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Ecology and Conservation of the Crowned Lemur, *Lemur coronatus*, at Ankarana, N. Madagascar

With Notes on Sanford's Lemur, Other Sympatrics and Subfossil Lemurs

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Abstract. Forests of Ankarana limestone massif in northern Madagascar support one of the largest and least disturbed populations of Crowned Lemurs, *Lemur coronatus.* This paper reports a preliminary study of the ecology of this species in the Ankarana Special Reserve conducted at the end of the dry season in 1986, with additional information collected a year later. Crowned Lemurs occur in very high densities in the semi-deciduous canopy forest and this probably represents a dry season refuge for the species. They also use more open habitats, including sparsely vegetated limestone and degraded forest. Sanford's Lemur, *Lemur fulvus sanfordi,* also inhabits the Ankarana forests but is most abundant in degraded habitats. Crowned and Sanford's Lemurs had similar patterns of activity, which included nocturnal travelling and feeding bouts. Crowned Lemurs proved to be unusual among *Lemur* species in displaying low spatial troop cohesion and a lack of obvious troop hierarchy. *Strongyloides*-like enteric helminths infested about one third of Crowned Lemurs but were apparently not causing disease. Crowned Lemurs fall prey to the Fosa, *Cryptoprocta ferox,* and the young possibly also to the largest raptors. A total of seven living lemur species (including the very rare *Propithecus diadema perrieri* and *Daubentonia madagascariensis*) were confirmed at Ankarana by the authors, and three further species have been reported by other observers. In addition to these ten extant lemurs, four subfossil species have been discovered: three of them (*Hapalemur simus, Palaeopropithecus* and *Mesopropithecus*) by the authors. The possibility that all 14 lemurs were once sympatric is discussed. For the present, the lemurs of Ankarana are protected from hunting by local taboo. Nevertheless they are under severe threat from habitat destruction, despite Ankarana's Special Reserve status. Given the very restricted distributions of Crowned and Sanford's Lemurs, both must be considered as threatened with extinction.

Introduction

The Crowned Lemur, *Lemur coronatus,* survives well and even breeds in zoos [1]. There are now four specimens at Parc Tsimbazaza, the zoological gardens at Antananarivo, and an additional 29 outside Madagascar [2]. There have been some studies of these captive individuals [3–5] but the only research to have been carried out on the species in the wild is detailed in an unpublished thesis [6], with a few observations reported by Petter et al. [7] and Tattersall [8].

L. coronatus are only found to the north of the Fanambana River, which is itself in the extreme north of Madagascar (fig. 1). The forests of the Ankarana Massif are the westernmost point of the species' range [8] and are probably their most important remaining stronghold. Sanford's Lemur, *Lemur fulvus sanfordi,* also has a very restricted range. It used to be found as far south as Sambava [7] but Ankarana may now mark the southernmost extent of its range [8]. Most of the work for the present study was carried out as part of the 1986 Anglo-Malagasy expedition to Ankarana [9]. It is the most extensive to be completed on these sympatric *Lemur* species and the first to published on their ecology at Ankarana. However, this was a survey of poorly habituated lemurs and the results must be regarded as preliminary.

Habitat

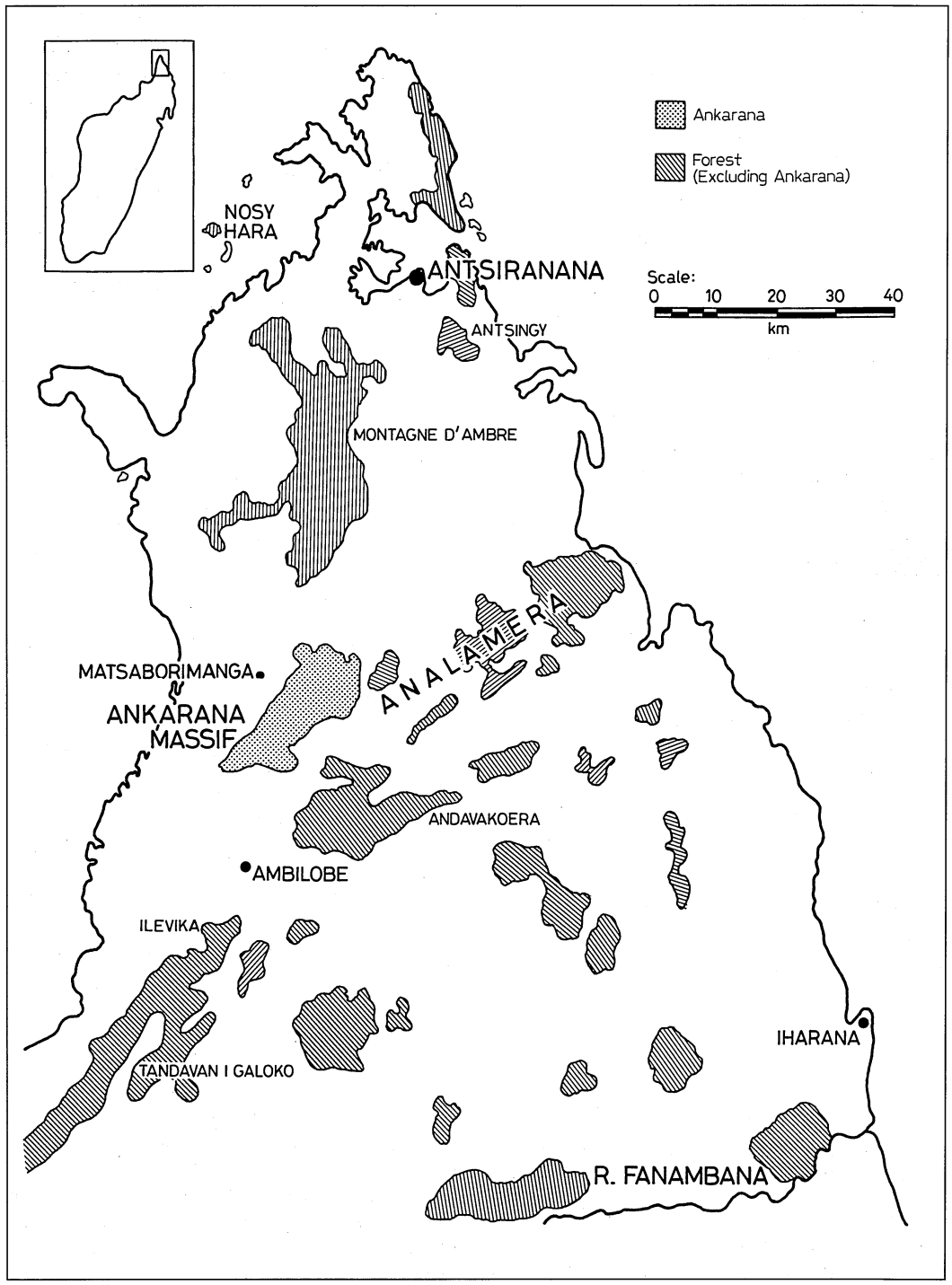
Ankarana is a small (28 × 8 km) limestone massif lying about 75 km south of Antsiranana (Diégo-Suarez) at the northern tip of Madagascar: about 13 °S, 49 °E. It was designated the 'Réserve Spéciale d'Ankara' (sic) in 1956 and comprises 18,220 ha [10] of forest growing around and on an outcrop of impressive pinnacle karst or 'tsingy' (fig. 2). About half of the reserve is barely vegetated tsingy (fig. 3); the remainder is limestone rubble covered by scrubby xerophytic vegetation, with small pockets of semi-deciduous dry tropical forest in the 200-m-deep canyons, steep-sided depression and collapsed caves [11, 12].

The forests are transitional to low broken scrub around the edge of the Ankarana Massif. This is surrounded by Western shrubby savannah with palms [13] which effectively isolates the reserve forest habitats. The dry season is from May to October (fig. 4) and annual rainfall is about 2000 mm [14].

Methods

Data were collected on the behaviour and ecology of *L. coronatus* at Ankarana between 26th August and 10th October 1986 by the authors, with additional observations by P.D.S. between 3rd September and 5th November, 1987. Although the study centred on *L. coronatus,* data were also collected on *L. f. sanfordi* and other sympatric lemurs. Two contrasting methods were employed. The first was the Spot-Check technique [15]: the authors walked a series of trails and noted details on all lemurs encountered. Trails used varied from little-used ox-cart tracks (where the canopy was breached overhead) to narrow, forest trails cut by expedition members and which they used to move about the area on foot. Although distances between key sites were small, travel between them

Fig. 1. Sketch map of northern Madagascar showing the position of Ankarana. Matsaborimanga was the nearest village to our base camp inside the Ankarana Massif and Ambilobé was the nearest town. Forests which remain north of the Fanambana River are denoted approximately as recorded on the 1:500,000 national map published in 1982 by Foiben Taosarintanin'i Madagasikara.


Ankarana
Forest
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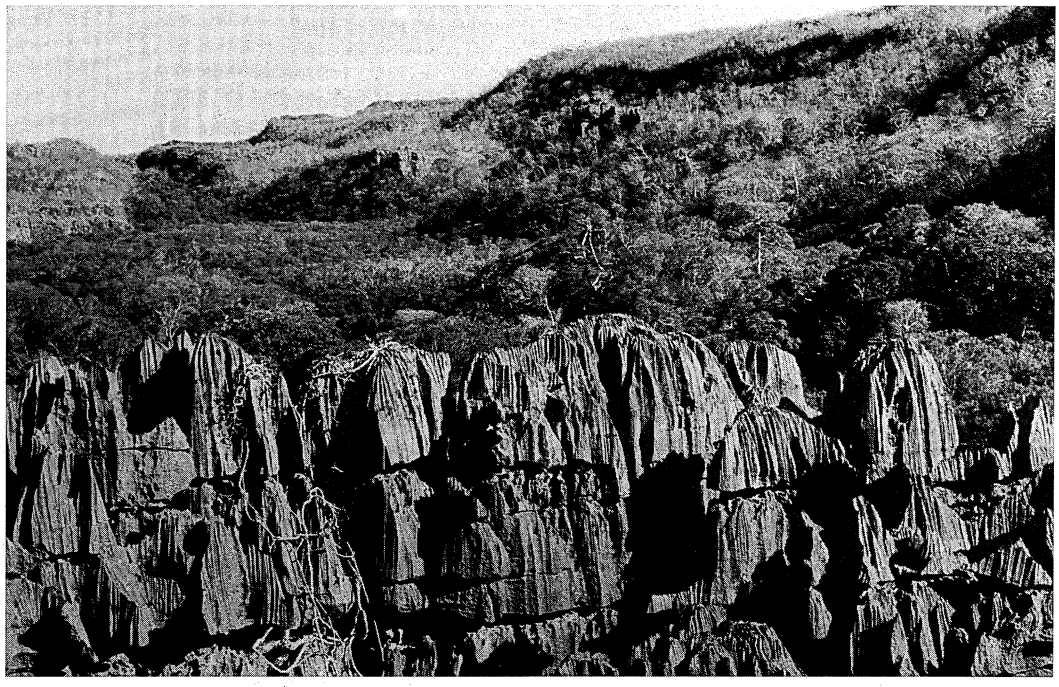


Fig. 2. Looking along Canyon Forestier just above the Second River Cave. The foreground is sparsely vegetated tsingy or pinnacle karst. Immediately below this is a strip of primary canopy forest growing above a subterranean river and beyond, stretching up to the horizon, is scrubby dry vegetation within the canyon. The limestone to the right of the picture is able to support some xerophytic vegetation, including *Pandanus* and *Ficus* spp. (photo, Jane Wilson).

often took up a great deal of time. For example, the early trips from base camp to the Second River Cave, a distance of 5 km, took 5 h to walk. The terrain hampered the repeated coverage necessary for the complete survey of all habitats used by lemurs.

For each lemur sighting, time of observation was recorded as well as species; numbers and sex of adults, sub-adults, juveniles and infants; activity and forest level when lemurs were first seen. Activity was divided into six categories: travelling (i.e. rapid travelling from one place to another); moving (or browsing within the area of one or two trees); eating; resting; grooming; scent-marking (i.e. rubbing the anal region on a tree trunk or rock), and disturbed (staring at the observer combined with grunting vocalizations and penduluming of the tail, or flight). Data from troops where any individuals were exhibiting disturbed behaviour were discounted.

In the forested parts of Ankarana the diurnal lemurs were tolerant of observation as long as observers did not approach closer than about 10 m. Closer observation was possible if lemurs moved towards the observer, but advances by the observer were rarely tolerated. Flight distance was only 3–4 m at the Second River Cave, where visibility was better. Although lemurs usually tolerated our presence whilst they were resting, feeding or moving, the longest period of continuous observation was only 3 h 40 min for a resting group. Observation times were more typically 5–15 min, presumably because these lemurs were poorly habituated. Lemurs were also disturbed by attempts to follow them while they were travelling. This, with the difficulties of moving over the tsingy, made all-day troop-follows impracticable. Sanford's Lemurs were more wary than the Crowned Lemurs.

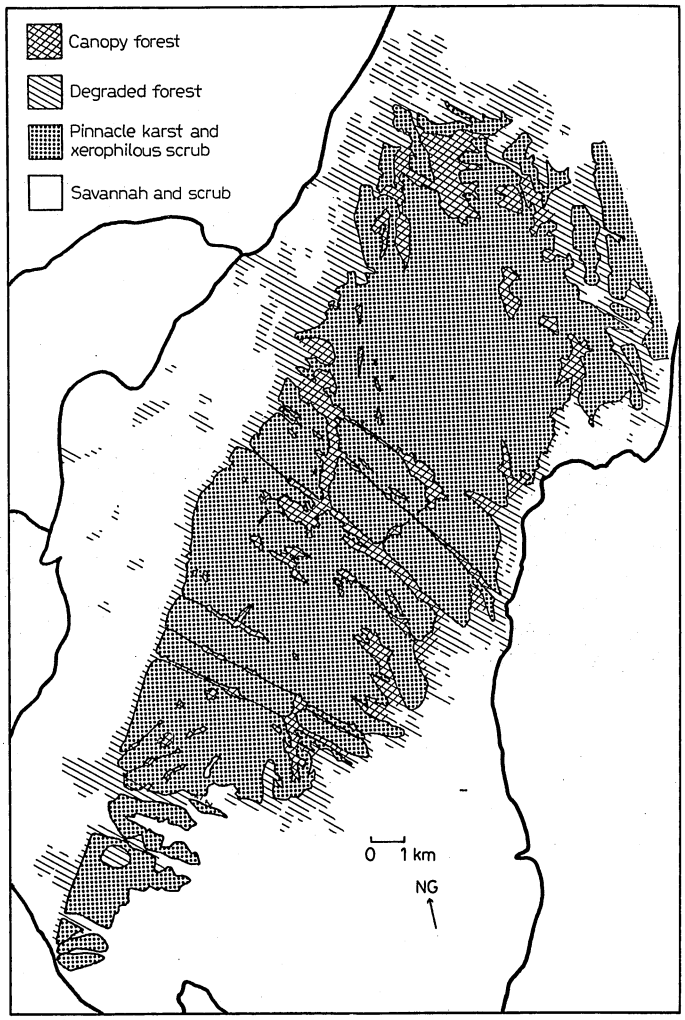


Fig. 3. Map of Ankarana showing major vegetation types. Heavy black lines denote dirt roads which are impassable in the wet season. Vegetation has been omitted beyond these tracks but comprises savannah with palms, patchy degraded forest and rice paddy along suitable rivers. The tsingy is about 200 m high and supports few plants towards the south and west, but it becomes covered with xerophytic scrubby forest towards the north and east. Data from aerial photographs (taken in 1949, available from Foiben Taosarintanin'i Madagasikara in Antananarivo) and from ground surveys conducted in 1986 (drawn by Simon Fowler).

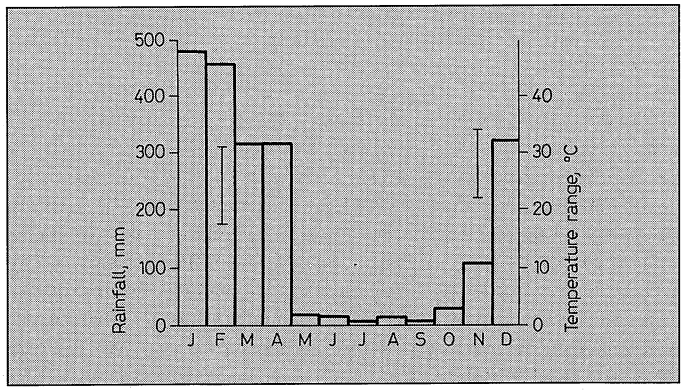


Fig. 4. Mean monthly rainfall at Ambilobé (20 km south of Ankarana) and temperature ranges at Ambilobé during the coolest and hottest months [14].

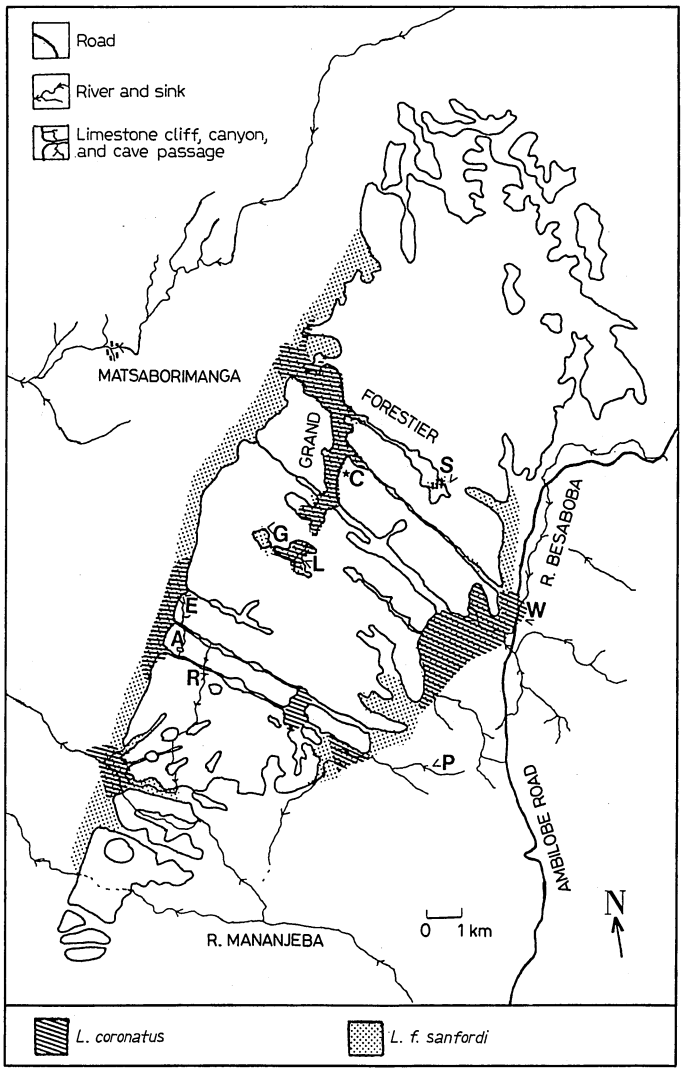


Fig. 5. Map of Ankarana showing approximate distributions of the two *Lemur* spp. Most time was spent surveying lemurs in the richly forested Canyon Grand and Canyon Forestier. Lemur populations in the forests north of the Canyon Grand were inadequately surveyed and an incomplete picture was obtained of lemur distributions on the east of the Massif. A = la Grotte d'Andrafiabé subfossil site, C = base camp in Canyon Grand. Waterholes used by Lemur spp. during the dry season: E = la Grotte d'Andrafiabé entrance and water hole; G = green lake; L = little river; P = stagnant green pool; R = River Styx water hole; S = Second River Cave water hole; W = water hole by the Antsiranana to Ambilobé road. Lemurs were seen close by but were not seen drinking there during the short time the area was watched (S.V. Fowler, pers. comm. 1986).

The second recording method involved watching the section of closed canopy forest 100 × 50 m at our campsite for 6.5 weeks, 20 h/day. A continuous 11-day watch was also kept on a contrasting section of dry river gallery forest near the Second River Cave water hole (fig. 5). Since we had supposed our *Lemur* subjects to be diurnal species, we had neither night-sights nor radio-tracking equipment to follow their nocturnal behaviour. Only noisy activities such as travel and vocalizations could therefore be recorded after dark. A total of 224 h of direct visual observation was made of Crowned Lemurs and 125 h of Sanford's Lemurs. These observations were supplemented with notes on vocalization and noisy activities (such as travelling) after dark.

Notes were made of locomotion in Crowned Lemurs during the first few seconds of observation. It was not possible to make notes on more than the first few jumps even though a simple short-hand system of arrows was used (table 1). The numbers of observed

Table 1. Locomotor observations for *L. coronatus*

Short-hand symbol	Activity	Observations	
		n	%
	Leaping between small branches and leaves in canopy	171	27
	Running along horizontal branches	133	21
	Bounding along horizontal branches	117	19
	Vertical clinging and leaping	95	15
	Bounding up or down vertical trunks (taking off from hind legs)	55	9
	Walking up or down sloping (approximately 30–60°) trunks	27	4
	Walking or running up vertical trunks	12	2
	Walking down vertical trunk head first	2	0.3
	Leaping from sloping (approximately 45°) branches	8	1
No symbol	8-metre vertical drop onto leaves and small branches	2	0.3

Symbols in the column on the left indicate the short-hand used when making notes in the field.

leaps, runs, etc. were counted and crudely expressed as a percentage of total observations.

Fresh faeces collected from Crowned Lemurs were inspected for dietary composition. Subsequently some were examined for evidence of enteric parasites using a modified Kato thick-smear technique [16]. Peanut-sized samples of faeces were passed through a 150-µm Endecotts test sieve, the resulting material smeared onto a microscope slide and a cover slip applied. These temporary wet preparations were then examined immediately using a MacArthur miniature microscope. The presence of any helminths or eggs was noted.

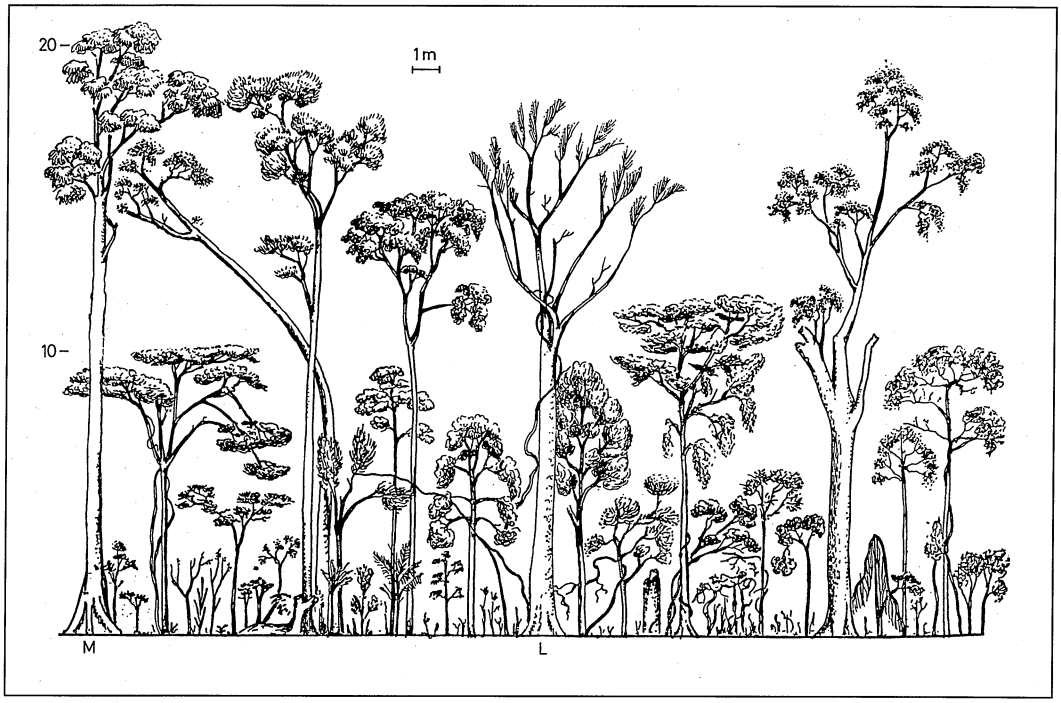
Forest profiles were drawn by GSR (fig. 6, 7) and herbarium specimens collected of the principal plants eaten by the lemurs.

During the course of cave exploration in 1981, 1986 and 1987, subfossilized lemur remains were found and photographed. These discoveries provided valuable insights on Ankarana's past lemur fauna.

Results and Discussion

Habitat Use

Lemur coronatus. Crowned Lemurs were sighted in canopy forest much more frequently and in greater numbers than in edge or degraded forest (table 2; fig. 5). The species undoubtedly also thrives in degraded habitats at Ankarana, but our data contradict observations made elsewhere suggesting that the species actually favours degraded forest [7]. Lemurs were not seen in the driest canyons, where the vegetation was dominated by leguminous trees (*Mesonovium* sp.), and leafless shrubs. However, dried lemur faeces found in these areas indicated that the habitat was used in other seasons, probably



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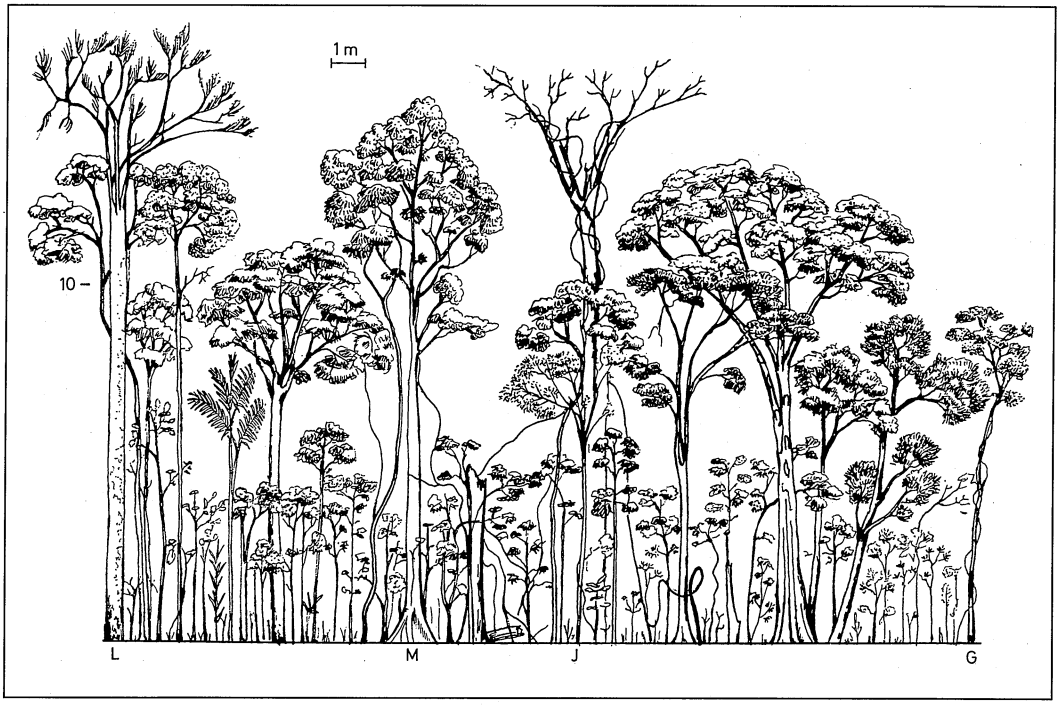

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towards the end of the wet season when trees bear fruit. *L. coronatus* were seen on the bare tsingy, either crossing to a neighbouring forest patch or, after the first rains, feeding on the sparse vegetation growing there. The patchiness of all habitats at Ankarana means that it is possible for a troop to range over a diversity of types in one day, making use of particular features (abundant water, food or good resting places) that may be peculiar to each. Thus, they are able to use habitats which in isolation would not support their needs.

Table 2. Number of sightings of *L. coronatus* and *L. f. sanfordi* at different locations at Ankarana, August–October 1986

	Sightings of *Lemur* spp.	
	canopy forest	degraded or edge forest
L. coronatus		
Observed	62	15
Expected	45	32
L. f. sanfordi		
Observed	33	52
Expected	50	35

The χ^2 test ($\chi^2 = 29.5$; $p \leq 0.001$) suggests that *L. coronatus* is more abundant in canopy forests while *L. f. sanfordi* occurs more frequently in degraded or edge forest than would be expected by chance.

The numbers are derived from lemur populations in small sub-areas with very limited observations in edge forest. Even within the canopy forest (which was surveyed much more thoroughly) populations were patchy with high variability in densities and this confounded accurate censusing.

Fig. 6. Forest profile of approximately 100 m encompassing edge forest bordering the savannah which surrounds the Ankarana Massif. M = Moraceae; L = Leguminoseae.

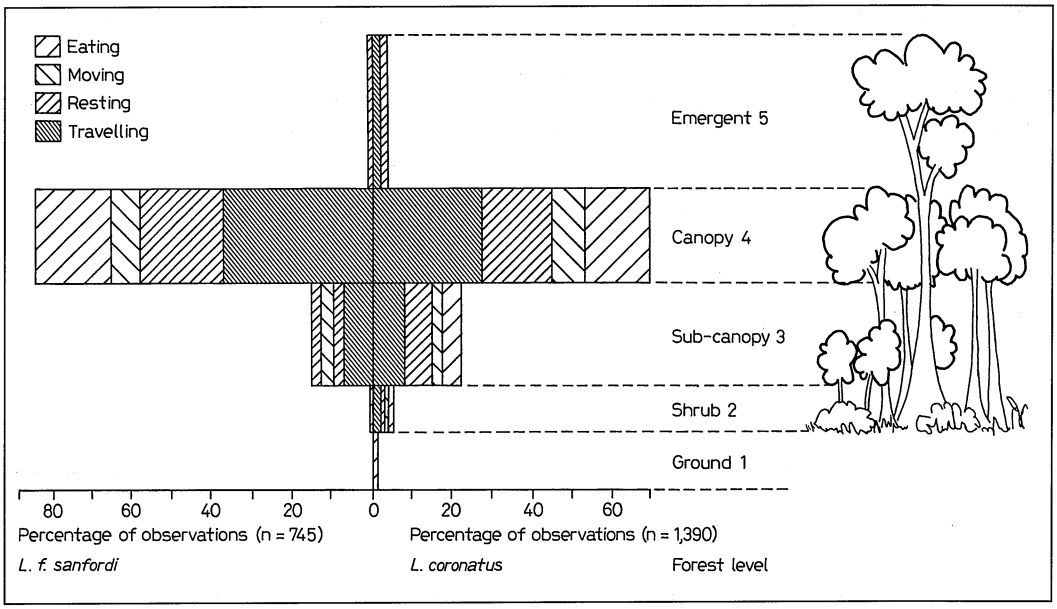
Fig. 7. Profile of about 100 m of canopy forest close to base camp in Canyon Grand. This area has been selectively logged since a track was cut into the canyon in the 1940s. The top of the canopy was about 25 m above the ground. L = Leguminoseae; M = Moraceae; J = cf. *Jasminum* sp.; G = *Grewia* sp.

L. coronatus were observed at all forest levels (fig. 8, 9); however, they appeared very reluctant to travel on the ground (level 1). Ground level forest observations at Ankarana were almost invariably of individuals that had descended to eat fallen fruit. Observations of Crowned Lemurs frequently travelling on the ground have been made in degraded forest to the north of Ankarana [7]. Yet at Ankarana, they were normally seen to leap from sapling to flimsy sapling, just tens of centimeters off the ground, or to walk on fallen logs (classified as level 2 in this study) when travelling low in the forest. Forest structure at Ankarana probably differs sufficiently to explain such behavioural differences; in the canopy forests there is no need to travel on the ground.

Lemur fulvus sanfordi. Sanford's Lemurs were observed most often in edge and degraded forest but they also frequented canopy forest (table 2; figure 5). *L. f. sanfordi* favoured canopy (level 4) and sub-canopy (level 3) where these were available (fig. 8). They were rarely recorded in the shrub (level 2) or emergent (level 5) layers and were never seen on the ground nor on the tsingy at Ankarana. However, they descended to ground level at Montagne d'Ambre and presumably they also do so in the most degraded areas at Ankarana.

Interspecific Interactions between the Two Lemur *Species*

Generally *L. f. sanfordi* and *L. coronatus* tolerated each other and were often seen



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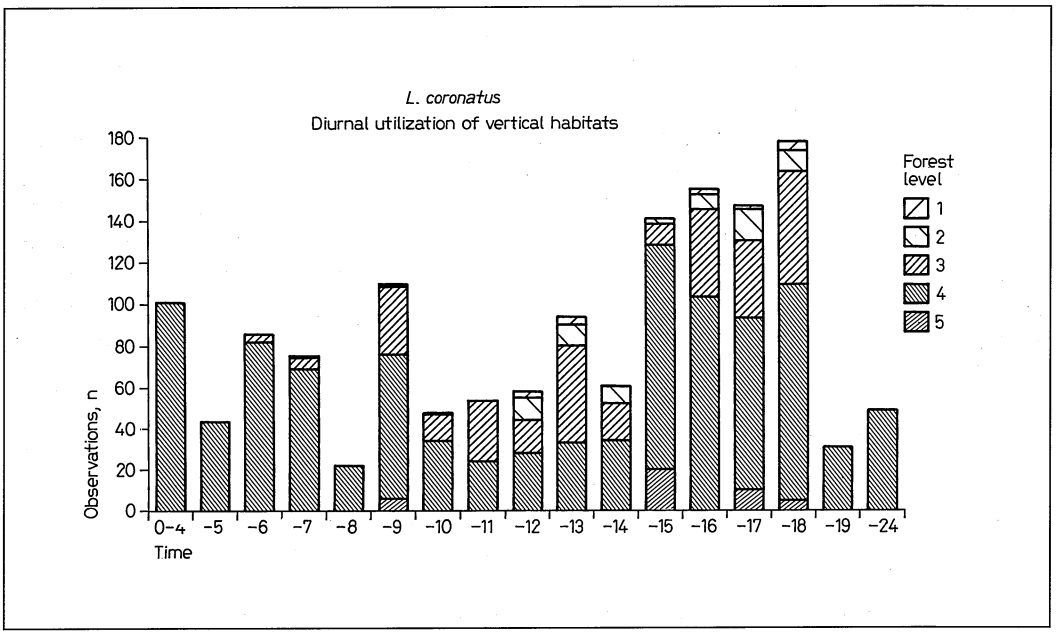

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Fig. 8. Layers within the canopy forest used by the lemurs; forest levels follow the work of Richards [17]. Histograms show the activities of *L.f. sanfordi* and *L. coronatus* at various forest levels during daylight hours.

Fig. 9. Use of different forest levels by *L. coronatus* according to time of day. 0–4 means observations in the interval from midnight to 4 a.m.; –5 means observations between 04.01 and 05.00 h; –24 means 19.01 h until midnight.

Table 3. Plants providing fruits most commonly eaten by *Lemur* species at the end of the 1986 dry season (August–October) at Ankarana

Plant family	Plant species	*L. coronatus*	*L. f. sanfordi*
Logoniaceae	*Strychnos sp.*	+	+
Logoniaceae	*Strychnos madagascariensis*	+	+
Logoniaceae	*Strychnos spinosa*	+	+
Apocynaceae	*Landolphia perrieri*	+	+
Ebenaceae	*Diospyros sp.*	+	+
Caesalpiniaceae	*Tamarindus indica*	? +	+
Moraceae	3 *Ficus* spp.[1]	+	–
Oleaceae	*Noronhia* sp.[1]	+	–
Pandanaceae	3 *Pandanus* spp.[1]	+	–

[1] Xerophytic *tsingy* species.

feeding together in *Strychnos* trees where fruit was abundant. Travelling in mixed species troops was never observed. Aggressive interactions between species occurred under several circumstances, for example if infants were in the troop or there was competition over a scarce resource. Crowned Lemurs carrying infants became agitated and aggressive if approached by Sanford's Lemurs, and a male in the troop would usually chase away the larger Sanford's Lemur. This contrasts with conflicts over single localised resources (such as safe access to a water hole or large, scarce fruit). In the six such conflicts observed, adult female Sanford's Lemurs played the most aggressive roles and displaced Crowned Lemurs.

Food and Water

The present study was carried out at the end of the 6-month dry season. At this time most vegetation was shrivelled and food for herbivores was scarce. Drought-adapted tsingy plants bore no fruit or leaves until the first rains fell in ealy October when *Ficus* spp. became covered in tiny fleshy fruits which were particularly favoured by Crowned Lemurs.

Most of the Ankarana canyons, where there is the richest canopy forest, are irrigated by subterranean rivers and remain exceptionally green, even at the end of the dry season. These forests act as an important dry season refuge for the lemurs. High population densities in these canyons are probably a result of immigration of troops that make use of other habitats during the rest of the year. In the selectively logged Canyon Grand, there was an abundance of fruits of a *Strychnos* liana which were a key food for both *Lemur* species at the end of the dry season. At the edge forests, 8-cm diameter fruits of *Strychnos spinosa* (locally known as *Moketra*) were taken by lemurs. *Tamarindus indica* grows along the forest edges and provides another source of fruit. Food plants are listed in table 3.

L. coronatus dealt with fruit by pulling them towards the mouth with either hand, sniffing and rejecting certain fruit and biting

others off the stem. Fruits up to about 1 cm in diameter were swallowed whole. The 2-cm green fruits of *Strychnos* lianas were peeled with a series of circumferential bites and the flesh was chewed off the toxic seed, which was allowed to fall to the ground. Occasionally *L. coronatus* were seen licking leaves, probably for hemipteran honeydew. Leaf-eating was observed only in forest where fruits were not so abundant, such as close to the Second River Cave. Otherwise *L. coronatus* only rarely ate leaves during the study period.

The scarcity of surface water in the dry season at Ankarana may dictate the lemurs' apparent preference for fruit: it is probable that they eat more leaves during the wet season. Faeces found in the dry scrubby canyons (where lemurs were never observed during our dry-season study) were composed almost entirely of altered fibrous vegetable material. This may suggest that consumption of a high proportion of leaf foods is only possible if abundant water is available for metabolic detoxification.

During the dry season both *Lemur* spp. visited waterholes to drink, usually in the late afternoon or at dusk. Seven sites were identified (fig. 5). Of these, the Second River Cave was especially interesting. This appeared to be the only dry season water source of about 3 km and was used only by Crowned Lemurs. Although Sanford's Lemurs frequently drank at other waterholes at Ankarana, and were occasionally seen feeding close to the Second River Cave, they were never observed entering to drink. Lemurs had to descend 5 m into a vertical shaft with a narrow exit and many of the limestone boulders on their habitual route to the water have become polished. Unlike at other waterholes, lemurs drank at the Second River Cave between 10.30 and about 16.30 h when plenty of light penetrated the cave. It is possible that troops range considerable distances in order to drink. Individuals did not drink at the cave every day, although some drank on two successive days. Lemurs did not always visit the water hole with the same troop members. Use of this drinking site (and probably others too) ceased entirely after rain, when *L. coronatus* could be observed licking water from fallen dead leaves and from puddles in rocks.

Activities and Circadian Rhythms

Lemur coronatus. L. coronatus were active from before first light at 4.30 h until after dark at 18.15 h, but generally rested between about 10.30 h and 14.30 h (fig. 10, 11). Early-morning activity often comprised travelling, generally in the canopy (level 4) or sub-canopy (level 3) (fig. 9). Our data possibly over-emphasise travel time since observers would be likely to notice moving animals more often than static ones during many short observations.

Travelling was interspersed with bouts of feeding, which increased in duration as the morning progressed. By 09.00 h movements were restricted to a small area (encompassing the canopy of two or three trees), where eating, moving, or resting were the predominant activities. Often one troop member would be asleep while others were actively feeding. *L. coronatus* sometimes rested alone in forks of trees. More usually they rested in groups of two or three on a horizontal branch. Often they wrapped their tails around themselves and each other. The rest period was generally followed by further travelling. In the evenings there were longer bouts of feeding and more vocalizations than in the mornings.

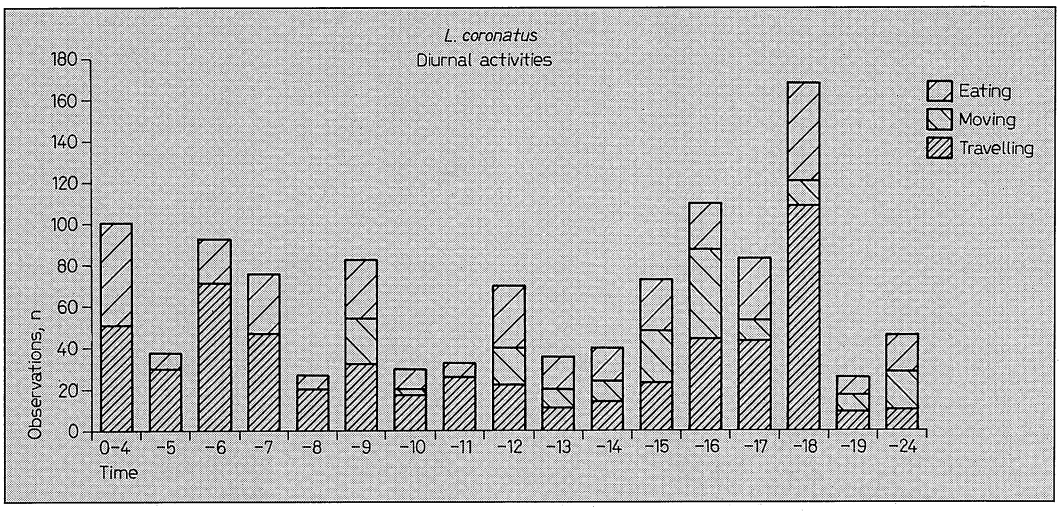

Fig. 10. Change in activities of *L. coronatus* throughout the day. 0–4 means observations in the interval from midnight to 4 a.m.; –5 means observations between 04.01 and 05.00 h; –24 means 19.01 h until midnight.

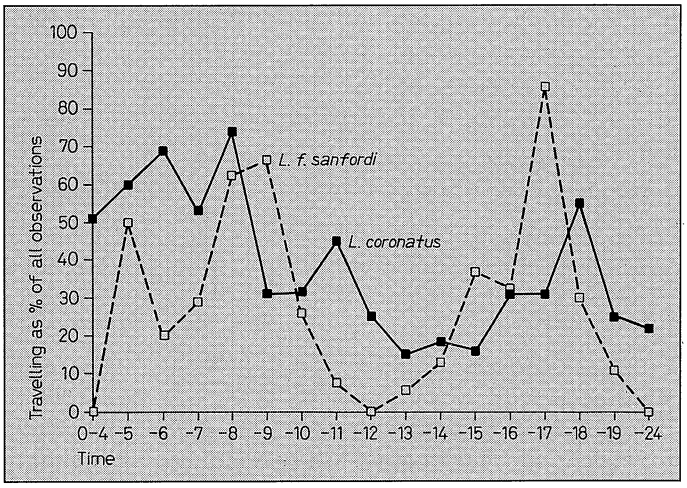

Fig. 11. Proportion of time each *Lemur* species spent travelling throughout the day. This plot of travelling observations divided by the sum of the travelling, resting, moving and eating observations for each time interval should eliminate observer bias. 0–4 means observations in the interval from midnight to 4 a.m.; –5 means observations between 04.01 and 05.00 h; –24 means 19.01 h until midnight.

Eighteen days' observation of Crowned Lemurs near to the green lake (G in fig. 5) revealed that certain troops followed the same routes day after day and were not ranging in a random manner. They travelled to feed on *Ficus* fruits which ripened continuously during the period of observation.

Most groups settled within half an hour of dusk (at 18.00 h), although travelling for some groups went on for up to 2 h after

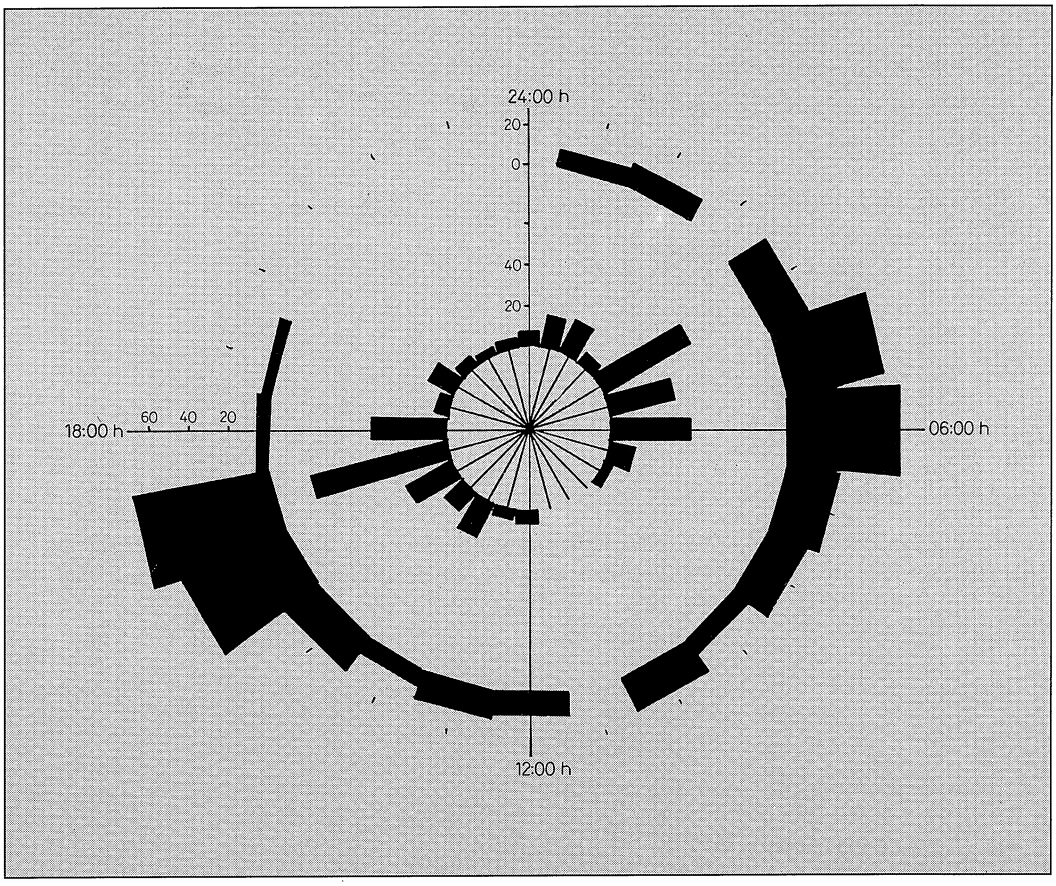

Fig. 12. Circadian activities of *L. coronatus.* This diagram represents a 24-hour clock, the inner circle indicating numbers of vocalizations and the outer circle travel. The radial scales for both vocalizations and travel are identical.

nightfall. Feeding and travelling between midnight and 02.00 h was also commonly noted. Nocturnal activity appeared to be independent of lunar phase. Sporadic loud shrieks were heard at night. On one occasion, at least, shrieks were provoked by cries of the predatory Fosa, *Cryptoprocta ferox;* on another, in response to unusually heavy October rain. Figure 12 represents activities recorded during constant watches in two small forest areas close to camp sites. This shows that *L. coronatus* is not strictly a diurnal species.

Lemur fulvus sanfordi. Data collected on the behaviour of *L. f. sanfordi* were scanty but figure 11 shows similarities in travelling and other activities which confirmed our subjective impressions. The activities of Sanford's Lemurs resembled those of Crowned Lemurs, although they became much more

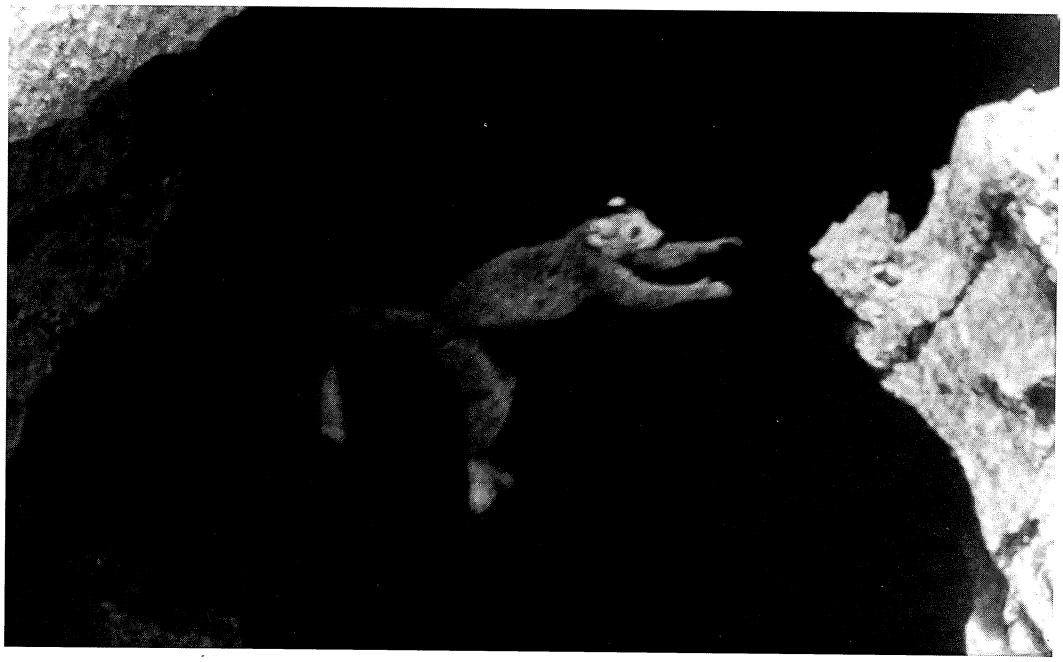

Fig. 13. An adult male Crowned Lemur leaping out of the Second River Cave after drinking there (photo, Jane Wilson).

inactive around midday. Sanford's Lemurs were also active at night.

Nocturnal activities of Lemur *species.* The *Lemur* genus was traditionally regarded as diurnal, but many members of the genus have nocturnal activity phases. *Lemur mongoz* becomes nocturnal during some seasons [8], and both *Lemur rubriventer* (Bernhard Meier, pers. comm. 1986) and *Lemur catta* (RD Martin, pers. comm. 1988) are active at night. *L. coronatus* and *L. f. sanfordi* were considered as strictly diurnal species [6], although some activity after dusk had been recorded for *L. coronatus* at Montagne d'Ambre [8]. Nocturnal activities during September and October were confirmed for both *Lemur* species during this study.

Locomotion

Lemur species are 'arboreal quadrupeds' of the branch-running and -walking type but they also exhibit elements of 'clinging and leaping' locomotor styles [18]. Crowned Lemurs generally travelled using horizontal or sloping branches; but they also jumped extremely well between the fine branches in the canopy, between the trunks or from rock to rock (fig. 13). Preliminary locomotor data for *L. coronatus* are given in table 1.[1]

[1] Slow-motion film of *Lemur coronatus* travelling in the open (and also eating, drinking) was obtained during 1987. This could be of value to researchers interested in locomotion. Enquires about this material should be addressed to National Geographic Films, New York, USA.

Morphology and Reproduction

Lemur coronatus. Adult Crowned Lemurs weigh just over 1.7 kg in semi-captivity (Peter Kappeler, pers. comm. 1987). *L. coronatus* are sexually dichromatic. The brown male has a triangular 'crown' of black fur between his ears; the female is grey with a subtle light brown 'V' of fur resembling the males' crown.

Crowned Lemurs were born from mid-September onwards. Births coincided with the first (light) rains, which stimulated a leaf flush and the appearance of more fruit. The first newborn *L. coronatus* was seen on 12th September 1986 and 24th September 1987. In both years the first births occurred in the richest canopy forest of Canyon Grand near base camp. Infants continued to be born over the next 5 weeks and the least births occurred in the drier forests, where far fewer fruits were available. Arbelot-Traqui [6] did not record births until late October, perhaps because she did not penetrate far into the Massif.

As with other *Lemur* species, infant Crowned Lemurs are carried by females. However, as the infants grew older and became more adventurous, they moved short distances from their mothers and would sometimes cling to the backs of adult males. Females with young acted as a focus for grooming by individuals of both sexes. The 1-year-old juvenile males were about half adult size and had adult pelage, except for subtle tail fur patterns reminiscent of those of the Ring-tailed Lemur, *L. catta.* The juveniles were less adept at moving through the trees and on several occasions they fell without apparent injury. One yearling fell 10 m onto branches which he managed to grasp and prevent further descent. Had the fall been onto the limestone beneath, he certainly would have been killed. Sexual maturity is attained at 20 months in both sexes [5].

Lemur fulvus sanfordi. Sanford's Lemur is also sexually dichromatic; the female is an unremarkable uniform dark brown while the male is grey-brown with handsome white whiskers. We noted the first newborn Sanford's Lemurs on 23rd September 1986. This was also earlier than previously recorded elsewhere in its range [6].

Troop Structure

Lemur coronatus. L. coronatus were notable for the relatively low spatial cohesion of the groups observed. Indeed, we found it very difficult to define *L. coronatus* troops and this hampered accurate population assessment. A group of individuals (behaving like a troop) would often move closer together, apparently communicate or even rest together, but then would split up and leave individuals behind. In some instances the remaining individuals would continue resting for an hour or more before following the individuals which had departed. Groups of two or three Crowned Lemurs were commonly encountered and apparently solitary individuals of either sex were not uncommon. A typical troop comprised five individuals: two adult females, two adult males and a sub-adult or juvenile. The largest troop seen comprised nine lemurs plus two infants.

Ano-genital scent marking of prominent rocks and trunks was frequently performed by both females and males during travelling. Excepting this, intraspecific interactions were rarely observed in *L. coronatus.* Antagonistic behaviour like that observed at a waterhole between troops of *Lemur fulvus fulvus* [19] were never seen, although it was

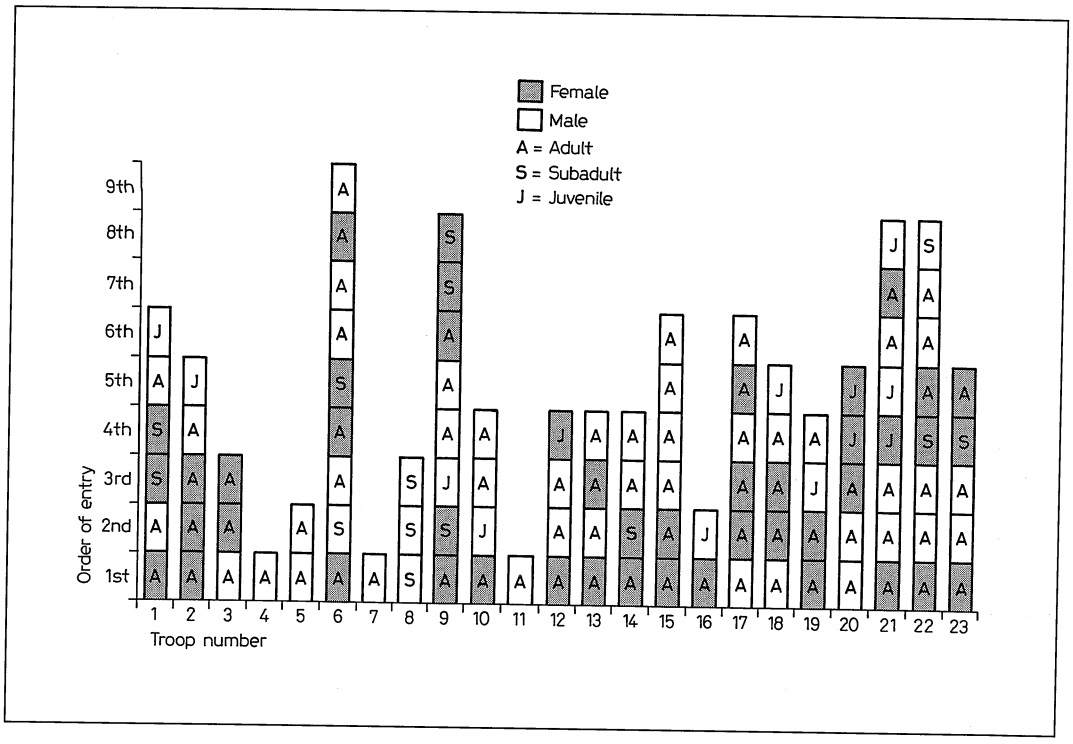

Fig. 14. The order in which members of *L. coronatus* troops entered the Second River Cave to drink. Adult females most often lead. The order in which troop members left the cave was invariably quite different.

interesting to note that troops would wait until others had departed before they would enter the Second River Cave water hole. Small groups of *L. coronatus* feeding on isolated fig bushes on the tsingy would often depart rapidly when larger troops advanced towards them.

Interactions between *L. coronatus* group members revealed little troop hierarchy. While travelling, troops were usually led by females, particularly when there was perceived danger (fig. 14). However, the leader role often rotated between individuals during travelling and sometimes no leadership was apparent at all. *L. coronatus* progressed follow-my-leader style in only half of the travelling observations.

Lemur fulvus sanfordi. An average troop comprised 9 individuals: 4 adult males and 5 adult females, although *L. f. sanfordi* were seen in larger troops of up to 15 individuals. Our subjective impression was that troops inhabiting the Montagne d'Ambre were smaller, usually comprising only 6 individuals. Sanford's Lemurs at Ankarana exhibited greater troop cohesion than Crowned Lemurs. Solitary individuals were never seen. *L. f. sanfordi* almost invariably travelled one behind the other and were always led by a female.

Population Densities

Lemur coronatus. There are numerous difficulties in censusing forest primates. Even under the most favourable research conditions, population estimates are only approximations [20]. Accurate and consistent troop counts proved very difficult to obtain at Ankarana and the figures given below must be regarded as crude estimates. The highest density of *L. coronatus* occurred in the richest canopy forest in the Canyon Grand and was about 5 adults/ha. Such high population density was seen only in an area of no more than 200 ha of selectively felled forest where *Strychnos* lianas were unusually abundant.

The average density of *L. coronatus* throughout the forested areas of Canyon Grand and Canyon Forestier was just over 1/ha but even this density was untypically high. The few areas of canopy forest which exist at Ankarana provide dry season browsing for lemurs all over the Massif. Thus, a tiny area of forest supports one of the highest densities recorded for a 2-kg forest primate [21, 22]. These estimates, which give an equivalent population of about 500 Crowned Lemurs/km^2, are comparable to the highest lemur densities ever recorded: 1,200 *Lemur fulvus rufus*/km^2 [23] and 1,000 *L. catta*/km^2 [24]. These population densities were recorded in southern gallery forest rich in Tamarind trees and are much higher than densities over the rest of the species' ranges [25]. The Tamarind-rich forest provides plenty of fruit at the end of the dry season when food might otherwise be at a premium and this probably attracts lemurs from poorer forests. This parallels the situation in the selectively logged Canyon Grand. The high *L. coronatus* density, then, reflects a concentration of lemurs into the few areas which remain green throughout the dry season.

Lemur fulvus sanfordi. Satisfactory population estimates were not obtained for *L. f. sanfordi.* Only five distinct *L. f. sanfordi* troops were recorded in the Canyon Grand and two in Canyon Forestier areas; in these forests there were on average less than 25 *L. f. sanfordi*/km^2. However, they were less dependent upon canopy forest and were much more numerous in edge and degraded vegetation. Over the Ankarana region as a whole *L. f. sanfordi* outnumber *L. coronatus.*

Lepilemur septentrionalis ankaranensis. The solitary nocturnal folivore, *Lepilemur septentrionalis ankaranensis* [26] also exists in high densities in parts of the Canyon Grand and this further boosts the lemur biomass in this especially important forest remnant. Using hand torches, eye-reflections were noted. In the richest 200 ha of canopy forest near base camp, where they achieved their highest density, individuals were noted at approximately 30-metre intervals. Population densities were much less in other parts of Ankarana but nevertheless the reserve is a significant refuge for a species which is disappearing elsewhere in its range [27].

The canopy forest acts as a dry-season refuge for the lemurs. The forest in which the highest lemur densities occur has a dense unbreached canopy at 30 m above the ground. The total area of this type of forest remaining at Ankarana probably totals no more than 5 km^2. This, the richest and most extensive area of forest, is relatively accessible and could be clear-felled in a matter of weeks. This would have disastrous consequences for the populations of Crowned Lemurs, *Lepilemur* and numerous endangered non-primate species. There is a larger area of

low, dry canopy forest in the north of Ankarana which we were unable to survey properly. Here, water is less abundant and the limestone canyons are much lower so the forest is not as effectively protected from the drying effects of the winds. Lemurs are present here but in much lower densities than in the high canopy forests.

Predators and Responses to Them

In marked contrast to the lemurs of the Montagne d'Ambre National Park, *L. coronatus* and *L. f. sanfordi* at Ankarana were relatively unafraid of man. This is because the Ankarana lemurs are protected by local taboo (fady) against hunting. By 1987 Crowned Lemurs were sufficiently habituated that they would take fruit from within 2 m of people at base camp. Observers were most likely to alarm the lemurs if they surprised them or attempted to use hides. Openly following lemurs into the Second River Cave to take flash photographs of them caused no alarm, but an unfamiliar, half concealed object (a jerry can) placed on the lemurs' habitual route to the water was treated with considerable suspicion.

Fosa faeces[2] were found which comprised grey fur and broken bone (apparently of *L. coronatus*). This suggested that *Cryptoprocta ferox* is a predator of lemurs at Ankarana. The Fosa is Madagascar's largest carnivore, capable of hunting in trees as well as on the ground and was seen frequently near the Second River Cave. Its presence provoked alarm and agitation, expressed as staring and grunk-shriek alarm vocalizations with tail-penduluming through an angle of about 70°; often this also stimulated the lemurs to defaecate and urinate in unison. Such grunt-shrieks stimulated all lemurs drinking inside to leave the cave rapidly. The normal response to the presence of a Fosa, even to its distant cries, was to flee upwards.

L. coronatus were, however, more frequently distressed by perceived threats from the air and usually fled downwards, sometimes nearly to ground level. Escape rather than staring, shrieking and tail penduluming was the usual initial response. Given the speed of strike of some birds of prey, this is an appropriate behaviour. Several authors have noted the alarm with which lemurs respond to raptors [19, 23, 28, 29] although few if any would be capable of taking an adult *Lemur.* However, the largest raptors at Ankarana were seen flying off with rodents at least four times the size of infant Crowned Lemurs and not much smaller than yearlings. It seems reasonable to suggest, then, that the largest raptors can take young lemurs. Table 4 lists raptors and other potential avian predators at Ankarana which might at least be capable of taking ailing infants.

Often 'threats' from the air were only rustling leaves or swooping and noisy but harmless birds, especially the 32-cm long *Falculea palliata, Coracopsis vasa* (length 50 cm) and even Madagascar Turtle Doves, *Streptopelia picturata* (length 28 cm). *L. coronatus* seemed unable to differentiate noisy from harmful birds. This is in contrast to reports of other *Lemur* species which were reputedly able to distinguish dangerous from harmless birds and fruit bats [19, 23, 28].

Parasites

Faeces were examined from 25 Crowned Lemurs; nine samples contained eggs and/or

[2] The faeces are available for study at the British Museum (Natural History) Mammal Section, London SW7 5BD, UK.

Table 4. Raptors and other potential avian predators of young lemurs at Ankarana (from bird list compiled by Phil Chapman and members of the 1986 expedition)

Species	Common name	Length, cm [30]
Falco newtoni	Madagascar kestrel	30–33
Falco zoniventris	Madagascar banded kestrel	36
Aviceda madagascariensis	Madagascar cuckoo falcon	40–45
Milvus migrans	Yellow-billed kite	60
Gymnogenys radiatus	Madagascar harrier hawk	60–62
Buteo brachypterus	Madagascar buzzard	48–51
Accipter francesii	Madagascar goshawk	30–35
Accipter madagascariensis	Madagascar sparrowhawk	34–40
Haliaeetus vociferoides	Madagascar fish eagle	80
Otus rutilus	Madagascar scops owl	26
Corvus albus	Pied crow	45

rhabditiform larvae of a nematode similar to *Strongyloides.* Egg and helminth counts in the faecal samples were low (less than 50 eggs/g wet faeces). This implies a minimal worm burden, unlikely to cause disease in the lemurs. Just over one third of the lemurs were infected and this contrasts with 100% infection rates (with higher worm burdens) in Mountain Gorillas [31]. Interestingly, the worm infecting Crowned Lemurs closely resembled the commonest parasite of Gorillas.

Eggs of helminths such as *Strongyloides,* which are excreted in faeces, generally need a period of maturation in soil before they are capable of infecting another host. If such a maturation period is needed before worms are infective, this would preclude coprography as a transmission route for worms: a mechanism proposed in Gorillas [31]. Coprophagy was never observed in the lemurs. The Mountain Gorilla, a terrestrial primate, would experience greater exposure to such parasites, through living close to infected soil. Infection of arboreal Crowned Lemurs is less likely to occur and might explain lower prevalence rates. *Diospyros* sp., the ebony, is eaten by Crowned Lemurs. This is used by local people as an anthelminthic [32] and might possibly also limit parasitic worm populations in the lemurs.

Lemurs have been cited as possible reservoirs of *Trichuris trichiura,* a troublesome parasite of man in the tropics [33]. This nematode is common in the Malagasy people [34] but was not recorded in the lemurs at Ankarana.

Other Lemurs at Ankarana

Subfossil Discoveries

In 1981 members of a Southampton University expedition discovered incomplete remains of four subfossilized *Hapalemur simus* within la Grotte d'Andrafiabé cave system [35]. At this time, museum specimens of this species totalled 15 worldwide [36]. In 1986 a further 18 specimens of *H. simus* (fig. 15) were collected from the same site. Further examples were left in situ since they were too firmly imbedded in calcite to be

removed without damage. Bones of *Propithecus diadema* were collected, constituting the first record of this species at Ankarana. A single, almost complete, *Mesopropithecus* (including hand bones never seen before for this species) was also found; this is the first time this subfossil species has been found in northern Madagascar [37]. Specimens collected in 1986 remain at Département de Paléontologie, Université de Madagascar, Antananarivo.

Another complete *Mesopropithecus* was located and sections of upper jaw and limb bones from a giant lemur, probably *Paleopropithecus* sp., were found in the First River Cave by P.D.S. in 1987. An *Archaeolemur* skull was also found recently by French cavers [38].

The subfossils at Andrafiabé Cave were found singly or occasionally in pairs, amongst large boulders just beyond the limit of light penetration into the cave. They had not been washed in, since bones had not accumulated in corners nor were they mixed with detritus or silt. Some skeletons were found on top of clean white calcite, which would have been stained by flood waters. It also seemed unlikely that the lemurs had been brought into the cave by a carnivore, since the remains were not in caches: many skeletons were complete and undamaged. None of the small bones (ribs and digits) of the 1987 *Mesopropithecus,* for example, were broken or displaced. Nor was there any evidence that there had ever been a hole in the cave roof through which lemurs might have fallen.

The main accumulation of subfossils was 15–30 cm above a small dried-up lake close to the cave entrace. It is probably that the lemurs came into the cave to drink (just as they still do at the Second River Cave) and were frightened deeper into the cave by the appearance of a predator, such as a Fosa. Lemurs generally flee upwards when threatened in such circumstances and the obvious escape route for the lemurs would have been up over the large boulder pile just beyond the lake. This path would have rapidly led them into a maze of boulders and absolute darkness. Once beyond the limit of light penetration into the cave, they would have been unable to find their way out. (This incidentally was nearly the fate of one of the authors!) The observation that the common extant lemurs are not well represented at the

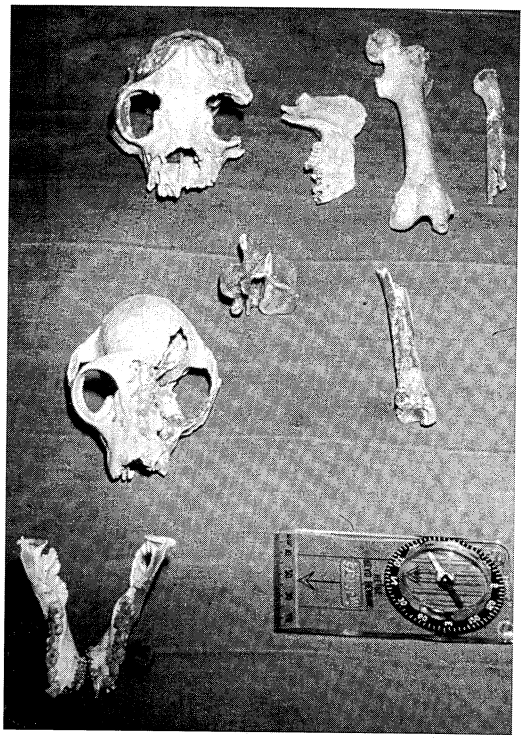

Fig. 15. Subfossil finds from la Grotte d'Andrafiabé, included skulls of *Hapalemur simus* and *Mesopropithecus.* The *Mesopropithecus* is the larger (photo Paul Stewart).

Table 5. Lemurs recorded from Ankarana

	Common	Infrequent	Rare	Subfossil
Lemur coronatus, Crowned Lemur	+			+
Lemur fulvus sanfordi, Sanford's Lemur	+			
Lepilemur septentrionalis ankaranensis, Sportive Lemur	+			
Daubentonia madagascariensis, Aye-aye[1]		+		
Microcebus murinus, Grey Lesser Mouse Lemur		+		
Hapalemur griseus, Grey Gentle-lemur			+	
Propithecus diadema perrieri, Diademed Sifaka[2]			+	+
Cheirogaleus sp. Fat-tailed Dwarf-Lemur			+	
Avahi laniger, Woolly Lemur[3]			+	
Phaner furcifer[3, 4]			+	
Hapalemur simus, Broad-nosed Gentle-lemur[5]				+
Mesopropitheus sp.				+
Paleopropithecus sp.				+
Archaeolemur sp.				+

[1] The Aye-aye was only seen five times, but its feeding damage was common throughout the massif. This was in the form of gnawed conical holes in dead and living wood. Typically 8 cm in diameter, 5 cm deep with 2- to 3-mm-wide tooth marks.

[2] Only one sighting of live specimen; possibly vagrant from the Analamera forests to the East.

[3] Benjamin LeNormand, pers. comm. 1986, and Patryck Vaucoulon, pers. comm. 1987.

[4] Unconfirmed single sighting in a hole in a tree (D. Checkley, pers. comm. 1986).

[5] Some of the subfossil *Hapalemur simus* skeletons could be as little as 50 years old (M. Vuillaume-Randriamanantena, pers. comm. 1986) and recent feeding damage similar to that produced by this critically endangered species was found in a bamboo forest in one of the remoter parts of Canyon Forestier.

subfossil site is consistent with the fact that the lake is now dry, and so no longer attracts lemurs to drink.

Lemur Sympatry at Ankarana

The lemurs which have been recorded from Ankarana are listed in table 5. At present ten species of lemurs are sympatric there and of these the commonest, *L. coronatus* and *L. f. sanfordi,* appear to be the closest competitors. Indeed how these two *Lemurs* with very similar frugivorous diets, habitat use and diurnal activity patterns coexist is worthy of further study. Our study was conducted at the end of the dry season when food was probably the most limiting resource. Yet food niche partitioning between these two species was not apparent.

In addition to the ten extant lemurs, subfossil evidence indicated that at least four other species have lived at Ankarana. One of these, the bamboo-feeding *Hapalemur simus,* may not be extinct at Ankarana (see footnote 5 in table 5). It is probable, then, that this species co-existed with the extant species.

The demise of the three large subfossil lemurs at Ankarana must have been brought about by anthropogenic ecological changes which progressively isolated the forests of

the Massif. Such ecological isolation would not only have put pressure on the lemurs living there but would also have limited any immigration of additional lemur species. All fourteen species could have been sympatric before Man arrived on Madagascar. This number of sympatric species is comparable with the highest primate diversities recorded in African and South American rainforest and exceeds any previous records for semi-deciduous forest [21].

Conservation

Threats to the Ankarana Reserve and Its Lemurs

Ankarana is a small isolated reserve. Its forest boundaries have remained essentially unchanged for at least the last 50 years (see aerial photographs available from FTM). Sadly, most other forests in the region are tiny remnants of those which existed 50 years ago. The Montagne d'Ambre National Park to the North and the Analamera Reserve to the East are being destroyed by logging, burning and grazing. Interchange between disjunct lemur populations which must have been possible when the forests were contiguous, becomes less and likely as forest boundaries shrink away from Ankarana. Loss of forest at Montagne d'Ambre also threatens the flow of the Anoranotsisilona River which drains off the mountain's southern slopes to feed Ankarana's subterranean rivers and irrigate the canyon forests. Loss of primary forest elsewhere also makes Ankarana's forests a more attractive commercial logging proposition. The loggers' inroads provide access for local herders to burn and graze land – as has happened in southern Ankarana. Once the forests of the major canyons have disappeared, the inaccessible forests of the Massif are unlikely to be large enough to support viable lemur populations. At present lemurs are protected by local taboo against hunting. Such traditional protection is no longer effective in nearby Montagne d'Ambre and Analamera reserves. It is only a matter of time before lemurs are also hunted at Ankarana.

The large healthy population of *L. coronatus* and *L. f. sanfordi* found at Ankarana after at least 50 years of isolation might imply that this little ecological island has sufficiently primary production to maintain lemur populations in a secure equilibrium. However, further extinctions might be expected because of its isolation [39]. As the surrounding forests disappear and topsoil is eroded, Ankarana is at increasing risk of protracted drought. And the isolation of Ankarana's lemurs combined with their high population densities at certain seasons also make them unusually susceptible to disease. Either could reduce the local lemur population below a level from which they could recover.

Conservation Status of L. coronatus *and* L. f. sanfordi

Nationally the problems now facing *L. coronatus* and *L. f. sanfordi* are much the same as those which threaten them at Ankarana. Logging, burning and grazing are annually reducing the forest habitat available to both species over their already dangerously small ranges. Hunting exacerbates the problems of declining populations.

L. coronatus is now only found north of the River Fanambana and probably no further west than Ankarana [8]. The forest in this part of the island covers an area of

1,800 km^2 (fig. 1), according to maps published in 1982. However, much forest has been cleared since the surveys were done for these maps and that which remains is degraded and may comprise habitats unsuitable for the lemurs. For example, the 190 km^2 of mapped forest at Andavakoera is degraded and no lemurs were seen there in 1987 (Andy Hawkins, pers. comm. 1988).

The area of forest around the Montagne d'Ambre National Park has suffered badly too. It is depicted on the 1982 map as covering about 403 km^2, but at least 80% of this has been cleared. The map also shows that the forests of Ankarana are only separated from those of Montagne d'Ambre by about 10 km of savannah, whereas the gap is now around 30 km and some of this is completely devoid of vegetation. The degraded and rapidly shrinking forests of Montagne d'Ambre, the few tall gallery forests within the 347 km^2 Special Reserve of Analamerana (Andy Hawkins and Jörg Ganzhorn, pers. comm. 1988) and the very dry Antsingy Forest and Forêt des Sakalavas [6] may be the only other significant refuges of the two *Lemur* species. In these forests Crowned Lemurs survive at population densities considerably lower than at Ankarana and at both Montagne d'Ambre and Analamerana they are hunted (Jörg Ganzhorn, pers. comm. 1988). In addition to these populations, a small colony of Crowned Lemurs has been released on the little uninhabited limestone island of Nosy Hara (fig. 1). Before the release G.S.R. determined that the vegetation there was similar to that of Ankarana and that the island would be a suitable habitat for the lemurs.

The remaining area of forest in the extreme north of Madagascar which provides suitable Crowned Lemur habitat can now be no more than 1,300 km^2: in reality it is probably far less. Further ground surveys are required to determine actual forest areas, how many Crowned Lemurs remain and what are the chances of the species continuing survival in these threatened refuges.

The very restricted and shrinking ranges of both *L. coronatus* and *L. f. sanfordi* must be a cause for grave concern. No conservation programme has yet been initiated, and the plight of these unique and delightful animals appears to be largely unrecognised.

Postscript

During just 3 weeks in May 1988, one third of the forest within Canyon Grand was clear-felled by the Kharma Sawmill Company of Ambilobé (Patryck Vaucoulon, pers. comm. 1988). It is uncertain exactly what effect this clearance will have on the lemurs. The resulting food deprivation is likely to particularly stress the pregnant lemurs and may reduce this year's births. At worst it could kill tens or perhaps hundreds of Crowned Lemurs during the present (1988) dry season in this, their most important refuge. This destruction must also threaten the continuing survival of the Aye-aye at Ankarana. It is not yet known whether complete clearance of the Canyon Grand is planned.

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