



Fig. 5. *Lemur catta* in Ambohibe forest with (from left to right) Charles DeHaes, Director General WWF-International; Elwyn Simons, Director of Duke's Primate Center; Winnifred Carter, Member of the boards of WWF-US and the Duke Primate Center; and Bodo Randrianasolo, a Malagasy student studying at Duke (photo by R. A. Mittermeier).

have become habituated to humans; this lack of fear becomes a critical weakness should they be reintroduced to an area where poaching occurs. At present, lemurs are frequently poached both within and outside of the protected areas of Madagascar. Only when the protection of parks and reserves is greatly improved and laws against the hunting of lemurs and other rare animals are enforced, will reintroduction into the natural habitat become a viable option. Meanwhile, we at Duke will study how lemurs readjust to wild conditions.

Before releasing the animals in 1981, Dr. Glander carried out research at the Duke Primate Center which showed that lemurs are very selective about feeding on native North Carolina leaves. After sniffing and biting, they rejected leaves containing high components of alkaloids and tannins. It appeared that lemurs released outdoors would not poison themselves. However, more than one scientist at the time believed that like apes, these cage-reared lemurs when released would not forage for themselves in the enclosures, but would wait to be fed. They suggested that these "naive" lemurs would misjudge jumping distances and fall from the trees or be captured by aerial predators such as hawks or owls.

Ambohikely and Ambohibe are surrounded by chain-link fences that run through the middle of a 9 m wide, cleared corridor. This corridor prevents escape by jumping through the tree-tops and since lemurs do not like to cross open country, they are seldom seen close to the fences. Three sets of mildly electrified wires run near the ground and near the top of the fences. Like live-stock guard fences, they carry a low voltage that surprises and repels the lemur without causing any harm. After a few contacts with the wires by some individuals in the days immediately following release, all lemurs in the enclosures avoided these fences. The lemurs are, therefore, living on an island of natural habitat that has totally different plant species from anywhere in Madagascar, but provides an environment broadly similar in tree and branch substrate as those in part of their native range. It is made up of bamboo thickets, an understory of small trees and vines, as well as a shady cover of mature hardwoods and pines.

Up to the present time, the two enclosures have held six different species of lemurs: 3 crowned lemurs, *Lemur coronatus*; 7 brown lemurs, *Lemur fulvus*; 9 ruffed lemurs, *Varecia variegata*; 22 ring-tailed lemurs, *Lemur catta*; 6 black lemurs, *Lemur macaco*; 2 mongoose lemurs, *Lemur mongoz*. Some of these groups have spent several years in the enclosures and much has been learned about the ability of these species to readapt to semi-free ranging conditions in a natural environment.

Since the enclosures are uncovered above, and in a few places have been penetrated by burrowing, the lemurs are sharing the environment

with many other animals. Deer, raccoon, fox, squirrels, wild turkeys, hawks, owls, snakes, and vultures have occasionally been seen in or above the enclosures. There have been no deaths due to aerial predators or resulting from disease carried by local mammals. The *Lemur catta* troop has suffered one death suspected to be from predation by a fox and another from a copperhead snake bite. In spite of these incidents and the social rejection of several individuals, the troop size has grown from 8 to 22, with only two unrelated males added in 1985, for outbreeding and to study assimilation of new group members. Presumably because of the greater space, most of the other species released in the enclosures have also increased faster than comparable troops occupying smaller cages.

What has been learned from these experiments in captive conservation? Of initial interest was the fact that only a few minutes or hours after release, all species took to the trees and began to fully explore the vertical dimensions of their habitat that includes oaks, gum and pine trees over 40 m tall. In spite of the fact that all but two of the introduced animals were born and raised in cages less than 5 m high, there have been hardly any injuries caused by falls from the tree-tops, nor have any animals been poisoned by eating the wrong plants. Within minutes after initial release, most of these lemurs began foraging for wild food products. For instance, the troop of 14 *Lemur fulvus* found a crab apple tree in about two hours and stripped it of its half-ripened fruit.

Over the years, long lists of native plants preferred by the various species have been compiled by a succession of researchers. Such items include maple and sweetgum buds and leaves, pine catkins and dried needles, fresh poison ivy leaves and clover, as well as tulip tree blossoms,



Fig. 6. Jonah Andrianarivo (left) and Hanta Rasamimanana, Malagasy students at Duke, with lemurs in Ambohibe (photo by provided by E. Simons).

and in August, wild scuppernong grapes. In order to eat this new growth, all species readily climb to the highest tree branches to feed. At certain times the brown lemurs, led by their captive-born matriarch, Ursula, go on foraging expeditions for mushrooms found under the leaf litter. The *Lemur catta* have been seen to eat insects, a phenomenon never observed in the wild. Likewise, the brown lemurs have been seen capturing and eating birds. Since Duke Forest is deficient in wild fruits and is mainly deciduous, all lemurs in the natural habitat enclosures are fed a supplemental diet of monkey chow and fruit. Because the winter environment of North Carolina occasionally has sub-freezing temperature periods, each enclosure has several sleeping houses heated by heat-lamps. Whenever the temperature falls below 25° F, the lemurs stay in these houses at night and are fed and watered inside, below 10° F they are locked in. We have learned about another important phenomenon: captive-born lemurs make predator alarm calls, triggered by both raptors flying overhead and by animals on the ground. Thus, it does not seem that lemurs need the long time period re-learning how to feed and survive in the wild the way apes do.

Nevertheless, returning lemurs to any part of their natural habitat in Madagascar is fraught with problems. Because some years ago imported sheep brought brucellosis onto the island destroying much of the livestock, there is great apprehension that any mammals brought onto the island might carry disease. For this reason a total ban on importing monkeys or apes (and by implication, lemurs as well) into the island has been enforced. Since the turn of the century, less than a dozen lemurs have officially been re-imported. The other block against reintroducing lemurs is the high rate of illegal and clandestine lemur hunting that goes on even in reserves. Since effective control against poaching does not exist in any reserve, reintroduced lemurs might well be caught and eaten within days of their release. Reintroduction in Madagascar will consequently have to wait until specific places exist where protection of the animals can be guaranteed.

Behavioral studies that can be carried out at Duke are different from those so far undertaken in the wild, in that ages and exact genealogical relationships are known for every individual animal. We have found out that caged lemur families often tolerate fewer adult females per group than lemur families do in the wild. In both Ambohikely and Ambohibé forests, social groups of *Lemur catta* and *Varecia variegata* have grown larger than would be tolerated by dominant individuals in an enclosed environment. Even while the *Lemur catta* group increased in size, one of the two matriline was slowly driving out the other. Such shifts cannot be documented in a wild troop where genealogical relationships are unknown. The brown lemur troop, Ursula's troop, is the oldest continuously maintained lemur social group in captivity, having been established for ten years in Duke's largest outdoor run before being

transferred to Ambohikely in 1981. In this habitat enclosure the total introduced population of fourteen, containing many juveniles, stabilized at around eight. In 1985, Ursula's group was moved to the larger enclosure where we will watch to see if a six times larger area will allow for a larger stable population. The ruffed lemur group in the large enclosure has grown to nine individuals with little conflict between the two adult (mother-daughter) breeding females. Large group size is of interest behaviorally as no adequate group size records for *Varecia variegata* have been compiled in the wild. Another aspect of behavior that was newly observed in our forest environment is the fact that ruffed lemur parents, like birds, leave their infants in nests and take turns guarding them.

* A growing number of scientists have begun to use our enclosures to gather behavioral data on lemurs. In addition to K. E. Glander, these include I. C. Colquhoun, R. Foerg, J. Ganzhorn, R. Hoffman, P. M. Keppler, M. E. Pereira, L. Taylor, and L. G. Vick. Their publications are, or will be, available by writing to the Duke Primate Center. Our forest enclosures are visited by several hundred scientists and students annually. Recent visiting primate conservationists include T. E. Lovejoy, G. M. Durrell, L. M. Durrell, R. A. Mittermeier, and from Madagascar, V. Randrianasolo and G. Ravelojaona. Not long ago, Charles DeHaes, Director of World Wildlife International, (Fig. 5) visited. His organization recognized many years ago that without financial help many species of lemurs were doomed in the wild. He was accompanied by Winnifred Carter and Margot Marsh, both of whom have contributed substantially to Duke's conservation efforts. The habitat enclosures also serve as training areas for American, European and Malgasy students. Bodo Randrianasolo studied primate field observation techniques in Ambohibé forest during the summer of 1984, Hanta Rasamimanana is now looking at lemur behavior in Ambohibé for her work at Berenty Reserve in Madagascar, and Jonah Andrianarivo is completing a Ph.D. in Forestry on the relationship between deforestation and dry rice farming in northwestern Madagascar (Fig. 6).

Just as this article is going to press, we have learned that Mr. and Mrs. Gordon Getty have contributed \$100,000 to the endowment of our center. Earlier pledges by Mrs. Jocelyn Alexander and her brother, Mr. Richard Arundel, will bring this endowment to above \$225,000.

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ARTICLES

Central and South America

A Synecological Study of a Primate Community in the Pacaya-Samiria National Reserve, Peru

A field study of a primate community at Cahuana, Río Pacaya, in the Pacaya-Samiria National Reserve of Peru, was carried out from February 1984 to February 1985, as part of a long-term study of the ecology and population dynamics of the primates in the reserve.

The study site is located at Cahuana Biological Field Station, on the middle Pacaya river ($5^{\circ} 26' S$, $74^{\circ} 34' W$), in the Tropical Moist Forest life zone of Holdridge (1967). The vegetation consists of pristine, evergreen, mesophytic primary forest and swamp, growing on low, seasonally inundated terrain of level relief. The annual climate pattern consists of a long rainy or wet season (October - June), and a short dry season, with less than 200 mm of rain per month (July - early October).

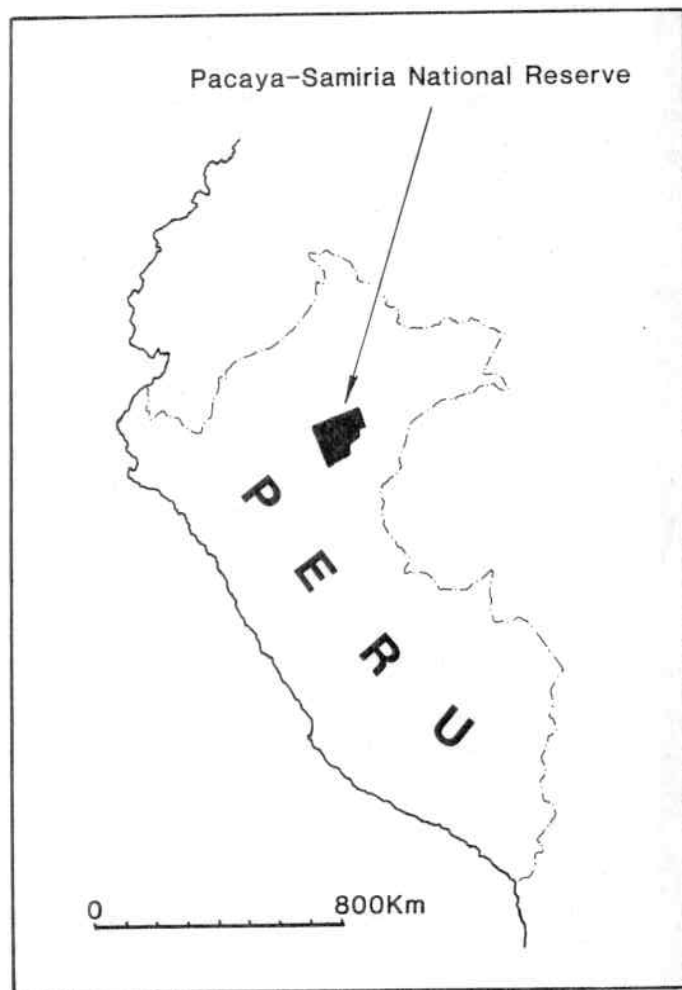


Fig. 1. The location of the Pacaya-Samiria National Reserve in Peru (map by S. D. Nash).

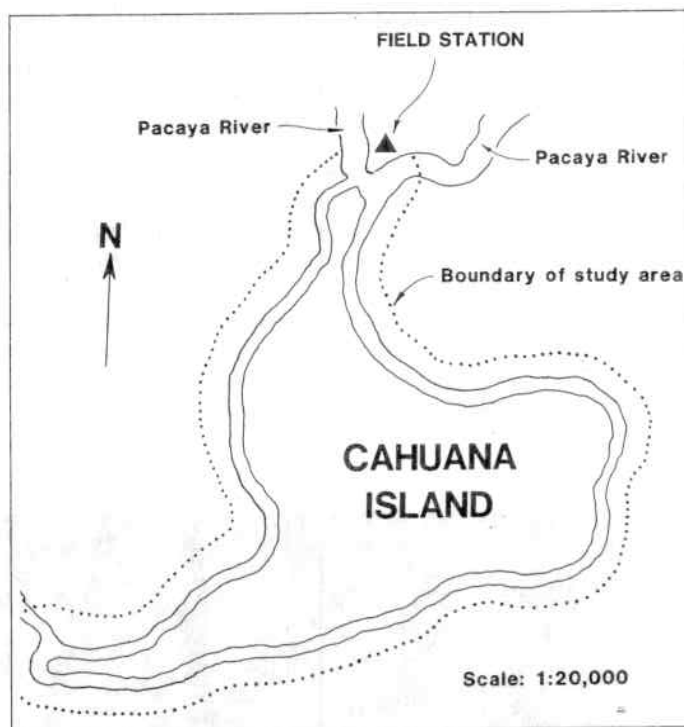


Fig. 2. Location of Cahuana Biological Field Station in the Pacaya-Samiria National Reserve, Peru (map by S. D. Nash).

The waters of the Pacaya river start rising in October, and between February and June all or nearly all the terrain is inundated by the flood. Monthly mean maximum temperature varies from 31° – $33^{\circ}C$ and monthly mean minimum temperature from 22° – $24^{\circ}C$. Phenologically, the wet season is characterized by an abundance of fruits, which begin to decrease in number towards the end of the wet season and become notably scarce in the dry season.

At Cahuana, the study area extended over 8.5 km^2 of forest, swamp and oxbow lake (Fig. 2). Of this, approximately 7.2 km^2 consisted of forested terrain and thus suitable primate habitat; the remaining 1.3 km^2 was open swamp and lake surface. The central part of the study area was occupied by the Cahuana Island, with about 4 km^2 of forest habitat.

The following 5 principal forest habitat types often grading into one another, were recognized within the study area:

Old-levee forest - Old levee terrains were the highest in the study area and supported the tallest, lushest, and most species-rich forest area. The trees formed a multi-stratified and continuous canopy. During the annual flood, the forest floor was inundated only shallowly and for a relatively short period. In years of lower than average flood, these terrains were not inundated.

Low-ground forest - The largest portion of the area consisted of tall, mixed forest growing on lower terrain and thus subjected to deeper and

more protracted inundation, even in years of relatively low flood. This forest had a lower plant species diversity, and a more uneven and broken canopy. In contrast to the old-levée forest, lianas grew in profusion here and non-woody forest floor plants were scarce. Moreover, fruit production was more strictly seasonal, being limited almost exclusively to the flood season.

Young-levée forest - The lake sides were bordered to a large extent by narrow strips of slightly elevated terrain, that supported a dense, mixed ('gallery') forest, partly isolated from inland forest by a belt of low-lying backwater swamp. These strips were much lower than the old levees and were subjected to deep and protracted inundation. The vegetation was similar but less varied and of lower stature than that of the low-ground forest. Fruit production was limited mainly to the flood season.

Cecropia forest - Pure or nearly pure stands of *Cecropia* trees grew on recently-formed river and lake banks. The undergrowth consisted exclusively or predominantly of *Paspalum* spp. reeds.

Backwater swamp - Swamps remained inundated or damp for all or most of the year. Swamps ranged from sparsely wooded to treeless. The vegetation was mostly low shrub and herbs and small stands or dispersed trees of *Bombax munguba* and *Cecropia* sp. Also *Ficus trigona* trees were sometimes present.

Forest types that are common in the region and present in other parts of the reserve, but which were noticeably absent from the study area included high-ground forest (i.e. tall, mixed forest not subjected to inundation) and *Mauritia flexuosa* palm swamp.



Fig. 3. Forest on Cahuana Island (A. Young).

The Primate Species of Pacaya

Surveys done along the course of the Pacaya river (except along its uppermost section) and additional information provided by the reserve guards have shown that 10 species of monkeys occur in the area.

Callitrichidae	<i>Cebuella pygmaea</i> (pygmy marmoset)
	<i>Saguinus fuscicollis</i> (Saddle-back tamarin)
Cebidae:	<i>Aotus nancymai</i> (owl monkey)
	<i>Saimiri boliviensis</i> (squirrel monkey)
	<i>Cebus albifrons</i> (white-fronted capuchin)
	<i>Cebus apella</i> (brown capuchin)
	<i>Pithecia hirsuta</i> (saki monkey)
	<i>Ateles paniscus</i> (black spider monkey)
	<i>Lagothrix lagotricha</i> (woolly monkey)
	<i>Alouatta seniculus</i> (howler monkey)

Also *Callicebus moloch* is known to occur at the periphery of the headwaters of Pacaya, in the southern tip of the Reserve, where it has been sighted at Machin Caño, near the left bank of the Ucayali, a few kilometers north of Monte Bello village. Of these, *C. pygmaea* and *A. paniscus* were absent from the lower and middle Pacaya. Both occur in the upper Pacaya but within the reserve both species appear to be more common in the Samfria river basin, where they may be largely confined to somewhat higher terrains. All the remaining 8 species were present in the study area and were included in this study, except the entirely nocturnal *Aotus nancymai*, and *Saguinus fuscicollis*, which was subject of an earlier detailed study there (Soini and Cópula, 1981; Soini and Soini, 1983; Soini, 1985). This study emphasized two species, *Lagothrix lagotricha* and *Pithecia hirsuta*, since very little previous information on their ecology and population dynamics existed.

Methods

Throughout the study period, field observations on the primates were done daily, for 20 or more days each month. Primate troops were located by walking along previously cut and marked trails, or by following compass bearings when outside the trail system, and by scanning the forest of the river and lake banks from a dugout canoe. Upon having located a troop, it was often followed for one or several hours and occasionally for a whole day. Troop locations and movements were plotted on a large-scale map. The census and home range utilization data were derived from the cumulative records of troop locations and movements and, particularly, from simultaneous or successive sightings of contiguous conspecific troops.

When encountering a troop, data were recorded, whenever possible, on troop size and composition, type of forest, vertical level and activity of the troop. If the monkeys were feeding, the type and taxonomic identity of the food plant, and the plant part fed on, were recorded. In order to obtain quantitative information on the food preferences, every time an individual or a troop was found feeding in a given fruit tree (or other plant) one feeding observation was scored; if later one or several individuals fed from a different tree of the same or other species, another observation was scored, and so on.

Herbarium specimens of some 200 food plants were collected and delivered to competent botanists for taxonomic identification. However, most of these are still pending identification; hence only a preliminary analysis of each primate species' feeding ecology is presented here; a more complete analysis will have to wait until the identification process has been completed.

Ecology and Population Dynamics

Lagothrix lagotricha

Social organization. The study population was composed of heterosexual troops and solitary individuals. No all-male or all-female groups were present. Observed troops ranged in size from 2-20 animals. A more intensive monitoring of several troops showed that these were not entirely independent units but that 2-3 such troops formed a larger social unit or clan.

Troop size and composition. Long-term observations (1979-85) in the study area and contiguous areas have shown that the usual size range for the troops is 5-9 self-locomoting animals, to which 1-3 carried infants may be added in the birth season; trios composed of one adult pair accompanied by one immature appear also to be relatively common. Units larger than these usually turned out to be coalitions of 2 or more such groups within the clan; this may, however, not always have been the case.

In 1984, the woolly population of the Cahuana Island lived in 4 troops; 3 of these often associated with one another and thus formed a clan, whereas the 4th troop apparently did not associate with the other troops and hence may have been an independent unit. The compositions of the 3 associated troops, just before the beginning of the birth season, were as follows:

		A	B	C
Adults	M	2	2	1
	F	1	3	1
Subadults	M	X	X	X
	F	1	X	X
Juvenile 2	M	1	1	X
	F	X	X	X
Juvenile 1	M	X	X	1
	F	X	X	X
	?	X	1	X
Infants	M	X	X	X
	F	1	X	X
	?	X	1	X
TOTAL		6	8	3

The 4th troop had 5-6 members, including 1 adult male and 1-2 adult females. In most troops the number of adults of each sex ranged between 1 and 3, and fully adult individuals made up 50-60% of the total study population. The composition of a troop tended to remain stable for periods of several months, but in the long-term the troop compositions were not stable. Thus, for example, during 9 months of continuous monitoring of troops A and B on the island, the composition of troop A remained fixed for about 5 months and, excepting recruitments through births and losses of infants, the only apparent change that troop B underwent was that the subadult female of troop A stayed mostly with troop B in January-February, 1985.

My observations on the island troops suggest that troops of a clan often coalesce for the night. In October-November, 1984, I followed troop A to its roost 12 times and on 4 of these, troops A and B coalesced and spent the night together or near one another; the 7 other times the two troops did not contact one another and spent the night in separate areas. Troop C seemed to associate more closely with troop B than with A, but sometimes all 3 troops coalesced. After having spent a night together, the troops usually drifted apart in late morning; sometimes they remained loosely together for one or a few days. Temporal subgroups were sometimes formed by an estrous female and her consort.

Solitary animals were seen infrequently. Both male and female solitaries were observed.

Population density. In mid-1984, the total number of woolies on Cahuana Island was fixed at 22-23 animals. This gives an ecological density of 5.5 animals/km².

The minimum number of woolies observed within the total study area was 74, but since a few animals were probably omitted in some of the troop counts, the total population was probably about 80 animals. This gives us an ecological density estimate of 11 animals/km² for the total study area. However, this figure probably somewhat overestimates the true density, due to the fact that the home ranges of all the troops outside the island extended far beyond the limits of the study area. A more reasonable estimate may be obtained by including only one-half of the

peripheral population of the study area in the density computation. This gives us a final density estimate of 7 animals/km² for the whole study area.

Annual population estimates for Cahuana Island (Table 1) suggest that since the establishment of our field station at Cahuana in 1979, the island population has been growing steadily, and in 5 years about doubled. This spectacular growth is undoubtedly a direct consequence of the full protection from hunting the island population has enjoyed through our continuous presence. Before this, the more vulnerable island population, in particular, seemed to have suffered from both illegal poaching and subsistence hunting by reserve guards. The comparatively low population density on the island probably indicates that the population has not yet reached the area's carrying capacity.

Reproduction. In the course of my long-term observations, I saw a minimum of 23 neonates (i.e., infants with natal coat, carried ventrally). All except 2 of them were born between September and April (60% of them in September-November); of the remaining 2, one was born in July and one towards the end of August (Table 1). These data suggest that *Lagothrix* has a discrete birth season that extends from the late dry season to mid or late wet season, with very few births occurring outside this season. Observations on many additional somewhat older infants, whose birth month could only be estimated, further support these findings.

Copulations were observed in January, February and September.

Infant care and development. Neonates have a light, straw-colored coat, which contrasts with the dark brown color of adults. The neonates were carried ventrally for the first 4-8 weeks and then on the back. There was usually a transition period of 1-2 weeks when the infants often rode on their mothers' flanks. The infants were carried frequently until 5-6 months of age, although they were seen moving around on their own during resting and feeding bouts already at 2-3 months of age. After the sixth month the infants were carried only infrequently, mostly in stressful or threatening situations and in difficult arboreal passages. Infants of nearly one year of age were still occasionally 'bridged' across gaps in the arboreal pathways. Infants in their second year of life still closely followed their mothers, particularly during travel and foraging. Three month old infants were already seen feeding on fruits, but at least some infants well in their second year still suckled occasionally.

Habitat preferences. For most of the year, *Lagothrix* showed a marked preference for tall, mature old-levée forest. However, a seasonal shift in habitat utilization was evident; from March thru June the low ground forest was used more intensively than the old-levée forest. This shift paralleled the fruiting pattern in that fruits were abundant in the low-lying terrain only during this season. The young-levée forest strips were visited relatively infrequently and only in March-April.

Most time was spent in the middle and (particularly) upper strata of the forest canopy, although they did feed often as well in emergent trees. Woolies only occasionally descended down to subcanopy levels. I once saw 2 individuals descend to the ground to pick up fallen fruits.

Roosting ecology. Troops always spent the night in the upper canopy stratum, often scattered over 3-4 trees that were sometimes up to 50-100m apart. I never saw troops spend consecutive nights in the same tree or travel long distances to reach a particular roost tree; rather, individuals (particularly subadult/adult males) often remained sleeping in the crown of the tree where they happened to be feeding at nightfall and where they would often continue feeding at daybreak.

Sleeping huddles or groups usually consisted of an adult female and her 1-2 immature offspring. In a small troop composed of an adult male and an adult female with her juvenile offspring, all three slept together. Also estrous females were observed spending nights in the company of single males. The woolies seemed to prefer sleeping on middle and distal parts of stout branches rather than near the bole.

All activities usually ceased at 18:00-18:15, i.e. well after sunset, and

started again at 5:15-5:45. The daily activity period was about 12.5 - 13 hours.

Home range and ranging pattern. The island clan's home range included nearly the entire island, and the total size of its home range was estimated to be about 3.5 km².

The day range of a troop was usually rather short, but occasionally up to 1-2 km long. On 7 successive days, in November 1984, troop A's ranging distance fluctuated between 100m and 550m, with a mean of 390m. The total sample of day ranges (n = 14), distributed over several months, gave a mean of 540m and a range of 100-950m. During foraging and feeding, the members of a troop were often highly dispersed, frequently over an area of one hectare or more, and the daily ranging distances given above refer only to straight-line distances the troop's core moved in a day.

Diet. The study population was observed feeding on fruits, seeds, flowers, leaves, shoots, and petioles of about 84 recognizable species of trees, lianas, hemiepiphytes and epiphytes. The total number of plant species included in their diet was evidently larger (probably well over 100 species), but in many cases it was not possible to recognize what the monkeys were eating high up in the canopy. Besides feeding on vegetal matter, I occasionally saw individuals carefully examine interiors of rolled-up leaves and lick up something from them, or catch small insects and arachnids by hand. They thus apparently also included a small amount of invertebrates in their diet.

The relative importance of different plant parts in the year-round diet of the population, as estimated on the basis of a total sample of 222 feeding observations, was:

Fruits	74%
Seeds	17%
Leaves & shoots	6%
Flowers	3%

Fruits were the quantitatively most important resource year round; the seeds were either discarded or swallowed intact. Besides ripe fruits, unripe fruits were also consumed, particularly those of *Coussapoa* sp. and *Inga aff. punctata*. Very immature fruits of the latter were eaten whole. *Ficus* spp. (about 13 species) were the quantitatively most important fruit source; they were eaten year-round and comprised 18% of all the feeding observations. Another Moraceae, *Coussapoa* sp., was an important staple in November-February, comprising 13% of all the feeding observations. *Inga* spp. (6 species) also scored 13% of all the feeding observations and were fed on mainly in November-March. Only one species of palm fruit, *Iriarteia exorrhiza*, was included in the observed diet (*Mauritia flexuosa*, an important palm fruit in other areas, did not occur in the study area); it was fed on mainly or exclusively by adult males, in October-April.

Although the population fed on seeds year round, they contributed very significantly to the diet only from October thru January, when 26% of all feeding observations were seeds. The most important species was a Lecythidaceae (*Echweilera* ?).

Leaves and shoots contributed significantly to the diet from September - December (9%); their consumption peaked in September-October, comprising then 17% of all feeding observations.

Flowers were a relatively insignificant food source, and were consumed mainly from September thru November.

In conclusion, feeding on seeds, leaves, shoots and flowers increased in the late dry season and continued high into the early wet season, thus coinciding with the seasonal low in the availability of ripe fruits, particularly of those of large size.

Relationships with other species. Woollies did not seem to actively associate with other monkeys. They were seen in circumstantial feeding associations with other species on 16 occasions: 8 times with *Alouatta*, 4 times with *Pithecia*, 3 times with *Saimiri*, and once with *C. apella*. These feeding aggregations occurred usually in large *Ficus* and *Ocoteia tamamuri* trees loaded with fruits, and overt interactions were usually

limited to mild mutual avoidance and occasional supplanting of other monkeys by woollies. However, a competitive and mildly agonistic relationship did seem to exist between *Lagothrix* and *Alouatta*, with the former being dominant over the latter. Once, when a woolly couple was feeding in a tree of relatively small crown diameter, a troop of *Alouatta* tried repeatedly to enter to feed there but was chased away by the woolly male. On several other occasions, I saw *Alouatta* troops lingering in the periphery of a particular fruit tree occupied by woollies, evidently waiting for the woollies to leave the tree before entering to feed in it.

Table 1. Annual population estimates of *Lagothrix lagotricha* on Cahuana Island from 1979-1984, based on counts made around midyear, i.e. before the onset of the birth season.

Year	No. of animals
1979	11-12
1980	12-13
1981	15
1982	approx. 20
1983	21-22
1984	22-23

Pithecia hirsuta

Social organization. The study population of *P. hirsuta* was composed of monogamous family troops and pairs, and solitary individuals. Temporary coalitions and aggregations between such troops were observed occasionally, but more commonly contiguous troops did not associate even when they found themselves near one another. In such circumstances the troops often entered into a vigorous vocal exchange (sometimes with both sexes participating), sometimes accompanied by visual threat displays. Nevertheless, contiguous home ranges often overlapped extensively, and during hundreds of hours of observations only once was a troop seen physically attacking another troop. *P. hirsuta* does not appear to be territorial in the way callitrichids and some other monogamous cebids (notably *Callicebus* spp.) are.

Troop size and composition. The troops ranged in size from 2-8 animals, with a mean size of 3.8 and modal size of 4 (Fig. 4).

Annual population censuses since 1981 showed that troops contained 2-5 adults, with an average of 1.4 (1-3) males and 1.1 (1-2) females. More often than not, the troops contained only one adult of each sex, and the modal troop composition was one adult pair with 2 offspring. Any additional adults were usually, or perhaps always, matured offspring of the breeding couple.

Troop composition was extremely stable, indicating that the troops were essentially closed social units. Thus, for example, in the 8 best-studied troops (monitored for 2-6 years, for a total of 34 'troop years') only 3 cases of single immigrations into three of them occurred. All 3 immigrants were adult males that joined the respective troops, and became permanent members of them, 1, 3, and 4 years after I had started monitoring the respective troops. It is quite likely that the immigrants were biologically related (sons or brothers) to one or both the adults of the respective troops.

Long-term monitoring of the study population showed that it had the following average age-sex composition:

Adult males	39%
Adult females	32%
Subadult males	4%
Subadult females	5%
Juveniles	14%
Infants	5%

Adults make up about 70% of the total population and immatures 30%. Reproductive and potentially reproductive couples comprised about 84% of the adult population or about 60% of the total population.

Population density. At the end of 1984, the total number of saki troops on Cahuana Island was 11 and the total number of individuals 51. The ecological population density on the island was thus 12.8 animals/km².

The total number of troops found within the overall study area was 23 and the total number of individuals 103, which gives us a density estimate of 14.3 animals/km² for the total study area. Although peripheral troops that ranged only very marginally into the study area were not included in the census, the above estimate probably slightly overestimates the true density, due to the fact that the home ranges of several study area troops extended well beyond the limits of the study area. The density estimate obtained on the island probably comes closer to the true overall ecological density, which is therefore estimated to be about 13 animals/km².

Reproduction. Long-term observations showed that *P. hirsuta* has a well-defined birth season that extends from September to December, i.e., from late dry season to early wet season. Each troop had only one reproductive female, and offspring were normally produced at 2-year and 3-year intervals. When an infant is lost at an early age, this interval may be decreased to one year. Although a few births occurred every year, the births in the population tended to be synchronous; nearly all the troops produced young in 1981, very few in 1982, many again in 1983, and only few in 1984. On the average, 45% of the troops produced offspring in a given year.

Copulations and sexual play were seen only in April and May, which suggests that the females may have a seasonal ovulation pattern; however, more observations are needed to confirm this.

Infant care and development. The natal coat pelage appears short, rather sparse and nearly black. As the pelage becomes denser and longer it turns lighter in color; infants of 2-8 weeks usually exhibit markedly lighter coat color than adults. In most juveniles I observed, the characteristic adult facial-hair pattern of the corresponding sex becomes unequivocally evident only at about 2.5 - 3 years of age.

Infants were apparently carried exclusively by their mothers; although subadult/adult daughters also may have participated to some extent. Contrary to many other monogamous primates, the males of this species did not participate at all in the carriage and direct care of the infants; in fact, they did not allow infants on their backs even in threatening situations. Nevertheless, brief cuddling and grooming of young infants by fathers were seen a few times.

During its first week of life, the infant was carried ventrally, mainly wrapped transversally across the lower abdomen or the inguinal region. From the second week onward the infant is carried mainly on the upper dorsum. The infant started leaving its mother's back in the second month of life, and at 3-4 months it was largely self-locomoting. Upon 4 months it was carried only in difficult passages and in stressful or threatening situations; in such situations it may still seek refuge on its mother's back up to 7-8 months of age. Self-locomoting infants often followed their mothers at their heels, but by 7 months these infants usually moved quite independently within the troop. In threatening situations, such as the sudden appearance of a human being, young juveniles often hid, remaining silent and motionless, while the mother and other troop members fled a short distance, vocalizing loudly as they moved away from the hiding juvenile, thus attracting the attention of the potential predator towards themselves and away from the juvenile. (This juvenile behavior is, by the way, a potential source of considerable bias in troop size counts in population censuses or short-term observations, and it may explain some of the smallest average troop size counts reported for *Pithecia* populations in the literature.)

Infants seemed to be suckled at least to the eighth month, but complete weaning occurs probably only at 1 year of age. They feed on fruits already at 2-3 months, and mothers often shared their food with their offspring at least into the second year of life. In one observed case the mother still opened the tough pods of *Inga* sp. for her 26-month-old daughter, who apparently was not yet able to open them by herself.

Habitat preferences. *P. hirsuta* commonly occupied both the tall old-levee forest and the low-ground forest. The young-levee forest was seasonally utilized intensively. During January or February, when *Xylopia ligustifolia* starts bearing ripe fruits, many of the troops shifted to the young levees, where this tree was abundant. Here they stayed (most of the time) until June and then returned to the tall old-levee forest and low-ground forest. They were not to be seen on *X. ligustifolia* again until the next year.

Although *P. hirsuta* utilized every level of the forest vegetation at least occasionally, their activities were largely confined to the middle and upper canopy strata. They occasionally fed in emergent trees and also in sub-canopy levels, particularly while in young-levee habitat. They were never seen on the ground or at levels below 3m.

Roosting ecology. Troops were observed in their sleeping sites only three times; in all cases, the site consisted of a stout horizontal branch located in the upper canopy stratum.

Home range. The home range limits were determined quite accurately for 2 contiguous troops (nos. 1 and 2) and less accurately for a third contiguous troop (no. 3). The respective home range sizes were 9.7 ha, 24 ha, and 40-42 ha. The home ranges of troops 2 and 3 overlapped extensively; approximately 70% of the home range area of troop 2 was also utilized occasionally by troop 3. In contrast to this, the home ranges of troop 1 and 2 had only a very narrow zone of overlap (0.2 ha) that represented only about 2% of the total home range area of troop 1 (troop 1 occupied a peninsula and had only troop 2 as a neighbor). My observations on the use of space by these and other troops in the study area suggest that, in general, large troops occupy larger home ranges than small troops.

Diet. The study population fed principally on fruits, seeds, leaves, and flowers. Also insects, particularly ants, were consumed. In the total year-round sample of 250 plant feeding observations, involving about 64 plant species, the relative frequency of the different food items was:

Fruits	55%
Seeds	38%
Leaves	4%
Flowers	3%

Fruits were the quantitatively most important resource in all seasons except early wet season (October-December) and contributed from 22% - 74% to the seasonal samples. Both ripe and unripe fruits were consumed. *Xylopia ligustifolia* (in January-March), *Ogcocodia tamamuri* and *Inga* spp. were the most frequent fruit sources.

The quantitative contribution of seeds in the seasonal samples ranged from 25% - 68%, surpassing that of fruits in the early wet season sample. Both mature and immature seeds were consumed. The quantitatively most important seed sources were a Lecythidaceae (*Echweilera* ?), *Inga* aff. *punctata*, and a liana pending taxonomic identification. These 3 species comprised 31% of all seed-feeding observations.

Flowers contributed from 3% - 10% to the seasonal samples. Of these, the inflorescence of *Iriarteia exorrhiza* palm was the most important and was fed on intensively from August - October.

Young leaves contributed from 1% - 14% to the seasonal samples.

Relationships with other species. *Pithecia* did not seem to actively associate with other species of monkeys. Circumstantial or passive associations with all the other species present except *C. albifrons* were observed occasionally. Of 35 occasions in which *P. hirsuta* was observed in the same feeding tree with other monkeys, 31% were with *Alouatta*, 29% with *Saimiri*, 17% with *Saguinus*, 12% with *Lagothrix*, and 11% with *C. apella*. Agonistic interactions occurred only with *C. apella*; twice I saw *C. apella* enter a tree where a saki troop was feeding and chase the sakis out from the tree by rushing towards the feeding sakis and even grabbing at them. The sakis did not put up any resistance and fled immediately, vocalizing excitedly.



Fig. 4. A view of Cahuana Island from the Field Station (photo by A. Young).

Alouatta seniculus

Social organization. The study population was composed of heterosexual troops, all-male groups, and solitary animals. Both one-male and multi-male heterosexual troops were present. Long-term annual censuses showed that about 55% of the troops had only one mature male and about 45% had 2 males ($n = 60$ troops); 2 troops had, at least temporarily, 3 seemingly mature males. Most troops had 2 or 3 adult females, but about 23% of the troops had only one mature female.

All-male groups were composed of 2-3 subadult/adult males. Solitary animals were mostly subadult/adult males, although at least 2 solitary females were observed repeatedly in the study area.

Each troop occupied a relatively small vocally and visually advertised/defended territory.

Troop size and composition. Annual censuses of the study area troops showed that stable, heterosexual troops ranged in size from 2 - 13 animals, including carried infants and peripheral troop members. The usual size range was 3-8 animals, the modal size 5, and the mean size (± 1 S.D.) 5.5 ± 1.6 ($n = 74$).

The age-sex composition of the heterosexual troops (including peripheral members) was as follows:

Adult males	26%
Adult females	34%
Subadult males	7%
Subadult females	2%
Juveniles	21%
Infants	10%

Thus, approximately 60% of the population consisted of adult animals. A troop had usually 1 or 2 ($x = 1.3$) adult males and 1-3 ($x = 1.8$) adult females. Troops of 2 animals consisted of apparently newly-formed, stable adult pairs without offspring. The average numbers of immature animals per troop were: 0.4 subadult males, 0.1 subadult females, 1.1 juveniles, and 0.6 infants.

Population density. Cahuana Island was inhabited by 24 stable, heterosexual troops, containing a total of about 137 animals (including peripheral troop members). Besides these, the population included, at any given moment of time, at least 2 incipient couples and 2-3 solitary animals. The total island population was thus around 144 animals, which makes an ecological population density of 36 animals/km². My data from the remaining portion of the study area suggest that this is a good estimate for the entire study area as well.

Reproduction. During long-term monitoring of the study population I saw a total of 38 neonates of known dates or months of birth. These birth records spanned every month of the year except August, indicating that *Alouatta* breeds year round. However, most neonates, as well as other still very young infants, were seen from October - April and very few were seen in June - September, indicating that, in the dry season, births were either infrequent or neonatal mortality was much higher, or both.

Most troops had 1 or 2 reproductively active females, and my observations suggest that intervals between a female's successive offspring fluctuated normally between about 1.5 and 2 years. After an early death of an infant, however, a female may produce her next offspring after a considerably shorter interval.

Infant care and development. In their first month of life the infants were carried ventrally, but from the second month on, they rode mainly on their mothers' backs. In the fourth month of life, infants became largely self-locomoting, but they were still carried occasionally well into the fifth month. Only adult females were seen carrying infants; males apparently did not allow infants on their backs even in threatening situations. In a few instances, however, males were observed defending threatened infants by boldly approaching the source of danger.

Habitat preferences. Howlers utilized all the available forest types, including to some extent the *Bombax munguba* swamps not utilized by other primates. Nevertheless, troop densities seemed to be higher in and about tracts of tall, old-levee forest than in the other available habitat types.

Howlers occupied mainly the highest forest strata; troops spent most time in the crowns of large emergent and upper canopy trees. Feeding at lower levels also occurred, and in the March-May period troops spent a considerable amount of time feeding on tender leaves and shoots of vines at very low levels (often only 1-3 m above ground or water surface) along the water front or other edge situations. Feeding at such low levels was relatively infrequent in October-February and was never seen in the July-September period. Howlers did not normally descend to the ground, but a female was once seen doing so in order to pick up her apparently debilitated offspring that had fallen down to the ground, and a subadult male once ran a considerable distance on the forest floor when I surprised him feeding in low shrub vegetation. A dispersing subadult male was once seen to deliberately descend into the water and swim across the 80m-wide Pacaya river. Such voluntary crossing of major open water bodies was never seen being done by other primate species.

Home range. The three best studied troops occupied home ranges of 9 ha, 6 ha, and 5-6 ha. The home ranges of contiguous troops overlapped to a varying extent. The vegetation in the above 3 home ranges was mostly tall, old-levee forest, and my observations on troops inhabiting less favorable habitat types suggest that these often occupied larger home ranges.

Roosting ecology. Howlers spent the nights on large branches of emergent and upper canopy trees, huddled in one or a few groups. Daily

activities usually ceased before nightfall, but howling activities occurred occasionally at any time of the night. At dawn, feeding often started well before sunrise.

Diet. Howlers were observed feeding on fruits, leaves, petioles, leaf buds, vine shoots, and flowers. No feeding on seeds was observed. In the total sample of 103 feeding observations, 72% were fruit feeding, 25% leaf feeding, and 3% flower feeding. However, this sample probably underestimates the true proportion of leaves and shoots in the diet of the howler population, because fruit feeding was usually a more conspicuous activity than leaf feeding. In fact, leaf feeding was often surmised but not ascertained, due to poor observation conditions, when howlers were found in trees that were not fruiting. Leaves and shoots probably make up more than 30% of the diet.

Both ripe and entirely unripe fruits were eaten from over 20 different species. The most commonly eaten fruits included *Ficus* spp. (7 or more species), *Clarisia racemosa*, *Xylopia ligustifolia*, *Cecropia* sp., *Ogcodeia tamamuri*, and *Inga* spp. (3 or more species).

Feeding on leaves was observed every month of the year and included leaf buds, young leaves, flush leaves and mature leaves. In some species only the apical tips were consumed (e.g., *Couroupita amazonica* and *Ceiba pentandra*).

Relationships with other species. Howlers did not actively associate with other monkeys. They were occasionally seen in circumstantial or passive feeding associations with all of the other species except *C. albifrons*. The species most frequently involved were *L. lagotricha* and *P. hirsuta*. As already pointed out, there seemed to exist a mildly agonistic relationship between the howlers and woollies.

Cebus apella

Social organization. The study population was composed of heterosexual, single-male and multi-male troops, usually containing 2-3 adult females. Small groups of 2-4 animals were also seen often, but these seemed to be dispersed subgroups of larger troops rather than autonomous troops. Also solitary individuals were observed in the population.

Troop size and composition. Long-term observations on 10 troops indicated that these were composed of 6-11 animals; most troops had 8-10 animals, with a mean of 8.7 and mode of 8 animals.

The best studied troop had the following composition: 2 adult males + 2 adult females + 1 adult/subadult + 2 juveniles + 1 self-locomoting infant + 1 carried infant. The compositions of other troops were not determined accurately, but most troops seemed to contain 1-2 adult males, 1-3 adult females, and several immature animals. Adults comprised about 40-46% of the population.

Population density. There were 4 or 5 troops of *C. apella* on Cahuana Island, with an estimated total of 35-44 animals. The estimated ecological population density was 8.7 - 11.0 animals/km².

The total number of troops ranging within or into the overall study area was 10 ± 1 and the estimated total number of individuals in them 87 ± 9 . This would give us a density estimate of 11 - 13 animals/km². However, since at least 5 of the troops ranged well beyond the study area limits, the true density was probably somewhat lower. Inclusion of only one-half of the peripheral troops in the density calculation gives us an estimate of 9 ± 1 animals/km², which is here considered the best estimate of the ecological density in the total study area.

Reproduction. In the course of long-term observations, I saw a total of 11 neonates of known month of birth. These births were distributed over nearly every month from October - June, suggesting that *C. apella* breeds year round. However, the lack of observed births in the dry season (July-September) may be significant, but further observations are needed to confirm this.

Infant care. The infants were always carried dorsally, initially diagonally on the neck or the shoulder region and later lengthwise on the middle back. Whether other troop members besides the mothers participated

in the carriage of the infants could not be ascertained. The infants were carried at least to the fourth or fifth month of life.

Habitat preferences. *C. apella* was a habitat generalist, utilizing all the available forest types, except relatively open backwater swamps. They were seen most frequently in sub-canopy and lower canopy levels and only relatively infrequently in the upper canopy levels.

Diet. *C. apella* were observed feeding on invertebrates, honey, fruits, seeds (nuts), leaves, shoots, meristems, petioles, pith, and nectar. The invertebrate diet included, among other items, wasp larvae and pupae, ants and ant eggs, and large snails. The snails were picked up from the damp or shallowly inundated forest floor. The shell was broken by banging it repeatedly against a tree bole or branch.

In the total sample of 96 plant feeding observations, 71% involved feeding on fruits, 16% on leaves, shoots, meristems, and petioles, 7% on seeds (nuts), and 3% on pith.

Couroupita amazonica (cannon-ball tree) was the most frequently eaten fruit, particularly in the late wet season and throughout the dry season (June-October). To break open this hard-shelled and heavy (up to 3.4 kg) fruit, *C. apella* pounded it persistently against a stout branch. Other important fruits included *Inga ingoides*, *Xylopia ligustifolia*, *Cecropia* sp., and *Abuta fluminum*.

In the dry season when fruits were scarce, feeding on bamboo shoots, *Cecropia* petioles and flush leaves (or leaf buds), pith, *Scheelea* palm nuts (and mesocarp), and the basal parts of *Bromelia* leaves became prominent. In August-October about 50% of the feeding observations were these items.

Relationships with other species. *C. apella* formed frequent or nearly permanent associations with *Saimiri* troops. On the 243 separate occasions on which *C. apella* groups were observed, they were with *Saimiri* troops 180 times (= 74%) and not with *Saimiri* troops 63 times (= 26%). The frequency of association showed seasonal changes, being most frequent in April-May and December.

Cebus albifrons

Social organization. The study area population lived in single-male and multi-male troops, containing 2 or more adult females. No all-male groups were seen; neither were solitary individuals seen in the study area. Generally, *C. albifrons* troops appeared more cohesive than *C. apella*, with the troop members less dispersed during foraging and feeding.

Troop size and composition. Long-term observations showed that the troops had an average size of 8.3 animals and a range of 5-10 ($n = 8$). Troops usually had 1-2 adult males and 2-3 adult females; however, there may have been more adults in some of the troops. Adults comprised about 40-50% of the population.

Reproduction and infant care. In the course of long-term observations I saw a total of 6 carried neonates, all born between December and March or April. These, and observations of somewhat older, carried infants, suggest that *C. albifrons* has a well-defined birth season occurring in the middle wet season, synchronously with that of *Saimiri*.

Other troop members besides mothers seem to participate in the carrying of infants; a subadult male was seen once carrying an infant for at least one-half hour while actively foraging and feeding. Infants were always carried on the back.

Population density. The total number of troops living on Cahuana Island was 2 or 3, and the estimated total number of individuals 17-25. The ecological population density was thus estimated at 4.2-6.2 animals/km².

The total number of troops living within or ranging well into the study area was estimated to be 6 (troops could not usually be individually identified). Correcting for the fact that the home ranges of 3 of the troops extended far beyond the study area limits (i.e., by including only one-half of those troops), the ecological population density for the overall study area was estimated to be about 5 animals/km².



Fig. 5. River bank in the Pacaya-Samiria Reserve (photo by A. Young).

Habitat preferences. Observations of *C. albifrons* troops were not frequent enough to warrant a judgement about their habitat preferences. They were, however, seen in all the major forest types except for relatively open swamps and *Cecropia* forest.

Diet. *C. albifrons* were observed feeding on invertebrates, seeds, fruits, leaf and flower buds, and the basal parts of *Bromelia* leaves. In 12 out of 17 feeding observations, they were eating fruits. Also *C. albifrons*, like its congener, fed on the large and hard-shelled *Couroupita amazonica* (cannon-ball) fruits, although it was my impression that it was less successful in opening them than the more powerfully-built *C. apella*.

C. albifrons also preyed on the large snails, searching for them in the shallowly inundated or damp forest floor. It handled them the same way *C. apella* did.

Relationships with other species. *C. albifrons* was observed in close association only with *Saimiri*. However, compared to *C. apella*, it seemed to associate with *Saimiri* only infrequently; of 24 separate opportunities in which I observed *C. albifrons* troops, they were alone 21 times (= 87%) and with *Saimiri* only 3 times (= 13%).

Saimiri boliviensis

Social organization. The *Saimiri* population was composed of heterosexual, multi-male troops, all-male groups, and solitary males. Within the heterosexual troops, adult/subadult males often moved as a discrete subgroup, somewhat separated from the main group of females and juveniles. During foraging, large troops sometimes split into 2 separate, heterosexual subgroups that occasionally moved a few hundred meters apart for several hours. Independently ranging all-male groups were seen

in every month of the year, but they were particularly ubiquitous from January thru June. The troops did not show any territorial behavior.

Troop size and composition. Repeated troop size counts in the study area showed that most troops consisted of 25-45 self-locomoting animals. The mean size for the 9 best-studied troops was 32 animals, and the observed range 12-50 (approx.) animals. The troops had 3-8 adult females and 3-6 adult males. Usually the troops had more immature animals than adults; approximately 30-37% of the troop members were adult animals. However, in small, apparently incipient troops, adults may outnumber immatures; for example, in one troop of only 12 animals, 58% were adults.

The all-male groups were usually composed of 3-4 males, with an average size of 3.5 and observed range of 2-5 ($n = 57$ groups). Most of these males were subadults, but also a few apparently fully adult animals were included. Some all-male groups seemingly maintained stable compositions for several months, but the groups did not appear to remain stable over long periods of time.

Population density. The total number of heterosexual troops on Cahuana Island was 6, containing a total of about 192 individuals. Besides these, the population included an estimated annual average of 4 all-male groups, for a total of about 14 extra-troop males. The ecological population density on the island was thus estimated at 51 animals/km².

Although not all the troops observed within the limits of the overall study area could be individually identified, the total number of heterosexual troops that habitually ranged within or into the study area was estimated to be 15. The home ranges of 9 of these ranged far beyond the study area limits. The adjust for this, only one-half of those troops

were included in the respective density calculation. On the basis of this, and considering a similar proportion of extra-troop animals as on the island, the overall ecological density was estimated to be about 50 animals/km².

Reproduction. Long-term observations of the study population showed that *Saimiri* had a well-defined birth season extending from late December to April, with a peak period in January-February. No births were observed outside this period.

The maximum number of visibly pregnant females and/or carried infants observed per troop ranged from 4-8, suggesting that most adult females reproduce annually. Conspicuously "fattened" males (a physiological condition associated with the mating season) were seen from June to November. Females carrying infants (which were always carried on the back) were commonly seen up to late April, and still (though rarely) in June, suggesting that 3 months old infants are largely self-locomoting.

Habitat preferences. *Saimiri* was a habitat generalist, utilizing every available type of forest habitat, including relatively open swamp habitat. It spent more time at and near forest edges and in open-canopy vegetation than any of the other species.

Saimiri foraged and fed at every vertical level of the forest. However, they seemed to spend most of the day in sub-canopy and lower canopy levels. On the river and lake banks, as well as in other edge situations, they often spent considerable amounts of time in low shrub and herbaceous vegetation, including on the ground combing for insects and feeding on fruits of such herbaceous low ground plants as *Physalia peruviana*. The foraging often took them into low shrub vegetation of virtually treeless parts of swamps that were not utilized by any of the other primate species.

Home range and ranging pattern. The best studied troop occupied a home range of about 40 ha, and the home ranges of contiguous troops overlapped extensively. On one seemingly typical day when the movements of the troop were monitored from dawn to dusk, its path length was 1900 m and its ranging distance 950 m.

All-male groups appeared to be much more sedentary than the troops, often remaining for several weeks within an area of one hectare or less.

Roosting ecology. Troops were observed spending the nights in the middle and upper crown of medium to large trees, often dispersed over 2-4 trees. The troops settled for the night well after sunset, usually around 18:15; and started moving out from the roost tree before sunrise, usual-

ly around 5:30 local time. The daily activity period was normally 12.5-12.7 hours.

Diet. *Saimiri* fed mainly on invertebrates and fruits. Nectar was also an important resource in the early dry season, when fruits were scarce, accounting for 33% of all feeding observations in June-July. Seeds and flowers were also eaten, but relatively infrequently. In the year-round sample of 111 plant feeding observations, 91% involved fruit feeding, 6% nectar feeding, 2% seed feeding, and 1% flower feeding.

Inga spp. (approx. 6-8 species) were the most frequently eaten fruits. Other highly important fruit sources included *Ficus* spp. (4+ species), *Cissus* sp., *Ogcodeia tamamuri*, and *Xylopia ligustifolia* (in February-March only). *Combretum fruticosum* and *Ceiba pentandra* were the principal nectar sources.

Relationships with other species. It seemed that all the *Saimiri* troops in the study area moved in frequent or semi-permanent associations with *C. apella*. *Saimiri* troops were also seen a few times in a similar association with *C. albifrons*. All-male groups and solitaries were only seldom seen associating with *Cebus*. They did, however, associate frequently with *Saguinus fuscicollis* troops, often following the latter for several days. *Saimiri* troops were also occasionally seen in circumstantial or 'passive' feeding associations with all of the other monkey species.

Two species of birds, *Crotophaga major* and *Monasa nigrifrons*, often followed *Saimiri* troops, catching insects that these stirred into flight.

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Africa

A Resurvey Of Tana River Primates And Their Habitat

Introduction

The Tana River subspecies of the red colobus (*Colobus badius rufomitatus*) and crested mangabey (*Cercocebus galeritus galeritus*) were the subject of several surveys and more detailed ecological studies between 1972 and 1976 (Andrews *et al.*, 1975; Groves *et al.*, 1974; Homewood, 1975, 1976, 1978; Marsh, 1978a, 1978b, 1978c, 1979a, 1979b, 1980, 1981a, 1981b, 1981c). These studies contributed to the establishment in 1976 of a Tana River Primate National Reserve, designed to protect some of the best remaining areas of riverine forest and populations of these monkeys. In addition, Allaway (1979) carried out a study of elephants in the Tana River region and a Management Plan for the Reserve was gazetted (Marsh, 1976).

Since 1976, no intensive studies have taken place in the Reserve, although Hughes (1984) has carried out a broad study of forest regeneration on the river and the government has monitored at intervals the regional distribution of cattle and large mammals by means of aerial surveys (Peden, 1984). The objectives of the present study were therefore to resurvey the status of the two rare Tana primates and their habitat, and to assess the effectiveness of the Reserve designed to protect them.

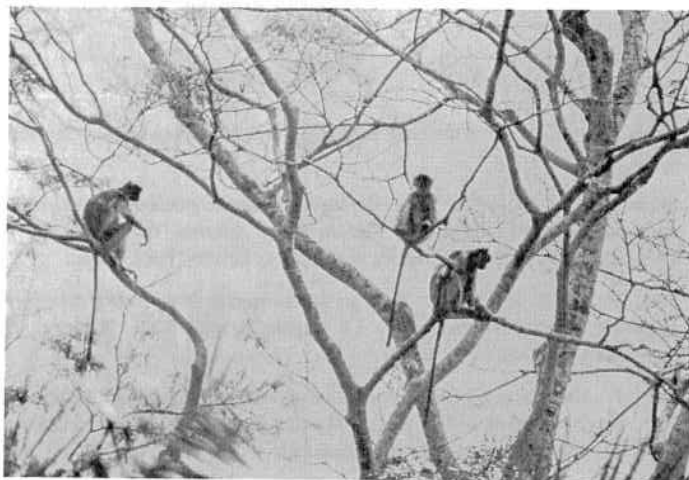


Fig. 1. Red colobus group in an *Albizia gummifera* tree. This species, ranked fourth in the study group's diet in 1974, but 58% of the trees in the group's range died between 1975 and 1985 (photo by C. Marsh).

Itinerary and Methods

The survey and report were carried out over eight weeks in January and February, 1985. Some four weeks were taken up with logistic arrangements, discussions, protocol, and preparation of the report, leaving 29 days in the field from January 17th to February 15th. In carrying out the survey the author was accompanied by Mrs. Barbara Decker and Mr. Robert Barton whose assistance permitted more intensive coverage of many forests than would otherwise have been possible.

The main method of survey was to visit and search as many as possible of the 70 odd forest patches in the two monkeys' 60 km range between Wenje and Garsen. Notes were made on all encounters with primates and on the species composition and condition of each forest. Aerial photographs taken in 1969 at a scale of 1: 50,000 were carried in the field to help with identification and interpretation of habitat. On nearly all trips, local guides were employed and questioned carefully on land-use and habitat changes. Counts of group size and composition were made whenever possible.



Fig. 2. An adult male mangabey selecting ripe fruits of *Ficus sycomorus*. This species was the highest ranking food source for both colobus and mangabeys at Mchelelo. There has been a heavy mortality in the species throughout the Tana forests since 1975 (photo by C. Marsh).

In some of the larger forests the survey team divided into two parties and criss-crossed the forest following compass bearings in a series of transects some 100-200 m apart, designed to maximize the chances of locating all primate groups. It remains possible, of course, to "miss" groups, particularly after 10.00 hrs in the morning. Confidence in our estimate of the number of groups in each forest is therefore a function of the size of the patch and the number of times a survey was repeated. Since the rare monkeys appeared less common in many forests than they had been in the 1973-1975 surveys, it was decided to sacrifice visits to some of the more inaccessible forests in favor of more intensive coverage of the principal and better known patches. Outside the Reserve and south of Mnazini, the only forests visited were those between Kulesa and Hewani at the southern limit of the range.

Survey Results

Red Colobus. Estimates of the number of groups of each species in each forest together with pre-1975 estimates are given in Table 1. A list and maps of all these forests are given in Appendix A. Within the Reserve, 20 out of 24 named forest patches were visited. Of these 20 forests, red colobus were found in 10, compared with 17 patches known to have been inhabited formerly. Moreover, in all but three occupied patches the estimated number of groups had declined. In all, only 15 groups were located between Wenje and Mnazini (two of these were on the west bank outside of the Reserve), compared with a comparable former minimum estimate of 39 groups in the same area and excluding the three patches not revisited this time.

The most spectacular and certain decline has been in the long thin forest strip known as Guru West, which was surveyed 17 times in 1973-74 and contained at least six and probably eight groups. During three repetitions of this route in 1985, we could locate only one group and two solitary males.

The Mchelelo study area immediately south of Guru formerly contained two groups of variable composition, but averaging 28 individuals in all. Only a single group of seven individuals was confirmed in this study during a dozen visits totaling 26 hours. No colobus could be found in the adjacent Congolani West forest and Congolani Central apparently contained only one group where formerly there were either three or four. Group counts of red colobus are notoriously difficult and prone to underestimation in a short study. Nevertheless, the six best counts of the survey had a mean size of 9.8 and a range of 6-13 (Table 2). These figures can be compared with a 1975 mean group size of 18 and a range of 12-30 for 13 groups (Marsh, 1979b).

Table 1. Number of Groups of Four Primate Species Found in Each Surveyed Forest Patch

	Ref. no.	No. Visits	1985					1975	
			Colobus	Mangabeys	Sykes	Baboons	Colobus	Mangabey	Notes
Kanjonga	1	1	0	2	5		0	4	Formerly considered jointly by Dhardo Abio
Wenje E.	2	1		2			1	1	
Maroni E.	5	2		1			1	0	
Kipende W.	3	2	1	0	1	1	2	0	
Maroni W.	4	2	0	0			1	0	
Makere W.	6	2	1	0			6-8	3-4	+ 2 solitary male R.C.
Guru W.	10	3	1	2	5		1-2	1	
Guru E.	9	1	1	1	1		2	2	+ 1 solitary male R.C.
Mchelelo W.	11	12	1	1	3		1	0	big males occasionally visit
Mchelelo E.	12	1	0	0	1		3-4	2	
Congolani	13	3	1	1	2	1	1	1	
Congolani W.	14	3	0	0	1		4-6	2-3	+ 1 solitary R.C.
Sifa E.	16	2	2	3-5	3		1	1	
Sifa W.	17	3	0	0	0		1	0	
Hadridu	19	1	0	0	0		0	1	
Mariadadi	18	6	0	0	0	1	2-3	1-2	
Baomo N.	21	1	0	1	2	1	6-8	5-6	
Baomo S.	22	4	4	5-7	4-5	3	3	2	
Mnazini N.	26	1	1	2	3	0	3	2	
Mnazini S.	27	2	2	1	4	2	0		
Wema E.1	56	2	0		1		0	0	1 solitary male R.C.
Wema W.1	53	1	0	0	1		1-2		1 solitary male R.C.
Hewani W.1	58	1	0	1	1		1	1	
Hewani W.2	62	1		1			0	0	
Hewani E.1	59	1	0	0			1	0	
Hewani E.2	60	1	1				1	0	
Hewani E.3	61	2	1	0	0		3	2	1 solitary male R.C.
Hewani S.2 (Home)	64	1		2	3	1			
N ^o 28	Total		17	26	41	10	46	31	

Table 2. Counts of Six Red Colobus Groups

Forest	Adult Males	Unsexed Adults	Adult Females	Subadult Females	Juveniles	Sub-Juveniles	Infants	Total
Mchelelo	1		3	1	1	1		7
Sifa E.	1		7		4	1		13
Makere W.	1		11		1			13
Baomo S.	1		4				1	6
Mnazini S.	1	3	5		1			10
Hewani E.3	2		4	1	1	1	1	10
Mean	1.1	0.6	5.6	0.3	1.3	0.6	0.3	9.8
Mean as %	12	5	58	3	14	5	3	100
		78%				22%	100	
Compare Marsh (1979)		66%				34%	18.0	

A more robust comparison, since it is less affected by incomplete counting, can be made of the proportion of infant and juvenile age-classes. Collectively, these made up only 22% of the 1985 sample compared with 34% in the earlier study, which is itself a smaller proportion of juvenile classes than Struhsaker (1975) has reported for this species in the Kibale Forest, Uganda. Apparently, then, over the past 10 years the Tana red colobus groups have declined by about two thirds in number, by about half in mean size and perhaps 10% in the percentage of young animals. The estimated population in 1975 of 1,200-1,800 may thus be reduced to perhaps 200-300 animals. This amounts to a crash in the population to a very critical level.

Mangabeys. Compared to observations of red colobus, changes in the abundance of mangabey groups appear much less severe. Among the 28 surveyed patches 26 groups were accounted for out of a former estimate of 31 groups. Seven patches appear to have lost groups, two may have gained one and the remainder either contained the same number

of groups or have never been reported to contain mangabeys. Significantly, all but one of the forests from which mangabey groups seem to have been lost are also patches from which a large proportion of colobus groups have also gone. These are Guru West, Mchelelo, Congolani, Congolani West, Sifa West, and Mnazini South. The other area of mangabey loss was a woodland area called Mariadadi which never contained colobus and is based on a now defunct flood channel near Congolani. Mangabey groups are still abundant in the three largest forests of Wenje East, Sifa East and Baomo South and may even have increased in Sifa East.

No group counts of mangabeys were obtained in this study, but several encounters gave impressions of 15-30 animals and were thus similar to many pre-1975 encounters. Counts of three groups reported by local assistants numbered 35, 15 and 26 animals. Interestingly, very few infants were seen and then only at the end of the survey in February. Homewood (1976) reported a discrete birth season between November and February. Possibly the season is late this year. If the original estimate

of 1,100-1,500 is accepted and if no change in group size has occurred then the population would now number around 800-1,100.

Sykes Monkeys and Baboons. Survey results for Sykes' monkey (*Cercopithecus mitis*) have not previously been reported, but are included here in Table 1 for the purpose of future comparisons. Essentially, the species is thriving in almost all the forests that contain colobus and mangabeys as well as in other patches, such as Congolani West, that now contain neither. However, the Mchelelo forests seem to have lost one group: there used to be four groups, but only three were found in this survey.

Baboons (*Papio cynocephalus*) remain abundant in the flood plain generally, and at least two groups roosted in the Mchelelo forest. Counts of these obtained by R. Barton are given in Table 3.

Other Wildlife. No formal attempts were made to estimate the abundance of wildlife other than primates, but some casual observations may be noted. Firstly, all the other specifically forest-based mammals were seen in this survey. These include red duikers, bush pigs, bush buck and the squirrels *Paraxerus palliatus* and *P. ochraceus*. Of these, only *P. palliatus*, the red bush squirrel, seemed perhaps less common than recalled from 1973-75. Some conspicuous forest birds, including the trumpeter and crowned hornbills, Fischer's touraco and the green pigeon remain common. Mr. R. Barton has also added some species to the bird list included in the Management Plan for the Reserve.

Good recent rains in areas away from the Tana probably explain a general paucity of plains game sightings during this survey, but giraffe, wart hog, zebra, Peter's gazelle, impala and oryx were all seen in or near the Reserve. Only the dik-dik, which is a resident, non-water dependent species and formerly the most consistently seen ungulate seemed oddly scarce in this survey (also Allaway, pers. comm. 1984).

Among the very large mammals, black rhino and elephant population crashes in the past decade are common knowledge. We saw no evidence of rhino in the Reserve and only a few sightings of fresh elephant spoor (but this will have been largely a seasonal consequence of rains elsewhere). Peden (1984) has reported a decline in the estimated elephant population for Tana River District from about 9,500 in 1977 to 1,400 in 1983, an apparent decline of 85%.

Certainly, the Pokomo were happy to report greatly reduced crop losses to elephants in recent years. The role of principal mammalian pest now seems to be shared between baboons and waterbuck. J. Allaway (pers. comm. 1984) has noted a loss from river bank erosion of at least three out of 11 former elephant drinking points on the west bank of the river in the Reserve. One of the most accessible remaining points is in the middle of the Baomo South forest, but the elephant paths to it have now largely overgrown from reduced use. Some of the bush understorey in this forest that was formerly very heavily browsed now seems to be recovering. Also, many saplings of *Acacia robusta* that were damaged by elephant in 1973-75 have nevertheless survived and grown up to 10 m in height (see below). It seems likely that the early 1970's was a time of heavier browsing pressure than either earlier (perhaps due to compression of ranging patterns) or later (due to population reduction by hunting).

Of the remaining big mammals, lions were heard often and buffalo, although not seen, are apparently still common in the forests in the late dry season. Hippopotamus are also abundant and reported by Pokomo to have increased in number considerably in recent years. Certainly, their trails are now more widespread in the forests than they were in 1973-75. Twenty or so animals were resident in the river at Mchelelo



Fig. 3. The Tana River subspecies of the red colobus, *Colobus badius rufomitatus*, recently reduced to a population of perhaps 200-300 animals (photo by R.A. Mittermeier).

during the survey, but following the flooding in December of several major splay lakes, most of the population had apparently moved away from the river. Some careful dry season river counts of this species are needed to monitor the population.

Finally, by repute at least, crocodiles have increased in both number and size in the river and splay lakes. Eight animals to a maximum size of around 3-4 meters were seen at Mchelelo. There have been several recent incidents of attacks on people, the most recent being at Maroni in January of this year.

A project to capture crocodiles for a farming project in Mombasa has been in operation for the past 18 months and continues to remove small crocodiles and eggs from a long stretch of river between Garsen and Wenje. According to the current project manager, they have captured some 50 large (2 m and above) animals, 200 small animals and an unspecified number of eggs. Although these figures may be underestimates, the animals are evidently not rare at present. Crocodiles are an eminently manageable species in terms of maintaining a sustained yield without endangering the population, but this requires close monitoring by scientists not involved commercially. On principle, it seems wrong to harvest from within the reserve, especially as formerly both waterbuck and baboons were being shot as bait within the reserve (J. Allaway, pers. comm., 1984).

Table 3. Counts of Two Baboon Groups at Mchelelo

	Adult Males	Adult Females	Subadult Males	Subadult Females	Juvenile	Infant	Total	Max. Count
Group 1	6	19	5	4	11	11	56	63
Group 2	8	23	4	8	26	13	82	82
Mean as %	10	31	7	8	26	18	100	—

Table 4. Re-Enumeration of All Trees (Other than Palms) 10 M Tall Within 9 Ha of the Former M Group's Range at Mchelelo

Family	Species	# of trees 1975	# of trees 1985	% change	% Colobus diet in 1974
Anacardiaceae	<i>Sorindeia obtusifoliolata</i>	82	76	- 7	19.6
Ebenaceae	<i>Diospyros mespiliformis</i>	78	71	- 9	0.8
Leguminosae	<i>Albizia gummifera</i>	41	17	-58	9.6
Sapindaceae	<i>Blighia unijugata</i>	18	15	-17	1.9
Sapindaceae	<i>Majidea zanguebarica</i>	14	13	- 7	4.4
Guttifera	<i>Garcinia livingstonei</i>	14	16	+14	1.3
Sterculiaceae	<i>Sterculia appendiculata</i>	10	10	0	3.0
Leguminosae	<i>Acacia robusta</i>	13	10	-23	15.0
Moraceae	<i>Ficus sycomorus</i>	10	6	-40	29.4
Moraceae	<i>Ficus natalensis</i>	8	5	-38	4.2
Leguminosae	<i>Albizia glaberrima</i>	8	7	-13	2.9
Sapotaceae	<i>Mimusops fruticosa</i>	7	6	-14	0
Leguminosae	<i>Tamarindus indica</i>	5	5	0	2.3
Anacardiaceae	<i>Lannea stuhlmanii</i>	4	5		0.7
Mimosaceae	<i>Acacia elatior</i>	3	3		0
Sapotaceae	<i>Pachystela brevipes</i>	2	2		0.6
Boraginaceae	<i>Cordia ghoezii</i>	2	5		0.1
Moraceae	<i>Ficus depauperata</i>	1	1		0
Moraceae	<i>Ficus bussei</i>	1	1		1.1
Ebenaceae	<i>Diospyros natalensis</i>	1	0		0
Ulmaceae	<i>Celtis wightii</i>	1	1		0.1
Euphorbiaceae	<i>Antidesma venosum</i>	1	1		0
Sterculiaceae	<i>Cola clavata</i>	1	1		0
Alangiaceae	<i>Alangium salvifolium</i>	0	1		0.9
Euphorbiaceae	<i>Excoecaria venenifera</i>	0	1		0
Erythroxylaceae	<i>Erythroxylum fischeri</i>	0	6		0
Leguminosae	<i>Casseea singuena</i>	0	1		0
Total		325	286		

Changes in the Vegetation

Forest Area. Since at least 17% of the former forest area between Wenje and Garsen was lost between 1960 and 1975, most of it to cutting for farmland, further changes in forest areas were of particular interest in this study. To locate and measure any recent changes a set of aerial photographs were taken privately in January, 1985, using a specially mounted Nikon camera on a Cessna 182. Two runs from Wenje to Garsen were made at elevations of 2500 and 3000 feet taking overlapping photographs centered on the river. These give calculated image widths of 1,016 m and 1,219 m, respectively. These slides were subsequently used to map further changes in forest cover by comparison with a map



Fig. 4. These scattered acacias are all that remains of the upper canopy over much of the range of Homewood's former study group of mangabeys at Mnazini (photo by C. Marsh).

drawn in 1974 from the best available aerial photography (1969 and 1960 survey of Kenya prints, plus aerial survey updating). This latest exercise was further assisted by an excellent series of 1979 maps and 1:60,000 scale photographs, and technical advice from Eco Systems Ltd., a company that specializes in aerial surveys and photointerpretation. The resulting map together with names for all forest and woodland areas between Wenje and Garsen is given in Fig. 8.

Only two significant areas that were forested in 1975 are no longer forest, and in neither case is human cutting a factor. About half of the 70 ha Mnazini South forest has been lost to grassland, apparently because of heavy, scouring floods caused by a break in the riverbank in 1982 followed by a severe fire in 1983. The other area lost is about 50 ha of the 100 ha Guru West forest which must now be considered bushland rather than forest. Apart from these two areas, other losses south of the reserve have been negligible.

Considerably more information on forest classification and the distribution of farmland could be plotted from these photographs, but this is regrettably outside the scope of the present study. The original photographs have been left with the Institute of Primate Research for future reference.

Forest Composition. While the gross forest area along the river has changed little over ten years the species composition and structure of many forests has altered greatly. With the possible exceptions of Sifa East and Mbazini North, all the main forests show signs of degeneration with the loss of some old trees not being replaced by younger growth. This was broadly predictable from the virtual absence of saplings and small trees of most forest species during the earlier study period (Marsh, 1976), but the form and sequence of change is of great interest. One formal comparison that can be made is of the number of trees over 10 m in height within 9 ha of the former M group's home range at Mchelelo (Table 3).



Fig. 5. View of the Mchelelo forest in 1975 (photo by C. Marsh).



Fig. 6. Same view of forest in 1985. Discounting the differences between wet and dry seasons in the two shots, the major change is the growth of *Hyphaene* palm and *Acacia robusta* trees to about 10 m height. The secondary growth follows the abandonment of the area as farmland in 1969. While this regeneration of colonizer species is encouraging, none of the evergreen forest species appears to be maintaining itself (photo by C. Marsh).

Excluding palms, there were formerly some 325 trees 10 m or more in height within 36 mapped 0.25 ha quadrats (four trees counted in 1985 appear to have been missed in 1975). A recount of the same area in 1985 showed 286 trees, or a net loss of 12%. While a few minor species of small tree have increased in number by growth (e.g. *Cordia ghoeztii*), all but one of the 13 species with formerly five or more stems in the sample has decreased in abundance. The greatest proportional decline is for *Albizia gummifera* (–58%) with losses of more than 20% also recorded for *Acacia robusta*, *Ficus sycomorus* and *F. natalensis*. Unfortunately these are all important red colobus food sources with respective ranks in the annual diet of the former study group of 4, 3, 1 and 6.

Two informal assessments of regeneration were made in this survey. One was a search along 400 m of trails in Mchelelo recording tree seedlings and saplings 10m tall within about 2.5 m of the trail. The results were as follows:

- Cordia ghoeztii* — 3 saplings from 2 to 6 m in height
- Acacia robusta* — 12 seedlings to 1.5 m in height
- Albizia gummifera* — c. 50 seedlings to 1.5 m in height mostly close to adults of the same species
- Garcinia livingstonei* — c. 30 seedlings to 1 m in height
- Diospyros mespiliformis* — 12 seedlings to 1 m in height
- Sorindea obtusifolia* — Several hundred seedlings to 20 cm in height all close to adults of same species

Immediately north of the Mchelelo forest is an area that was cleared for farms in 1966, but has been abandoned since 1969. By 1975 the area had developed a fairly dense stand of bushes to about 2–3 m in height, dominated by *Pluchea discorides* and *Phoenix reclinata*. Now *Pluchea* is much less abundant but both *Phoenix* and *Hyphaene* palms are common and reach 10 m or more in height. Half a dozen bush species are also common together with scattered trees 5–10 m tall of *Acacia robusta*, *Albizia gummifera* and *Ficus sycomorus*. There are the only forest species to have established themselves, but are evidently growing strongly (Figs. 5, 6).

Although these observations are casual they suggest that several tree species are producing a crop of seedlings but that within the forest these are not (or at least have not been) surviving to sapling or larger size. Outside the forest, three species, at least, have established themselves as trees. These three all presently have high rates of adult mortality in the mature forest. High rates of establishment and growth but shorter lifespan are characteristics of colonizer species such as these.

Similar changes are evident in several of the other major forests. Almost everywhere, large specimens of *Acacia robusta* and *Ficus sycomorus* have fallen down or show signs of crown dieback. Thus, for example, remaining forest in Guru West and the northern portion of Mnazini South (Homewood's former study area), which were dominated by *Acacia* are now largely reduced to bushland. On the other hand, in parts of Mnazini South, at least, there is a good population of young acacias now some 2–6 m in height.

A crucial element in any understanding of the forest dynamics is the conditions permitting establishment to sapling size of the non-colonizer evergreen trees such as *Pachystella*, *Diospyros*, *Sorindea*, *Blighia*, and *Sterculia*. It was therefore interesting to find one small portion of Mnazini North where all these species occur as saplings or small trees. Their location was on the outside of a riverbank where the forest still floods regularly, depositing silt and sand, but not clay.

Discussion

Vegetation Changes. An explanation of the dynamics of the Tana forests must lie principally in knowledge of the conditions required for establishment and growth of seedlings in the common tree species. Hughes (1984) has also noted the absence of sapling-sized regeneration at a number of sites along the river, but the details of her enumeration plots are not yet available. As a first hypothesis, it is suggested that there are two kinds of survivorship pattern among the commoner trees. First, there is a class of colonizer species, including *Acacia robusta*, *Albizia gummifera* and *Ficus sycomorus*, which require high light intensity but not necessarily regular flooding to achieve establishment to sapling size. These are the only species currently regenerating, while a cohort of old trees of these species is in the process of dying off. Their age is not known, but must be at least 40–50 years.

A second class of species is apparently slower growing, shade tolerant, and currently almost completely lacking in younger growth. The older trees are dying off but in a less synchronized manner than the colonizing species. On the basis of girth increment measurements, Hughes (1984) suggests that most of these trees are in the age range of 60–100 years which places their establishment in the period 1880–1920. She suggests that these species require regular flooding for growth when young to provide sufficient water and/or nutrients, and that rainfall was apparently higher at the end of the last century than for most of this century. Hence, conditions may have favored the establishment of what have now become senescent forests on high, sandy levees which are rarely flooded.

A model of forest turnover thus begins with an *establishment phase* on a low-lying sandy levee close to the river, and subject to frequent flooding. Such areas are usually at points where the river has recently changed course and has yet to build up high levees. After establishment, trees are much less dependent on floods since their roots can presumably tap the water table through the porous sand of the levee. This may be termed the *growth phase* of the forests, but it is accompanied by a decline in regeneration creating an increasingly bimodal pattern of size classes (i.e. big trees and seedlings, but few saplings). This is due to the accre-

tion of sediment on the levees and a consequent decline in flood frequency. A third, *senescent phase* is reached when the big trees begin to die and can then be replaced only by a small class of colonizer species which do not require regular flooding for their establishment.

In terms of a forest typography (e.g. Marsh, 1976), Mixed Evergreen and *Pachystella* (Types I and II) are characteristic of the growth phase of the cycle. *Acacia* Type III forest probably occurs either in the senescent phase or as a secondary formation following clearance by man during the growth phase. *Garcinia* (Type IV) forest remains an edaphic variant of lower-lying, clay soils on the backwater edge of the levees (i.e. further from the present river course).

Several management implications stem from this model. Firstly, the decline of the main forest remnants on the river is not due principally to either human removal of large trees or undergrowth, or to elephant damage. This is not to deny any significance to these factors in accelerating the process of senescence, but they are of secondary importance only. Secondly, the key areas where generation could occur are low-lying riverside areas favored by the Pokomo for farms. Many of these sites are already occupied and in the remainder succession is probably hindered by the fires that occasionally sweep through grassland and bushland areas.

A third consequence of recognizing the importance of flooding for regeneration is that the gradual taming of the river by upstream dams can only worsen the present problem. A quantitative model of peak flow frequencies based on calculations by the Tana River Development Authority and shown to the author shows that common events, i.e. small floods, will become less frequent while the occasional really big flood (e.g. such as occurred in 1961 and 1968) will be hardly affected. The present absence of a class of small trees of around 18 or 24 years old, corresponding to establishment in those years, suggests that frequent but small floods may be the crucial requirement. Very large floods actually kill off many trees through the development of anoxic conditions in the soil.

A further consequence of dam building may be to reduce sediment load in the river which will slow down the geomorphological processes of meander development, cutting off ox-bows and levee deposition. The river will tend to entrench in its present course.



Fig. 7. River dynamics. Although new ox-bow lakes have been cut since 1975 this river bend has cut more than 50m into the edge of the flood plain in the past 10 years (photo by C. Marsh).

Primate Population Changes. The survey results indicate a decline in the red colobus population over ten years of about 5/6 and of mangabeys of about one quarter (more if mangabey group sizes have declined). An interesting feature of the decline is that it has apparently been mediated through both declines in group size, and the extinction or dissolution of whole groups. Unfortunately, no study was in progress to document

the behavioral correlates of these changes. Nor is it known if the decline is continuing. However, the paucity of juveniles in the remaining population suggests that this may be the case and that the population has not yet begun to rebuild.

In the continuing absence of any hunting of these animals, there remain at least three possible explanations for the decline. One is that a disease epidemic has occurred to which red colobus have been particularly susceptible. Dr. P. Waser (pers. comm.) reported seeing three sickly colobus in 1977 at Mchelelo, but there is no other direct evidence of a possible epidemic. Telling against such speculation is the widespread distribution of the decline, including the Sifa East forest which is separated by the river from westbank forests and Hewani South (the Home forest of Andrews *et al.*, 1975), which is isolated and about 40 km south of Mchelelo.

A second possibility, suggested by a Pokomo guide, was that the drought in 1984 reduced the animals' food supply disastrously. Several Pokomo, incidentally, acknowledge that red colobus have vanished from previous haunts but maintain that they have merely moved to other forests. Having visited nearly all forests in the Reserve, this is not plausible. Local informants were also uncertain as to the date of colobus disappearance.

The drought hypothesis is unfortunately not supported by the rainfall data from Hola, which is the nearest station. 1984 was a dry year at Hola (286 mm), but there have been four drier years since 1963, including two prior to the 1973-75 study period. Nor does anyone recollect any major defoliation of the forests.

A remaining possibility is that the colobus population has declined because the forests have become senescent. In support of this is a loose connection between patches in which colobus have declined most markedly and where most trees seem to have been lost (e.g. Guru, Mchelelo, Congolani, Mnazini South and Hewani South). However, even in these forests, the colobus decline seems disproportionate to the loss of trees. There would therefore have to be some threshold effect relating a relatively modest loss of trees to a large loss of monkeys.

Two observations may be relevant here. First, as noted earlier, the four species to have declined most at Mchelelo are four of the most eaten and most strongly selected food species. *Ficus sycomorus* trees, in particular, may have a disproportionate influence on the colobus carrying capacity because they are very productive of both fruit and young leaves, and asynchronous in their fruiting pattern. An interesting analysis that could be performed with phenology data collected during 1973-75, would be to calculate the likelihood of, say, a two or three month gap in the year without fig fruits as a function of the number of trees available to the animals. It is possible that below a certain small number of trees the probability of a major gap occurring in the annual food supply increases very rapidly, constituting a threshold effect of the kind proposed.

Secondly, some of the populations in which big declines have occurred seem in retrospect, at least, to have been vulnerable to a crash. The Guru, Mchelelo and Congolani forests each supported a density of about 8-10 groups per km² in habitat dominated by figs and *Acacia*. These were the highest densities in any forests and perhaps the populations were already above the long term carrying capacity of their habitat due to earlier excisions for agriculture. Another class of "vulnerable" forest were several small patches of *Acacia* or *Garcinia* (Types III and IV) forest, that were characterized on dietary grounds as marginal because of their low diversity of colobus food species. Very slight changes might convert these to inviable habitat. Maroni West, Congolani West, Sifa North and the northern part of Mnazini South were of this kind, and each supported one group but now contains none.

Another aspect of the habitat requirements of red colobus that became apparent during this resurvey is their virtual inability to utilize secondary forests. This is probably due both to their requirement for dietary diversity, and to their reluctance to move across open ground and thus colonize new habitat. Most of the series of *Acacia* Type III forests comprising Wenje East are late secondary and probably lack colobus for one or both of these reasons. Revealing, also, is the situation around

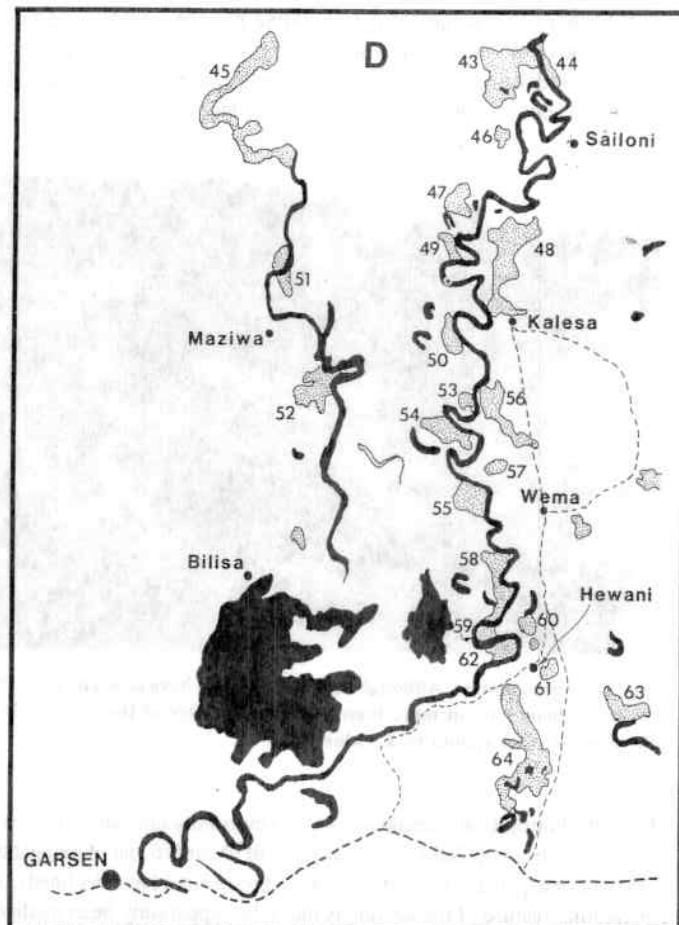
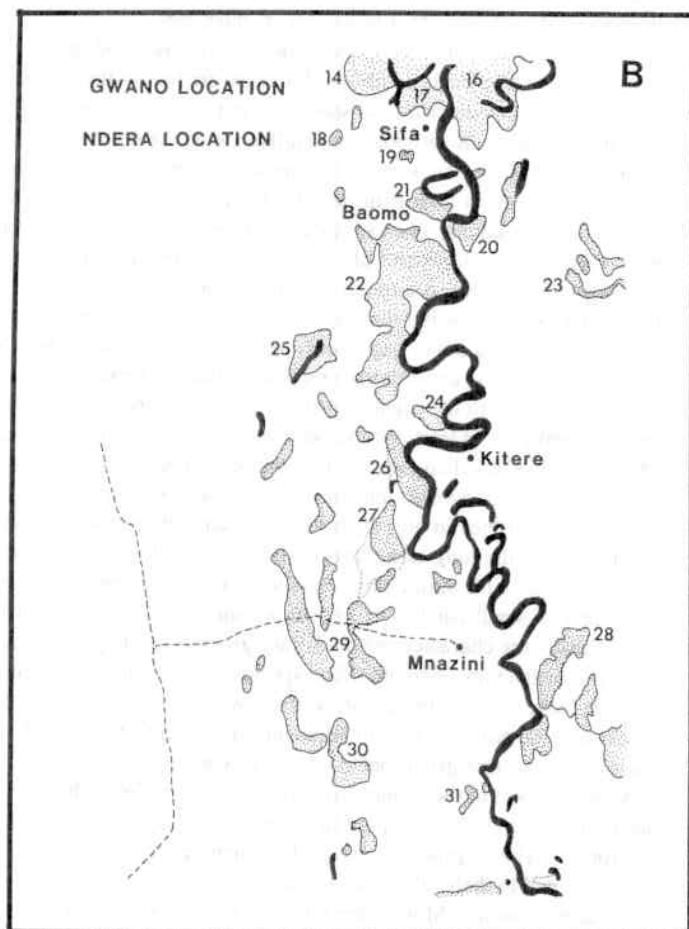
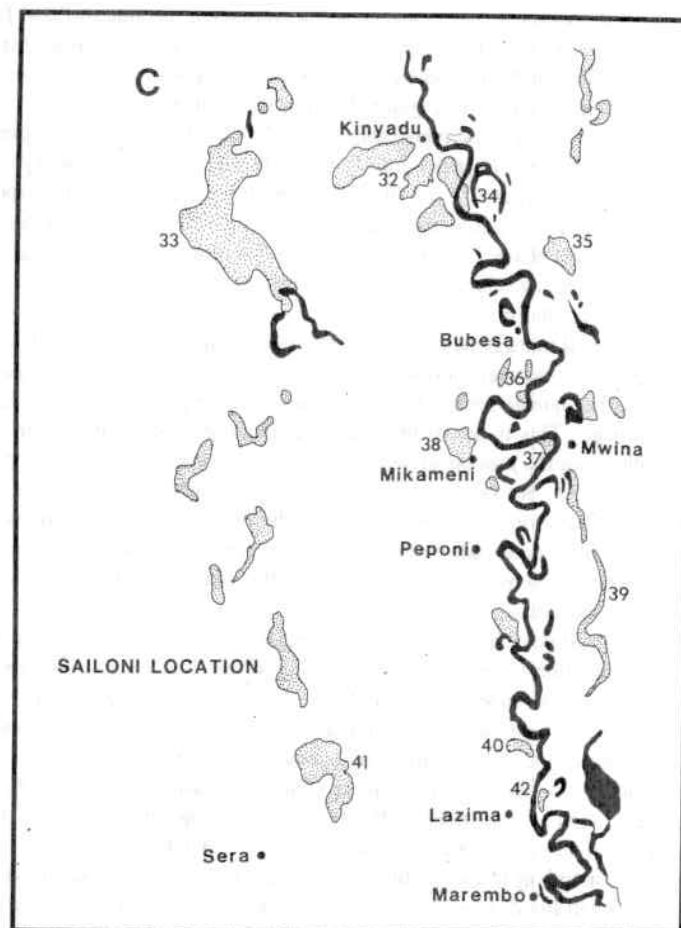
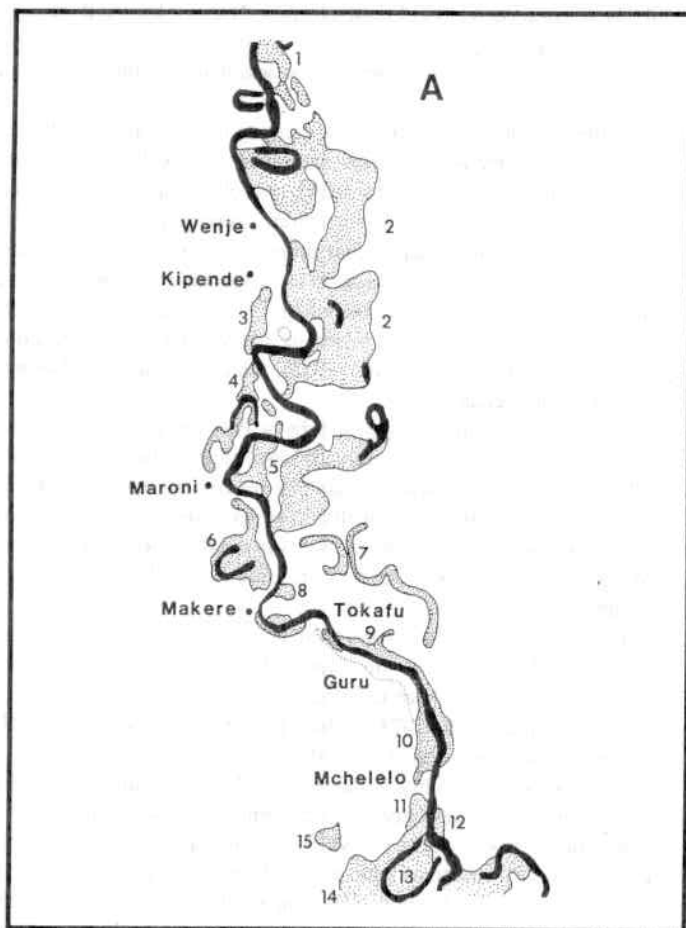


Fig. 8. (a,b,c,d). Location of forest tracts in the Tana River region (maps by S. Nash from author's originals).

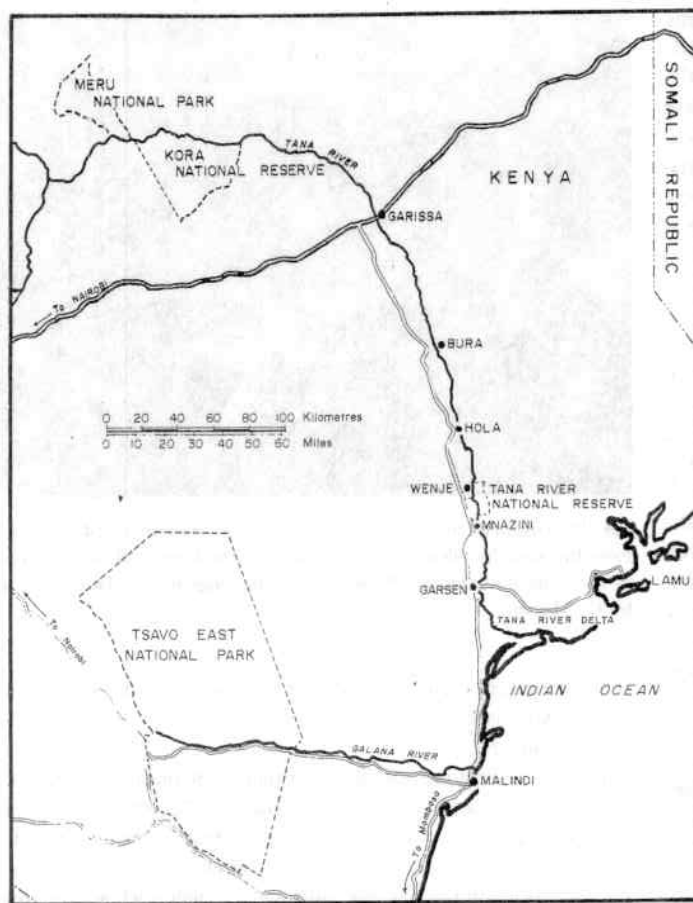


Fig. 9. Map of Eastern Kenya showing the location of the Tana River National Reserve (map provided by the author).

Reference List of Forests From Just North of Wenje to Garsen

- | | |
|-----------------------|----------------------------------|
| 1. Kanjonga East | 34. Kinyadu East |
| 2. Wenje East | 35. Bubesa East |
| 3. Kipende West | 36. Bubesa West |
| 4. Maroni West | 37. Mwina West |
| 5. Maroni East | 38. Mikamani |
| 6. Makere West | 39. Unnamed Woodland |
| 7. Kwechi | 40. Lazima North |
| 8. Makere East | 41. Sera |
| 9. Guru East | 42. Lazima East |
| 10. Guru West | 43. Marembo West |
| 11. Mchelelo West | 44. Marembo East |
| 12. Mchelelo East | 45. Giritu Woodland |
| 13. Congolani Central | 46. Sailoni West 1 |
| 14. Congolani West | 47. Sailoni West 2 |
| 15. Unnamed Woodland | 48. Kulesa East |
| 16. Sifa East | 49. Kulesa West 1 |
| 17. Sifa West | 50. Kulesa West 2 |
| 18. Mariadadi | 51. Maziwa North |
| 19. Hadribu | 52. Maziwa South |
| 20. Baomo East | 53. Wema West 1 |
| 21. Baomo North | 54. Wema West 2 |
| 22. Baomo South | 55. Wema West 3 |
| 23. Lemu | 56. Wema East 1 |
| 24. Kitere West | 57. Wema East 2 |
| 25. Mkombeni | 58. Hewani West 1 |
| 26. Mnazini North | 59. Hewani East 1 |
| 27. Mnazini South | 60. Hewani East 2 |
| 28. Mnazini East | 61. Hewani East 3 |
| 29. Unnamed Woodland | 62. Hewani West 2 |
| 30. Matalani North | 63. Hewani South 1 |
| 31. Mungaveni | 64. Hewani South 2 (Home Forest) |
| 32. Kinyadu West | 65. Lango la Simba Woodland |
| 33. Matalani South | |

Hewani in the extreme south of the species' range. The large forest of Hewani South (the Home forest) is now in an advanced state of degeneration because of its distance from the present course of the river, and only a solitary male colobus could be found there. In four small patches between Kulesa and Hewani, two or more solitaires were seen and one group reported, but three of these are old cultivation forests dominated heavily by mango and fig trees alone. On the other hand, small but healthy (in terms of juvenile composition) groups remain in the two tiny Hewani East 2 and 3 patches (10 ha in total), just as they were 10 years ago. Although low in stature, these are both primary forests, fairly rich in tree species, close to the river and still liable to flood. Young tree growth was evident in both.

In sum, it seems that red colobus achieve highest densities in primary riverside forests just as these start to senesce, whereafter they are vulnerable to a sharp decline. The period from 1975 to 1985, happens to have been a time of transition from peak maturity of many forests into senescence. This has been the primary cause of a crash in the colobus population and a lesser decline among mangabeys. The relative rarity of the two subspecies has thus reversed, with the colobus definitely now the rarer and more endangered of the pair.

While mangabey groups have declined much less than those of red colobus, the most conspicuous changes have been in some of the same forests (e.g. Guru West, Mchelelo, Congolani and Mnazini South), which further supports the importance of habitat senescence. The lesser decline accords with Homewood's (1975) characterization of the species as a generalist well suited to unstable flood plain environments. In particular, ability to forage in the understorey as well as in trees, to eat insects as well as fruit, and to range widely in feeding parties of variable size may all aid survival in a changing habitat. Sykes' monkeys and baboons both appear to be thriving, but both these species are less specialized and more widely distributed in East Africa.

Management

Context. Following the gazettement of the Tana River National Reserve in 1976, at least four wardens have been posted there, the first of whom was Mr. Japeth Mkunga and the most recent, Mr. David Ngambo, who took up his appointment in January 1985. A few suggestions and observations of changes and developments since the production of a Management Plan for the Reserve in 1976, are offered here with the intention of being of use to the present and future wardens, and other Government officers.

Habitat Management. Since the establishment of the reserve no significant losses of forest to farmland have occurred. Restrictions imposed on the District Commissioner's orders through the Chiefs of Gwano and Ndera Locations have also probably had some affect in reducing removals of both understorey poles and large trees for canoes. During this survey, five recently cut (probably less than 1 year-old) large trees were found in Sifa East, and one each in Baomo North and Mnazini North. However, a count of canoes on the river between Wenje and Mchelelo totaled 31, which is a significant decline from a 1975 figure of 41 over the same stretch.

Although no forest has been cleared recently in the Reserve, a serious management problem arose in 1984 with the establishment, in April-May for a few weeks and again in December, of some 40 shambas on the east bank of the river near Makere in a splay lake, called Tokufu. This is an area of seasonally flooded grassland occasionally used in the past for rice and maize growing after medium-sized floods. On these two occasions, however, the prime reason for planting this land, rather than riverside shambas, was to assert traditional ownership rights. It was thus a gesture of objection to alienation of the land for the reserve. It has also become a political issue, known by Pokomo throughout much of the District. The question of land and other Pokomo rights was given careful consideration in the original boundary proposals and Management Plan, and every effort made to devise regulations that would conserve forest and wildlife while minimizing loss of local amenities and tradi-

tional rights. The suggested policy for farms was that existing farms should have a right to remain but that new ones should not be cleared.

The dilemma posed by the present situation is that while new settlements are contrary to the general conservation objectives of the reserve and set a disturbing precedent, the area in question is not even potentially forest land since it is a splay lake. Nor are the settlements permanent or by people immigrating from areas outside the reserve. In these circumstances, the long-term interests of the reserve may be served best by a degree of temporary tolerance, while maintaining the principle that such forms are a privilege and not a right.

More fundamentally disturbing is the conclusion of this study that most of the protected forest area is becoming senescent from natural causes. In the absence of man, regeneration would probably be most active in low-lying bankside locations, many of which are now farmed or occasionally burned. A strict protectionist recommendation would therefore be to persuade or force the 300 or so people who live in the Reserve to leave. In this author's view such a solution was and remains both morally unacceptable and politically impossible. In any case, the conditions necessary for forest regeneration are essentially an unproven hypothesis and in need of further research. Furthermore, it is possible that any forthcoming up-stream dams, by decreasing even marginally the frequency of small and medium-sized floods, will in any case prevent the necessary conditions for widespread regeneration. Management should aim to prevent fires and maintain the status quo with respect to shambas, but in no circumstances attempt to evict long-standing owners and farmers of this land. A classical national park cleared of people is not an option in this case, even if the survival of two subspecies is at stake.

Cattle-grazing and related dry-season burning by the Orma and Waldeigabra are another serious problem of habitat management. In recent years, pastoralists have grazed in the Reserve largely without restriction, and some semi-permanent settlements are established near the main road. While tolerance during extreme droughts, as in 1984, is probably unavoidable, settlements should not be permitted, nor grazing in any but extreme circumstances. Competition between cattle and wildlife occurs for grazing, and also for use of watering points on the river, of which few now remain.

Roads, Boundaries, Buildings and Staff. Most of the track cut in the Reserve in 1975 is still drivable, especially the road from Makere via Mchelelo south to Baomo to the main road. The road from Baomo to Mnazini required some minor clearing this time, but was drivable as far as Nkano. The extent of boundary demarcation is uncertain, but all the lines on the west bank appear to have been cut. All the roads and cut-lines need rebrushing.

Construction of headquarter buildings was begun in 1976 at a site some 3 km west of Makere just on the boundary of the reserve. Although a location outside the reserve is sensible, it is not clear why a site was selected so far from the river and Makere village. This increases water supply costs and isolates the administration from the local community. The buildings have yet to be completed due to lack of funds, and the riverside pump had to be removed recently to prevent its loss to the river at Makere where a meander has incised deeply into the edge of the flood plain where it abuts onto the dry plains country. At the time of writing, the new warden, Mr. Ngambo, is due shortly to receive a vehicle from the Department of Wildlife Conservation and Management and to move in to the half-completed H.Q. buildings. Junior staff, comprising a corporal and two rangers, are presently housed at Wenje. It would help greatly if money could be found to complete the H.Q. buildings and reinstall the water supply system, so that all staff can be based there. Similarly, the entrance gate at Baomo remains half completed. Finally, the airstrip cleared in 1975 has been subsequently gravelled and remains serviceable. This was completed with part of the funds allocated to the Tana River District Council, principally to permit air carrier services to the Baomo Lodge. No further funds remain with the County Council.

Visitors and the Baomo Lodge. At present, no more than a few dozen visitors reach the reserve each year, most of whom register as required

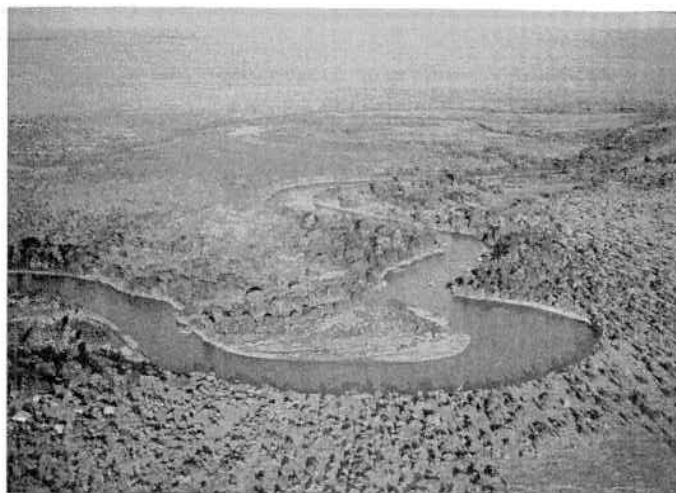


Fig. 10. This bend at Makere Ya Gwano has moved about 50 m since 1975. Note the sand bar deposit on the inside of the bend and the undercutting of the opposite bank which here marks the edge of the flood plain (photo by C. Marsh).

with the ranger post at Wenje. No formal campgrounds exist, but several groups have used sites at Guru and Mchelelo, both of which are attractive and suitable.

In 1977, a most remarkable investment took place in the Reserve, in the form of a permanent lodge at Baomo. Recommendations in the Management Plan for a site in the Guru Forest with almost flood-proof access were overlooked in favor of another attractive site at Baomo. The road access to this place floods easily and the camp itself also occasionally floods and is prone to undercutting of the bank on the outside edge of a bend in the river. This unwise siting might have been reprieved had not the owners invested heavily in wooden buildings with concrete floors, rather than a tented camp. Thus, the enterprise was handicapped from the start by being closed for up to four months in the year. Nevertheless, it operated from 1977 until 1981 when it closed and was put up for sale. There being no buyer, it is now quickly deteriorating and it is hard to suggest any use for it other than salvage purchase of some of the building material.

The principle cause for regret in this unhappy tale is that the only commercial source of revenue and local employment, and thus tangible benefit from the reserve has now ended. It is also difficult for any other prospective entrepreneur to gauge the viability of another, better sited camp. By several accounts, the Baomo Lodge was quite popular with visitors, especially those with experience of other parks and reserves, offering a combination of game drives, boat trips and guided walks in the magnificent Baomo Forest. Drawbacks to the site were its distance from the airstrip (c. 13 km via-a-vis 4 ha from the Guru site), the awful state of the Malindi-Garsen road and the climate (but no hotter than, say, Tsavo East). Although no visitor figures were available, one former partner in the enterprise maintained that a camp on the Tana could still be viable if set up and marketed properly. An important aim of the Reserve management should be to encourage and assist any entrepreneur bold enough to try.

External Developments Affecting the Reserve. The most important local development has been the establishment of a 99 ha irrigation scheme by the Ministry of Agriculture, at Mnazini on the southern boundary of the Reserve. Alternate crops of rice and maize are planted by 99 tenant farmers, and for the two years that it has been in operation it seems to have been generally popular. Certainly, this is a more appropriate site for development than grandiose schemes such as Bura. One important consequence of the scheme is that it reduces any pressure on remaining forest or other Reserve land in the Ndera location. A stronger line can therefore be taken here with any new farms like those at Tokafu, at the Gwano location to the north.

Since 1975, the large Bura irrigation scheme has been operated with very large capital expenditure and, by repute, momentous problems of many kinds (see Saha, 1982). One consequence of this is that the Pokomo of Gwano and Ndera have no desire to move voluntarily or be "resettled" on the scheme. As an option for reducing pressure on the reserve, this is therefore a non-starter for the foreseeable future.

Another large-scale irrigation scheme, this time for rice production, is currently planned for the delta and pre-delta zone on the east bank from Sailoni in the north extending for several kilometers south of the Lamu-Garsen road. As with the Bura scheme, an environmental impact assessment has been carried out, but is unlikely to influence major decisions. Among the predicted problems are very serious risks to people, livestock, and fisheries from pesticide poisoning, loss of important grazing areas, and considerable engineering costs and risks associated with the erratic behavior of the river. There are also serious questions about the economic value of a rice scheme carrying such heavy overheads, and of the relatively small scale of local employment that will be created on a highly mechanized scheme. Work on the project is expected to begin soon.

A relatively minor consequence of this scheme relative to the social consequences will be the likely loss through woodfuel cutting or reduced flooding of the remaining forest patches between Sailoni and Hewani. These total about 7 km² out of a 1974 total of 37 km² of forest between Wenje and Garsen. Only the southernmost six of these forests were surveyed in this study, but on the basis of 1974 observations they contained about 10-15% of known colobus and mangabey groups.

An indirect consequence of both the Bura and delta rice schemes is that by disturbing large areas of habitat to the north and south, they increase the importance of the reserve as the one remaining area on the whole river below Garissa with relatively intact riverine habitat, and significant populations of wildlife in addition to the rare Tana primates. An internal World Bank environmental appraisal of the Bura scheme in 1983 pointed this out and recommended strongly increased funding and support for the Tana River National Reserve. To date, this has not been forthcoming from any of the principal agencies involved, viz. the Department of Wildlife Conservation, the Tana River Development Authority or the World Bank itself.



Fig. 11. Forests based on old courses of the river can persist for at least a century, but tend to degenerate at their outer edges as the ox-bow lakes become silted (photo by C. Marsh).

Research and Funding Needs. Notwithstanding the long-term external pressures on the Tana reserve and the senescent condition of many of the remaining forests, the area is still home to two of Kenya's rarest mammals — now rarer than ever, living in one of the most complex and unique habitats in East Africa. At the national level the reserve should probably rate either in the highest category of priority for resources, or at the top of the second division, depending on whether financial or

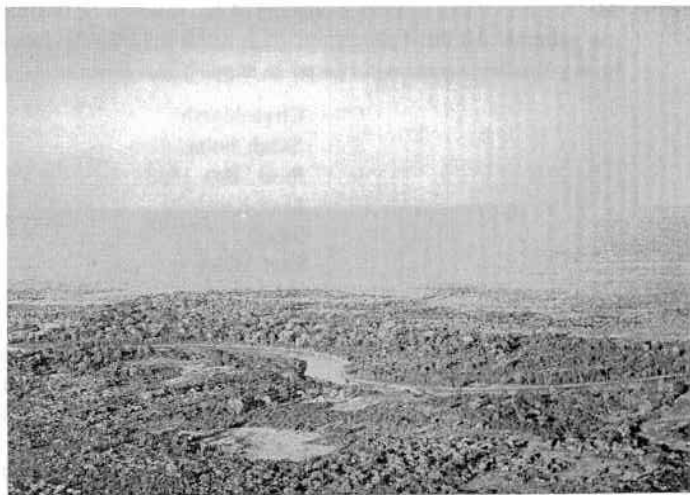


Fig. 12. This forest on the opposite (east) bank of the river at Baomo is one of the largest remaining intact blocks (photo by C. Marsh).

biological values take precedence. The reserve currently has a warden and three rangers who will shortly have transport, but have only a half-completed infrastructure for which to operate. Also, while a substantial body of research literature exists on the reserve and its fauna and flora, some outstanding problems relevant to management remain. A realistic minimum package of support should include the following:

1. Support for a second major study of red colobus and their habitat. The reason for this is to document the manner in which the population has declined, including behavioral and ecological correlates of the change, and to determine whether it has ceased or will continue. Related to this must be a proper study of regeneration of the forest. This should include quantitative sampling of seedling, saplings and trees in selected forest types, in combination with seed germination experiments to determine the establishment requirements (light/shade; flooding/no floods) of the principal tree species.
2. As part of the background to management of the reserve, and also the planning of the proposed rice irrigation scheme in the delta and other developments, there is a need for an ecological and social study of Pokomo traditional agriculture systems. Efforts should be made to quantify the yield of different crops from both bankside and backwater swamps in differing flood and rainfall conditions. One far-reaching application of this study would be to quantify the reduction in food production that can be expected from the predicted reduction in flood frequency, height and duration resulting from dam construction on the upper river. Results of such a study would doubtless be "sensitive", but there is no escaping the need for this study granted the scale of developments already implemented or planned for the Tana River. Responsibility for funding and providing all relevant data, especially the river flow model, should rest with the Tana and Athi River Development Authority.
3. Management of the reserve must be supported with sufficient funds to complete the basic infrastructure of headquarter buildings and entrance gate, together with maintenance funds for these and the roads, cut-lines, etc. Carefully used, even a few thousand dollars could go a long way towards addressing these needs. Ideally, a small research station should also be built, for which Mchelelo remains probably the best site.

In terms of personnel available to fulfill these three needs, at the time of writing a fortunate situation exists. An excellent young warden, Mr. David Ngambo, has recently been appointed to the Reserve. A primatologist married to an experienced engineer is keen to begin a study of the colobus and their habitat for a Ph.D. and to assist in any way possible with the development of the reserve. Their names are Barbara and Fred Decker. Finally, a capable and qualified Pokomo school teacher,

Mr. Kenneth Pakia, is keen to conduct M.Sc. research on Pokomo land-use patterns. All these people and their needs are warmly commended to any funding agencies prepared to support this Reserve.

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Both in the field and in Nairobi, I was assisted greatly by Mrs. Barbara Decker and Mr. Robert Barton. Hopefully the Deckers will be able to take up the study in more detail shortly. It was also a pleasure to work once more at the Tana with Jumar Galana, Dhardho Abio and Bakari Kahwa, and to make the acquaintance of David Ngambo and Kenneth Pakia. The Tana River National Reserve owes a particular debt to Chief Joseph Heribai of Gwano Location, who has been at the difficult edge of implementing Government policy for the area. Dr. J. Allaway and Dr. D. Western offered useful discussion of some of the more speculative ideas in this report. EcoSystems Ltd. provided office space, mapping facilities and technical advice in Nairobi. Dr. R. Malpas kindly loaned his word processor.

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Towards a Conservation Policy for Madagascar's Eastern Rain Forests

Most discussions of Madagascan biogeography divide the island into four zones or sometimes five zones: the west, the south, the high plateau region, the east, and the northeast. The case for regarding the humid forests in the east as a distinct biotome rests largely on their exceptional biological diversity. The first general treatise on Madagascar's flora by Perrier de la Bathie (1921) listed 200 plant genera and 1,800 species in the west, compared with 500 genera and 5,500 species in the east. As in other humid tropical forest regions of the world, this diversity derives in part from the general conditions which favor plant growth such as rainfall and warm temperatures. Much additional local diversity is generated in Madagascar's eastern rain forests by the mountainous terrain which imposes variation in drainage, exposure to sun and wind, and extremes of temperature.

The tropical forests of eastern Madagascar also vary from north to south, being distributed as a thin rectangle some 1,500 km long from 13°S to 25°S. Variation in forest structure and species composition also follow differences in altitude; evergreen forest growing along the coast as series of Myristicaceae and *Anthostema* (0-800 m), become series of *Tambourissa* and *Weinmannia* through the medium altitudes (800-1,300 m) and turn into lichen forests at high altitudes (less than 2,900 m). In contrast, the western and southern forests are not normally found higher than 200 m.

Species diversity in Madagascar's eastern forests seems to be particularly high. Perrier de la Bathie's (1921) figure of 102 species of plants in 100 m² sampled at 220 m near Maroantsetra slightly exceeds those obtained by the author in some sample plots of the same size: 68 species, at 560 m in Betampona, National Reserve No. 1; and 57 species, at 1000 m in Zahamena, National Reserve No. 3. These figures indicate an altitudinal effect on plant diversity similar to that found elsewhere in the world and illustrate a relatively rich flora. Recent estimates of plant species diversity in Madagascar by Rauh (1979), White (1983), and Guillaumet (1984), range from 8,200-12,000 species. This would, if correct, increase Lebrun's (1960) area-richness index (based on the

SIZE DISTRIBUTION OF NATURAL & SPECIAL RESERVES BY REGION

A <1,000 ha
 B 1,000-10,000 ha
 C 10,000-100,000 ha
 D >100,000 ha

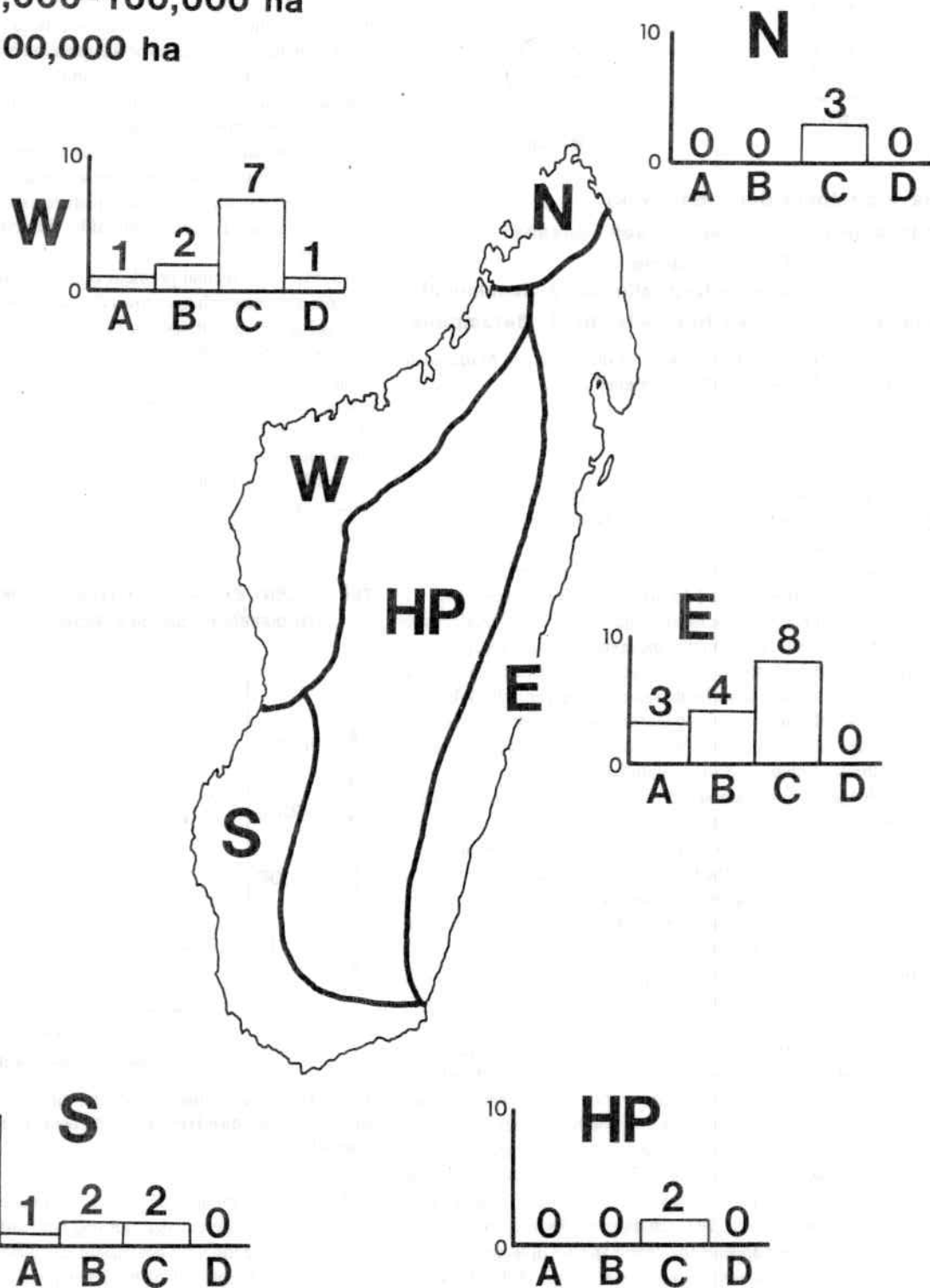
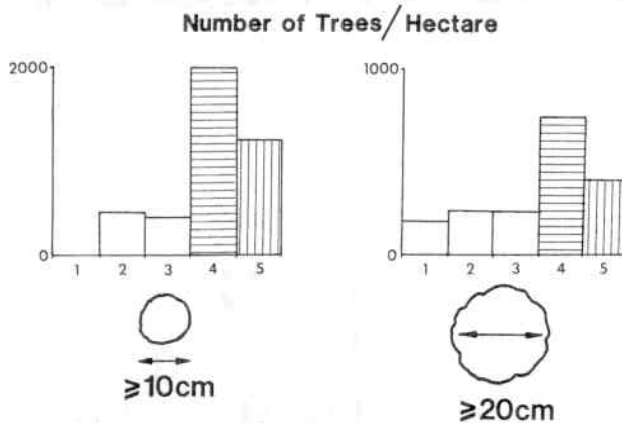


Fig. 1. Size distribution of natural and special reserves by region (figure by S. D. Nash based on author's original).

TREE DENSITY IN TROPICAL RAIN FORESTS OF THE WORLD AND MADAGASCAR

(After Richards, 1966)



- 1 Malaysia (Mount Dulit, Sarawak)
- 2 South America (Morabelli Creek, Guyana)
- 3 Africa (Okomu Forest, Nigeria)
- 4 Madagascar (Reserve Naturelle No. 3, Zahamena)
- 5 Madagascar (Reserve Naturelle No. 1, Betampona)

Fig. 2. Tree density in tropical rain forests of the world and Madagascar (figure by S. D. Nash based on author's original).

number of species occupying 10,000 km²) from 5,406 to between 5,684-8,318; values superior, for instance, to South Africa's Cape Province (maximum index value of 5,636).

Although the Malagasy rain forest formations are generally low by world standards (few trees exceed 45 m), tree density is high (Fig. 2).

More information is needed on forest structure in eastern Madagascar in order to know whether, for example, the apparently high species diversity is dependent on high species abundance. This sort of information will be of great significance in assessing reserve design criteria. Whatever the case, however, the high species endemism (approximately 90%, Perrier de la Bathie, 1936), together with the dense and diverse vegetation make these forests unique and of exceptional value.

Our knowledge of distribution of the dominant fauna in eastern Madagascar is limited and survey work is urgently needed. However, sightings and collection records of lemurs, which are summarized in Tattersall (1982), indicate that the main zoogeographical barriers in the east are the primary river systems: the Mananara, the Mangoro, the Antainambalana, and the Tsaratanana highlands (Fig. 4). At present, the northern sectors are richer in lemur species diversity than the southern ones, although it is by no means certain that this was always the case, and so our initial attention is drawn to the latter for immediate protection measures.

The second major consideration governing lemur conservation in eastern Madagascar concerns their biology and population dynamics. With the possible exception of *Microcebus rufus*, eastern lemur species are larger than congeners in the west and south. Furthermore, their maturation rates are slower and some evidence exists to suggest that they also reproduce at a slower rate (Pollock, 1975). The few reports available suggest that infant mortality in the west and south may be higher than in the east (Jolly, 1966; Richard, 1975; Budnitz and Dainis, 1975). From the only studies available it appears that lemur species diversity is higher in the east but species abundance and biomass are lower (Table 1). These few data suggest that lemurs occupying the eastern forests in Madagascar demonstrate a cluster of life history traits equivalent to the "k-selected"

Table 1. Lemur Diversity and Biomass in Regions of Madagascar

Region	Total no. of lemur spp.	No. of folivorous lemur spp.	Biomass (kgs/ha)
West/South ¹	7	4	58-74
South ²	5	3	18
East ³	11	8	4.6-5.8

Key

1. Antserananomby; data from Sussman (1972)

2. Berenty; data from Charles-Dominique and Hladik (1971)

3. Analamazotra; data from Pollock (1975)

mainland tropical rain forest fauna and flora. Consequently, their ability to respond reproductively to a population crash is limited and reserves must be carefully designed to minimize environmental perturbations.

Reappraisal of the nature protection system in Madagascar must start with an examination of the extensive existing reserve network. This consists of 36 National Reserves, Special Reserves and National Parks well distributed across the different vegetational and climatic zones. In general, the reserve network receives adequate legislative support, although enforcement is heavily compromised by understaffing and transportation problems.

Another fundamental problem is reserve size. Much theoretical and now practical research has shown that large reserve size is a critical factor in slowing the rate of species extinctions over the long-term (Frankel and Soule, 1981). The smallest official reserve in Madagascar is 520 ha and thirteen others are less than 1,000 ha. In the east, half of the reserves are less than 10,000 ha (Fig. 1). Although the largest number of reserves is to be found in the eastern region, their average area (23,300 ha) is the lowest of all the regions (south — 27,560 ha; west — 27,190 ha; north — 30,070 ha). The east is intermediary in the percentage of remaining forest cover that exists in protected areas (south 3.8%, east 6.1%, west 11.7%).

TEN PERCENT EXTINCTION RATES FOR DIFFERENT RESERVE SIZES WITH DIFFERENT SPECIES RICHNESS (After Terborgh, 1975)

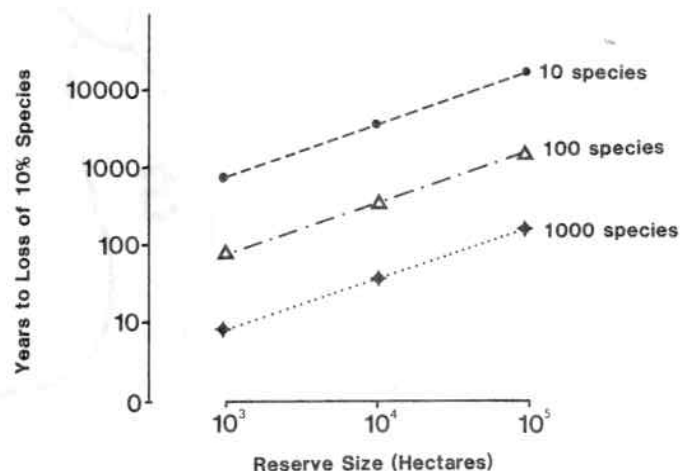


Fig. 3. Ten percent extinction rates for different reserve sizes with different species richness (after Terborgh, 1975; figure by S.D. Nash based on author's original).

By way of example, 10% species extinction rates can be calculated for reserves of different sizes starting with different numbers of species. In Fig. 3, the extinction coefficient calculated for birds on Caribbean islands by Terborgh (1975) has been applied to the Malagasy arena using species numbers of the same order as the numbers of Malagasy vertebrates (885 species), mammals (112 species) and primates (21

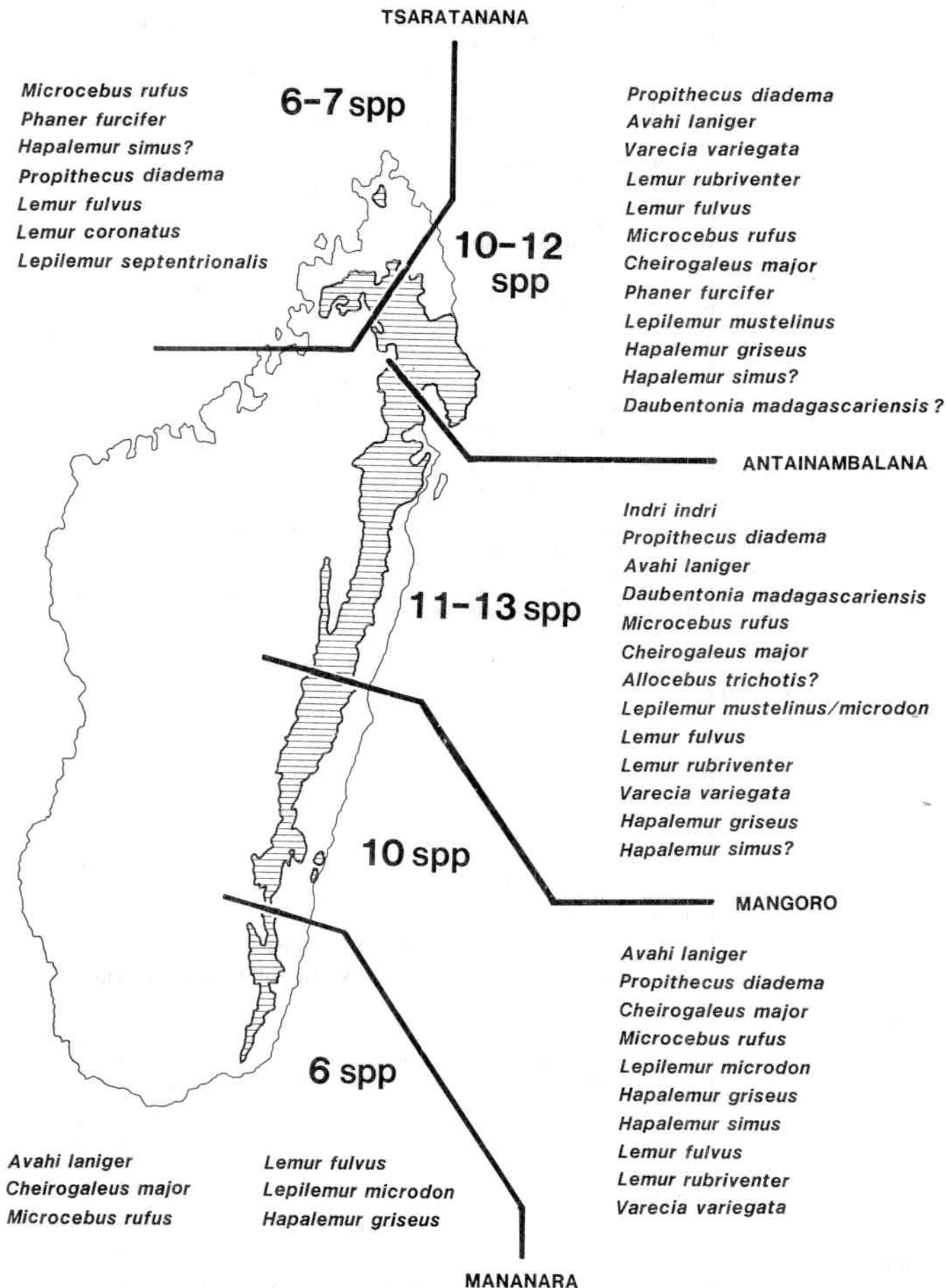


Fig. 4. The distribution of primate species in relation to major river systems in Madagascar (figure by S. D. Nash based on author's original).

species). It is probable that at least for mammals and primates, the extinction rates shown underestimate the true rate because of the higher mobility of birds. This approach, while unlikely to quantitatively define species extinction prognoses in Madagascar, does illustrate the relevant features of the problem:

1. Since almost half of the eastern reserves are less than 10,000 ha the numbers of extinctions in the existing protected areas over the next 100-200 years could be substantial. A reduction in the size of a reserve by 90% increases the extinction rate by about 50%.

2. As a consequence, it is wiser to regard the smaller reserves such as Analamazotra (810 ha), Nosy Mangabé (520 ha), Mangerivola (800 ha), and Betampona (2,228 ha) as refuges for particular species rather than reservoirs of substantial proportions of biological diversity. Such species-oriented reserves will increasingly require attention and management intervention by scientifically competent conservation administrators.

Fortunately, however, the objectives for nature conservation in eastern Madagascar are not simply confined to the maintenance or creation of large, northern forest tracts. This is because although forest fragmentation is rapidly becoming extremely serious, especially in the western region, most eastern reserves maintain a degree of genetic communication with nearby forested areas. Most of these, however, are being disturbed or slowly destroyed by local exploitation.

As the protected areas become more and more isolated, the significance of the analogy drawn with island communities will strengthen. A study by DeLord (1965) estimated eastern forest destruction to occur at a rate of 150,000 ha each year for hill rice farming, of which at least 10,000 ha will show no regeneration.

Furthermore, encroachment on the reserves by local people is continuing. This takes the form of selective logging and slow perimeter erosion, especially where reserve boundaries are not physically marked. The effect of reserve shrinkage by this method is very obvious, especially in the smaller reserves, because of the large areas easily disturbed or destroyed. At Reserve Naturelle No. 1 (Betampona), one of the few protected forests near the eastern coast, human pressure on natural habitats is great and the undisturbed area of this reserve has now been reduced from the official 2,228 ha established in 1927 to about 1,000 ha (pers. obs.).

In conclusion, the little information available suggests that lemurs (and their predators) can be regarded as key species in defining the principles governing the design and protection of nature reserves in eastern Madagascar. Because they are likely to be particularly susceptible to population fluctuations their long-term future probably resides in the areas of greatest size, with highest diversity, and the lowest pressure from human populations. These are the reserves of Zahamena (73,160 ha), Marojejy (60,150 ha), Masoala (30,000 ha, now degazetted), and Ambatovaky (60,050 ha). The smaller reserves of less than 5,000 ha are best managed as species preserves with substantial research, education and tourism potential. It is important to stress the lack of scientific information available on which to base a rational conservation policy. It is certain that knowledge of the factors regulating lemur and other vertebrate populations will play a central role in deciding their future. Finally, efforts must be made to ensure that a flow of genetic information is maintained between reserves and other natural or semi-natural areas. This demands a national strategy of forest protection and management based on biological principles, national economic development and the local needs of the Malagasy villagers.

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Acknowledgements

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Lemur Conservation in Madagascar: the Status of Lemurs in the South

Many biologists believe that Madagascar should be considered the top conservation priority in the world. The isolation of Madagascar and its variety of climates has led to an exceptional richness of plant species. There are at least 10,000 species of flowering plants and, in some groups, over 80% of the species are unique to Madagascar. Five percent of the species on earth are found on this island and two-thirds of these are endemic. Thus, 3% of the plant species on earth are endemic to Madagascar. Of all vegetation zones of Madagascar, the Southern Domain is among the most unusual. In this dry region, intermixed with deciduous riverine forest, dense brush and scrub, and grassland, are the xerophytic Didiereaceae forests (Fig. 9). These forests are physiognomically much like the deserts found in the southwestern United States and Mexico, but are composed of species unrelated to American forms. In fact, southern Madagascar has among the highest percentage of generic and specific plant endemism in the world. Close to 50% of the genera of

undisturbed vegetation of the South are found only in Madagascar, as are 95% of the species (Koechlin, 1972). The family Didiereaceae is endemic to the dry southern regions of Madagascar.

The lemurs of the Southern Domain of Madagascar include two species active during the day, *Lemur catta* and *Propithecus verreauxi*, and four nocturnal species, *Microcebus murinus*, *Cheirogaleus medius*, *Lepilemur mustelinus leucopus* and *Phaner furcifer*. Although sympatric in many areas, these species also live in different habitats and are thus most successful in different types of vegetation. There have been very few biological surveys in recent years and it is almost impossible to give an accurate estimate of the current condition of the forests or of the lemur populations in southern Madagascar at the present time. However, given our knowledge of the habits of these lemurs, and of the general distribution of primary vegetation, some general impressions of the current conservation status of these species can be formed.

Usually distribution maps of a primate species include an outline of the total area in which the species is found. For example, Figures 4 and 5 include the borders of the ranges of *L. catta* and *P. verreauxi* in southern Madagascar. However, only about one-third of this area (about 20,000 km² vs. a total of about 60,000 km²) contains primary forest vegetation (according to Landsat photographs taken in 1985). Furthermore, each primate species is not found in all available forest vegetation.

The last vegetation map of Madagascar was printed in 1965, probably from aerial photographs collected in the early 50's (Humbert and Cours-Darne, 1965). This map lists five major types of natural vegetation in the Southern Domain of Madagascar. These are: high bush (including both Didiereaceae forest and dense *Euphorbia* bush), discontinuous bush areas, woodland savannah, grassland, and riparian forests along major rivers. Of course, evergreen rainforest is present in the Southeast of the island. Only the continuous bush areas and riparian gallery forests are extensively used by the lemurs of the South. This is a total area of much less than 20,000 km².

The area generally available to the lemur populations is much less than we might assume from looking at published distribution maps. Furthermore, if we examine the distribution of each species individually, we find further restrictions of their ranges due to particular species specific ecological necessities. We will briefly review the habitat preferences of the lemurs of southern Madagascar and point out how these preferences relate to the distribution of each species.

Lemur catta (Fig. 1) is likely the most widely distributed lemur in the South. Its ability to exploit resources both in the trees and on the ground make the ring-tailed lemur quite adaptable (Sussman, 1974). However, unlike many ground-living monkeys, *L. catta* is not successful in open tree savannah nor in grassland. Furthermore, although it does eat some planted crops, these plants make up a very small portion of the diet. Thus *L. catta* does not become a commensal of man in any part of its range, nor does it become a major agricultural pest. The basic habitats of *L. catta* are the natural vegetation types of dense euphorbia bush, riparian forest, and the edges of these two habitats (Sussman, 1977). *L. catta* is not found deep within the Didiereaceae forest. Given its dependence on these two, fairly restricted, and locally diminishing vegetation types, we must be careful in assuming that *L. catta* is one of the less endangered lemurs. It is the only species of lemur essentially restricted to the Southern Domain. Furthermore, because it travels mainly on the ground, the ring-tailed lemur is often hunted with dogs and in some areas may be very vulnerable to hunting pressures. It is imperative that we learn the distribution of this species within the south and southwest of the island and get estimates of population density in various vegetation types. *Lemur catta* may have much lower population densities than we imagine.

The sifaka, *Propithecus verreauxi verreauxi* (Fig. 2), of the South and Southwest, has a wide distribution. It is found in Didiereaceae forest and in riparian forest, but is not found in dense brush and scrub vegetation. Also, like *Lemur catta*, it does not exist in tree savannah or open grassland. *P. verreauxi* is not successful in edge vegetation nor in areas which necessitate prolonged travel on the ground (Sussman, 1977). It

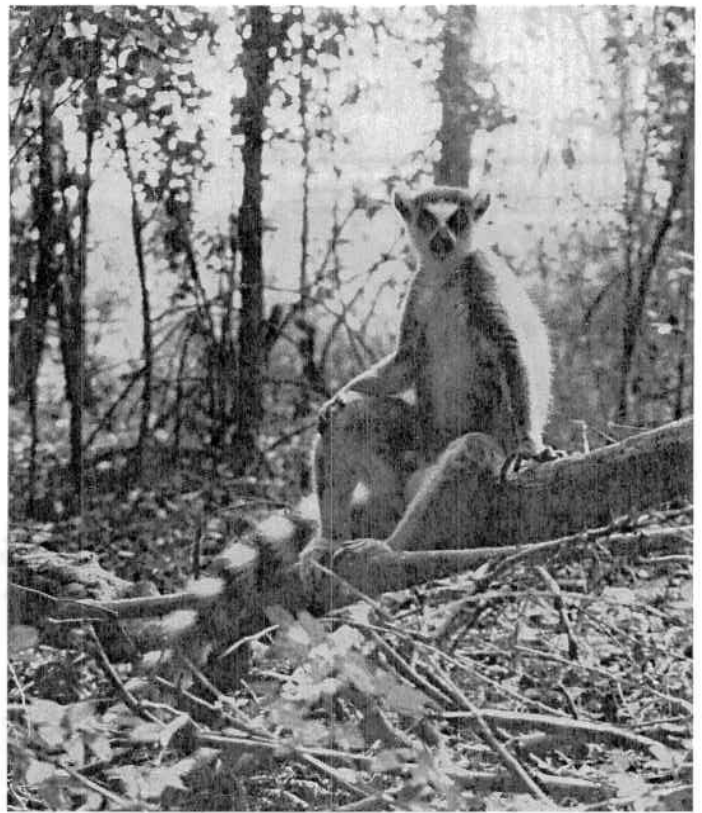


Fig. 1. *Lemur catta*, one of the two diurnal species of *Lemur* found in southern Madagascar (photo by R.W. Sussman).

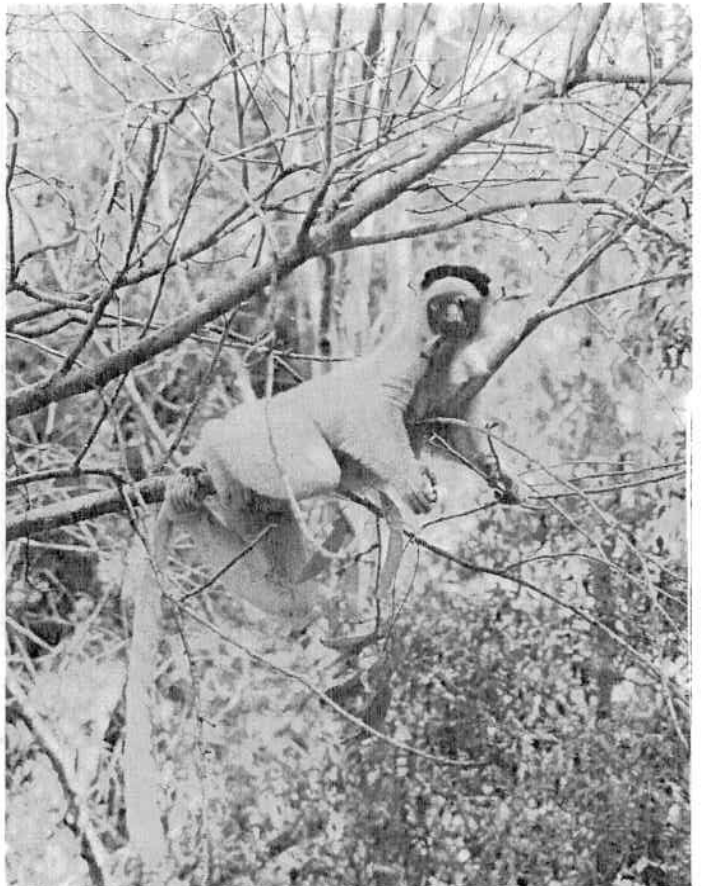


Fig. 2. *Propithecus verreauxi*, the second diurnal species found in southern Madagascar (photo by R.W. Sussman).

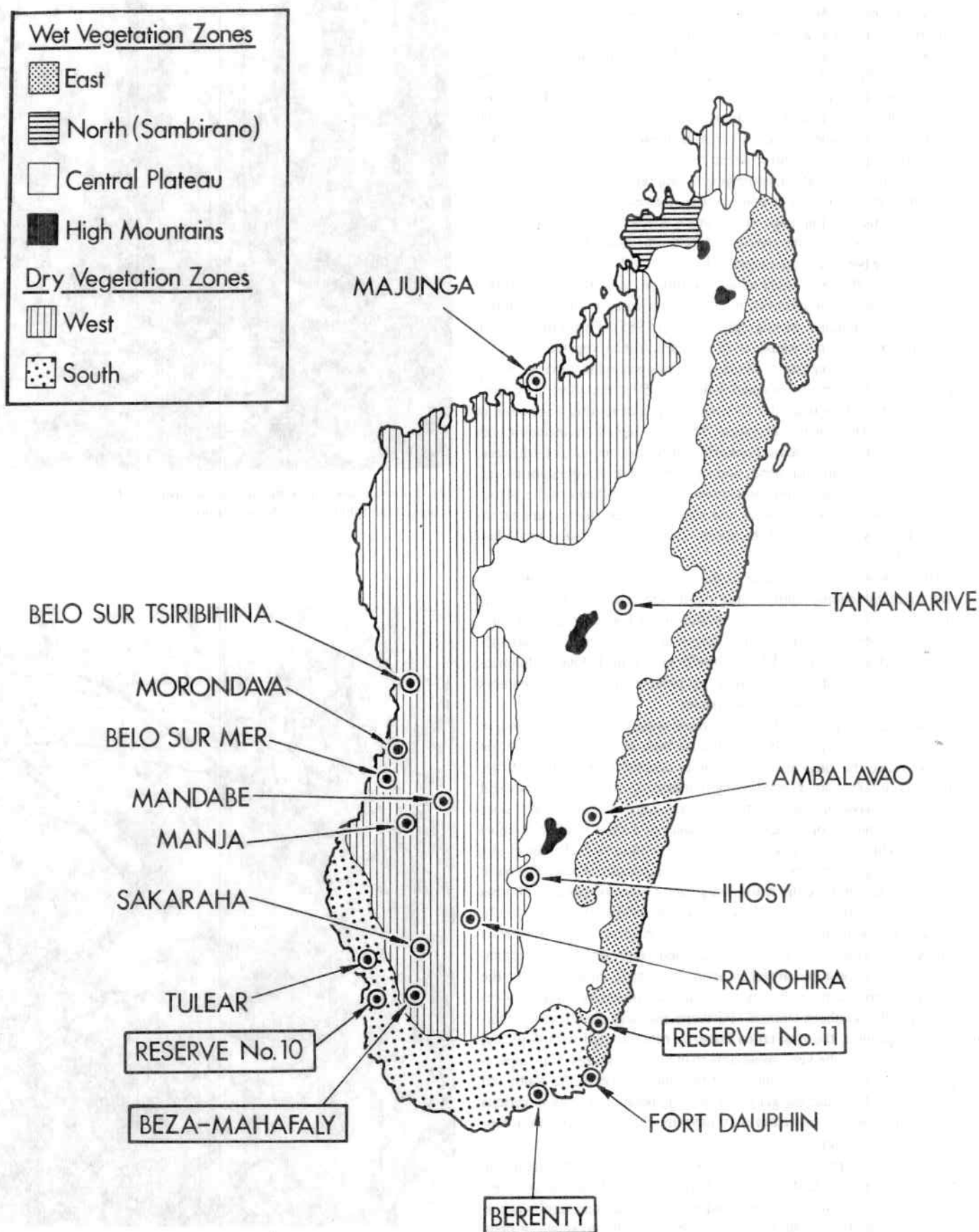


Fig. 3. Vegetation types of Madagascar and the location of the reserves in the southern portion of the island (Figure by S.D. Nash).

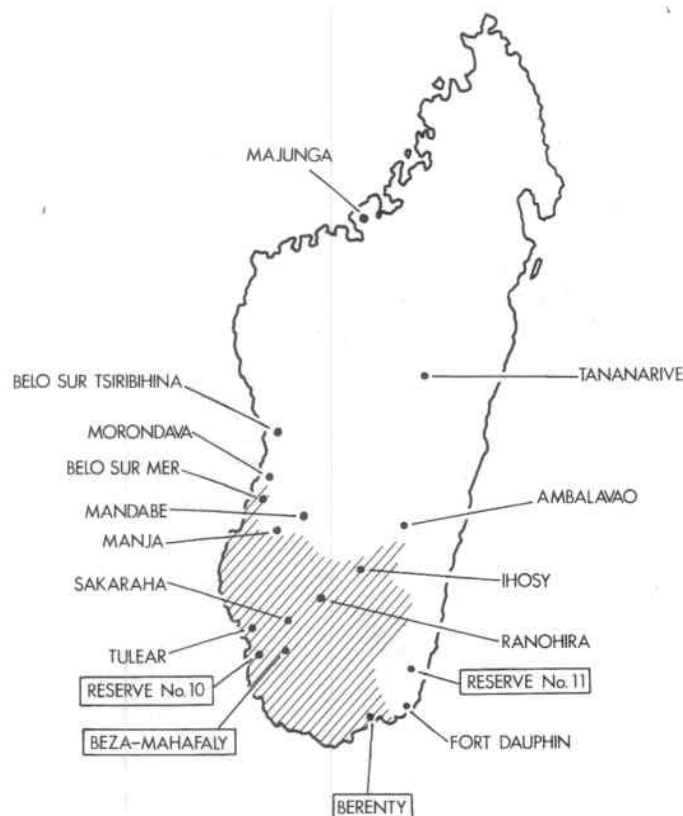


Fig. 4. Geographical distribution of *Lemur catta*. Populations are not continuous within these areas but are only found where suitable primary vegetation exists (map by S.D. Nash).

does not utilize human crops. Thus, although the species has wide geographic distribution, it is entirely dependent on the two natural vegetation types of the South with continuous, relatively high "canopies" or with closely spaced, relatively high, vertical supports. Both the Didiereaceae forest and the gallery forest are quite restricted in climatic requirements and in area, and may be becoming more so. The South must be surveyed to determine the status of these two important climax vegetation types. The continued existence of the sifaka of the South is dependent upon the health of these unique forests. Furthermore, the large, white sifaka is the easiest target in the South for a lemur hunter, and we suspect that the sifaka is already gone from some perfectly adequate forest areas.

Microcebus murinus (Fig. 7), the mouse lemur, is one of the most geographically widespread and adaptable of all lemurs. It is found in its highest density in transitional, generally low vegetation zones and tree fall areas within Didiereaceae, brush and scrub, and gallery forests (Martin, 1973). Densities are lower in deep forest. The mouse lemur is active during the night and enters a period of torpor during the cold, sparse winter months. Since these animals are usually dependent upon areas of dense undergrowth, extensive grazing by cattle and goats may be destroying some of their optimal habitat in the South. It must also be emphasized that the mouse lemur may actually occur in relatively low densities naturally. We know very little about its specific distribution and ecological preferences throughout southern Madagascar.

Cheirogaleus medius (Fig. 11) is another nocturnal species found in the South. We have almost no information on its distribution within this region. Although in some dense, deciduous riparian forests, population densities may be high, this species normally occurs at very low densities and is difficult to locate. *C. medius* stores fat in its tail during the winter months and is able to hibernate for 6 to 8 months at a time (Hladik *et al.*, 1980). Probably because of its need for a rich diet before hibernation and its requirement for adequate hibernation sites, it seems to be restricted to natural riparian forests in the South and is most successful in the center of these forests and not in edge habitats. As far as we know it does not inhabit Didiereaceae forest.

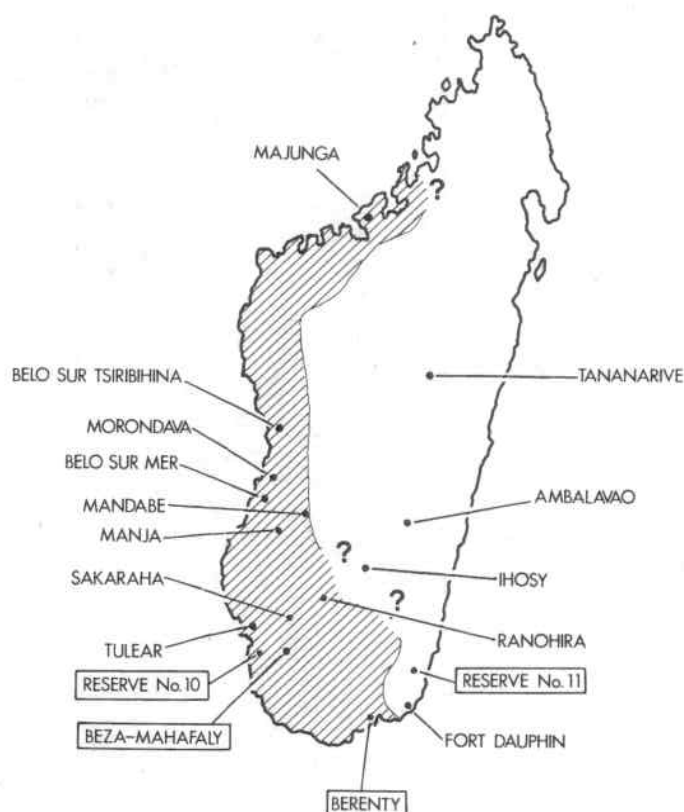


Fig. 5. Geographical distribution of *Propithecus verreauxi*. As with *Lemur catta*, populations are found only in areas with suitable primary vegetation (map by S.D. Nash).

Lepilemur mustelinus leucopus (Fig. 8) is a nocturnal, folivorous lemur whose general distribution and choice of habitats in the South are very similar to those of *Propithecus*. It is found only in primary Didiereaceae forest and in the remaining gallery forests of the region, and has a higher population density (twice as high) in the latter type of forest (R.J. Russell, pers. comm.). Since *Lepilemur* has only been studied in the forests near Berenty in the Southeast (Charles-Dominique and Hladik, 1971; Russell, 1977) and in the deciduous forests of the west (Hladik *et al.*, 1980), we know virtually nothing about its precise distribution or population densities in the southernmost portion of the Southern Domain. The diet of *Lepilemur* is quite specialized and monotonous, with a very few species accounting for a great proportion of the plant food eaten. This dependency on a few species of plant may affect the densities of this lemur in different areas.



Fig. 6. *Phaner furcifer*, a specialized gum eater which may exist in one reserve in southern Madagascar (photo by R.W. Sussman).



Fig. 7. *Microcebus murinus*, the smallest living lemur (photo by B.Z. Freed).



Fig. 8. *Lepilemur mustelinus*, a nocturnal folivore of southern Madagascar (photo by R.W. Sussman).

Table 1. Lemur species of the South and habitats in which they are found

Species	gallery	Habitats		
		Didiereaceae	low brush and scrub	dense edge habitats
<i>L. catta</i>	X		X	X
<i>P. verreauxi</i>	X	X		
<i>M. murinus</i>	X	X	X	X
<i>C. medius</i>	X			
<i>L. mustelinus</i>	X	X		
<i>P. furcifer</i>	X			

Phaner furcifer (Fig. 6) may be found in one small gallery forest region of the South, in Reserve No. 11 along the Mananara River (Russell and McGeorge, 1977). However, if it is still found in this region, its density is extremely low. We doubt if *Phaner* exists anywhere else in southern Madagascar.

A summary of the general habitat preferences of the five species of southern Madagascar is found in Table 1.

There are two Natural Reserves in southern Madagascar, Tsimanampetsotsa (No. 10) and Andohahela (No 11), and one Special Reserve (the University Reserve, Beza-Mahafaly). The private reserve of Berenty is also found in this region (Figs. 4, 5). *Lemur catta*, *Propithecus verreauxi*, *Lepilemur mustelinus* and *Microcebus murinus* are found in all of these reserves. *Cheirogaleus medius* may also be in these reserves but in very low densities. *Phaner* is only found in Reserve No. 11, if

at all. Andohahela is unique in that it contains areas within both the dry Southern Domain and the rainforests of the Eastern Domain (see O'Connor, Pidgeon and Randria, p. 49). According to O'Connor and Pidgeon (pers. comm.), in the wet forests of the reserve such species as *Lemur fulvus*, *Propithecus diadema*, *Avahi laniger*, *Microcebus rufus*, *Cheirogaleus major*, *Haplemur griseus*, and one of the eastern subspecies of *Lepilemur mustelinus* may be present.

The special university reserve of Beza-Mahafaly and the private reserve of Berenty are well demarcated, fenced, and guarded. Both are quite small. Studies of the population densities and of the behavior and ecology of the lemurs in these reserves have been done or are planned. At Beza-Mahafaly, an intensive education program and parallel agricultural project are underway. Similar projects are planned for Natural Reserve No. 11. However, Reserve No. 10 has not been surveyed in recent years. Furthermore, these reserves are not well delineated and there has been extensive encroachment of their boundaries, especially at Andohahela. Thus, the precise area of remaining natural vegetation and the condition of these forests are not known at this time.

Recommendations for Immediate Action

Given our extremely limited knowledge of the state of the natural forests, of the current status and precise distribution of the lemur populations of the South, and of the current status of the Natural Reserves of this region, we make the following specific recommendations for immediate action:

1. extensive surveys and studies of the vegetation and habitat types;
2. production of a vegetation map as an integral part of these vegetation studies and surveys;



Fig. 9. Didiereaceae forest. The physiognomy of these forests are much like the deserts found in Southwestern United States and Mexico but the family Didiereaceae is endemic to southern Madagascar (photos by R.W. Sussman).



Fig. 11. *Cheirogaleus medius*, a nocturnal species found in the south that hibernates 6 to 8 months of the year (photo by B.Z. Freed).



Fig. 10. R. Sussman with a *Propithecus verreauxi* (photo provided by authors).

3. studies of the amount and reasons for encroachment on natural vegetation in the area and, in light of findings, suggestions (as well as practical aid) for alternative production methods to replace means of production that are destructive to this vegetation;
4. surveys of the distribution and density of lemur populations paralleling the vegetation surveys (lemurs may serve as indicator species, giving us an indication of the health of the natural vegetation);
5. delineate the borders of Natural Reserves No. 10 and 11 and guard well, conduct basic research on the flora and fauna in these reserves, initiate education, training and development programs for local inhabitants similar to those being conducted at Beza-Mahafaly;
6. finally, we recommend that new areas, located during the above recommended surveys, be suggested as either larger Natural Reserves or small Special Reserves, and that the suitability of these areas, both as reserves and for the local inhabitants, be examined carefully. If found suitable and locally compatible, new reserves should be established, especially those protecting areas with Didiereaceae and gallery forest.

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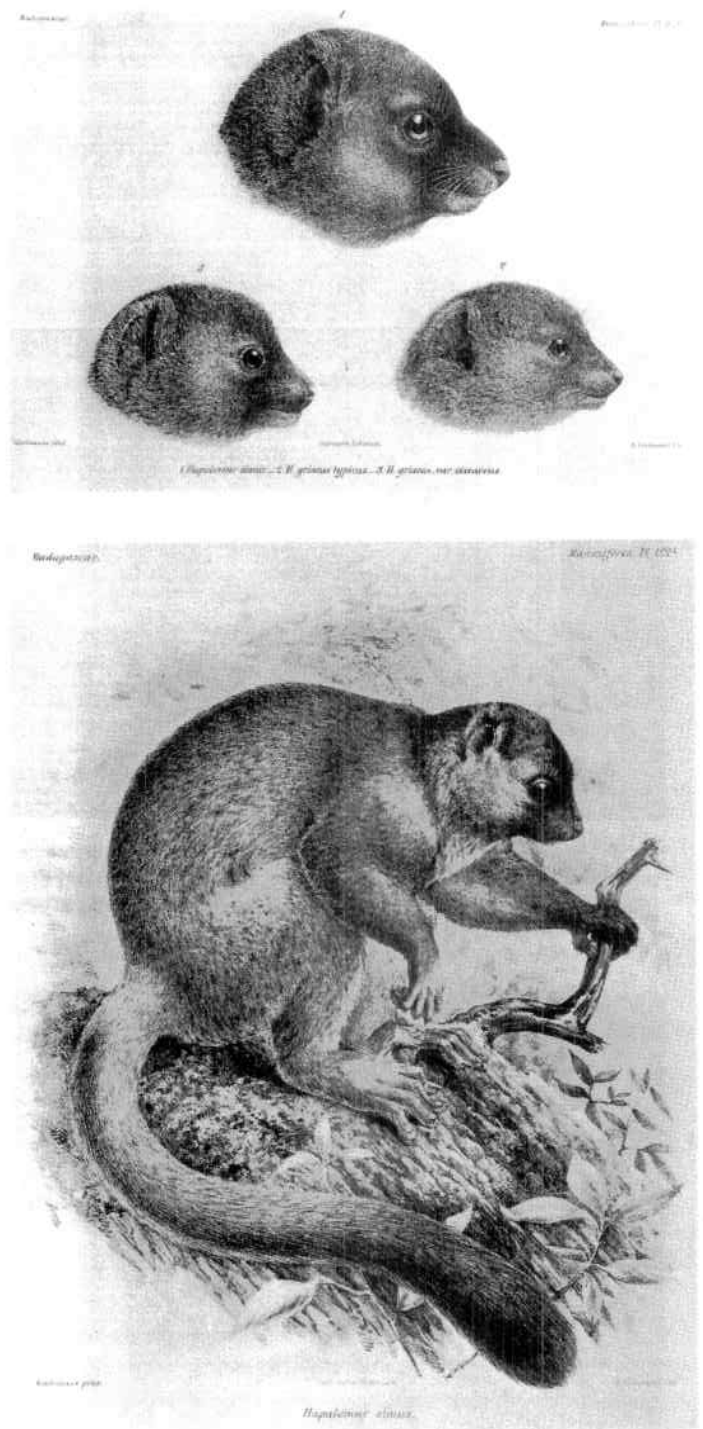
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Hapalemur simus: Endangered Lemur once Widespread

The greater bamboo lemur or broad-nosed lemur (*Hapalemur simus*), has become very scarce. Today it lives only in the bamboo forests east of Fianarantsoa. However, several hundreds or thousands of years ago it was distributed throughout northern, northwestern, central, and eastern Madagascar, overlapping extensively the geographic range of its congener, *Hapalemur griseus*. Remains of *H. simus* have been recovered from the subfossil sites Anjohibe (northwest coast), Andrafiabe (north, Ankarana massif), and Ampasambazimba (Itasy basin, central Madagascar). Those from Ampasambazimba were actually discovered eighty years ago (Standing, 1905), but only recently recognized as belonging to *Hapalemur simus* (Mahé, 1976; Vuillaume-Randriamanantena et al., 1985); additional subfossil remains of *H. simus* were discovered in 1981 and 1983.

The pace of *H. simus*'s recent demise can be estimated from museum collection records (Table 2). In the late nineteenth century, a small but significant number of individuals were found at widely dispersed eastern rainforest localities — from the Bay of Antongil in northeast Madagascar to central Betsileo country (near Fianarantsoa) in the southeast. Judging from the small number of individuals captured at that time we can deduce that *Hapalemur simus* had already become rare but was, nevertheless, widespread.

Hapalemur simus was unknown prior to 1870. Its type description was based on a zoo specimen of unknown provenance (Gray, 1870). Until additional specimens were shipped to Europe, there was a certain amount of skepticism regarding the validity of this species (Schlegel,



Figs. 1, 2. *Hapalemur simus*, plates drawn by Keulemans for Grandidier's classic volume on the Lemurs of Madagascar.

1876). Additional individuals did arrive, however, and the dispute over the existence of *H. simus* ended. But by the early 1900's, capture of *H. simus* also ended. Isolated mid-twentieth century reports of *H. simus* were actually based on its confusion with a population of large-bodied *H. griseus* (e.g., Allen, 1918; Hill, 1953; Lamberton, 1956) — a confusion that would not end until J.-J. Petter and A. Peyrieras (1970) visited the alleged *H. simus* retreat in the reed beds surrounding Lake Alaotra and found instead the animal that Rumpler (1975) would later name *Hapalemur griseus alaotrensis*.

By the mid-1960's persistent failure to find living *H. simus* had convinced some primatologists that this species was extinct (Napier and Napier, 1967; Walker, 1967). However, unknown to most primatologists,

Subfossil *Hapalemur simus* sites ◆

Recent *Hapalemur simus* sites..... Vondrozo



Fig. 3. Map of Madagascar, showing current distribution of the three subspecies of *Hapalemur griseus* (*griseus*, *occidentalis*, and *alaotrensis*), and collection sites for *H. simus* (map by S. D. Nash based on author's original).

Peyrieras had already in 1964 or 1965 rediscovered *H. simus* near Vondrozo, southeast of Fianarantsoa and west of Farafangana (pers. comm.). Then in 1972, two individuals were captured by Petter and Peyrieras near Kianjavato, on the Route de Mananjary, due east of Fianarantsoa. No survey of the area has been conducted since, and both individuals captured in 1972 have died. We conclude that, if this species has not disappeared, it remains today only in the bamboo forests of southeast Madagascar.

Subfossil and recent *H. simus* site locations are shown in Fig. 3. Since not all specimens have associated locality data, the map is incomplete even for known *H. simus* material. Furthermore locality records are often imprecise. Some nineteenth century sites seem to have disappeared completely; others are difficult to locate because they were recorded incorrectly (sometimes with phonetic interpretations of the place name) or because their name was so common as to suggest multiple site alternatives. In some cases, only the collector's itinerary remains; there are no maps or field notes.

The worst offender was J. P. Audebert, late nineteenth century collector for the Dutch National Museum of Natural History (Leiden). Audebert captured numerous lemurs in northeast Madagascar, but most of his capture sites are now untraceable. Audebert was responsible for a most interesting discovery of *H. simus* at a site far north of the species' current refuge. Audebert called it "Passumbee," a name that does not exist in Malagasy. Collection records inform us that Audebert was in Mananara in northeast Madagascar on September 5, 1876 and that he was at "Passumbée" (collecting *Lemur rubriventer*) on the same day. He captured a *Hapalemur simus* on September 8, 1876 and by September 12 was back in Mananara. Our guess is that "Passumbée" represents the Malagasy place name Ampasimbe — a name common in the eastern rainforest. In particular, there is an Ampasimbe on the northeast coast, south of Mananara (and the Bay of Antongil) and across from the island of Saint Marie, and there is another Ampasimbe (a stream) west of the Mananara River. Since the northern Mananara River is not navigable past about 6 km from its mouth (A. Peyrieras, pers. comm.) and since the stream is too far inland to have been reached by foot in one or even several days, we think it far more likely that Audebert traveled south along the eastern coast of Madagascar toward the coastal village of Ampasimbe. But we can only state with certainty that Audebert's Ampasimbe was within about a day's journey of Mananara, by foot or by boat. This is the region we have marked "Passumbee?" in Fig. 3.

Other nineteenth century collection sites are almost as difficult to locate. Within a single week in June, 1881, M. Lantz collected two *H. simus* for the Paris Museum National d'Histoire Naturelle; the specimens are marked "Ambakobé" and "Ampazénambé," east coast, Madagascar. A turn of the century map of Madagascar shows two such sites (spelled "Ambakobé" and "Ampasinambé") northeast of Fianarantsoa (Pelet, 1900). We have been unable to find modern villages with these names at the precise locations indicated on that map, but we think it highly likely that these were the Lantz sites and that they have simply since disappeared. (We note, also, that several Ampasinambos and at least one Ambakobe exist today in that general area.)

In 1961, Rothschild bequeathed a specimen of *H. simus* to the British Museum (Natural History). It may have been collected by C. I. Forsyth Major during the late nineteenth century (as were most of the specimens in the Rothschild collection). Major collected extensively in eastern Madagascar during this period (Vinanitelo, Ampitambe, Ambohimandroso).

Another *H. simus* belonging to the British Museum Waters collection came from Central Betsileo country. Catalog records list it as coming from "Nandisen, Central Betsileo." We interpret this as Nandihizana, another common Malagasy place name. An 1895 map of Madagascar shows a Nandihizana in Central Betsileo country, due north of Fianarantsoa (Laillet and Suberbie, 1895).

Additional nineteenth century and very early twentieth century specimens exist; they unfortunately lack locality data (they include the type specimen, Gray 1870, at the British Museum; two *H. simus* at the

Museum für Naturkunde der Humboldt-Universität; and another at Harvard's Museum of Comparative Zoology).

Our knowledge of the paleodistribution of *Hapalemur simus* has increased markedly in the past five years due to extensive paleontological fieldwork in northern Madagascar by British, American and Malagasy researchers. In 1981, the bones of several individuals of *Hapalemur simus* were discovered in a cave near Andrafiabe, Ankarana massif, in the extreme north of Madagascar, by members of an expedition of biologists and speleologists from the University of Southampton. These cranial and postcranial remains are now in the collections of the British Museum (Natural History).

In 1983, the paleontological team of the American-Malagasy Cenozoic Research Group discovered a skull of *Hapalemur simus* in a cave at Anjohibe, near Mahajanga. This cranium is preserved in the collections of the Service de Paléontologie, Université de Madagascar, Antananarivo.

Yet, curiously, some of the best evidence for the expanded paleodistribution of *Hapalemur simus* has been in the collections of the Académie Malgache for eighty years; it consists of fragmentary remains of several individuals from the richly fossiliferous subfossil site of Ampasambazimba in central Madagascar. Ampasambazimba is located in the Itasy basin, far from either Anjohibe or Andrafiabe (see Fig. 3). Unfortunately, H.-F. Standing (1905; 1912), who first described *H. simus* material from Ampasambazimba, was apparently unfamiliar with the morphology of *H. simus*. He gave these fossils a new name — *H. gallieni*.

Standing's confusion was compounded by Lamberton (1936, 1939), who not only failed to recognize the specific identity of the fossils at hand, but gave them generic distinction by calling them *Prohapalemur*. Clearly the sparsity of *H. simus* materials in museum collections hampered the correct identification of these subfossil materials.

The synonymy wasn't recognized until 1976, when Mahé compared so-called *Prohapalemur gallieni* at the Académie Malgache directly with *H. simus* materials from the British Museum (Natural History). He did think it necessary, however, to distinguish the Ampasambazimba fossils from extant populations of *H. simus* by giving the former subspecific status. (He made a taxonomic error in naming them *Hapalemur simus robustus*. Should subspecific separation of Ampasambazimba from extant *H. simus* be warranted, the correct taxonomic name would be *Hapalemur simus gallieni*).

Until very recently (Vuillaume-Randriamanantena *et al.*, 1985), Mahé's conclusions (outlined in several paragraphs of his lengthy treatment of lemur craniometry) went unnoticed by most Malagasy primate specialists who continued to speak of *Hapalemur gallieni* (e.g., Tattersall, 1982; Jolly *et al.*, 1984). Then Vuillaume-Randriamanantena *et al.* (1985) explored this taxonomic problem from the vantage point of a far larger sample of recent *H. simus*, including subfossil *H. simus* material from northern Madagascar that was unknown in 1976 (Tables 1 and 2).

These researchers were able to corroborate Mahé's assessment of the specific identity of so-called *H. gallieni* fossils, but they rejected his subspecific separation of these from other *H. simus* samples. Specimens of *H. simus* seem to conform to a pattern of size variation exhibited by many other lemurs from Madagascar, where samples from the central portion of the island tend to be larger than sister taxa living in the north or east. Specimens of *H. simus* from Ampasambazimba do tend to be larger than specimens from both the north and east. However, they often do not deviate as markedly from northern and eastern *H. simus* as do specimens of the largest subspecies of *Hapalemur griseus*, i.e., *H.S. alaotrensis*, from other *H. griseus*. It is highly likely that subspecies of *H. simus* existed, but they cannot be determined from current samples.

Unfortunately, we cannot follow the history of the demise of *Hapalemur simus* from northern and central Madagascar nearly as well as we can trace its retreat within the eastern rainforest over the past hundred years. We do not know, for example, whether this species had disappeared from northern and central Madagascar before or after humans arrived there (approximately 1,500 years ago). We do now have ex-

Table 1. Subfossil <i>Hapalemur Simus</i>		
Museum and ID#	Collector/Date	Locality
British Museum (Natural History) London 82.372 (Includes postcrania,* multiple individuals)	J. Wilson September 20, 1981	Grotte d'Andrafiabe, Ankarana Massif
Service de Paléontologie Antananarivo 82.202	E. Simons, R. MacPhee, and M. Vuillaume- Randriamanantena 1983	Grottes d'Anjohibe, Near Mahajanga
Académie Malgache Antananarivo (includes three partial lower jaws, one facial portion of a cranium, two maxillary fragments) AMH1, AMH2, AMH3, AMH4	H.-F. Standing 1905 and 1912; C. Lamberton 1936	Ampasambazimba, Itasy Basin

*Clavicle, radius, ulna, femorae, vertebrae, sacrum

Table 2. Specimens of <i>Hapalemur Simus</i>		
Museum and ID#	Collector/Date	Locality
Service de Zoologie Université de Madagascar Antananarivo, male Z9BG	J.-J. Petter & A. Peyrieras February 11, 1972 (Deceased 1978)	Kianjavato, near Mananjary, east of Fianarantsoa
Service de Zoologie Université de Madagascar Antananarivo, female (unnumbered)	J.-J. Petter & A. Peyrieras February 11, 1972 (Deceased 1972)	Kianjavato
Museum of Comparative Zoology Harvard University MCZ 6341	Purchased from E. Gerrard, Jr., 1880	Unknown
British Museum (Natural History) London 1870.9.2.2 TYPE	Zoo specimen Deceased 1870	Unknown
British Museum (Natural History) London 1884.10.20.4	J. Waters 1884	"Nandisen" (= Nandihizana?) Central Betsileo
British Museum (Natural History) London 1961.6.8.1 (immature)	Rothschild coll. (Bequeathed 1961)	Unknown probably eastern rainforest
Laboratoire de Zoologie, Museum National d'Histoire Naturelle, Paris, male 1882-1553	M. Lantz June 12, 1881	"Ambakobé" (= Ambakobe)
Laboratoire de Zoologie, Museum National d'Histoire Naturelle, Paris, female 1882-1552	M. Lantz June 5, 1881	"Ampazénambé" (= Ampasinambé?) (= Ampasinambo?)
Rijksmuseum van Natuurlijke Historie, Leiden <i>Hapalemur simus</i> a	J. Audebert September 8, 1876	"Passumbée" (= Ampasimbe?) Near Mananara
Museum für Naturkunde der Humboldt-Universität, Berlin MZB 5511 female	Darling no date	Unknown
Museum für Naturkunde der Humboldt-Universität, Berlin MZB 16510 (not quite mature)	zoo specimen June 2, 1913	Unknown

cellent radiocarbon data for the subfossil site Ampasambazimba in central Madagascar (thanks to the recent efforts of the American-Malagasy Cenozoic Research Group). Once thought to be one of the youngest subfossil sites (around 1,000 years old), Ampasambazimba is now known to be one of the oldest of dated subfossil sites (about 8,000 years old at the deepest fossiliferous layers) (see MacPhee *et al.*, 1985). But the ages of the two northern caves that have yielded *H. simus* have not yet been determined, and it is not clear, in any case, that we will ever know whether subfossil *H. simus* from northern and central Madagascar were exactly contemporaneous. The specific age of the specimens of *H. simus* from Ampasambazimba cannot be determined unless the level at which they were found is known. Since it is not we must depend on discovering more subfossil *H. simus* from central Madagascar to answer this question directly.

Nevertheless, we can conclude that *Hapalemur simus* once occupied at a minimum eastern, central, northern, and northwestern Madagascar — perhaps it lived everywhere except the arid south. Its demise at least partly post-dates the arrival of humans in Madagascar. The distribution of the broad-nosed lemur at the turn of the century, while restricted in comparison to its apparent earlier spread, was nevertheless broad. A marked constriction in range seems to have occurred in the early twentieth century. *H. simus* averted extinction by retreating into isolated pockets of dense eastern forest — in other words, by living a precarious existence in a tiny portion of its nineteenth century range.

Analysis of the numerous remains of extant lemurs in museum collections around the world should help us document the pattern of constriction in geographic range among other Malagasy lemurs. Some bones of miscellaneous extant lemurs from subfossil sites have not yet been properly identified, and there is ample evidence that *Hapalemur simus* is not the only Malagasy lemur whose range has changed markedly during the past 100 years. Careful documentation of past distributions may help us understand the causes of the disappearance of much of Madagascar's magnificent fauna.

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Fig. 3. A *Hapalemur simus* in the Parc Tsimbazaza in 1975 (photo by G. Peters).

A Note on the Ecology and Behavior of *Hapalemur griseus*

The primates of Madagascar evolved in an environment dominated by conventional rain forests in the east, deciduous or dry scrub-forests with closed canopy gallery forests along the water courses, and thick spiny xerophytic vegetation in the west and south. Only in the central highlands were there meadows or savannas, and these were probably studded with trees, copses and patches of forests in the wetter parts (see Dewar, 1984; MacPhee *et al.*, 1985). Of the 20 extant species, only *Lemur catta* has been observed spending much time on the ground (Jolly, 1966; Sussman, 1975) or occupying areas of poor tree density (Ratsirarson, 1978). Terrestrial habits in some of the larger sub-fossil genera such as *Hadropithecus* and *Megaladapis*, were probably heavily penalized by human populations as man permanently colonized the central plateau for the first time sometime after 500 AD (Brown, 1978). Now largely treeless and heavily eroded, the vast central spine of Madagascar has become a sterile core supporting scattered human populations clustered around areas of permanent water.



Fig. 1. Juvenile female *Hapalemur griseus* "alaotrensis" kept as a pet by a villager at Ambatosoratra on the east coast of Lake Alaotra (photo by J.I. Pollock).

Forests cover about 20.3% of Madagascar's surface based on an annual destruction of 20,000h/year (see Chauvet, 1972) since 1968, when the last accurate measurements were made (Rakotomanampison, 1984). One half the lemur species have become extinct probably through the combined effects of direct human predation, forest clearing and disturbance, and fires which destroy habitat and fragment populations.

One species of Malagasy primate has, however, exhibited remarkable adaptive abilities by successfully occupying the most specialized habitat of any primate species in the world. The gentle lemur, *Hapalemur griseus* (Fig. 1), can be found not only in many forests along the eastern escarpment, but also amongst the banks of reeds growing in Madagascar's largest lake, Lake Alaotra. The habits of this lemur, which is about the size of a small cat, are poorly known except that it has been determined to feed largely on bamboo, to live in small family groups, and to be active mostly at dawn and dusk (Petter and Peyrieras, 1970).

As with most other lemurs, the distribution of *Hapalemur* is poorly known. However, populations discovered in the Ampasindava peninsula (Betsch, J.M. in Petter and Peyrieras, 1970), and on Cape Masoala, together with those at Sambava and Vohemar (Petter and Peyrieras, 1970), indicate that *H. griseus* is possibly the most widely distributed lemur in this half of the island. An apparently very localized western form, however, may exist only in the Lake Bemamba area west of Antsalova. This form is said to be smaller and has been awarded sub-specific

status, viz. *H. griseus occidentalis*, in an unconventional fashion (see Tattersall, 1982). Collecting records indicate a much wider distribution in the past which could have covered most of the northwest and north of the island. The population living in the reed beds of Lake Alaotra has been given subspecies status, *alaotrensis*, on the basis of its larger size (Tattersall, 1982), and this is followed by Petter *et al.* (1972). However, only one individual of this supposed new subspecies has been measured, and details of the comparison are not convincing. For example, although the mean head-plus-body length of the nine Archbold Expedition *H. griseus griseus* was 284 mm. (Tattersall, 1982), Hill's (1953) value was 365 mm (unknown sample number), whilst that of the single *H. g. "alaotrensis"* was 380 mm. Furthermore, the hind foot length of the Archbold animals ranged from 75-93 mm, values substantially greater than the 50 mm *H. g. "alaotrensis"* (Tattersall, 1982). Karyological examinations have been effective in separating only *H. griseus occidentalis* (2N=58 with 50 acrocentrics) from *H. griseus griseus* and *H. griseus alaotrensis* (2N=54 with 42 acrocentrics; Rimpler & Albignac, 1973). It seems at present, until a wider sample of individuals are examined and measured carefully, that there is no reason to regard the Lake Alaotra form as more than a substantial isolated population of *H. g. griseus*.

A second species of substantially larger size, *H. simus*, is known by recent collection from rain forest in the Ranomafana area west of Ifanadiana. Thanks to Tattersall's careful research at the Rijksmuseum in Leiden, Holland, a second locality in the Bay of Antongil region has been identified. The discovery of *H. simus* remains in the cavernous Ankarana massif by a Southampton University expedition (Wilson, 1981) makes it very likely that this extremely rare lemur is still, or has been until recently, widely distributed in appropriate habitats throughout the wet eastern forest, and the intermediary environments in the central plateau, area (Godfrey *et al.*, 1985, and this volume) and the extreme north.

In the course of an 18-month field study in eastern Madagascar in 1972/3, *H. griseus griseus* were frequently observed moving and feeding, usually in the early morning (Fig. 2). On several occasions, especially during the summer months, these animals were disturbed while active before dawn in secondary forest close to the Reserve de Faune at Analamazoatra. At Maroantsetra, Petter *et al.* (1977) also report an evening activity period between 16:00 - 21:00. In the course of frequent nocturnal surveys at Analamazoatra, *H. griseus* were not discovered active in the middle period of the night, but in captivity at Duke University Primate Center periodic short bouts of night activity are usual (pers. obs.).

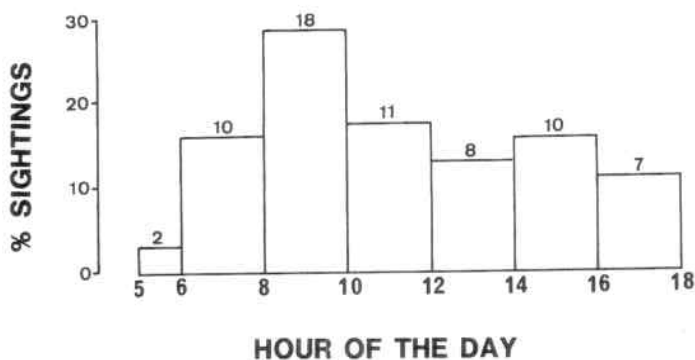


Fig. 2. The hourly distribution of active *Hapalemur griseus* sightings in three study areas in eastern Madagascar (figure by S. D. Nash based on author's original).

H. griseus griseus usually live in groups of 2-5 individuals, although single animals and much larger aggregations occur on occasion. In this study, group counts were made on 55 occasions (Table 1) of which 40 are regarded as accurate. The mean group size of 2.6-2.9 is similar to

that reported for the "family-group living" *Indri indri* (Pollock, 1975) and *Lemur mongoz* (Tattersall and Sussman, 1975). However, my observations of group composition include a high probability of the presence in some groups of more than one breeding adult female. In particular, the presence in some groups of 3 adults and 2 infants or young each following or carried by a different adult, suggest that nuclear family units may not explain all social group compositions in this species. The twinning rate in *H. griseus* is unknown, but there has been only one twin pregnancy in the ten occurring in the captive population at Duke, with one of the twins dying soon after birth. Although at Duke a close infant association with the male in captive groups has been observed, Petter *et al.* (1977) in reporting the presence of more than 1 adult female in some groups, agrees with the present interpretation that a variety of group compositions occur in *H. griseus*.

Table 1. *Hapalemur* Group Size

No. of groups:	Group size								Total
	1	≥ 1	2	≥ 2	3	≥ 3	4	≥ 5	
	4	2	13	7	13	6	7	3	55

Because of their size, cryptic appearance and flight behavior (fleeing on the ground or near ground level) it is frequently difficult to be confident of *H. griseus* group sizes. In this table only groups in which animals are counted three times within an observation period are included. On 18 of the 55 counts only minimum group sizes were ascertained (numbers prefixed by " "). The size of groups in which all animals were counted (mean = 2.62, n=37) is very similar to the size of groups in which all animals may have been counted (mean = 2.65, n=55).

All Malagasy lemurs for which there is information, breed seasonally and exhibit very sharp birth peaks. Petter and Peyrieras (1970) report one captive *Hapalemur* birth in France in late May, breeding having been observed in early January, and at Duke most *H. griseus* births have been in June. Because reproductive activity in the northern hemisphere is 6 months out of phase with Madagascar (due to seasonal photoperiodic differences), these birth dates are equivalent to November and December in the wild. At Maroantsetra, *H. griseus* births are reported to occur in December and January (Petter and Peyrieras, 1970). Further south at Analamazoatra, infants were observed by the author in November and January, with small but independently moving young seen in each of the subsequent five months. These observations are consistent with a birth season starting in late October and continuing into January. The gestation period of 140 days (Petter and Peyrieras, 1970) is exceptionally long for a primate less than 1 kg in body weight.

The diet of *H. griseus* is poorly known except that much of its time is spent feeding on bamboo shoots and stalks. The animals are often found in or close to bamboo thickets which generally grow in thick clumps within the forest. The feeding mechanism described by Petter *et al.* (1977) and Milton (1978) involves substantial manual dexterity and high plant part selectivity. Of the 36 varieties of bamboo present in Madagascar today, some 14 exist within the distribution range of *H. griseus* as presently known (Wei Chih Lin, 1970). Because different bamboo species are adapted to different altitudes, *H. griseus*'s wide altitudinal distribution (0-2,000 m) probably requires it to feed on several species (Table 2). Six of the 12 endemic bamboo species are found only in the northern highland regions of Marojeje and Tsaratanana, and can only be locally significant for *H. griseus* if they exist there. Five of the other species are vine-bamboos which may be of less importance as they grow in a dispersed fashion on other vegetation. It is, therefore, most likely that the free-standing *Ochlandra capitata* and the two introduced species, *Phyllostachys aurea* and *Dendrocalamus giganteus*, are of greatest nutritional importance for *H. griseus*. *H. griseus* has also been observed at Analamazoatra to feed on surface grasses, fig leaves and fruit, and in the west on the fruit of *Flacourtia ramontchi* (Petter *et al.* 1977). These authors also report the presence of seeds of the genus *Dypsis* in the faeces of a wild *H. griseus*.

Table 2. Madagascan Bamboo Species and Observed Food Species for *Hapalemur*

Endemic bamboo species present within the distribution range of <i>H. griseus</i> . (After Wei Chih Lin, 1970)	
<i>Arundinaria marojejensis</i>	High altitude species, very localized (1,800-2,100 m)
<i>Arundinaria madagascariensis</i>	High altitude species (2,000-2,800 m)
<i>Cephalostyrium madagascariensis</i>	Climbing bamboo @800 m
<i>C. perrieri</i>	50-500 m
<i>C. riqueri</i>	800-1,200 m
<i>C. chapelieri</i>	800-1,200 m
<i>Nastus aristatus</i>	Climbing bamboo 900-1,450 m
<i>N. perrieri</i>	Climbing bamboo 1,000-1,700 m
<i>N. tsaratanensis</i>	2,000 m, Very localized
<i>Ochlandra capitata</i>	40-900 m
<i>Perrierbambus tsaratanensis</i>	Very localized, high altitude
<i>Schizostachyum perrieri</i>	Very localized, 2,000 m
Non-endemic species of bamboo within <i>Hapalemur</i> range	
<i>Phyllostachys aurea</i>	Widespread
<i>Dendrocalamus giganteus</i>	Widespread, 1,000-1,400 m
Other observed forest foods	
<i>Ficus pyrifolia</i> young leaves	
<i>Gaertnera macrostypula</i> berries	

The distribution of *H. griseus occidentalis* in the west and both subspecies in the north has also been linked to vegetational zones rich in bamboo (Tattersall, 1982). However, one distinct habitat occupied by *H. griseus*, the marshes of Lake Alaotra, contain no bamboo, its role being replaced by the dominant reed, *Phragmites communis*.

Lake Alaotra is a long, shallow lake, at 750 m, formed by tributaries draining the line of modest hills running from Antanimenambaka (in the north) to Andilanatoby (in the south). These tributaries which feed the Sasomangana, Sahabe, Sahamloto and Anony Rivers, carry water down a gentle gradient from 1,000-1,300 m, through marshy zones which, by means of dykes and dams, have been used to create the most productive wet rice paddies in Madagascar (Aldegheri, 1972). Although it has been reported that as recently as 1900, the lake was 8 m deep (Petter and Peyrieras, 1970), its present day average depth of 2.5 m is regulated by the overflow control formed by the rocky sills at Ambatofafana on the lake's only outlet, the Maningory River. According to Hardyman (pers. comm), no water-level changes occurred between 1946 and 1973. The southern and western borders of the lake basin are composed of vast expanses of marsh dominated by the common reed, *P. communis* (baratratra), and papyrus, *Cyperus imerinensis* (zozoro); (Perrier de la Bâthie, 1921). This vegetation formation of about 800 km² is generally too insecure to walk on and must be visited by dug-out canoe. To the northeast of the marsh an expanse of clear water covers some 200 km². The water-level of the lake varies by ± 1.5 m according to the season. Heavy erosion around the lake has followed destruction of the forest, especially in the east, and silting up of the paddies is a major conservation problem in the area. The nearest natural forests now lie on the western edge of National Reserve No. 3 (Zahamena), some 40 km to the east of the lake.

Prior to human habitation in this area, probably about 1,500 years ago, this forest grew down to the lake's edge, providing a means of direct access to the reed beds for *H. griseus* and other species. Forest clearing has now isolated a population of *H. griseus* in the reed banks which provide a suitable bamboo substitute from the same botanical family, Graminae. Of the 7 plant species commonly found in the marsh (Table 3), the papyrus and reed are overwhelmingly dominant. The latter root in the lake bottom, whereas the *C. imerinensis* forms floating colonies that accumulate in size and attach themselves to each other and the more

stable reed stands. The reeds have culm diameters ranging from ½ cm to 5 cm and stand up to 3 m above the dry season water level, providing just adequate supports for this 850 gm vertical-clinging-and-leaping lemur. Both in their forest habitat and in the marsh, *H. griseus* flee either directly from disturbance at normal heights or, more often, drop to the ground and freeze or move quietly away. This flight behavior is extremely effective in the dense reed beds, and the higher reed diameter low down facilitates their leaping locomotion by providing firmer supports.

Table 3. Common Plants Living in Lake Alaotra Reed Beds

<i>Cyperus imerinensis</i>	Cyperaceae
<i>Phragmites communis</i>	Graminae
<i>Polygonum senegalensis</i>	Polygonaceae
<i>Jussiaea sp.</i>	Oenotheraceae
<i>Solanum nigrum</i>	Solanaceae
<i>Tynophodrodin lindleanum</i>	wild taro
<i>Eichornia crassipes</i>	water hyacinth

During the three days spent at the Eaux et Forêts research station just north of Ambatosoratra in 1984, four attempts in the early morning, evening and late evening were made to observe *H. griseus*. The nearest reed banks lie about 7 km across the lake, due west, and are frequented by fishermen in dug-outs. One adult *H. griseus* was observed in this area at 0730 feeding on *Phragmites* shoots, before rapidly disappearing into the reed mass. The flight distance of about 50 m suggested hunting pressure which was confirmed by interviewing local people.

According to the indigenous population, the diet of *H. griseus* or *band-ro*, as they are known, is mostly the young *Phragmites* shoots which are available throughout the year. The apical or terminal shoots are probably less accessible than shoots derived from lateral nodes which can be bitten off and eaten while the animal clings to the base of an adjacent reed. These feeding sites also afford a rapid means of escape from any arboreal predator (e.g. the viverrid *Galidia elegans* and snakes such as the boa *Sanzinia madagascariensis*; Petter *et al.*, 1977) and probably completely prevent aerial attack by large rapacious birds such as *Buteo brachypterus* and *Polybioides radiatus*. The soft fleshy bases of the papyrus stems are also bitten off and consumed by *H. griseus* according to local people.

The main threat to *H. griseus* on Lake Alaotra, however, is man. Utilization of the lake and marshes for fishing and obtaining materials involve some destructive practices. Fishermen can obtain up to 40-50 kg fish per day in this highly productive shallow lake. Working alone or in small groups of dug-outs, they make temporary camp sites on the reeds by bending them down to form a 2 m x 2 m platform which is then overlaid with cut reeds.

Reed bank edges are favored fishing sites which can be enlarged by burning the reeds at the end of the dry season. Because of water level differences of 100-150 cm between seasons, the fires open up new areas for the fishermen as the water table rises. These provide improved access to central parts of the reed mass, probably creating simultaneously new attractions for the fish and easier fishing conditions. These fires, either intentionally (Webb, 1953; Peter and Peyrieras, 1970) or coincidentally, result in animal captures as they flee their native ranges, and can dramatically affect habitat availability.

Competition between *H. griseus* and man for plants also occurs as the stalks of *Phragmites*, cut and split or laced together whole, form the basic material for screens, barriers and fencing. The papyrus shoots woven together are used to furnish Sihanaka dwellings with floor mats, and to make simple fish traps. The *amamamy* plant (*Solanum nigrum*) is picked to be eaten like spinach, and wild taro (*Tynophodrodin lindleanum*) also provides an occasional source of food. The swollen stems of the water-hyacinth (*Eichornia crassipes*) are used as fishing floats, and, according to Webb (1953), are also eaten by semi-aquatic native pigs (*Potamochoerus larvatus*).

Direct hunting is probably not a major threat to *H. griseus* on the lake, although they are caught on occasion and kept as pets. Local merchants with access to firearms hunt ducks in the season and probably shoot lemurs if they can. All lemurs are, however, protected by law in Madagascar and such activities are acknowledged locally to be illegal. The existence of a local taboo or *fady* against hunting *H. griseus* was described to the author at Andreba and is reported to exist at Anororo, on the western bank, by Petter *et al.*, 1977. It is unclear how effective such beliefs are in protecting lemurs. In the forests, *H. griseus* are always sympatric with larger, more visible and less secretive species to which any hunting or trapping is usually directed.

H. griseus, both in the forest and on the lake, probably spend most of their feeding time selecting parts of a single species of Graminae. By exhibiting this behavior they prove to be the most specific feeder of all primates, the nearest folivorous competitors being *Colobus guereza* (46.8% feeding time spent on several parts of one species, *Celtis durandii*; Oates, 1977) and *Presbytis senex* which feeds on 2 species for 45% of its feeding time (Hladik, 1978).

Table 4. Nutritive Composition by Percentage Dry Weight of the Lake Alaotra *Haplemur* Foods and Two Important Foods for the Wolong Giant Pandas (after Schaller *et al.*, 1984)

	Protein	Simple sugars and starch	Hemi- cellulose	Cellulose +lignin	Ash	NGR ¹
<i>Haplemur griseus</i> foods on Lake Alaotra ²						
<i>Phragmites</i> ³	14.4	18.6	< 41.4	< 27.6	4.29	0.52
<i>Cyperus</i>	9.3	18.1	< 24.0	< 26.0	5.27	0.36
Giant Panda foods at Wolong						
<i>Sinarundinaria</i>						
leaf ³	15.5	12-14	35.5	36.4	8.4	0.43
new shoot	14.8		33.9	41.9	6.4	0.35
<i>Fargesia</i>						
leaf	14.4	@4	33.0	38.2	8.8	0.38
new shoot ³	17.6		32.5	36.2	8.7	0.49

Key:

1 NGR = nutritive quality ration (Schaller *et al.*, 1984) = % protein ÷ % (cellulose and lignin)

2 Samples from 3 plants taken in September 1984, and pooled for analysis

3 Top selected foods

To exist successfully on a virtual monoculture implies a close affinity between the animals' needs and the composition of the plant. If little intraspecific variation is present in biochemical composition, perhaps to be expected in a semi-aquatic plant, control over diet can only be achieved through intake variation. (It is assumed that *H. griseus* have a small or negligible animal matter component in their diet as suggested by Petter and Peyrieras, 1970, although this remains to be shown for the Alaotra form). Table 4 shows the relevant chemical composition of a sample of young shoots of papyrus and reed from Lake Alaotra collected in September 1984, together with data on two significant foods eaten by another tall-grass eating specialist, the giant panda (*Ailuropoda melanoleuca*), in Wolong province in China (Schaller *et al.*, 1984). In the panda study, some species of *Bambusa* and *Phyllostachys* contained very substantial amounts of protein (less than 30.1%) but the two main panda foods had a protein composition very similar to that of Alaotra *Phragmites communis* shoots. Furthermore, the cellulose plus lignin content of the latter was lower than panda bamboo giving the Madagascan reeds the highest nutritive quality ratio (NGR) in the comparison. This ratio was found to be the best predictor of food selectivity in the Wolong pandas. By estimating and measuring food consumption parameters, Schaller *et al.* (1984) concluded that pandas were obtaining protein sufficient or in excess of their requirements from a bamboo-only diet, and that the limiting dietary components were likely to be soluble carbohydrates or/and fats. The energy requirements of *H. griseus* are probably greater than the panda per unit of body weight, and proportionately more food may therefore be required. However, food intake rate on a monoculture of reeds or bamboo may be as much dependent on hand

and mouth dexterity as on body size, and it seems unlikely that sufficient metabolizable energy cannot be easily consumed. The continuous productivity of the reed, its even and abundant distribution, its rhizomatous reproductive capabilities, and its high nutritive value make it an ideal primate food.

Table 5. Mineral Content of *H. griseus* Foods on Lake Alaotra and Comparisons with Other Species and Recommended Feeds

	Major minerals (% dry matter)					Trace minerals (parts per million)			
	P	K	Ca	Mg	S	Fe	Mn	Zn	
<i>P. communis</i>	.38	3.45	.16	.12	.18	66	49	35	
<i>C. imerinensis</i>	.25	4.65	.13	.13	.11	87	340	23	
<i>Celtis durandii</i> ¹ (all leaves)	.48	1.69	1.2	.25		185	44	44	
Swamp plants ²	.56	3.19	1.46	.57		1530	192	1330	
Captive primates ³	.2	?	> .3	.1		?	?	15	
<i>Sinarundinaria</i> ⁴			> 1.0	.1		?	?	15	
<i>Fargesia</i> ⁴			< 1.0						

Key

1. The main land-based food for *Colobus guereza* at Kibale (after Oates, 1978)
 2. The mean values for swamp-living plants in the above study.
 3. Values given in the National Research Council's (1978) assessment.
 4. The main giant panda bamboo foods (after Schaller, 1984)
- The values given for the *Hapalemur* foods were obtained from an analysis performed by the Agronomic Division of the North Carolina Department of Agriculture and derive from three samples of each species taken in September 1984, and pooled for analysis.

Alluvial soils in the Alaotra basin are enriched by vegetation decomposition and run-off concentrations of minerals leached from the deforested watershed. Although this probably affords better plant growth conditions in the lake basin itself, poor soil chemical composition in the surrounding area (Riquier, 1965) is reflected especially in low calcium profiles of the marsh plants (Table 5). Both the calcium concentration and the calcium to potassium ratio of *Phragmites* and *Cyperus* are low. For *Colobus guereza* at Kibale Forest in Uganda, the land-based and swamp-living food species contained ten times as much calcium (Oates, 1978). Both Hladik and Guegen (1974) and Oates (1978) have speculated that soil consumption by primates may not be a strategy for obtaining minerals, but a digestive aid of a mechanical nature or a detoxification system. It is perhaps relevant that geophagy is denied the marsh-living Lake Alaotra gentle lemurs. It is noteworthy that an artificial diet fed to captive *Macaca mulatta* containing a similar calcium concentration (0.15%) to *Phragmites*, resulted in pathological osteoporotic changes over a number of years (Griffiths *et al.*, 1975). The main bamboo foods of giant pandas analyzed by Schaller *et al.*, (1984) also contained calcium at substantially higher concentrations than the Lake Alaotra reeds. The United States National Research Council's (1978) recommendation for captive primates of 150 mg calcium/kg body weight/day, can be just met by the Lake Alaotra gentle lemurs by consuming about 800 gm *P. communis* or 980 gm *C. imerinensis* daily, assuming the samples analyzed were typical of the animal-selected swards. It is of interest that in the past some captive *H. griseus* maintained largely on domestic vegetables and calcium-rich primate feed (Purina Regular Monkey) at Duke University Primate Center have experienced soft tissue hypercalcification, suggesting a low calcium-adapted physiological system (Gray *et al.*, 1982).

Little information is available on the digestive properties of bamboo-feeding specialists such as pandas, *H. griseus*, *Rhizomys sp.*, *Hapalomys longicaudatus* (Musser, 1972) and perhaps the red panda, *Ailurus fulgens*, and the golden monkey, *Cercopithecus mitis kandti* Schaller *et al.* (1984). Schaller *et al.*, 1984 have suggested that the short gut-to-body length ratio of pandas (4.1-7.7) indicates a poor adaptation to their 99% bamboo diet, invoking the high faecal output and substantial faecal nutritive composition as evidence. The gut-to-body-length ratio of an *H. simus* examined by Beddard (1901) was 6.1, and that of an adult female *H. griseus griseus* dissected by the author was between 4.0 and 4.5 depend-

ing on the measurement method. However, it is very difficult to say how panda nutrition is limited, and both Hill and Rewell (1948) and Hladik (1967) have warned against unitary interpretations of the intestine-to-body length ratio. The latter author offers a more substantial analysis based on gut surface area and microvilli density and structure, but his studies did not include *H. griseus*.

The niche occupied by *H. griseus*: middle strata and bamboo thicket, vertical-clinging-and-leaping, crepuscular, graminivorous, is probably one of the most successful of any lemur. In the forest of Analamazoatra, a population density of 47-62 individuals/km² were estimated to produce a biomass of 0.3-0.5 kgs/hectare. Their range in the east lies throughout the non-degraded forest areas which now cover approximately 50,000 km². This means that the remaining total population size must be very substantial, although forest destruction and fragmentation in the east is a serious threat. The status of the western subspecies is unknown. On the lake itself virtually all of the 800 km² is likely to be suitable *H. griseus* habitat, although access to much of this area is impossible, making verification difficult. Because size and pelage coloration is variable in *H. griseus*, it is not possible, without further information, to regard the *alaotrensis* form as a distinct subspecies worthy of separate conservation action. The Lake Alaotra habitat is, however, of great conservation importance, especially as the only locality for the Madagascar pochard, *Nyroca innotata*.

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The Status of Primates in Bangladesh and a Description of their Forest Habitats

Introduction

This report presents the results of an 18 month field survey of the status of primates in the forested and non-forested areas of Bangladesh. Between December, 1979 and June, 1981, ten species of primates were recorded present in Bangladesh (Table 1).

Table 1. Primates Recorded from Bangladesh

Species	Vernacular English and Bengali Names	
Family Lorisidae		
<i>Nycticebus coucang</i> (Boddaert, 1785)	slow loris	lajjawati/lajuk banar, mukhluka banar, naiphonda in Chittagong
Family Cercopithecidae		
Subfamily Cercopithecinae		
<i>Macaca mulatta</i> (Zimmermann, 1780)	rhesus macaque/ monkey	banar/bandor
<i>Macaca assamensis</i> (McClelland, 1840)	Assamese macaque	asami/bora banar
<i>Macaca nemestrina</i> (Linnaeus, 1766)	pigtailed macaque	ulu/ultaleji banar
<i>Macaca arctoides</i> (I. Geoffroy, 1831)	stumptailed macaque	chotoleji banar
<i>Macaca fascicularis</i> (Raffles, 1821)	longtailed/crab- eating macaque	borleji banar/ parailla banar
Subfamily Colobinae		
<i>Presbytis entellus</i> (Dufresne, 1797)	common langur	hanuman
<i>Presbytis pileatus</i> (Blyth, 1843)	capped langur	mukhpura/lal hanuman
<i>Presbytis phayrei</i> * (Blyth, 1847)	Phayre's leaf monkey	kala hanuman/ chasmapara hanuman
Family Hylobatidae		
<i>Hylobates hoolock</i> (Harlan, 1834)	Hoolock gibbon/ white-browed gibbon	ulluk, hulu banar, banamanush

* Mountfort (1969) recorded the dusky leaf monkey (*Presbytis obscurus*) from Bangladesh. Gittins (1980), however, contends that *P. obscurus* and *P. phayrei* are indistinguishable in the field and are probably conspecific.

Previous status surveys of primates in Bangladesh include those of Khan (1979), Gittins (1980), Green (1980), Khan and Ahsan (1981a; 1981b) and Gittins and Akonda (1982). Khan's (1979) report was preliminary in nature. Green (1980) was not able to survey the Sunderbans and Chittagong Hills, the largest remaining forest tracts in the country, and Gittins and Akonda's (1982) study was also incomplete, not including the forests of the Chittagong Hills. The results of this study, which include all the major forest types and tracts of Bangladesh, have increased our knowledge of the status of primates in this country, and will provide a basis for their future management.



Fig. 1. The location of Bangladesh in Asia (map by S. D. Nash).

Climate and Geography

Bangladesh lies between 20° 3'-26° 45' N, and 88°-92° 56' E, and encompasses an area of approximately 142,450 km² (Fig. 1). Its climate is characterized by hot, rainy humid summers, and dry, mild winters. The summer or monsoon rains are preceded by a period of frequent thunderstorms from March through May. In the early part of the summer the mean maximum temperatures approach 37°C, with temperatures of 43°C being recorded in some of the drier western districts. The heavy monsoon rains begin in early June and continue almost to the middle of October. Total rainfall varies considerably between regions; Rajshahi receives only 1,550 mm, while Sylhet and Cox's Bazaar may receive between 3,300-4,000 mm. Bangladesh can be conveniently divided into two main physical regions: a vast alluvial plain, and marginal hills in the east and southwest with a few hillocks in the north. Five large rivers feed the alluvial plain, three of which — the Ganges (Padma), Brahmaputra (Jamuna) and Meghna, and their tributaries — criss-cross the entire country before emptying into the Bay of Bengal. All of these rivers originate in the high mountains of neighboring countries. Their alluvial deposits account for more than 90% of the total land area of Bangladesh, and the delta formed by the Ganges and the Brahmaputra is reported to be the largest in the world (Rashid, 1967; Anon., 1981). The highest land here is under 15 m in elevation.

North of Dhaka, in the central part of the country, is a large area of comparatively high land with reddish soils known as the Madhupur Tract. Its northern portion slopes gently to the foot of the Garo Hills in India. A few of the smaller foothills are within Bangladesh. To the northeast of this tract is a large area of low depressions known as the *haors* (Rashid, 1967) and to the northwest a group of high, clay terraces dating from

the Pleistocene known as the *barind*. Hill country also predominates in the Chittagong region of southeastern Bangladesh, the ranges running north to south. A few peaks rise above 1,000 m including Keokradeng, Mowdokmual, Reng Tiang and the Pyramid Hills (Fig. 2).

The largest swamp forest of the world, the Sunderbans, lies in the southwest. The greater part of the Sunderbans is within Bangladesh, with a smaller portion entering the Indian state of West Bengal.

Survey Areas and Study Methods

A large portion of Bangladesh was surveyed during this study, including most of the country's forested areas. In addition, surveys were conducted in non-forested areas in the districts of Comilla, Barisal, Dhaka, Dinajpur, Faridpur, Jessore, Khulna, Kushtia, Pabna and Rajshahi, as these areas were reported to harbor primates.

Census and data analysis basically follow the line transect method of



Fig. 2. The districts of Bangladesh showing the distribution of *Macaca mulatta* and *Presbytis entellus* (map by S. D. Nash based on authors' original).

Southwick *et al.* (1964), Southwick and Cadigan (1972), Freese (1975) and Green (1978). Observers move in a line through the forest, measuring the approximate distance covered and recording the primate groups encountered. During the study the effective transect width ranged from 10-200 m. The linear distance of the transect is later translated into a square kilometer equivalent (Green, 1978) for the purpose of determining population densities. The survey was conducted mainly on foot, and partly by canoe, motorboat and motor vehicle. In most areas, one or two villagers or indigenous natives were hired as guides. Censusing was conducted during 355 days of this study from dawn to dusk, though not usually during periods of heavy rain. Observation periods ranged from 2-30 minutes depending on visual conditions. If after this time only one individual was sighted it was recorded as isolated, two or more individuals constituted a group (gibbon vocalizations coming from one direction at the same time were also considered a group).

The average group size for each species in each forest type was calculated and used to make density estimates by multiplying by the total area available to the species. The total population of non-forest inhabiting primates was determined by multiplying the observed average group size by the number of reported primate groups.

Forest Types and their Distribution

Most species of primates in Bangladesh live in forested areas, which can be characterized as either *sal* (moist deciduous), evergreen or mangrove. Forests are reported to cover 22,297 km² of the country, but Green (1978), considers this figure to be an overestimate based on information from Forest Department Statistics, and reports by Chowdhury (1968; 1973), Baten (1969), and others (Anon., 1969; 1970; 1973; 1974; 1976; 1979). A recent report by the Bangladesh Agricultural Development Corporation (Anon., 1981) states that not much more than 10% of the country is forested, and that most of this remaining forest is concentrated in the extreme south and southeast. Timm (1981) observes that although Bangladesh is commonly reported to have 16% forest cover, satellite analyses put the figure closer to 7%. Evidence indicates that the extensive floodplains were never completely forested (UNDP/FAO, 1971). Today, forests are restricted to the lowland mangroves in the southwest, and the higher land areas in the north-central and south-east portions of the country (Fig. 3). The Forest Directorate divides the forest areas of Bangladesh into ten main Divisions: Chittagong Hill Tracts (CHT) North, CHT South, Chittagong, Cox's Bazaar, Sylhet, Dhaka, Mymensingh, Tangail, Northern (Dinajpur, Rajshahi and Rangpur), and Sunderbans. In addition, another nine divisions are recognized by Hendrich (1975), Rashid (1977) and the Bangladesh Forest Administration Progress Report (Anon., 1979). All forests are legally classified as either Reserved, Acquired, Protected, Private, Vested, Khas or Unclassed State Forest (USF).

Sal or Moist Deciduous Forest

All *sal* forest in Bangladesh lies within the Dhaka, Mymensingh and Tangail Forest Divisions, and is represented in a single contiguous unit known as the Madhupur Tract. This tract is 112 km long (north to south), between 8-21 km wide, and is bordered by the Bangshi and Banar Rivers. The annual rainfall in this region is approximately 2,300 mm, and the elevation about 20 m.

Indigenous tribes and farmers inhabit much of the Madhupur Tract. The farmers cultivate paddy, jute, pineapple, jackfruit, banana, plantain, mustard and cassava, among other crops. Homesteads and agricultural plots are interspersed with forest, which continues to decrease in area each year. Almost every part of the forest, including Madhupur National Park, has some settlers. It is generally agreed that about 30% of this tract is already being exploited by squatters.

Sal forest is dominated by the coppice tree (*Shorea robusta*). This species covers approximately 80% of Madhupur Tract. The tree species found in association with *S. robusta* are listed in Table 6.

In addition to the Madhupur Tract, *sal* forests are also found along the northern border of Bangladesh from Mymensingh to Jamalpur, and in the Sylhet, Dinajpur and Rangpur Districts.

Evergreen Forests

Evergreen forests within Bangladesh include those found in the Chittagong, Cox's Bazaar, CHT North, CHT South, and Sylhet Divisions. The forests of the Chittagong Division lie within the Sadar subdivision and extend from the Feni River in the north to the Cox's Bazaar Forest. They are bordered on the west by the Bay of Bengal, and to the east are contiguous with the forests of the Chittagong Hill Tracts Districts. The Cox's Bazaar Forest lies between the southern extremity of the Chittagong forests, the Burmese border in the southeast, and the Bay of Bengal to the south and west. Cox's Bazaar enjoys a modern climate and the annual precipitation is approximately 3,500 mm.

The forests of CHT North and South lie within the Districts of Chittagong Hill Tracts and Bandarban. These forests are bounded on the east by the hills of Tripura and Mizoram of India, and the Arakan hills of Burma. The climate is typically subtropical, with a long dry season extending from November to May, and rainstorms from June to September. The average temperature varies between 24°C in December and 35°C in May. Annual precipitation is approximately 2,540 mm.

At present, the forests of Sylhet District occur patchily in broad valleys bounded on the east, north and south by low hills. The Khasia and Jaintia Hill Ranges of India lie to the north. The southern portion of the District is covered largely by tea estates, spread over an area of approximately 43,000 ha. In the southeast there are about six hill ranges (Patharia, Harargaj, Rajkandi, West Bhanugach, Tarap and Rhaghunandan) which vary in altitude between 50-100 m. These ranges contain the best quality forests of Sylhet, and also adjoin Private and Unclassed State Forests. Most dry land areas have already been cleared and agriculture is practiced throughout the Division. Earlier reports suggest that these lands once supported good quality forests. The annual rainfall ranges between approximately 2,400 mm (Srimangal) and 4,000 mm (Sylhet).

Several centuries ago, most of the hill areas were inhabited by indigenous tribes, including the Chakmas, Murangs, Tipras, Moghs, Khasias, Manipuris and Kukis, among others. To a large degree, they all practiced slash-and-burn or shifting cultivation, locally referred to as *jhum chash*. Today, plains dwellers are settling amongst the hills of several Forest Divisions. Both the indigenous peoples and these new settlers share responsibility for the destruction of wildlife and habitat that has occurred in this region.

The forests of Chittagong, CHT North, CHT South and Sylhet are similar and are broadly classified into tropical evergreen, semi-evergreen and deciduous types (Puri, 1960; Champion and Seth, 1968). Evergreen forests always contain some deciduous species. The tree species most commonly found in these forests are listed in Table 7.

Bamboo forests occur in pure stands over wide areas of these Forest Divisions. Frequently bamboo forms an undergrowth or borders mountain streams. Species common in bamboo forests include *kansh* (*Saccharum spontaneum*), sungrass (*Imperata cylindrica*), *khagra* (*Phragmites karka*) and *hogla* (*Typha elephantina*).

Savannah type forest is widely distributed in the same Forest Divisions which support evergreen forest, and also in the Unclassed State Forests. This is likely the result of regeneration following cultivation in hill areas. Any cleared area of evergreen forest is rapidly taken over by fast-growing sungrass (*Imperata cylindrica*), *Lantana camara*, *Eupatorium odoratum*, *Clerodendrum infortunatum*, and *Melastoma/Osbeckia* spp. These form an impenetrable scrub formation, which is occasionally dotted with *Microcos paniculata*, *Dillenia pentagyna*, *Albizia* spp., *Cassia* spp., *Sterculia villosa*, *Pterospermum semisagittatum*, *Lagerstroemia* spp., *Syzygium* spp. and *Careya arborea*, among others.

The swampy areas of these five Forest Divisions include ox-bow lakes and quiet streams. The permanent lakes support *baruna* (*Crataeva nurvala*), *hijol* (*Barringtonia racemosa*), *chitki* (*Phyllanthus reticulatus*), *pitali* (*Trewia polycarpa*), *panibaj* (*Celtis* sp.), *Saccharum* spp., and *Typha* sp.

Large areas of the evergreen and semi-evergreen forests have been clear-felled in the past, or are in the process of being cleared to practice monoculture of teak (*Tectona grandis*), champa (*Michelia champaca*), garjan (*Dipterocarpus* spp.), dhaki jam (*Syzygium grandis*), rubber (*Hevea brasiliensis*), gamari (*Gmelina arborea*), telsur (*Hopea odorata*), lohakath (*Xylia* sp.), jarul (*Lagerstoremia* spp.), mahogany (*Swietenia mahagoni*, *S. microphylla*), tea (*Camelia sinensis*) and Malayan oil palm (*Elaeis guineensis*).

Sunderbans or Mangrove Forest

The forest of the Sunderbans is a tropical humid or mangrove type that stretches from the Hoogly River of India in the west to the Meghna River of Bangladesh in the east. The Bangladesh Sunderbans is located at the southern extremity of the Padma and Jamuna delta in the Districts of Khulna and Patuakhali, between 21° 31' - 22° 30' N and 89° - 90° E. Most of the Sunderbans is inundated by the Bay of Bengal during the high tide of the monsoon period. The forest is intersected by many rivers, canals and *khals* of various widths. A number of rivers have indirect connections and receive the overflow of the Padma during the rains, including the Passur, Sibsah, Arpangasia and Malancha, and to some extent the Jamuna and Raimongal. The soil is silty, clay loam (Rashid, 1977) deposited originally by the Ganges. The climate is humid and the rainfall averages between approximately 1,650- 1,780 mm per year.

The Sunderbans is the only forest belt of Bangladesh which has no permanent human population, although across the border in India settlers are quite numerous.

Prain (1903) listed some 334 species of plants from the Sunderbans mangrove forest. The major species are listed in Table 5, following Curtis (1933), Choudhury (1968) and Mukherjee (1975).

Non-forested Areas

The non-forested areas in Bangladesh are on the flood plain and include some 85,650 villages, many towns and vast agricultural plots. Whatever forest may have existed in this area in the past has been cut to meet the daily demands for fuel wood, and for construction materials. There is now no forest in the villages of Bangladesh. The isolated trees and scattered forest remnants are composed of species listed in Table 8.

Primate Distribution

Macaca mulatta is still the most widely distributed of all the non-human primates of Bangladesh (Table 2). It inhabits all types of natural forests and also some villages, cities and urban forests. In these non-forested areas, its distribution is patchy. There is a genetic discontinuity between two neighboring populations e.g. the population of Dhaka city proper and the population of Dhamrai or Narayanganj (southeastern subdivision of Dhaka District).

Presbytis pileatus is also widely distributed, being found in all forests except for the Sunderbans and other coastal forests (they do, however, exist on Moheskhal Island), and the *sal* forest of Rangpur and Dinajpur. This species was found in only one village near Satkhamair, Dhaka district; here a few isolate individuals live in a nearby caprice *sal* forest. We did not see this langur west or south of the Jamuna and Pacma Rivers. Mukherjee and Gupta (1965), Mukherjee (1975, and pers. comm.) and Hendrichs (1975), and Southwick (pers. comm.) did not see *P. pileatus* in the Sunderbans. Akonda (1979), however, misleadingly reports their occurrence in Dinajpur, Rangpur and the Sunderbans at population densities of 5.1/km².

Presbytis pileatus and *P. phayrei* are sympatric in much of Sylhet and part of the Karerhat Range of Chittagong. We sometimes saw both species occupying the same tree with no apparent aggressive encounters.

Macaca assamensis, *M. nemestrina*, and *Presbytis phayrei* were encountered only in evergreen forests, whereas *P. entellus* was found nowhere in these forests. Instead, *P. entellus* was found in rural vegetation and in towns in the districts of Jessore and Kushtia, bordering the langur-rich Indian 24-Parganas District. This langur is restricted to

Table 2. Distribution of Primates in Forests

Species	Forest type	No. sighted groups	individuals	Mean group size
<i>Macaca mulatta</i>	sal forest	7	142	20.29
	evergreen forest	34	666	19.59
	Sunderbans (mangrove) forest	33	353	10.70
<i>M. assamensis</i>	sal forest	absent		
	evergreen forest	7	185	26.43
	Sunderbans forest	absent		
<i>M. nemestrina</i>	sal forest	absent		
	evergreen forest	3	128	42.67
	Sunderbans forest	absent		
<i>M. arctoides</i>	occurs only in the evergreen forest			
<i>M. fascicularis</i>	coastal forest of Teknaf Peninsula	4	48	12.00
<i>Presbytis pileatus</i>	sal forest	29	165	5.69
	evergreen forest	44	295	6.70
	Sunderbans forest	absent		
<i>P. phayrei</i>	sal forest	absent		
	evergreen forest	15	205	13.67
<i>P. entellus</i>	only in the non-forested areas of Jessore & Kushtia	8	89	11.13
<i>Hylobates hoolock</i>	sal forest	1	2	2.00
	evergreen forest	34	90	2.65
	Sunderbans forest	absent		
<i>Nycticebus coucang</i>	sal forest	1	2	2.00*
	evergreen forest	2	4	2.00*
	Sunderbans	absent		

*group size yet to be confirmed

Manirampur, Keshabpur, Jheaidah of Jessore and Chuadanga and Meherpur Police Stations of Kushtia.

All earlier reports, including Green (1978), noted *N. coucang* and *H. hoolock* from the evergreen forests. We have also recorded them from the moist deciduous *sal* forest of Mymensing, from the Balijhuri Range beyond Gazni Reserve, in Jamalpur district, bordering Tura hills of Indian Meghalaya.

Khan (1981) has reported *M. fascicularis* from the hilly streams of Cox's Bazaar Division in the Teknaaf Range. Rashid (1977) has reported it both from the Cox's Bazaar and CHT Divisions. Our present study confirms its presence in the Wykong of Teknaaf Range. It appears to prefer coastal vegetation along the Naaf River. The local report of its presence in the Chakoria Sunderbans (Cox's Bazaar Division) could not be confirmed during a survey in June, 1981. It is undoubtedly a rare species in Bangladesh.

Macaca arctoides is rare in the evergreen forest of Cox's Bazaar. It occurs primarily in the forests of Chittagong Hill Tracts, Chittagong and Sylhet, inhabiting forest similar to that of Cox's Bazaar.

Nycticebus coucang is the only primate of Bangladesh which is purely nocturnal and was difficult to census. We observed it twice in evergreen forests.

In all, 139 groups of seven different species of non-human primates were observed in evergreen forests.

The estimated primate group density in evergreen forests was 1.65/km² (Table 3). The density of primates in these forests is 18.5 individuals/km², as compared to 9.7 individuals/km² reported by Green (1978). This is possibly because our results are based upon census of a much larger forest area in different seasons. *Macaca mulatta* and *M. assamensis* appeared especially frightened of humans in the evergreen forests. They would typically drop to the ground and flee in the underbrush where it was difficult to count them. The group size estimates

we have given are observed group size and can, therefore, be considered a minimum for actual group size. Other species, especially *Presbytis pileatus* and *P. phayrei*, were much easier to count accurately.

Table 3. Primate Density in Different Forest Types, km²

Species	Sal Forest		Evergreen forest		Sunderbans		Coastal	
	Indiv.	Group	Indiv.	Group	Indiv.	Group	Indiv.	Group
<i>Macaca mulatta</i>	7.00	0.34	7.85	0.40	17.05	1.58	—	—
<i>M. assamensis</i>	—	—	2.18	0.01	—	—	—	—
<i>M. nemestrina</i>	—	—	1.51	0.04	—	—	—	—
<i>M. fascicularis</i>	—	—	—	—	—	—	25.26	2.11
<i>Presbytis pileatus</i>	8.12	1.43	3.48	0.52	—	—	—	—
<i>P. phayrei</i>	—	—	2.42	0.18	—	—	—	—
<i>Hylobates</i>	?	—	1.06	0.40	—	—	—	—
<i>hoolock</i>	—	—	—	—	—	—	—	—
<i>Nycticebus</i>	?	—	?	—	—	—	—	—
<i>cougang</i>	—	—	—	—	—	—	—	—
Totals	15.12	1.77	18.50	1.55	17.05	1.58	25.26	2.11

? occasional records only

Primates of Sal Forest

Only *M. mulatta* and *Presbytis pileatus* have been reported from sal forest by earlier authors. We were able to note two more species, *N. cougang* and *H. hoolock*, present in the Kornojhura area of the Bali-jhuri Range in Mymensingh Division. It is quite likely that these primates and other forest wildlife such as the gaur, elephant and tiger, travel between the forests of Bangladesh and India.

Altogether, we recorded 36 sightings of primates in the sal forest. Overall density was 15.12 primates/km² and 1.77 groups/km². The density of *M. mulatta* and *P. pileatus* (Table 3), are significantly lower than those reported by Green (1978) and Akonda (1979). As far as we can determine, both authors collected their information in and around Madhupur National Park. This represents only a small fraction of the Madhupur Tracts and the foothills of the Garo Hills, where the forests have been degraded and the primates are sparsely distributed. The same is true for most sal forest areas of Dhaka, Tangail and Mymensingh Divisions, which are literally devoid not only of primates, but also of other mammals, like deer and wild boar.

We encountered only *M. mulatta* in the Sunderbans, where it occurred throughout at an average density of 1.58 groups/km², and 17.05 individuals/km².

The coastal forest in Cox's Bazaar Division, other than the Sunderbans, probably does not exceed 10 km². The only primate occurring there is *M. fascicularis*.

In non-forested areas, we contacted 538 individual *M. mulatta* in 32 groups, most of these (289 individuals, 19 groups) were from Dhaka District. The remainder were from Rajshahi (24 individuals, 3 groups), Faridpur (62 individuals, 2 groups), Barisal (63 individuals, 4 groups), Comilla (85 individuals, 3 groups), and Chittagong (13 individuals, 1 group) Districts. We also received reports of the presence of 5 additional groups in the Districts of Dhaka(2), Comilla(2) and Faridpur(1). *Presbytis entellus* were also seen in non-forested areas. We sighted 2 groups (7 individuals) in Kushtia, and 4 groups (38 individuals) in Jessore District. Information regarding another 10 groups occurring along the border belt of Kushtia and Jessore was received in 1982 (Wahab, pers. comm.).

Overall Primate Population

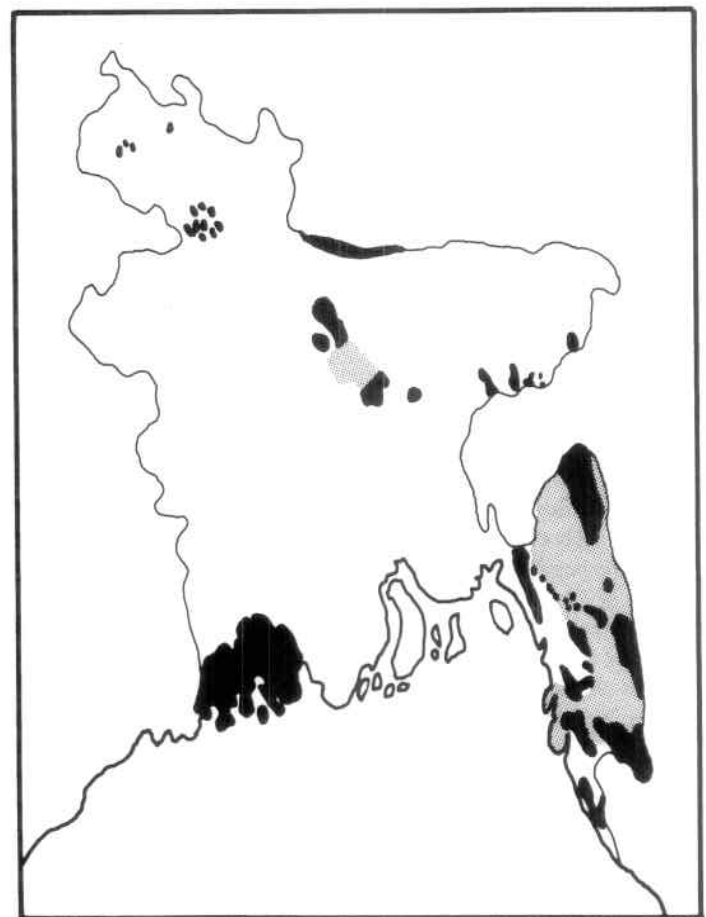
Based on areas of different forest types from Hendrichs (1975) and Green (1978), we have estimated the density of non-human primates in each forest type and the total numbers of primates in each forest (Table 3).

Table 4. Estimated Primate Population of Bangladesh

Forest type	Area of forest type/km ²	X Individuals/km ²	Total no. of primates
Sal forest	227.97	15.12	3,666
Evergreen forest	2,566.87	18.50	36,986
Sunderbans forest	4,071.00	17.05	88,442
Coastal forest	—	—	253
Non-forested areas	640 <i>M. mulatta</i> + 200 <i>P. entellus</i> = 840		
Total primate population of Bangladesh			130,187

* area quoted from Hendrichs (1975) and Green (1978)

The total estimated primate population of Bangladesh is 130,187 individuals. This can be compared with a similar estimates by Green (1978) of 140,00 and 126,025 by Khan and Ahsan (1981), and much higher estimates of 318,797 by Gittins (1980) and 318,200 by Gittins and Akonda (1982). We feel that major differences in estimates are due to problems in calculating total suitable primate habitat with remaining forested areas of Bangladesh. In addition, differences between the above-mentioned authors exist regarding density estimates of the different primate species in various forests. Green (1978) did not census the Sunderbans, the area which supports the highest number of primates.



MIXED FOREST & SCRUB

CONTINUOUS FOREST

Fig. 3. The remaining forested areas of Bangladesh (map by S. D. Nash based on authors' original).

Neither Gittins (1980) nor Gittins and Akonda (1982) censused the evergreen forests or the Chittagong Hill Tracts. These differences in sampling have also contributed to the discrepancies in total population estimates. Despite the fact that we repeatedly censused the Sunderbans, we are not yet satisfied with our estimates for this area.

Conclusion and Recommendations

Of all the forests in Bangladesh, the Sunderbans is the largest single tract and the most uniform with regard to floral composition. In addition, there are no human settlements in this forest type within Bangladesh, in contrast to the situation in India. The Bangladesh Sunderbans supports more primates than any other forest type (88,442 individuals), although only one species (*Macaca mulatta*).

We consider the entire *M. mulatta* population in the vicinity of villages and cities, to be very vulnerable. Many appear diseased and emaciated, and large numbers are or will be killed by local people because they are agricultural pests.

Since *Presbytis entellus* does not occur anywhere other than around villages and a few police stations in Jessore and Kushtia, we urge the Government Forest Department to protect this species. Efforts must be made to study this dwindling population before it is wiped out of Bangladesh.

The present Government ban on the export of the rhesus macaque and other non-human primates of Bangladesh is to be continued for at least another five years, during which time a proper survey is to be conducted to estimate the carrying capacity of all the major forest types of Bangladesh. This could be accomplished jointly by the Government Forest Department, the Department of Zoology at Dhaka University, and foreign assistance.

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Table 5. Plants Species of the Sunderbans

Species	Vernacular name
Trees and Shrubs	
<i>Lumnitzera racemosa</i>	kripa
<i>Heitiera fomes</i>	sundri
<i>Excoecaria agallocha</i>	gewa
<i>Sonneratia caceolaris</i>	ora
<i>S. apetala</i>	keora
<i>Avicennia alba</i>	sada ba-in
<i>A. officinalis</i>	ba-in
<i>Candelia candal</i>	goria
<i>Amoora cucullata</i>	amoor
<i>Xylocarpus molluccensis</i>	passur
<i>X. obovata</i>	dhundal
<i>Bicus retuse</i>	jir
<i>Aegiceras corniculatum</i>	khalshi
<i>Bruguera gymnorhiza</i>	kankra
<i>Cepiops decandra</i>	moth goran
<i>C. tagal</i>	goran
<i>Rhizophora apiculata</i>	garjan
<i>R. mucronata</i>	
<i>Syzygium fruticosum</i>	ban jam
<i>Brownlowia lanceolata</i>	sundrilata
<i>Pongamia pinnata</i>	karanj
<i>Thespesia populnea</i>	parash
Plants	
<i>Acanthus ilicifolius</i>	hargoza
<i>Acrostichum aureum</i>	hodo
<i>Hibiscus tiliaceus</i>	bola
<i>Phoenix paludosa</i>	hantal
<i>Nypa fruticans</i>	golpata
<i>Pandanus odoratissimus</i>	kewakanta
<i>Intsia bijuga</i>	bhadal
<i>Cynometra ramiflora</i>	singra
<i>C. mimisoides</i>	
<i>Cerbera manghas</i>	dacor
<i>Aegialitis rotundifolia</i>	tora
<i>Drypetes assamicus</i>	ban bakul
<i>Paramignya longispica</i>	ban nebu
<i>Sapium indicum</i>	bauul
<i>Diospyros peregrina</i>	gab
<i>Barringtonia racemosa</i>	hijol
<i>Tamarix</i> sp.	nona jhao
<i>Tamarindus indica</i>	tentul

Climbers

Entada pursaetha
Derris sinuata
D. uliginosa
Dendrophoe falcata
Mezoneuron cucullatum
Potypodium irioides
Sacrolobus globosus

S. carinatus

Grasses

Phragmites karka
Imperata cylindrica
Typa elephantina

Table 6. Tree Species of the Madhupur Tract

Species	Vernacular name
Upper Canopy	
<i>Adina cordifolia</i>	kaika
<i>Albizia procera</i>	koroi
<i>A. lebbeck</i>	
<i>A. chinensis</i>	
<i>Anthocephalus indicus</i>	kadam
<i>Bridelia retusa</i>	kanta koroi
<i>Dillenia pentagyna</i>	ajilu
<i>Lagerstroemia speciosa</i>	jarul
<i>Ficus benghalensis</i>	bot
<i>F. religiosa</i>	ashwatha
<i>Syzygium cumini</i>	jam
<i>Terminalia belerica</i>	bahera
<i>T. chebula</i>	haritoki
Middle Canopy	
<i>Azadirachta indica</i>	neem
<i>Bauhinia variegata</i>	kanchan
<i>Cassia fistula</i>	sonalu
<i>C. siamea</i>	minjiri
<i>Careya arborea</i>	kumbhi
<i>Mangifera indica</i>	um
<i>Spondias mangifera</i>	ampa
<i>Phyanthus emblica</i>	amloki
<i>Zizyphus rugosa</i>	banboroi
<i>Mallotus philippensis</i>	sinduri
<i>Saraca indica</i>	ashoka
<i>Streblus asper</i>	sheora
<i>Diospyros peregrina</i>	cab
<i>Garuga pinnata</i>	mahaneen
Lower Canopy/Lianas	
<i>Spatholobus roxburghii</i>	
<i>Entada pursaetha</i>	gila
<i>Zizyphus oenoplia</i>	
<i>Smilax aspera</i>	kumarika
<i>S. macrophylla</i>	" "
<i>Dioscorea</i> sp.	gach alu
<i>Acacia nilotica</i>	babul
<i>Wrightia tinctoria</i>	
<i>Hollarrhoena antidysenterica</i>	
<i>Microcos paniculata</i>	
<i>Woodfordia fruticosa</i>	
<i>Lantana camara</i>	
<i>Eupatorium odoratum</i>	
<i>Bambusa</i> sp.	
<i>Saccharum</i> sp.	
<i>Curcurum zedoaria</i>	sotthi
<i>Chrysopogon</i> sp.	

Table 7. Tree Species of Evergreen, Semi-evergreen and Deciduous Forests

Species	Vernacular name
Upper Canopy (30-50 m)	
<i>Dipterocarpus</i> spp.	garjan
<i>Artocarpus chaplasha</i>	chopalish
<i>Pterygota alata</i>	Buddha narikel
<i>Tetrameles nudiflora</i>	chundul
<i>Swintonia floribunda</i>	civit
<i>Hopea odorata</i>	telsur

<i>Bombax ceiba</i>	shimul
<i>Bursera serrata</i>	gutgutia
<i>Aphanamixis polystachya</i>	pitraj
<i>Acrocarpus fraxinifolius</i>	
<i>Toona ciliata</i>	toon
<i>Albizia</i> spp.	koro
<i>Duabanga grandiflora</i>	bandarholla

Second Story (15-20 m)

<i>Quercus</i> spp.	batna
<i>Syzygium</i> spp.	jam
<i>Amoora wallchi</i>	rata
<i>Mesua ferrea</i>	nageshwar
<i>Calophyllum polyanthum</i>	kamdeb
<i>Palaquium polyanthum</i>	tali
<i>Artocarpus lakoocha</i>	lakooch
<i>Lophopetalum wightianum</i>	raktan
<i>Mangifera longipes</i>	uriam
<i>Lannea coromandelica</i>	bhadi/jiol
<i>Lagerstroemia</i> spp.	jarul
<i>Trewia polycarpa</i>	pitali
<i>Gmelia arborea</i>	gamar
<i>Pterospermum acerifolium</i>	konak champa
<i>Stericula villosa</i>	
<i>Ficus</i> spp.	
<i>Terminalia</i> spp.	
<i>Dillenia pentagyna</i>	ajuli

Third Story (7-15 m)

saplings of species of the upper two canopies plus:

<i>Quercus</i> spp.
<i>Syzygium</i> spp.
<i>Vitex glabrata</i>
<i>Saraca indica</i>
<i>Mallotus philippensis</i>
<i>Macaranga</i> sp.
<i>Castanopsis indica</i>
<i>Meliosma pinnata</i>
<i>Garcinia</i> spp.
<i>Glochidion</i> spp.
<i>Cordia myxa</i>
<i>Elaeocarpus</i> spp.
<i>Streblus asper</i>

Undergrowth

<i>Meloanna bambusoides</i>	muli
<i>Burmusa tulda</i>	mitinga
<i>Bambusa teras</i>	parua
<i>Teinostachyum griffithi</i>	dalul bansh
<i>Neohouzeaua dulloo</i>	dalul
<i>Melocalamus compactiflorus</i>	daral
<i>Oxytenanthera nigrifolia</i>	kali
<i>O. auriculata</i>	
<i>Dendrocalamus longispatus</i>	bans
<i>Alsophila</i> sp.	tree fern
<i>Geodorum</i> sp.	ground orchid
<i>Daemonorops jenkinsianus</i>	galla bet
<i>Calamus latifolius</i>	hyna bet
<i>C. gurbu</i>	sundi bet
<i>C. tenuis</i>	sanchi bet
<i>C. flagellum</i>	
<i>Lantana camara</i>	
<i>Eupatorium odoratum</i>	

Creepers, Lianas and Epiphytes

<i>Tinospora cordifolia</i>
<i>Vitis</i> spp.
<i>Spatholobus roxburghii</i>
<i>Entada pursaetha</i>
<i>Derris</i> sp.
<i>Bauhinia</i> sp.
<i>Ipomoea</i> sp.

<i>Passiflora</i> spp.
<i>Vanda</i> spp.
<i>Dendrobium</i> spp.
<i>Viscum</i> sp.
<i>Dendrophoe falcata</i>
<i>Mikania cordata</i>

Table 8. Plant Species of Non-forested Areas in Bangladesh Listed in Order of Frequency

Species	Vernacular name
<i>Azadirachta indica</i>	neem
<i>Syzygium cumini</i>	kalo jam
<i>S. jambos</i>	golab jam
<i>Musa</i> spp.	kola
<i>Bambusa</i> spp.	bansh
<i>Dendrocalamus</i> sp.	
<i>Zizyphus mauritania</i>	boroi kul
<i>Diospyros peregrina</i>	gab
<i>Albizia lebeck</i>	siris
<i>A. procera</i>	sil koro
<i>A. richardiana</i>	belari/Richard's koro
<i>Bombax ceiba</i>	shimul
<i>Erythrina ovalifolia</i>	mandar
<i>E. variegata</i>	
<i>Lannea coromandelica</i>	jiol
<i>Cassia fistula</i>	sonalu/bandar lathi
<i>C. siamea</i>	minjiri
<i>Phoenix sylvestris</i>	khajur
<i>Borassus flabellifer</i>	tal
<i>Cocos nucifera</i>	narikel/dab
<i>Areca catechu</i>	supari
<i>Chukrasia tabularis</i>	chikrashi
<i>Trewia polycarpa</i>	pitali
<i>Crataeva nurvula</i>	baruna
<i>Cordia myxa</i>	bowla gota
<i>Salicocnea</i> sp.	panibaj gach
<i>Barringtonia racemosa</i>	hijol
<i>Acacia nilotica</i>	babla
<i>Psidium guajava</i>	piara
<i>Litchi chinensis</i>	litchu
<i>Euphoria longana</i>	ashphal
<i>Spondias dulcis</i>	amra
<i>Pithecellobium dulce</i>	ban tentul
<i>Dalbergia sissoo</i>	shissoo
<i>Swietenia mahagoni</i>	mahogany
<i>Anthocephalus chinensis</i>	kadam
<i>Polyalthia longifolia</i>	debdaro
<i>Delonix regia</i>	krishnochura
<i>Caesalpinia pulcherrima</i>	radhachura
<i>Murraya paniculata</i>	kamini
<i>Sesbania grandiflora</i>	bok phool
<i>Ficus benghalensis</i>	bot
<i>F. religiosa</i>	ashwatha
<i>F. hispida</i>	dumur/khiksa
<i>F. racemosa</i>	jaga dumur
<i>Streblus asper</i>	shorea
<i>Trema orientalis</i>	jinal
<i>Annona reticulata</i>	non phal
<i>A. squamosa</i>	ata phal
<i>Tamarindus indica</i>	tentul
<i>Terminalia arjuna</i>	arjun
<i>Phyllanthus emblica</i>	amlaki
<i>Averrhoa carambola</i>	karanga
<i>Zanthoxylum rhetsa</i>	bajna
<i>Mimusops elengi</i>	bakul
<i>Alstonia scholaris</i>	satim
<i>Enterolobium saman</i>	rendi koro
<i>Peltophorum pterocarpum</i>	halud krishnachura
<i>Bauhinia</i> spp.	kanchan
<i>Gliricidia sepium</i>	madder tree
<i>Butea monosperma</i>	palash

Primate Postage Stamps and Primate Conservation

The purpose of this paper is to examine briefly the significance of the increasing numbers of stamps on primates in regards to the preservation of the wild species in their natural habitats. We believe that the trends witnessed in stamps on primates can be duplicated for other species of animals as well, and that the changes in the way primates, at least, are now illustrated are a direct result of new data gathered by both behaviorists and conservationists, based on recent field research. The survey of primate stamps which we have undertaken to date lists some 500 different issues representing over 100 identifiable genera and species.

In order to illustrate these points, to further encourage an interest in primates, especially those endangered by the encroachment of man on their natural habitats, and to update the last checklist of mammals (Wagner and Stanley, 1973) published by the American Topical Association, we offer Table 3, a systematic list of primate stamps including the various countries of issue, and Table 4, a list of primate stamps published by country. (The numbers are primarily Scott's Catalog. Minkus numbers are followed by M. In the case of some Arab states, the only numbers of record are in the Official Trucial States Stamp Catalog, by M. Carus, 1976. These will be followed by TS. Dashes indicate no number on record.)

Table 1. Percentage Issues of Primate Stamps Worldwide

Area	# of Countries	# of Types of Mammal Stamps	# of Types of Primate Stamps		% of Primate Stamps to Total		% Increase
			1982	1985	1982	1985	
South & Central America	18	153	6	38	3.9	20.5	630%
Africa	50	1010	82	288	8.7	23.8	327%
Asia	23	323	24	92	7.4	23.5	383%

The adjusted percentages of primate stamps to the total collection of stamps on mammals in general is less than 10 percent in most areas; however, in some instances in certain countries, much higher ratios are achieved.

In reviewing the number of genera and species of primates now on stamps, the range and diversity of these animals is indicative of the increasing expression of interest by the issuing governments to bring to light the ever diminishing wild fauna of the world. In fact, a number of stamps carry titles demonstrating concern for the preservation of specific species, such as:

Jersey - 51, 52, 218, 220 - Wildlife Preservation Trust;
 Lesotho - 232 - World Wildlife Fund;
 French West Africa - 62 - Protection de la Nature;
 Ghana - 621, 625 - World Wildlife Fund;
 Ivory Coast - 210 - Reserve de Bouna;
 Peru - C411, C412 - Fauna Protegida;
 Madagascar - C67, C68, 321, 322, 323, 450 - Protection de la Faune;
 Equatorial Guinea - 753 - Endangered species;
 Mali - 318 - Endangered wildlife;
 Central Africa - 323, 328 - Endangered animals;
 Kenya - 92 - Endangered species.

The majority of the listing, with certain exceptions, represents primates in their natural surroundings and are issued by countries within whose

borders these animals may be found, yet it is of interest to note that specific countries such as Japan, India and Brazil, whose fauna include unique primates, have issued only a few stamps commemorating them. In general, primate stamps are relatively infrequent throughout South and Central America when compared to countries in Africa and Asia, although this situation has improved within the past few years. The vast majority of the non-human primate stamps (over 90% for the African sample) were issued after 1960, which is the approximate date of the commencement of the major field studies of the non-human primates by behaviorists representing several different biological disciplines (Ribnick, 1982).

Table 2. Percentage Issues of Primate Stamps from Selected Nations

Country	# of Types of Primate Stamps		% Increase
	1982	1985	
Malagasy Republic	10	43	430%
North Borneo	10	18	180%
Central Africa Rep.	5	10	200%
Rwanda	14	27	193%

When one compares the kind of stamps produced, it is reasonable to credit the behavior studies with influencing the manner in which primates themselves were depicted. For instance, the government of Gabon in 1964 issued a stamp (No. 173) of the gorilla which emphasized the ferocious nature of the animal, an idea which had persisted from travelers' tales and other folklore stemming back to the time of exploration of the continent by the early European explorers. Later dated issues of stamps of gorillas and chimpanzees by other governments de-emphasized aggression, recreating scenes of play groups (Rwanda, 1970:359; Republic of Guinea, 1969:534; 1977:753), mother-infant bonds (Rwanda, 1970:363, 366) and feeding (Fujeira, 1971), behavior which has been shown to be much more important by the behaviorists in the daily patterns of these animals. It is tempting to suggest that these studies played an important role influencing many governments to recognize the issues and problems facing them in terms of the preservation of the native primate species, an interest which was then, in part, translated into the production of new stamps.

It is our belief that one positive result of the proliferation of stamps on mammals in general, and probably the intent of the governments of the various issuing countries, is to broaden public interest in natural fauna as part of the national heritage. This may well be true for such entities as Jersey, where the non-human primates are not part of the native fauna, but interest in the preservation of many endangered species remains a strong concern. As Stephen Gartlan (1979) has recently remarked; "The situation for primates and their forest habitats is dismal, even desperate, in many parts of their range. But there are opportunities to ameliorate the situation; we need to identify the needs, the areas, the agencies involved, to offer our assistance and expertise, and to bring pressure to bear where this seems warranted."

It will be difficult to assess exactly what impact the increasing number of stamps advertising the behavior and conservation of different animal groups will have on the general public. However, stamp collecting, especially among young individuals, is well known to be an important hobby and thus we might expect an increasingly favorable and positive reaction in support of the conservation movement over time as a result. It is our belief that conservationists should encourage government participation at this level, as it is certainly one area where the efforts for both are mutually advantageous. In regard to the worldwide conservation movement, the advertisement of the dilemma of certain animal species is not only printed at the expense of the issuing government, but



Fig. 1. A selection of primate stamps (photos provided by authors).

distributed as well through the large and efficient international postal service. On the other hand, those governmental agencies involved in the production of stamps, even if they have no direct interest in the conservation problem, have had laid upon them an issue which has the potential of being highly popular and saleable. Increased sales, of course, would translate into increased revenues for general administrative purposes, some of which would include the funding of national parks and game reserves dedicated to the conservation of those very species now endangered.

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Wagner, R., and W. Stanley 1973. *Mammals of the World on Stamps*. Milwaukee, American Topical Association. Handbook No. 79, 6-8.

Table 3. Primate Species Depicted in Stamps of the World

Family: Pongidae

Gorilla gorilla

Belgium Congo — (310); Burundi — (9, 13, 359a, C150a, CB17a); Cameroun — (656, 747); Central African Republic — (328); Congo Democratic Republic — (347); Congo People's Rep. — (272); Czechoslovakia — (2380); Fújeira — (235M); Gabon — (173, C215); Guinea-Bissau — (458, 568); Japan — (1487, 1487a); Jersey — (220); Liberia — (768); Rio Muni — (20); Ruanda-Urindi — (137, 141); Rwanda — (9, 60, 359, 360, 361, 362, 363, 364, 365, 366, 858, 1158, 1159, 1160, 1161, 1162, 1163, 1164, 1165, 5- no#s); Um al Qiwaín — (387M); Uganda — (285); Equatorial Guinea — (no#).

Pan troglodytes

Aden Q State — (no#); Ajman State — (no#); Angola — (691); Benin — (441); Bulgaria — (1487); Burundi — (358a, 518d, C259d); Columbia — (879a); Congo People's Rep. — (456); Cuba — (no#); Czechoslovakia — (1112); Equatorial Guinea — (1122M, 1069); French West Africa — (62); Fújeira — (729M, 732M, 732aM, 1229M); Gabon — (206); Ghana — (788); Guinea — (531, 532, 533, 534, 753, 685, 688a, C140); Guinea-Bissau — (461); Hadramud — (no#); Ivory Coast — (533); Liberia — (048, 103, 454, 765); Mali — (318); Mongolia — (707); Niger — (C202); Oman — (no#); Poland — (1891); Rwanda — (857); Senegal — (523, 523a); Sharjah — (943M); Sierra Leone — (586, 587, 588, 589); Tanzania — (203); Togo — (C318, C320a); Um al Qiwaín — (979TS)

Pan paniscus

Belgium Congo — (B29); Congo Democratic Rep. — (739); Congo People's Rep. — (275).

Pongo pygmaeus

Ajman State — (2789TS, 2608TS); Comoro Is. — (311M); Equatorial Guinea — (1117M); Germany (Berlin) — (9N275a); Germany D.R. — (1631); Fújeira — (1228M); Indonesia — (475); Jersey — (218); Labuan — (96, 97, 123, J3); Malaysia — (182); North Borneo — (103, 104, 108, 186, 199, 211, 214, 229, 292, J13, J23, N7, N22, N22a); Sarawak — (198, 216); Singapore — (202); Um al Qiwaín — (1238TS); Equatorial Guinea — (no #)
Ajman State — (2786TS)

Hylobates agilis

Hylobates concolor
Hylobates lar

Hylobates moloch
Hylobates sp.

Family: Cercopithecidae

Subfamily: Colobinae

Colobus abyssinicus

Colobus badius

Colobus guereza

Colobus kirkii

Colobus polykomos

Colobus p. angolensis

Colobus p. satanas

Colobus ursinus

Colobus verus

Colobus sp.

Nasalis larvatus

Presbytis cristata

Presbytis francoisi

Presbytis geei

Presbytis obscura

Presbytis rubicunda

Rhinopithecus roxellanae

Subfamily: Cercopithecinae

Cercocebus albigena

Cercocebus torquatus

Cercocebus sp.

Cercopithecus aethiops

Cercopithecus albogularis

Cercopithecus cephus

Cercopithecus diana

Cercopithecus erythrotis

Cercopithecus hamlyni

Cercopithecus lhoesti

Cercopithecus mitis

Cercopithecus mona

Cercopithecus neglectus

Cercopithecus nictitans

Cercopithecus pygerythrus

Cercopithecus sabaeus

Erythrocebus patas

Papio hamadryas

North Vietnam — (no#)

Laos — (C60); Poland — (1892); Thailand — (1017).

Equatorial Guinea — (1126M)

North Vietnam — (no#); Singapore — (156).

Congo Democratic Rep. — (312, 347); Bophuthatswana — (10M); Burundi — (11, 15); Ethiopia — (C104); Fújeira — (1224M); German Democratic Rep. — (553); Guinea-Bissau — (462); Ivory Coast — (671); Ruanda-Urindi — (139, 143); Rwanda — (58, 61)

Ajman State — (2784TS); Fújeira — (1227M); Kenya — (92, 92a); Tanzania — (85, 86a); Uganda — (179, 180a)

Equatorial Guinea — (1116M); Rwanda — (859); Um al Qiwaín — (no#)

Central Africa — (146)

Ivory Coast — (210); Congo Democratic Rep. — (743); Rwanda — (444); Sharjah — (no#)

Burundi — (482c, C221c)

Ajman State — (no#); Cameroun — (718); Ivory Coast — (210, 210a)

Jersey — (51)

Ghana — (621, 625); Ivory Coast — (529); Togo — (C317, 1425)

Austria — (580)

Indonesia — (1014); North Borneo — (196, 211, 226, N4, N19)

Cambodia — (C19, C20, C21, C22, C23 stylized); Laos — (C15, C16); Thailand — (1020)

North Vietnam — (no#)

Bhutan — (713, 714, 715, 716); India — (1029)

Equatorial Guinea — (1118M); Ras al Khaima — (657)

Ajman State — (2315TS, 2787TS)

People's Rep. of China — (713, 714, 715); Nigeria — (450)

Equatorial Guinea — (1121M); Gabon — (264)

Congo Democratic Rep. — (740); Gabon — (330);

Ghana — (892); Paraguay — (2131M)

Kenya — (202)

Afars and Issas — (401); Central Africa — (C180); Congo Democratic Republic — (735); Kenya — (33); Liberia — (575); Rwanda — (863); Zambia — (no#)

Zambia — (no#)

Cameroun — (358, 365, 368); Congo Democratic Rep. — (736); Fernando Po — (241, 243); Gabon — (331)

Ajman State — (2545TS); Congo Democratic Rep. — (742); Guinea-Bissau — (463); Liberia — (288); Sharjah — (941M)

Guinea-Bissau — (570); Spanish Guinea — (335, 343)

Congo Democratic Rep. — (741)

Congo Democratic Rep. — (744)

Zambia — (no#)

Gabon — (332); Ghana — (451); Grenada — (305); St. Thomas — (no#); Rwanda — (861)

Ajman State — (2788TS); Congo Democratic Rep. — (737); Congo People's Rep. — (274)

Fernando Po — (240, 242)

Kenya — (33); Southwest Africa — (465)

Ajman State — (2785TS); Fújeira — (731M); St. Kitts-Nevis — (350, 351, 352, 353); Upper Volta — (152); Zaire — (852)

Central Africa Rep. — (B7); Mauritania — (142) Fújeira — (728M); Yemen Rep. — (no#); Guinea-Bissau — (457); Um al Qiwaín — (978TS)

<i>Papio cynocephalus</i>	Congo Democratic Rep. — (738); Rwanda — (105, 864); Upper Volta — (651)	<i>Lepilemur mustelinus</i>	Madagascar — (C117, 502)
<i>Papio anubis</i>	Afar-Issas — (C94); Dahomey — (255); Ethiopia — (C94); Guinea — (512, 514a); Liberia — (709); Oman — (no#); Sharjah — (944M); Togo — (472, 784, 804)	<i>Microcebus murinus</i>	Madagascar — (667)
<i>Papio papio</i>	Mauritania — (137)	<i>Varecia variegata</i>	Madagascar — (322, 668)
<i>Papio ursinus</i>	Bophuthatswana — (7M); Equatorial Guinea — (1131M); Lesotho — (61, 460, 232, 352, 400); Manama — (1422TS); Southwest Africa — (466); Swaziland — (167); Zambia — (no#)	Family Indriidae	
<i>Papio sp. indet.</i>	Chad — (C126); Czechoslovakia — (1770); Yemen — (336M); Togo — (C451)	<i>Indri indri</i>	Madagascar — (C68, C70, C90); Comoro Is. — (312M); Um al Qiwain — (1150TS)
<i>Theropithecus gelada</i>	Equatorial Guinea — (1127M); Ethiopia — (734); Guinea-Bissau — (459)	<i>Propithecus diadema</i>	Madagascar — (C67)
<i>Mandrillus sphinx</i>	Burundi — (480a, C219a, C225a); Central Africa — (C263); Chad — (C122); Cuba — (no#); Guinea-Bissau — (460); Poland — (2307); Rio Muni — (B7, B9); Russia — (5226); Sharjah — (940M)	<i>Propithecus verreauxi</i>	Madagascar — (C69, 669)
<i>Macaca arctoides</i>	north Vietnam — (no#)	Family: Daubentoniidae	
<i>Macaca cyclopis</i>	Formosa — (1716, 2179)	<i>Daubentonia</i>	Ajman State — (2536TS); Comoro Is. — (323M);
<i>Macaca fascicularis</i>	Philippines — (1404)	<i>madagascariensis</i>	Madagascar — (450, 666)
<i>Macaca fuscata</i>	Ajman State — (2549TS); Equatorial Guinea — (1129M); Japan — (1136)	Family: Lorisidae	
<i>Macaca mulatta</i>	Afghanistan — (754); Equatorial Guinea — (1128M); Fujiera — (730M); Um al Qiwain — (no#)	<i>Arctocebus calabarensis</i>	Central African Rep. — (144)
<i>Macaca nemestrina</i>	Equatorial Guinea — (1123M); Thailand — (1018)	<i>Loris tradigradus</i>	Ceylon — (440)
<i>Macaca philippinensis</i>	Philippines — (1404)	<i>Nycticebus coucang</i>	Malaysia — (297); Thailand — (1019)
<i>Macaca silenus</i>	India — (1030)	<i>Nycticebus pygmaeus</i>	north Vietnam — (no#)
<i>Macaca sylvanus</i>	Ajman State — (2549TS); Algeria — (673); Equatorial Guinea — (1124M); Fujiera — (1225M); Gibraltar — (156)	Family: Galagidae	
<i>Miopithecus talapoin</i>	Ajman State — (no#); Mozambique — (559); Spanish Guinea — (B36)	<i>Galago crassicaudatus</i>	Belgium Congo — (309)
Family: Cebidae		<i>Galago demidovii</i>	Ghana — (849)
<i>Alouatta caraya</i>	Ajman State — (2380TS); Guyana — (329b)	<i>Galago elegantulus</i>	Central Africa Rep. — (143); Fernando Po — (249)
<i>Alouatta seniculus</i>	Peru — (818)	<i>Galago inustus</i>	Rwanda — (860)
<i>Aotus trivirgatus</i>	Cuba — (no#); Equatorial Guinea — (1125M); Paraguay — (no#)	<i>Galago senegalensis</i>	Central Africa Rep. — (142); Kenya — (23); Malawi — (259, 262a); Mozambique — (555); Rwanda — (860); Somalia — (445); Togo — (1426); Uganda — (282); Um al Qiwain — (1232TS)
<i>Ateles geoffroyi</i>	Columbia — (715); Costa Rica — (C823); Salvador — (739, C485); Sharjah — (939M)	<i>Perodicticus potto</i>	
<i>Ateles sp.</i>	Austria — (580)	Central Africa Rep. — (145); Congo People's Rep. — (273); Ivory Coast — (202); Madagascar — (671); Manama — (575TS); Oman — (no#); Rio Muni — (68); Rwanda — (862)	
<i>Brachyteles arachnoides</i>	Brazil — (1926, 1927)	Family: Tarsiidae	
<i>Cacajao rubicundus</i>	Equatorial Guinea — (1130M); Peru — (C411, C412)	<i>Tarsius bancanus</i>	Sarawak — (181)
<i>Callicebus moloch</i>	Equatorial Guinea — (1119M)	<i>Tarsius syrichta</i>	Philippines — (1006); Manama — (1420TS)
<i>Callicebus torquatus</i>	Paraguay — (no#); Venezuela — (828)		
<i>Cebus albifrons</i>	Equatorial Guinea — (1120M)		
<i>Cebus capucinus</i>	Costa Rica — (C360); Panama — (498); Peru — (no#)		
<i>Lagothrix lagothricha</i>	Um al Qiwain — (966TS)		
<i>Pithecia pithecia</i>	Ajman State — (2579TS)		
<i>Saimiri oerstedii</i>	Ajman State — (2539TS)		
<i>Saimiri sciureus</i>	Guyana — (329c); Suriname — (363)		
Family: Callitrichidae			
<i>Callithrix aurita</i>	Fujeira — (1226M); Paraguay — (1670M)		
<i>Leontopithecus chrysomelas</i>	Jersey — (320)		
<i>Leontopithecus rosalia</i>	Brazil — (1439); Sharjah — (942M)		
<i>Saguinus sp.</i>	Ajman State — (2383TS)		
Family: Lemuridae			
<i>Cheirogaleus major</i>	Madagascar — (C118, 501)		
<i>Haplemur griseus</i>	Madagascar — (321)		
<i>Lemur catta</i>	Jersey — (52); Korea — (no#); Madagascar — (C60, 594)		
<i>Lemur macaco</i>	Madagascar — (595, C173)		
<i>Lemur mongoz</i>	Madagascar — (323)		
<i>Lemur sp.</i>	Madagascar (63-77, 119-124, 129, 383)		
		Algeria	673
		Angola	691
		Austria	580

Table 4. Countries and Their Primate Stamps

Country	Number	Nomenclature
Aden Q-state	—	<i>Pan troglodytes</i>
Afars-Issas	401	<i>Cercopithecus aethiops</i>
	C94	<i>Papio anubis</i>
Afghanistan	754	<i>Macaca mulatta</i>
Ajman State	2315TS	<i>Presbytis rubicundus</i>
	2379TS	<i>Pithecia pithecia</i>
	2380TS	<i>Alouatta caraya</i>
	2383TS	<i>Saguinus sp.</i>
	2536TS	<i>Daubentonia madagascariensis</i>
	2539TS	<i>Saimiri oerstedii</i>
	2541TS	<i>Macaca fuscata</i>
	2545TS	<i>Cercopithecus diana</i>
	2549TS	<i>Macaca sylvanus</i>
	2608TS	<i>Pongo pygmaeus</i>
	2784TS	<i>Colobus badius</i>
	2785TS	<i>Cercopithecus sabaeus</i>
	2786TS	<i>Hylobates agilis</i>
	2787TS	<i>Presbytis rubicundus</i>
	2788TS	<i>Cercopithecus neglectus</i>
	2789TS	<i>Pongo pygmaeus</i>
	—	<i>Cercopithecus talapoin</i>
	—	<i>Pan troglodytes</i>
	—	<i>Colobus p. satanas</i>
	—	<i>Cercopithecus aethiops</i>
	—	<i>Saimiri sciureus</i>
	—	<i>Macaca sylvanus</i>
	—	<i>Pan troglodytes</i>
	—	<i>Colobus sp.</i>

Country	Number	Nomenclature	Country	Number	Nomenclature
Belgian Congo	309	<i>Galago crassicaudatus</i>		C321	unident., C247 surch.
	310	<i>Gorilla g. gorilla</i>		C340	unident., C247 surch. & ovpt.
	312	<i>Colobus abyssinicus</i>		C615	unident. monkeys (4) in forest
	B29	<i>Pan paniscus</i>	Comoro Islands	879a	<i>Pan troglodytes</i>
Belgium	752	unident. monkey and buildings		311M	<i>Pongo pygmaeus</i>
Benin	441	<i>Pan troglodytes</i>		312M	<i>Indri indri</i>
	550	unident. monkeys holding jar		323M	<i>Daubentonia madagascariensis</i>
Bhutan	713-6	<i>Presbytis geei</i> (4)	Congo, Demo. Republic	344	Congo. ovpt. on Belg. Congo 309
Bophuthatswana	7M	<i>Papio ursinus</i>		345	Congo. ovpt. on Belg. Congo 310
	10M	<i>Colobus abyssinicus</i>		347	Congo. ovpt. on Belg. Congo 312
Brazil	1439	<i>Leontopithecus rosalia</i>		735	<i>Cercopithecus aethiops</i>
	1926-27	<i>Brachyteles arachnoides</i>		736	<i>Cercopithecus cephus</i>
Brunei	316	unident. monkey		737	<i>Cercopithecus neglectus</i>
Bulgaria	1487	<i>Pan troglodytes</i>		738	<i>Papio cynocephalus</i>
Burundi	9	<i>Gorilla g. berengei</i>		739	<i>Pan paniscus</i>
	11	<i>Colobus abyssinicus</i>		740	<i>Cercocebus torquatus</i>
	13	<i>Gorilla g. berengei</i>		741	<i>Cercopithecus hamlyni</i>
	15	<i>Colobus abyssinicus</i>		742	<i>Cercopithecus diana</i>
	358a	<i>Pan troglodytes</i>		743	<i>Colobus polykomos</i>
	359a	<i>Gorilla g. graueri</i>		744	<i>Cercopithecus lhoesti</i>
	480a	<i>Mandrillus sphinx</i>	Congo, Peop. Republic	272	<i>Gorilla g. berengei</i>
	482c	<i>Colobus p. angolensis</i>		273	<i>Perodicticus potto</i>
	518d	<i>Pan troglodytes</i>		274	<i>Cercopithecus neglectus</i>
	C149a	<i>Pan troglodytes</i>		275	<i>Pan paniscus</i>
	C150a	<i>Gorilla g. graueri</i>	Costa Rica	456	<i>Pan troglodytes</i>
	C219a	<i>Mandrillus sphinx</i>		C360	<i>Cebus capucinus</i>
	C221c	<i>Colobus p. angolensis</i>		C823	<i>Ateles geoffroyi</i>
	C225a	<i>Mandrillus sphinx</i>	Czechoslovakia	1112	<i>Pan troglodytes</i>
	C259d	<i>Pan troglodytes</i>		1770	<i>Papio</i> , sp. and tiger
	CB17a	<i>Gorilla g. graueri</i>		2380	<i>Gorilla gorilla</i>
Cambodia	C19-23	Hanuman Monkey God	Cuba	—	<i>Pan troglodytes</i> (1964)
	C24-27	C19-22 with surcharge		—	<i>Aotus trivirgatus</i> (1969)
Cameroun	358	<i>Cercopithecus cephus</i>		—	unident. monkey (1971)
	365	<i>Cercopithecus cephus</i>		—	<i>Mandrillus sphinx</i>
	368	<i>Cercopithecus cephus</i>		—	<i>Pan troglodytes</i> (1979)
	495	unident. monkey and vulture	Dahomey	255	<i>Papio anubis</i>
	656	<i>Gorilla g. gorilla</i>		1069	<i>Pan troglodytes</i>
	718	<i>Colobus p. satanas</i>	Equatorial Guinea	1116M	<i>Colobus guereza</i>
	747	<i>Gorilla g. gorilla</i>		1117M	<i>Pongo pygmaeus</i>
Central African Republic	142	<i>Galago senegalensis</i>		1118M	<i>Presbytis obscura</i>
	143	<i>Galago elegantulus</i>		1119M	<i>Callicebus moloch</i>
	144	<i>Arctocebus calabarensis</i>		1120M	<i>Cebus albifrons</i>
	145	<i>Perodicticus potto</i>		1121M	<i>Cercocebus albigena</i>
	146	<i>Colobus kirkii</i>		1122M	<i>Pan troglodytes</i>
	172	unident. monkey in clock face		1123M	<i>Macaca nemestrina</i>
	328	<i>Gorilla g. gorilla</i>		1124M	<i>Macaca sylvanus</i>
	450	<i>Pan troglodytes</i>		1125M	<i>Aotus trivirgatus</i>
	B7	<i>Erythrocebus patas</i>		1126M	<i>Hylobates moloch</i>
	C180	<i>Cercopithecus aethiops</i>		1127M	<i>Theropithecus gelada</i>
	C263	<i>Mandrillus sphinx</i>		1128M	<i>Macaca mulatta</i>
Sri Lanka	440	<i>Loris tardigradus</i>		1129M	<i>Macaca fuscata</i>
	C122	<i>Mandrillus sphinx</i>		1130M	<i>Cacajao rubicundus</i> and <i>Cacajao calvus</i>
Chad	C126	<i>Papio</i> sp.		1131M	<i>Papio ursinus</i>
	1716	<i>Macaca cyclopis</i>		1514M	<i>Macaca</i> sp.
China, Taiwan	1926B	monkey and man		1518M	<i>Nycticebus coucang</i>
	1929	monkey, man, children		—	<i>Pongo pygmaeus</i>
	1952	monkeys and deer		—	<i>Gorilla</i> sp.
	2179	<i>Macaca cyclopis</i>	Ethiopia	734	<i>Theropithecus gelada</i>
	2180	<i>Macaca cyclopis</i>		C104	<i>Colobus abyssinicus</i>
China, P.R.	713	<i>Rhinopithecus roxellanae</i>	Fernando Po	240	<i>Cercopithecus nictitans</i>
	714	<i>Rhinopithecus roxellanae</i>		241	<i>Cercopithecus cephus</i>
	715	<i>Rhinopithecus roxellanae</i>		242	<i>Cercopithecus nictitans</i>
	1547-54	unident. monkey king		243	<i>Cercopithecus cephus</i>
	1586	stylized monkey, 1980 New Year		249	<i>Galago elegantulus</i>
	1607b	unident. monkey, fox, hare	French West Africa	62	<i>Pan troglodytes</i> head
	1607c	unident. monkey, lion, hare		235M	<i>Gorilla gorilla</i> ssp.
	1607d	unident. monkey, lion, hare	Fujeira	728M	<i>Papio hamadryas</i>
	1853	unident. monkey		729M	<i>Pan troglodytes</i>
Columbia	715	<i>Ateles paniscus</i>		730M	<i>Macaca mulatta</i>
	C413	<i>Ateles paniscus</i> , 715 surcharged		731M	<i>Cercopithecus sabaeus</i>
	C247	unident. monkey fountain		732M	<i>Pan troglodytes</i>
				732aM	<i>Pan troglodytes</i>

Country	Number	Nomenclature
Gabon	1224M	<i>Colobus abyssinicus</i>
	1225M	<i>Macaca sylvanus</i>
	1226M	<i>Callithrix aurita</i>
	1227M	<i>Colobus badius</i>
	1228M	<i>Pongo pygmaeus</i>
	1229M	<i>Pan troglodytes</i>
	173	<i>Gorilla g. gorilla</i>
	206	<i>Pan troglodytes</i>
	264	<i>Cercocebus albigena</i>
	330	<i>Cercocebus torquatus</i>
Germany, Berlin	331	<i>Cercopithecus cephus</i>
	332	<i>Cercopithecus mona</i>
	C215	<i>Gorilla g. gorilla</i>
	9N275a	<i>Pongo pygmaeus</i>
	553	<i>Colobus abyssinicus</i>
Germany, D.R.	1631	<i>Pongo pygmaeus</i>
Ghana	451	<i>Cercopithecus mona</i>
	621	<i>Colobus verus</i> , 8 p.
	625	<i>Colobus verus</i> , 15 p.
	788	<i>Pan troglodytes</i>
	849	<i>Galago demidovii</i>
Gibraltar	892	<i>Cercocebus torquatus</i>
	156	<i>Macaca sylvanus</i>
Great Britain	157	unident. monkey
	1032	unident. monkey in menagerie
Greece	1068	fresco of blue apes
Grenada	305	<i>Cercopithecus mona</i>
Guinea	512	<i>Papio anubis</i>
	514a	<i>Papio anubis</i> , souv. sheet
	531	<i>Pan troglodytes</i>
	532	<i>Pan troglodytes</i>
	533	<i>Pan troglodytes</i>
	534	<i>Pan troglodytes</i>
	685	<i>Pan troglodytes</i>
	688a	<i>Pan troglodytes</i> , souv. sheet
	753	<i>Pan troglodytes</i> , 3 in strip
	852	stylized monkey
	857	stylized monkey
	C140	stylized monkey
	457	<i>Papio hamadryas</i>
	458	<i>Gorilla g. berengei</i>
	459	<i>Theropithecus gelada</i>
Guinea-Bissau	460	<i>Mandrillus sphinx</i>
	461	<i>Pan troglodytes</i>
	462	<i>Colobus abyssinicus</i>
	463	<i>Cercopithecus diana</i>
	568	<i>Gorilla g. berengei</i>
	570	<i>Cercopithecus erythrotis</i>
	254	unident. monkey on coin
	329b	<i>Alouatta seniculus</i>
	329c	<i>Saimiri sciureus</i>
	—	Overprint on 329b
Guyana	—	Overprint on 329c
	237	stylized monkey families, 10c
	238	stylized monkey families, \$1.30
Hungary	2340	unident. monkey in tree
India	1029	<i>Presbytis geei</i>
	1030	<i>Macaca silenus</i>
Indonesia	475	<i>Pongo pygmaeus</i>
	1014	<i>Nasalis larvatus</i>
Ivory Coast	202	<i>Perodicticus potto</i>
	210	<i>Colobus p. satanas</i>
	210a	<i>Colobus p. satanas</i> , souv. sheet
	529	<i>Colobus verus</i>
	533	<i>Pan troglodytes</i>
	671	<i>Colobus abyssinicus</i>
	940	monkey toy, Noborizaru
Japan	1136	<i>Macaca</i> by Minoo Falls
	1387	monkey toy, Osaka
	—	monkey toy, Osaka, souv. sheet
	1487	<i>Gorilla g. gorilla</i>

Country	Number	Nomenclature
Jersey	1487a	<i>Gorilla g. gorilla</i>
	51	<i>Colobus ursinus</i>
	52	<i>Lemur catta</i>
	218	<i>Pongo pygmaeus</i>
Kenya	220	<i>Gorilla g. gorilla</i>
	320	<i>Leontopithecus chrysomelas</i>
	23	<i>Galago senegalensis</i>
	33	<i>Cercopithecus pygerythrus</i>
	92	<i>Colobus badius</i>
	92a	<i>Colobus badius</i> , souv. sheet
	202	<i>Cercocebus</i> sp.
Korea	—	<i>Cercopithecus neglectus</i>
	—	<i>Cercopithecus neglectus</i> , souv. sheet
	593	stylized monkey and zodiac
	593a	stylized monkey, souv. sheet
	1184	monkey headed figure
Labuan	1184a	monkey headed figure, souv. sheet
	—	<i>Lemur catta</i>
	96	<i>Pongo pygmaeus</i>
	97	<i>Pongo pygmaeus</i>
	123	<i>Pongo pygmaeus</i> , Labuan ovpt. on 96
Laos	J3	<i>Pongo pygmaeus</i> , Post. due ovpt. on 97
	C15	Hanuman
	C16	Ninh Lapath
	C41	Hanuman
Lesotho	C60	<i>Hylobates lar</i>
	C76	Hanuman and Nang Matsa
	61	rock painting of baboons
	232	<i>Papio ursinus</i>
	352	<i>Papio ursinus</i>
Liberia	400	<i>Papio ursinus</i>
	460	<i>Papio ursinus</i>
	103	<i>Pan troglodytes</i>
	288	<i>Cercopithecus diana</i>
	454	<i>Pan troglodytes</i> (infants)
	575	<i>Cercopithecus aethiops</i>
	709	<i>Papio anubis</i> and Schweitzer
	765	<i>Pan troglodytes</i>
	768	<i>Gorilla g. gorilla</i>
	048	<i>Pan troglodytes</i>
Madagascar	63-77	<i>Lemur</i> sp. and zebu (15)
	119-124	<i>Lemur</i> sp. and zebu (6)
	129	<i>Lemur</i> sp. and zebu
	321	<i>Haplemur griseus</i>
	322	<i>Varecia variegatus</i>
	323	<i>Lemur mongoz</i>
	385	Lemur in tree
	450	<i>Daubentonia madagascariensis</i>
	501	<i>Cheirogaleus major</i>
	502	<i>Lepilemur mustilenus</i>
	594	<i>Lemur catta</i>
	595	<i>Lemur macaco</i>
	666	<i>Daubentonia madagascariensis</i>
	667	<i>Microcebus murinus</i>
	668	<i>Varecia variegatus</i>
Malawi	669	<i>Propithecus verreauxi</i>
	670	<i>Indri indri</i>
	671	<i>Perodicticus potto</i>
	C60	<i>Lemur catta</i>
	C67	<i>Propithecus diadema</i>
	C68	<i>Indri indri</i>
	C69	<i>Propithecus verreauxi</i>
	C117	<i>Lepilemur mustilenus</i>
	C118	<i>Cheirogaleus major</i>
	C173	<i>Lemur macaco</i>
Malaysia	C90	surcharge on C68
	259	<i>Galago senegalensis</i>
	262a	<i>Galago senegalensis</i> , souv. sheet
	90	unident. monkey, elephant, lion
	182	<i>Pongo pygmaeus</i>
	297	<i>Nycticebus coucang</i>

Country	Number	Nomenclature	Country	Number	Nomenclature
Mali	318	<i>Pan troglodytes</i>	Rwanda	58	<i>Colobus abyssinicus</i>
	—	unident. monkey and acrobats		60	<i>Gorilla g. berengei</i>
Manama	575TS	<i>Perodicticus p. potto</i>		61	<i>Colobus abyssinicus</i>
	1420TS	<i>Tarsius syrichta</i>		105	<i>Papio cynocephalus</i>
	1422TS	<i>Papio ursinus</i>		359-366	<i>Gorilla g. berengei</i> (8)
Mauritania	137	<i>Papio papio</i>		444	<i>Colobus polykomos</i> and antelopes
	142	<i>Erythrocebus patas</i>		857	<i>Pan troglodytes</i>
Monaco	845	unident. monkey		858	<i>Gorilla g. berengei</i>
	1133	monkey music band		859	<i>Colobus guereza</i>
Mongolia	707	<i>Pan troglodytes</i> on bicycle		860	<i>Galago inustus</i>
	C33d	unident. monkey and Explorer VI		861	<i>Cercopithecus mona</i>
Mozambique	555	<i>Galago senegalensis</i>		862	<i>Perodicticus potto</i>
	559	<i>Cercopithecus talapoin</i>		863	<i>Cercopithecus aethiops</i>
Netherland Antilles	B82	unident. monkey and turtle		864	<i>Papio cynocephalus</i>
Niger	C202	<i>Pan troglodytes</i> and leopard		1158-1165	<i>Gorilla g. berengei</i>
Nigeria	450	<i>Rhinopithecus roxellanae</i>		—	<i>Gorilla g. berengei</i> (5)
North Borneo	103	<i>Pongo pygmaeus</i>	Ryukyu	165	monkey toy, Bingata
	104	<i>Pongo pygmaeus</i>	Sabah	13	Sabah ovpt. on N. Borneo 292
	108	<i>Pongo pygmaeus</i> , Brit. prot. ovpt. on 104	Saint Kitts-Nevis	350	<i>Cercopithecus sabaeus</i>
	186	<i>Pongo pygmaeus</i> , face, 6c.		351	<i>Cercopithecus sabaeus</i>
	196	<i>Nasalis larvatus</i>		352	<i>Cercopithecus sabaeus</i>
	199	<i>Pongo pygmaeus</i> , face, 10c.		353	<i>Cercopithecus sabaeus</i>
	211	<i>Nasalis larvatus</i> , BMA ovpt. on 196	Saint Thomas	—	<i>Cercopithecus mona</i>
	214	<i>Pongo pygmaeus</i> , BMA ovpt. on 199	Salvador	739	<i>Ateles geoffroyi</i>
	226	<i>Nasalis larvatus</i> , crown ovpt. on 196		C485	<i>Ateles geoffroyi</i> and young
	229	<i>Pongo pygmaeus</i> , crown ovpt. on 199	Sarawak	181	<i>Tarsius bancanus</i>
	292	<i>Pongo pygmaeus</i> and Queen		198	<i>Pongo pygmaeus</i> and young
	J13	<i>Pongo pygmaeus</i> , post. due ovpt. on 104 (1901)		216	<i>Pongo pygmaeus</i> and young
	J23	<i>Pongo pygmaeus</i> , post. due ovpt. on 104 (1903)	Senegal	523	<i>Pan troglodytes</i>
	N4	<i>Nasalis larvatus</i> , Jap. ovpt. on 196		523a	<i>Pan troglodytes</i> , souv. sheet
	N7	<i>Pongo pygmaeus</i> , Jap. ovpt. on 186	Sharjah	939M	<i>Ateles geoffroyi</i>
	N19	<i>Nasalis larvatus</i> , similar to N4		940M	<i>Mandrillus sphinx</i>
	N22	<i>Pongo pygmaeus</i> , similar to N7		941M	<i>Cercopithecus diana</i>
	N22a	<i>Pongo pygmaeus</i> , two ovpts. on 186		942M	<i>Leontopithecus rosalia</i>
North Vietnam	—	<i>Hylobates concolor</i> (1961)		943M	<i>Pan troglodytes</i>
	—	<i>Presbytis francoisi</i> (1965)		944M	<i>Papio anubis</i>
	—	<i>Nycticebus coucang</i> (1965)		—	<i>Colobus polykomos</i>
	—	<i>Macaca speciosa</i>	Sierra Leone	586	<i>Pan troglodytes</i>
	—	<i>Hylobates</i> sp.		587	<i>Pan troglodytes</i>
Oman	—	<i>Perodicticus p. potto</i>		588	<i>Pan troglodytes</i>
	—	<i>Papio anubis</i>		589	<i>Pan troglodytes</i>
	—	<i>Pan troglodytes</i>		628	unident. monkey
Panama	498	<i>Cebus capucinus</i>	Singapore	156	<i>Hylobates</i> sp.
Paraguay	1670M	<i>Callithrix aurita</i>		202	<i>Pongo pygmaeus</i>
	2131M	<i>Cercocebus torquatus</i>	Somalia	445	<i>Galago senegalensis</i>
	—	<i>Aotus trivirgatus</i>	Southwest Africa	465	<i>Cercopithecus pygerythrus</i>
	—	<i>Callicebus</i> sp. (1985)		466	<i>Papio ursinus</i>
Peru	818	<i>Alouatta seniculus</i>	Spanish Guinea	343	<i>Cercopithecus erythrotis</i>
	—	<i>Cebus capucinus</i>		B35	<i>Cercopithecus erythrotis</i>
	C411	<i>Cacajao rubicundus</i>		B36	<i>Cercopithecus talapoin</i>
	C412	<i>Cacajao rubicundus</i>	Surinam	363	<i>Saimiri sciureus</i>
Philippines	1006	<i>Tarsius syrichta</i>		B117	unident. monkey, boy, spider
	1404	<i>Macaca philippinensis</i>		B242	unident. monkey
Poland	1891	<i>Pan troglodytes</i> , face	Swaziland	167	<i>Papio ursinus</i>
	1892	<i>Hylobates lar</i>		—	<i>Gorilla</i> sp.
	2307	<i>Mandrillus sphinx</i>		—	<i>Cercopithecus pygerythrus</i>
	—	ceramic monkey	Tanzania	85	<i>Colobus badius</i>
Ras-al-Khaima	657	<i>Presbytis obscura</i>		86a	<i>Colobus badius</i> , souv. sheet
	—	Set of 6. <i>Cercocebus</i> , <i>Hylobates</i> , <i>Mandrillus</i> , <i>Pongo</i> , <i>Pan</i> , <i>Gorilla</i>		203	<i>Pan troglodytes</i>
Rio Muni	20	<i>Gorilla g. gorilla</i>		—	<i>Colobus badius</i>
	68	<i>Perodicticus potto</i>	Thailand	1017	<i>Hylobates lar pileatus</i>
	B7	<i>Mandrillus sphinx</i>		1018	<i>Macaca nemestrina</i>
	B9	<i>Mandrillus sphinx</i>		1019	<i>Nycticebus coucang</i>
Ruanda-Urundi	137	<i>Gorilla g. berengei</i>		1020	<i>Presbytis cristata</i>
	139	<i>Colobus abyssinicus</i>	Togo	472	<i>Papio anubis</i>
	141	<i>Gorilla g. berengei</i>		784	<i>Papio anubis</i>
	143	<i>Colobus abyssinicus</i>		796	monkey toy
Russia	5226	<i>Mandrillus sphinx</i>		804	surcharge on 784
				1069	disney monkey cartoon
				1425	<i>Colobus verus</i>
				1426	<i>Galago senegalensis</i>

Country	Number	Nomenclature
	C168a	monkey toy
	C264a	monkey toy
	C317	<i>Colobus verus</i>
	C318	<i>Pan troglodytes</i>
	C320a	<i>Pan troglodytes</i> , souv. sheet
	C451	<i>Papio</i> sp. and young
Uganda	179	<i>Colobus badius</i>
	180a	<i>Colobus badius</i> , souv. sheet
	282	<i>Galago senegalensis</i>
	285	<i>Gorilla g. berengei</i>
Um al Qiwain	387M	<i>Gorilla g. berengei</i>
	966TS	<i>Lagothrix lagothricha</i>
	978TS	<i>Papio hamadryas</i>
	979TS	<i>Pan troglodytes</i>
	1150TS	<i>Indri indri</i>
	1232TS	<i>Galago senegalensis</i>
	1238TS	<i>Pongo pygmaeus</i>
	—	<i>Colobus guereza</i>
	—	<i>Macaca mulatta</i>

Country	Number	Nomenclature
Upper Volta	77-79	stylized monkey masks and face
	152	<i>Cercopithecus sabaeus</i>
	—	<i>Papio</i> sp. and leopards
	651	<i>Papio cynocephalus</i>
Venezuela	828	<i>Callicebus torquatus</i>
Viet Nam	—	<i>Macaca</i> sp.
	—	<i>Presbytis</i> sp.
	—	<i>Nycticebus coucang</i>
	—	<i>Macaca mulatta</i>
	—	<i>Nycticebus coucang</i> , 1D
	—	<i>Nycticebus coucang</i> , 2D
Yemen Repub.	336M	<i>Papio</i> sp.
Zaire	852	<i>Pan troglodytes</i> , ovpt. on Congo 735
	1083	unident. monkeys
Zambia	—	<i>Papio ursinus</i>
	—	<i>Cercopithecus alborgularis</i>
	—	<i>Cercopithecus mitis</i>
	—	<i>Cercopithecus aethiops</i>

APPENDIX

New Members of the IUCN/SSC Primate Specialist Group

The following members have been added to the group since the appearance of the last issue of *Primate Conservation*.

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Back cover. Male white-faced saki (*Pithecia pithecia*) from Suriname (photo by R. A. Mittermeier).

