 30°C, energy expenditure must be minimal (bearing in mind the insulation provided by the dense fur).

The sportive lemur does not have to move far to find its food: a

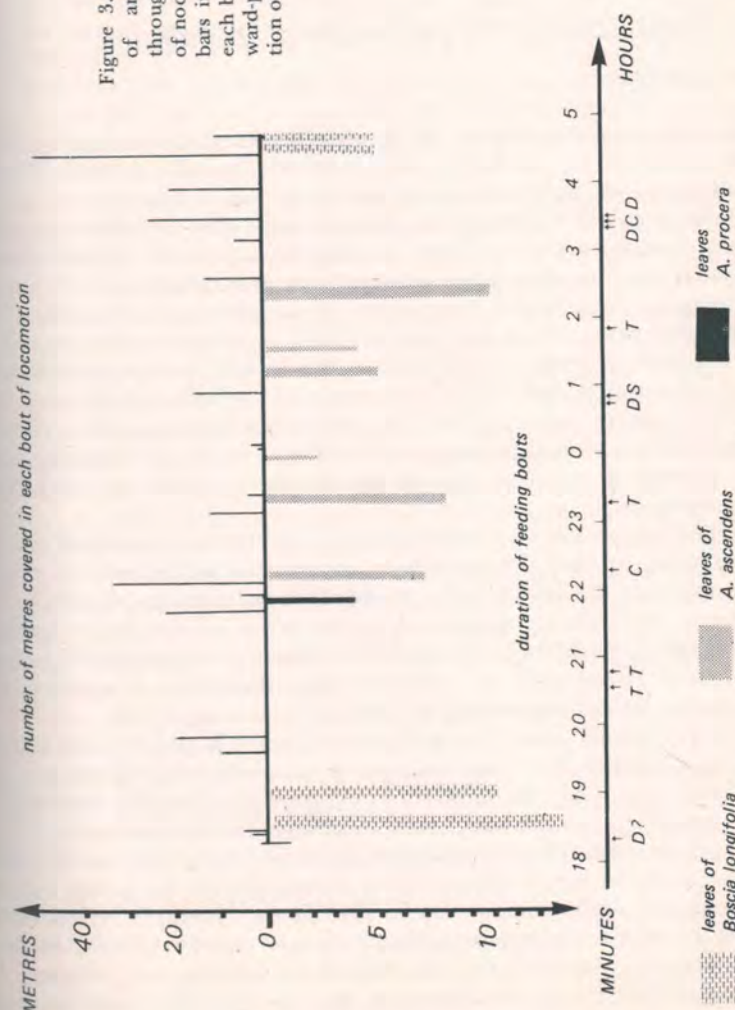


Figure 3. Diagram illustrating movement of an adult male sportive lemur through his home range in the course of nocturnal foraging. Upward-pointing bars indicate the distance travelled in each bout of locomotion, while downward-pointing bars indicate the duration of each feeding bout.

single leaf-bearing ramus will suffice for one night. Thus, the animal performs a minimal muscular effort in moving around (scarcely more than 10% of the total energy expenditure). This economic way of life necessitates maximal utilisation of a naturally poor food-source, from which celluloses can be assimilated only after bacterial degradation. Accordingly, caecotrophy is a specialisation permitting utilisation of a food-source which normally yields little energy. This process, which is common among rodents and lagomorphs, seems to be exceptional among primates; nevertheless, it is less efficient than rumination, which permits even better utilisation of ligno-celluloses.¹⁰

Adaptation to the environment: population densities

The economic life-style of the sportive lemur is further expressed in the utilisation of extremely small home-ranges within which it can find its food. In the Didiereaceae bush, the average area of each home-range is 2,300 square m., and we were able to calculate under field conditions that the food available in the month of September could (theoretically) have provided for a maximum of 50 days. Bearing in mind the irregularity in distribution of plants and territorial demarcation (see next section), this figure can be regarded as a *minimum* which is explained by the drought present throughout the observation period. This exceptional drought, which was far more marked than any in the ten years preceding the study, represented a critical period, in the course of which there is doubtless a process of equilibration between such populations and the environment.

The distribution of sportive lemurs in the Didiereaceae bush is not homogeneous, and the population counts that we carried out along the transects show that there are small population nuclei which are isolated to varying degrees. Various areas of the bush remain unoccupied, partly because of a lower density of edible plant species; but more frequently we observed that there was a scarcity of adequate diurnal shelters for the sportive lemurs to rest in.

In the gallery forest, the population density is greater than in the bush; it reaches 450 *Lepilemur* per square km., corresponding to a biomass of 2.7 kg. per hectare, as compared to 200-350 *Lepilemur* per square km. in the bush, which amounts to a biomass of 1.2-2.1 kg. per hectare. These population densities can be compared with those observed in a habitat entirely comparable to the gallery forest of southern Madagascar — that is, the alluvial forest of Ceylon. The biomass of a nocturnal prosimian (*Loris tardigradus*) found in the latter areas is extremely low, less than 0.25 kg. per hectare.¹¹ However, since *Loris tardigradus* is an insectivore, the 1:10 ratio of

the biomasses is quite in agreement with standard ecological relationships found when passing from one trophic level to one immediately above. (*Microcebus murinus*, which is also partially insectivorous, has a biomass of 0.23 kg./hectare in the Didiereaceae bush). If we consider the folivores living in the alluvial forest of Ceylon (that is, the two colobines *Presbytis senex* and *P. entellus*), there are biomasses of 10 and 15 kg. per hectare.³ These figures represent the maximum densities observed for animals whose 'dietary assimilation' is certainly better than that of *Lepilemur*, since their digestive system exhibits remarkable convergence with that seen in ruminants. In the gallery forest of South Madagascar, two large-bodied lemurs (the Sifaka, *Propithecus verreauxi*, and the Ringtail, *Lemur catta*) occupy ecological niches analogous to those of the colobines in Ceylon.

Therefore, the size of the *Lepilemur* home-range reflects, in the most arid area, more effective utilisation of the terrain. The biomass is very large in view of the low productivity of the Didiereaceae bush during adverse periods.

We carried out a complementary study of the distribution of the sportive lemur (*Lepilemur mustelinus mustelinus*) in the east coast rain-forest of Madagascar, which is dense and evergreen, and which doubtless has much greater primary production (study area: forestry station of Perinet). This other subspecies of *Lepilemur mustelinus*, which is 50-100% larger than the subspecies found in southern Madagascar, is sympatric with a nocturnal folivorous Indriid of comparable size — *Avahi laniger*. In the course of nocturnal counts, it was not always possible to distinguish between the two lemurs; but the overall density (of *Lepilemur* and *Avahi* together) is of the same order as that of *Lepilemur* in the dry forest of south Madagascar. Thus, one might ask whether the limiting factor governing such folivore populations is, in certain cases, something other than the level of food availability. However, the synecology of dense forests is much more complex — and hence much less well known — than that of dry forests. There are far more species in dense forests, the ecological niches are more specialised, and the conditions of observation are much more difficult.

Folivorous primate species share a large number of characters. They are the least active and the least mobile of all, though one must not confuse such slowness with that of the insectivorous lorises (*Loris*, *Arctocebus* and *Perodicticus*), where it represents a cryptic mechanism.¹² It is obvious that the ease with which such folivorous species can find their leaf diet removes any necessity to move over large areas, and the home ranges are small. Among the gregarious 'higher' primate species the folivorous forms (*Alouatta*, *Presbytis*, etc.)^{3,13} only defend small territories, compared with those of sympatric species which are frugivorous or insectivorous. Among the solitary nocturnal lemurs, individual territories are similarly smaller

in folivorous forms than in frugivorous or insectivorous species. *Lepilemur* would appear to represent the lower limit of such home-range restriction.

Social life

The Didiereaceae bush constitutes a habitat which is particularly favourable for observation. During our study period, at the end of the dry season, the bush had the appearance of a forest of dry trunks and branches without leaves, in which visibility was very good. In addition to this, it was relatively easy to drive sportive lemurs from their retreats during the daytime, by beating the vegetation, and subsequently to capture them. When disturbed, sportive lemurs take refuge at a height of 5-8 m. on a ramus of *Alluaudia* and observe the intruder without moving. With a little patience it is possible to approach the animal very cautiously with a noose suspended at the end of a long pole and to pass the noose around the animal's neck. Some captures took only 10 minutes, whilst others required more than two hours; but we were nevertheless able to capture 12 of a population of 13 sportive lemurs. After a standard examination (genital organs, mammary glands, teeth, body-weight, etc.), the animals were marked by clipping the ears and shaving the tail according to various patterns, and then they were released and observed. In this study area, strings attached at a height of 1 m. in rows 10 m. apart, each marked with numbers, permitted us to localise any observation to within 2-3 m. on a map, and thus to delimit individual territories.

1. Territories

As has already been mentioned, the territories are small.¹ Adult females range over 0.18 hectares (0.15-0.32), adult males over 0.30 hectares (0.20-0.46), and juvenile females over 0.19 hectares (0.18-0.20). For comparison, one can consider the following values taken for 2 lorid species (insectivorous and frugivorous prosimians): *Galago demidovii* – 0.8-2.7 hectares;¹⁴ *Perodicticus potto* – 7.5-15 hectares.¹⁵

The female territories are distinct from one another. However, we noted a certain range overlap and mutual tolerance between an old female and two young females of one and two years of age. (All the females were gestating in October, and reproduction takes place only once a year). The territories of the males are similarly separate from one another, but we did observe one case of overlap between the two smallest males in the population. However, these two individuals were never observed together in this common area. Although there is quite clear separation of territories between males and between

females, overlap of female territories with those of the males is the rule. The same applies, in fact, to the Loridae and to *Microcebus murinus*.^{14,15,16}

The largest of the males was associated in this way with 5 females, whilst the other males were associated with two, one and one female, respectively.

2. Territorial defence

All adult males and females exhibit scars on their ears, snouts and tails as witness to intra-specific fights. We have never observed such traces of former wounds with young females at one year of age. Although olfactory marking constitutes the principal means of territorial defence with most nocturnal species, *Lepilemur* exhibits a process which is quite remarkable. In the sportive lemur, which has such small territories of approximately 50 m. diameter, the territory-owner can easily survey the limits, which are absolutely rigid. The occupant of a territory, usually whilst squatting on a high ramus of *Alluaudia*, surveys his immediate neighbours, which are also located on elevated branches. Such mutual surveillance is particularly frequent with the males, which spend hours observing one another, often with only a few metres between them. When one of them moves, it is common to see the neighbour move in his turn along the territorial limit and come to rest facing his opposite number once again.

From time to time, two – and sometimes three – males exchange vocalisations as a duet or a trio. A duet consists of a rapid series of 'Heh, heh...' calls (aggression), followed by an abrupt, high-pitched 'Hiii' call (signalling). These two vocalisations are subsequently exchanged for a period of 10-20 seconds in a less precise order, and calm then returns. In fact, we counted many more duets of this kind when the moon was visible, and this indicates quite clearly that contact between neighbours is largely based on vision. In the course of reciprocal surveillance, we also saw a display consisting of powerful leaps against a support, or a simulation of jumping reminiscent (in a slow-motion form) of the rapid branch-shaking exhibited by monkeys. Side-to-side head shaking also occurs in territorial encounters.

The sportive lemurs deposited urine on the branches of the 'surveillance posts', but we never noticed any particular behaviour associated with such urination.

3. Social relationships

Even if there is nothing more than superposition of male and female territories, there must be relatively frequent encounters between individuals of opposite sex. When they do meet, one individual utters

a 'Hiii' vocalisation, and then both continue on their way.

During our period of observation, it was seen that males and females sleep in separate retreats each night; but that the same retreat may be used by a male and a female on successive nights.

A few days before our observations were completed, we removed – by way of experiment – the largest male, whose territory overlapped with that of five females. The very next night, all of the other males penetrated into this zone, and each one began to associate with one of the females. It is important to note that the males were all in a sexually inactive state (regression of the testes) and that the females were either gestating or immature. Two days after the experiment, one female was already accepting the presence of one of the males, which was seen sniffing at her ano-genital region.

Courtship behaviour, as with surveillance of territories where females occur, is thus independent of direct sexual behaviour, since it can occur outside the reproductive period. Obviously, this represents some kind of social behaviour, as is found in other nocturnal prosimians.

Conclusions

Lepilemur, whose phylogenetic relationship to other lemurs is difficult to establish, is distinguished first and foremost by its extremely specialised diet. Alongside primitive anatomical and behavioural characters resembling those of the Cheirogaleinae and the Lorisidae (closure of the vulva during sexual inactivity; transport of the infant in the mouth; social organisation; overlapping of male and female territories), one can see a series of adaptations directly or indirectly associated with the dietary regime: specialised dentition, modified digestive tract, caecotrophy, small territories. Social organisation is of a primitive type; but the system of visual territorial surveillance, which is unusual for a nocturnal mammal, is doubtless related to the very small area of the defended territories.

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