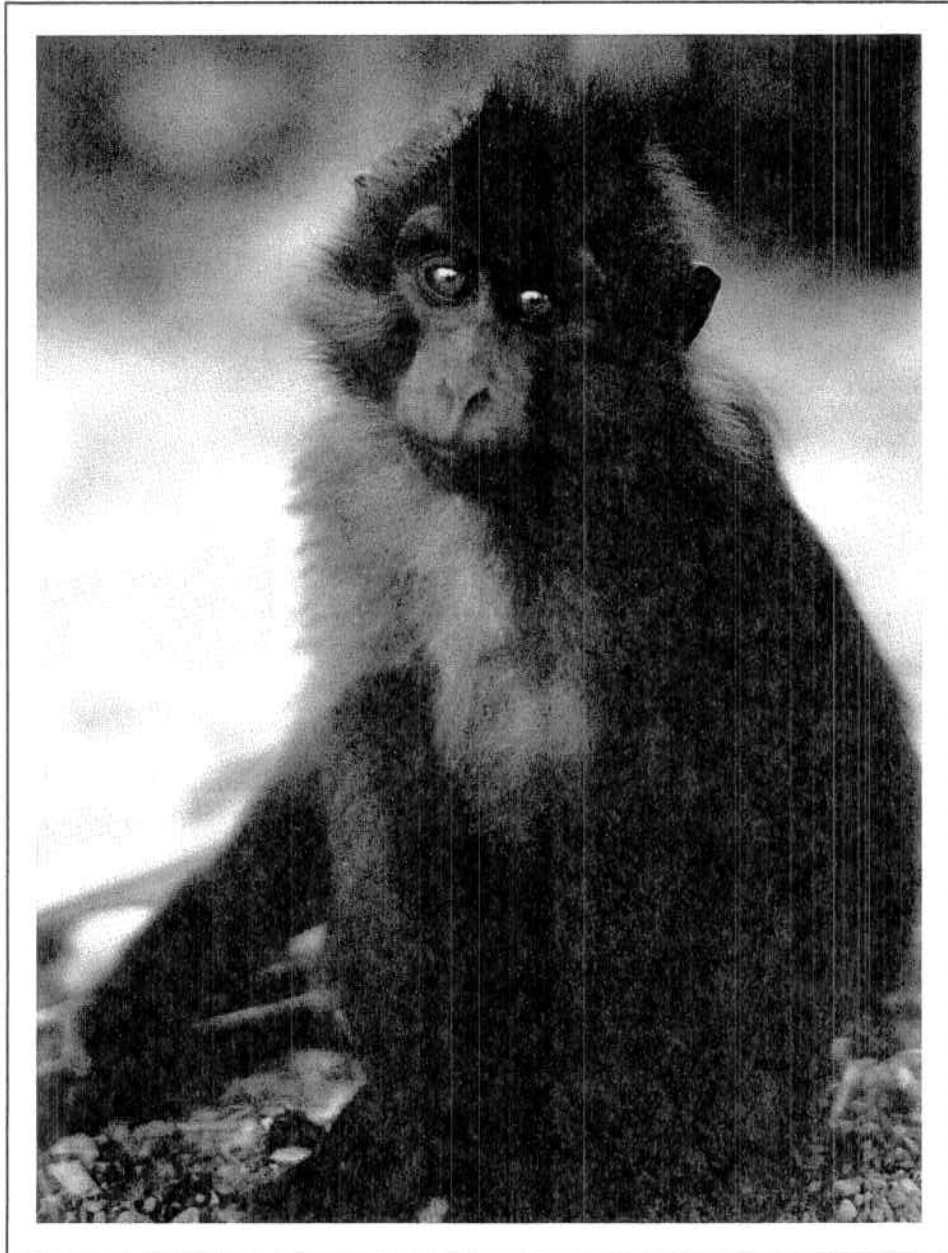


PRIMATE CONSERVATION

The Journal of the IUCN/SSC Primate Specialist Group

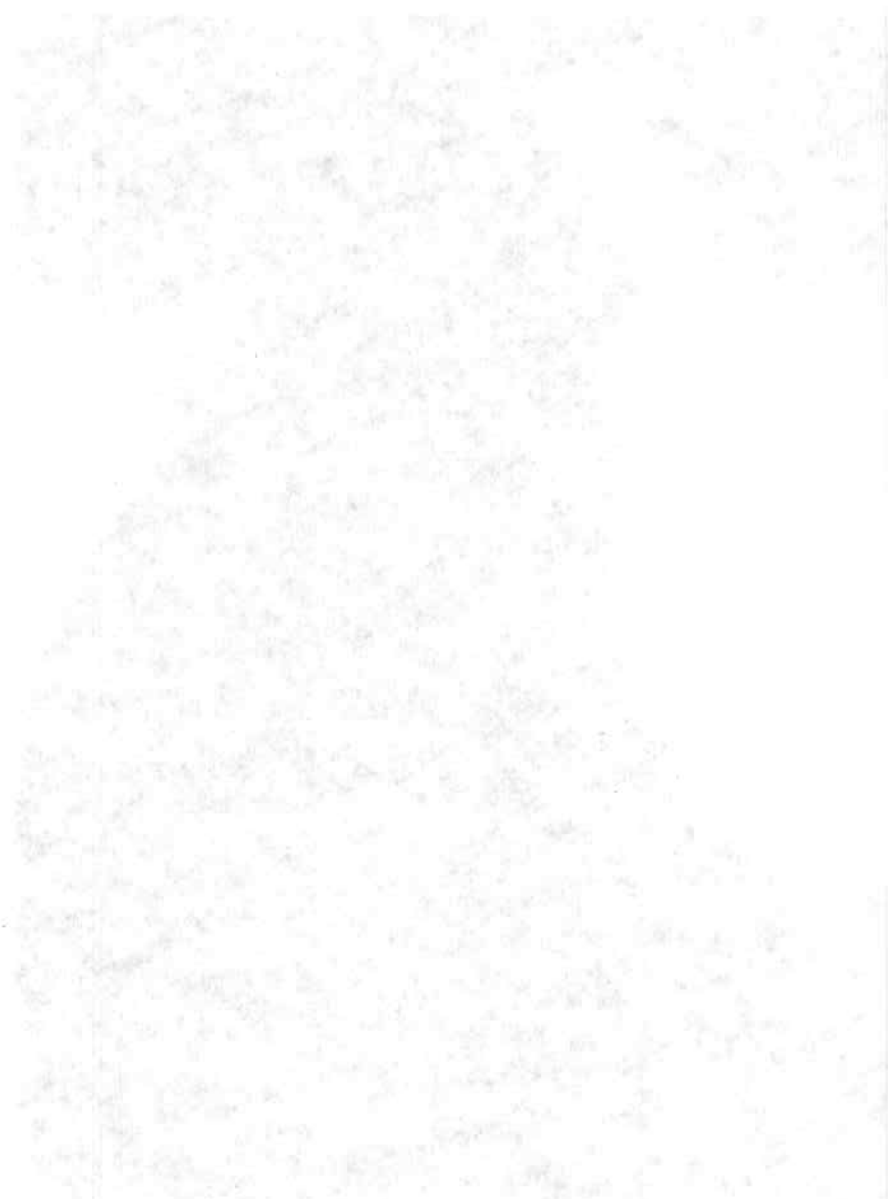
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A Word from the Editors

This issue of *Primate Conservation* has a good geographic spread, with excellent articles from all four of the major regions in which primates occur (Neotropics, Africa, Madagascar, Asia), and the quality of the contributions is as strong as it ever has been. We are delighted to be able to present this issue, and would like to give special thanks to those of you who helped to make it possible.

We would also like to make a special plea to all of you who have contributed, or plan to contribute, to *Primate Conservation* and our four regional newsletters. Please do your best to provide us with top-quality photographs and maps. Although you may be familiar with the animal(s) you study and the area in which they occur, remember that our publications have a wide international circulation, and most readers will not have had first-hand experience with the appearance and the range of your target species. Many of the excellent articles in this issue for example are hampered by lack of photos and, in some cases, quality maps clarifying the geographic locations under discussion. Keep in mind that if you have not been successful in taking good pictures, we have the capacity to provide illustrations from whatever source material you might have available. The same is true for maps. Please help us with these important aspects for enhancing our knowledge and awareness of the Order Primates.

Finally, we are pleased to announce the creation of a new foundation for primate conservation, entitled the Margot Marsh Biodiversity Foundation. It was created by the late Margot Marsh of La Jolla, California. Margot was a long-time supporter of the activities of the Primate Specialist Group, as well as a wide variety of other primate conservation activities. She was also a wonderful person with a tremendously strong personal commitment to the global biodiversity conservation issues that concern us all. In spite of her broad range of interests, she had a special fondness for primates, and consequently when she died in May 1995, she left special provision in her will for the creation of this new foundation dedicated exclusively to global primate conservation. The PSG was honored by the fact that many of its goals and activities were mentioned specifically in her will, and that the Chairman was named one of three Board Members for the Foundation. The final legal details are still being worked out, but more information on guidelines, objectives and application procedures will be included in the next issue of *Primate Conservation* as well as future regional newsletters. We are all delighted that Margot Marsh chose to focus her foundation on primates, and believe that her dedication will provide for significant advances in primate conservation and field research as we enter the 21st century.

Russell A. Mittermeier
Chairman, IUCN/SSC Primate Specialist Group
Anthony B. Rylands
Editor, *Primate Conservation*

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Long-term Studies of Primates at La Macarena, Colombia

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The Macarena mountains, of which the highest summit is about 1500 m, lie to the east of the Andes. The range is 30 km wide and extends north-south for 120 km. The Macarena National Park is the principal conservation unit in this region, which also includes three other adjacent national parks, and five reserves, covering a total of 15,600 km². In 1986, a research station was set up there, first called the Centro de Investigaciones Primatológicas Macarena (CIPM) but later renamed the Centro de Investigaciones Ecológicas Macarena (CIEM), on the west bank of the Río Duda on the border of the Macarena and Tinigua National Parks. All studies in CIEM have been made under cooperative projects between Colombia and Japan, the representative institutes of which are the Universidad de Los Andes and the Miyagi University of Education. The projects have been authorized by the Instituto Nacional de Los Recursos Naturales Renovables y del Ambiente (INDERENA), and every field study has been carried out with the permission of INDERENA through the Universidad de Los Andes. Here we present a summary review of the projects which have been or are currently being carried out at this Research Station.

The Study Site

The Centro de Investigaciones Ecológicas Macarena is located at 2°40' N and 74°10' W. Access involves a 3-4 hour bus journey from Bogotá to Villavicencio, the capital of the Department of Meta, followed by a shorter than one hour flight to the town of Macarena, and lastly a journey of several hours to two days by canoe and outboard; the time taken depending on the time of year and degree of flooding. A fast-flowing stream, the Raudal, one hour upstream from Macarena, is impossible to pass when the water is high, and in this case it is necessary to walk a 3 km trail carrying all the equipment. When the water is low, upstream navigation on the Raudal is difficult on account of shallows and fallen trees. While these geographical conditions make for difficult access to the study site, they have played an important role in protecting the forest from destruction by colonization. The number of *fincas* (estates) on the banks of the Guayabero diminishes upstream of the Raudal, and especially along the Río Duda.

The Río Duda, a tributary of the Río Guayabero, is part of the Orinoco basin, although, some tributaries of the Río Caquetá, a larger river of the upper Amazon basin, also rise 40 km west of the

Río Duda. The west bank of the Duda, where the study site is located, is generally hilly, being at the southern end of the Chamusa mountains, although the highest point of the study site is only 70 m above the level of the river (Hirabuki 1990). Between the hills and the river, there are a number of alluvial plateaux. The vegetation there is recent, 30 years old at most, while the hilly areas are covered by mature forest, including patches where vines or bamboos predominate, depending on the topography and drainage (Hirabuki 1990).

Mean annual rainfall at the study site is 2600 mm (range: 2200-3000 mm, over four years) (Kimura *et al.* 1994). There is a marked dry season from December through February or March, with less than 100 mm of rainfall each month. Leaves of a number of tree species fall at this time. Maximum rainfall occurs in June or July.

There are seven species of non-human primates at the study site (Izawa and Nishimura 1988): *Callicebus cupreus*, *Aotus vociferans* (?), *Saimiri sciureus*, *Cebus apella*, *Alouatta seniculus*, *Ateles belzebuth*, and *Lagothrix lagotricha*. Other species have also been confirmed for the region: *Saguinus nigricollis* (see Vargas, 1994), *Callicebus torquatus* around the Raudal, and *Cebus albifrons* in some localities between the Río Duda and the western slopes of the Macarena mountains.

History

Research at the Centro de Investigaciones Ecológicas Macarena dates back to October 1975, when Izawa and Mizuno, with the authorization of INDERENA, set up their camp at a site later called Puerto Chamusa. Ecological and sociological studies of the seven sympatric species, especially *Cebus apella* were carried out up to February 1977 (Izawa and Mizuno 1977; Izawa 1978, 1980). Field studies were begun again in August 1986, and the situation of the forest and the animals there seemed to be unchanged in spite of nearly 10 years absence. Since then the camp has been permanently occupied.

A further two camps were set up downstream of the Puerto Chamusa, at Puerto Paujil in 1990, and at Puerto Marimba in 1993. The three camps are connected by trails, involving a half hour walk between the first and second, and one and a half hours walk between the second and third. Having three camps has made it possible to diversify the projects, and also allows for the protection

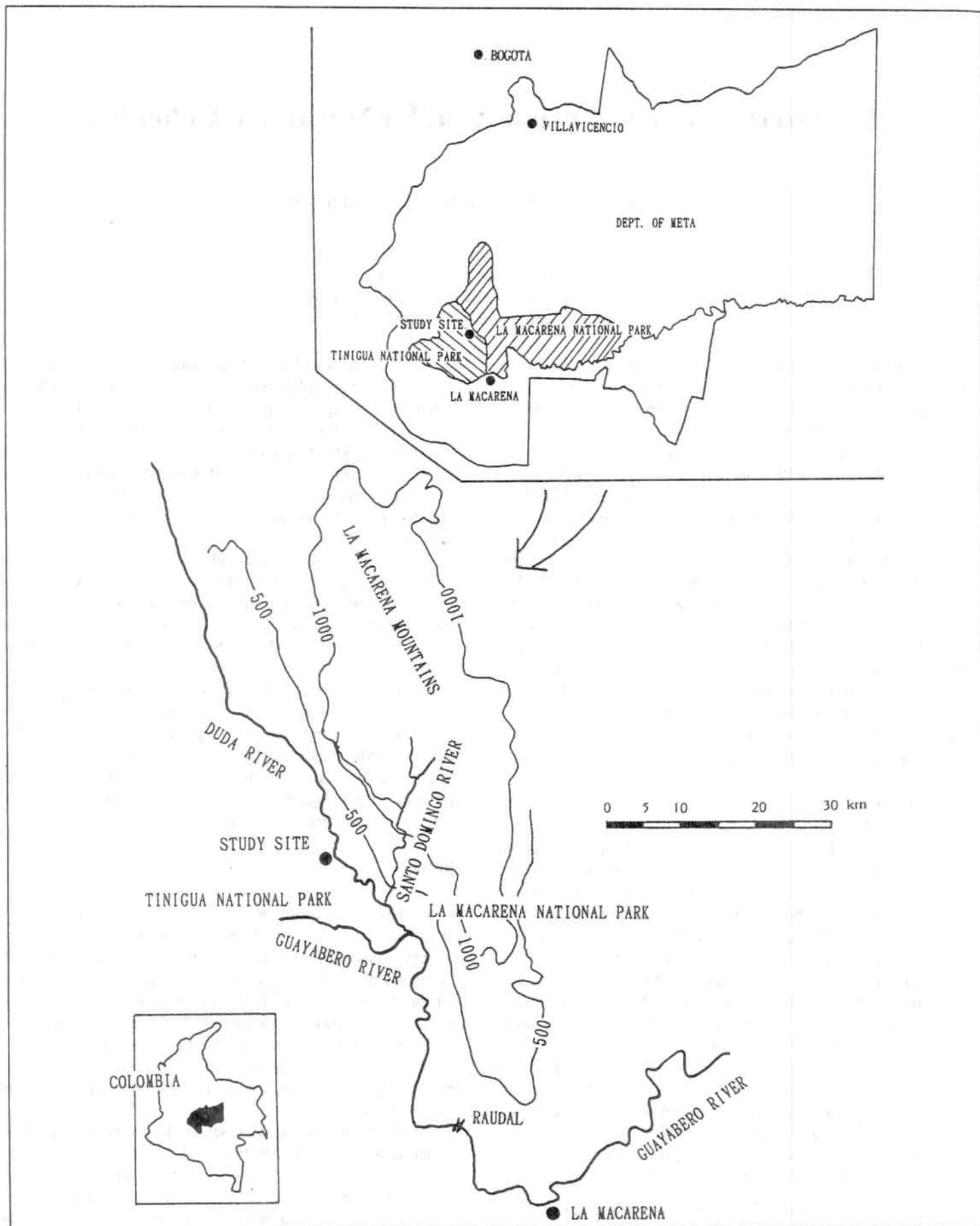


Fig. 1. Map showing the study and location of the Centro de Investigaciones Ecológicas Macarena (CIEM) (map provided by the authors).

of a more extensive area from hunting, logging and colonization than was possible previously.

Projects

The projects carried out at CIEM are of four types. The first involves long-term studies of the primates, with the aim of studying the social structure of each species based on historical studies of individuals and intra- and intergroup interactions. The second includes a number of other biological studies on the woody flora, vegetation structure, bird fauna, bird ecology and behavior, insect fauna and ecology, and seed dispersal.

The third group of projects involves field education of university students, especially from the Universidad de Los Andes, and is divided into the following three categories: a) one-month field exercise courses held twice a year, each attended by several, or up to 20, students; b) six-month field projects by 1-5 students, who are obliged to present full reports after their study; and c) more

prolonged field studies by university graduates who have participated in the six-month field projects. The fourth type of project involves environmental education for the public.

The projects of the first three categories were already underway during the first years when only one camp (Pto. Chamusa) had been set up. Currently, however, the camp of Pto. Marimba, established principally for public education, is also the site for some of the second and third types of project. The Pto. Paujil camp, originally an annex of Chamusa camp, has been the center for long-term studies of curassows (paujil) since 1992. The species studied, duration of the study, and personnel involved in the research on primates and birds at the Centro de Investigaciones Primatológicas Macarena are shown in Table 1.

Results

Cebus apella

In October 1986, a group of tufted capuchins, *Cebus apella* which had occasionally stolen bananas at the base camp began to eat them at ease in the presence of researchers. The composition, (including group division), behavior and social organization of this provisioned group, named MC1, has been observed continuously over the subsequent eight years by Izawa (1988a, 1990a, 1990b, 1992, 1994a, 1994b). Colombian students have also studied infant social development (Calle 1992a, 1992b; Escobar-Paramo 1989a, 1989b; Valenzuela 1992, 1994).

From longterm studies of the dispersal pattern of these tufted capuchins, it is now known that they live in a matrilineal society,

Table 1. Species studied, duration of the study, and personnel involved in the research on primates and birds at the Centro de Investigaciones Ecológicas Macarena (CIEM) ¹									
	1986	1987	1988	1989	1990	1991	1992	1993	1994
Primates									
<i>Cebus apella</i>									
Group MC1			[EP][CZ][PJ][VN]	[-----OS-----]			[AT]	[BM]	
					[-----IK-----]				
Group MC2									
<i>Alouatta seniculus</i>									
Group MN1									
Group MN2									
Group MN4									
<i>Lagothrix lagotricha</i>									
Group CR1									
Group CR12									
<i>Ateles belzebuth</i>									
Group MB1									
Group MB2									
<i>Callicebus cupreus</i>									
Group MR3									
Group MR4									
<i>Aotus vociferans(?)</i>									
Group TM1									
Birds									
<i>Mitu salvinii</i>									
Group PS1									
<i>Crax elector</i>									
Group PA1									

Colombian Staff: Primates - Henry Lozano (LH); Alvaro Sanabria (SA), CIEM. **Primates and birds** - Carlos Mejia (MC), Universidad de los Andes. **Plants** - Cesar Barbosa (CB), Inderena.

Japanese Staff: Primates - Kosei Izawa (IK), Miyagi University of Education; Koshin Kimura (KK), Nagoya Gakuin University; Akisato Nishimura (NA), Doshisha University; Shizue Otake (OS), JOCV. **Plants** - Yoshihiko Hirabuki (HY), Miyagi University of Education; Mikio Kobayashi (KM), Utsunomiya University; Tatsuyuki Oba (OT) and Masatoshi Hara (HM), Chiba Central Museum; Akihide Takehara (TA), Iwate University. **Seed dispersal** - Takakazu Yumoto (YT), Kobe University.

Colombian Students: Primates - Jorge Ahumada (AJ)², Maria G. Alterio (AM); Tita Alvira (AT); Maria I. Barrera (BM); Maria T. Becerra (BT); Alejandro Calixto (CA); Jaime Cabrera (CJ); Zoraida Calle (CZ); Gisele Didier (DG), Catalina Estrada (EC); Patricia Escobar-Paramo (EP); Ximena Garabito (GX); Angela Parrado-Rosselli (PA); Juan C. Pizarro (PC); Jairo Padraza (PJ); Marcela Porras (PM); Nelson Pinilla (PN); Rocio Polanco (PR); Santiago Palacio (PS); Maria T. Pulido (PT); Marcela Quifones (QM)²; Carolina M. Rodas (RC); Catalina Saravia (SC); Clara Solano (SL); Nicole Valenzuela (VN); Catherine Valdez (VC); Aida V. Wilches (WA); Nicole Zangen (ZN). **Primates and plants** - Pablo Stevenson (SP)². **Birds** - Mauricio Alvarez (AM)²; Luis Beltran (BL); Maria Clara (CM); Marisol Escaño



Fig. 2. An adult male *Cebus apella*. Photograph by K. Izawa.



Fig. 3. Red howlers, *Alouatta seniculus*, resting. Photograph by K. Izawa.

in which only males transfer, as has been found for other *Cebus* and most cercopithecoid species (Robinson and Janson 1987). Further aspects also demonstrate some convergence in their social behavior with matrilineal cercopithecoids; for example, closely related females rise in their dominance rank together, and members of a kin group act as a unit in group division. The ecology and social behavior of *C. apella* groups other than MC1 have been studied by Stevenson *et al.* (1991).

Alouatta seniculus

One group of red howlers, MN1, has been studied over eight years, principally by Izawa (1988b 1989) but with the help of a number of other researchers and students (Izawa and Lozano 1989, 1991, 1992a, 1992b, 1994; Ceballos 1989; Figueroa 1989). Another two groups, MN2 and MN4, have been studied over seven and four years, respectively, by Kimura (1992) and students of the Universidad de Los Andes. More than 20 group years of study of these red howlers have confirmed that they, like *C. apella*, also live in a matrilineal society. This is in sharp contrast to the dispersal pattern of mantled howlers (*A. palliata*), in which both males and females transfer between groups (Glander 1992). However, a number of observations lead us to infer that red howler females, especially young ones in large groups, may also disperse from their natal groups when solicited by solitary males to form new groups. First, although over 15 groups have been censused, the mean size of groups with established home ranges is 10, and groups of more than 20 animals have never been observed as they have in *A.*

palliata. Second, small groups composed of one male and one or two young females have been occasionally seen around the boundaries of the ranges of established groups over periods of several months.

It has become evident that there are considerable differences between the three howler groups in various aspects of their daily activity, including daily travel distance, diet, use of bamboos for sleeping site, and the timing of their beginning and end of their daily activity. There are also differences in social phenomena. Of 12 infants born into group MN1, eight were killed in relation to male takeovers, which occurred five times in seven years (Izawa 1993). In contrast, infanticide occurred only once in MN2, and has not to date been recorded for MN4.

Howler monkeys, along with spider monkeys, have been observed to eat soil (Izawa 1993). There are various studies on this behavior and the chemical properties of the soil eaten (Hirabuki and Izawa 1990; Izawa and Mizuno 1992; Izawa *et al.* 1992).

Lagothrix lagotricha

Humboldt's woolly monkey is one of the most common mammal species in the middle and upper Amazon and the upper Orinoco. However, longterm field studies of this species have been lacking until very recently because of high hunting pressure, making it difficult to secure a good study site. More than 10 groups of woolly monkeys have been recorded at CIEM, but none of them seem to have been hunted (Nishimura 1990a).

One group, CR1, has been observed for eight years, since the



Fig. 4. A spider monkey, *Ateles belzebuth*. Photograph by K. Izawa.

beginning of 1987 (Nishimura 1988, 1990b, 1994; Nishimura *et al.* 1992; Stevenson 1992). The results indicate that *Lagothrix* monkeys live in a patrilineal society, in which only females migrate between groups, whereas males are philopatric, as has been found for *Pan* (see Nishida and Hiraiwa-Hasegawa 1987), *Ateles* (see Symington 1990) and muriquis, *Brachyteles* (see Strier 1992), the latter two also of the subfamily Atelinae. Numerical values for the reproductive parameters of *Lagothrix* which have been obtained from this study include gestation period, interbirth interval, and age of the first copulation and the first birth, all of which are quite similar to those recorded for the other atelines (Nishimura *et al.* 1992). Woolly monkeys, on the other hand, differ from the other atelines in a number of aspects of intra- and intergroup relationships (Nishimura 1994). Group members, for example, almost always travel together in a single foraging unit, whereas spider monkeys and at least one muriqui population studied live in parties that show repeated fission and fusion (Symington 1990; Milton 1984).

The diet and activity patterns in relation to forest structure and phenology have been studied in another woolly monkey group, CR12, by Stevenson and others (1991, 1994). They also carried out a similar ecological study comparing three other sympatric species, *C. apella*, *A. seniculus*, and the long-haired spider monkey, *Ateles belzebuth*. Woolly monkeys were found to be normally as highly frugivorous as spider monkeys, although, unlike *Ateles* and the howler monkeys which have never been seen to ingest animal prey, they constantly eat considerable numbers of arthropods. On the other hand, woolly monkeys increased their

foliage intake when fruits were scarce, whereas at this time spider monkeys maintained a highly frugivorous diet by traveling in small parties and feeding on palm and other fruits that were distributed in small patches; a food source which is difficult for woolly monkeys, in larger groups, to exploit.

Other Primate Studies

One group of the long-haired spider monkey, *Ateles belzebuth*, MB1, has been observed over a number of years, and a second group, MB2, for six months. From these studies, especially of group MB1, group composition and its change, patterns of range use, daily activity, diet and social interactions are now well fairly understood (Ahumada 1989, 1992; Stevenson *et al.* 1991). Unfortunately studies of this species have been interrupted the last two years.

One group of night monkeys, probably *Aotus vociferans*, has been a regular visitor to the Chamusa camp since 1986. Recently Clara Solano, following a months preliminary survey with K. Izawa, made a six-month intensive study of this group, with the aid of A. Sanabria. Since then Sanabria has been continuing to monitor the night monkeys whenever they visit the camp.

Whereas the primates mentioned above are seen everywhere in the study site, titi monkeys, *Callicebus cupreus*, are largely restricted to the zone of vines and lianas that typically grow on the valley slopes (Izawa and Nishimura 1988). So far two groups of titis have each been studied for six months, by Rocio Polanco-Ochoa (1994) and Marcela Porra, respectively. The common squirrel monkey, *Saimiri sciureus*, has been the least studied. Almost nothing has been done but to record the location of groups, and occasionally check their size and composition.

Multispecific studies other than those by Stevenson and others mentioned above were carried out by Yoneda (1988, 1990) who made preliminary observations comparing tree size and height used by five sympatric species. Stevenson and Quiñones (1994) made a similar, but more extensive, study. Yumoto recently examined seed dispersal by howlers, woolly monkeys, and curassows. He measured dispersal distances for fruits (from the parent tree to where the seeds were excreted) while accompanying other researchers in their daily observations of habituated groups.

Birds

A checklist of bird species at CIEM was recently published by Mauricio Alvarez *et al.* (1993). Being based on a short term study, it is still incomplete, but a revised list is in preparation.

One group of the curassow, *Mitu (Crax) salvini*, was habituated by Marcela Santamaria in August, 1990. Since then she, Ana Maria Franco, and other students, have been observing the group for over four years. Curassows are monogamous, and the group studied contained the same couple throughout the study period, and on two occasions the young were observed dispersing. The research on these curassows includes studies of range use patterns, daily activity, diet, predator relations, intergroup relationship, courtship and other interactions between the male and female, and infant development. The results will be published soon.

Plants

A plant list based on the specimens collected by numerous re-



Fig. 5. Woolly monkey, *Lagothrix lagotricha*. Mocho, the b-male of Group CR1. Photograph by A. Nishimura.

searchers at CIPM was made by César Barbosa (1992). The list is far from complete, while comprising 100 families and about 500 species, but is very useful for the ecological studies of primates, birds and the forest. Forest structure and its relation to landform, soil, and succession has been studied principally by Hirabuki (Hirabuki 1990; Takehara and Hirabuki 1991; Hirabuki *et al.* 1991; Hirabuki and Barbosa 1992). Ecological and floristic studies of bambusoids have been carried out by Kobayashi and Izawa (1991, 1992, 1994).

Acknowledgments

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Observations of Two Threatened Primates in the Peruvian Andes

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In July-August 1994, surveys were carried out by a team of five British and Peruvian zoologists on an expedition organized from the University of Cambridge, U.K. in collaboration with the Asociación Peruana para la Conservación de la Naturaleza (APECO). The aim was to assess the conservation status and habitat requirements of the threatened and endemic birds and mammals in remaining areas of cloud forest and elfin forest on the Cordillera de Colán, a semi-isolated mountain range located in the Amazonas Department, northern Peru (see Fig. 1). These habitats were surveyed at altitudes of 1,500-2,650 m at two sites in the southern part of the range. Our conclusions regarding the importance of the Cordillera de Colán for the conservation of mammals are discussed elsewhere (Butchart *et al.* 1995). Here we detail our records and describe behavioral observations of two poorly known primates which are considered to be threatened (Groombridge 1993; Rylands *et al.* 1995): the yellow-tailed woolly monkey, *Lagothrix flavicauda*, and the Andean night monkey, *Aotus miconax*.

The Yellow-tailed Woolly Monkey, *Lagothrix flavicauda*

The yellow-tailed woolly monkey, *Lagothrix flavicauda*, was described in 1802, and collected again in 1925 and 1926, but was then presumed to have become extinct before its rediscovery in 1974 by Mittermeier *et al.* (1975). Graves and O'Neill (1980) observed the species in the wild in 1976, and it was also recorded by Parker and Barkley (1981) in 1979. Leo Luna (1980) carried out the first detailed study of the species, and concluded that it is found exclusively in humid and very humid montane forest above 1,800 m., at a few sites in the departments of Amazonas, San Martín, and Loreto, in northern Peru. The species is listed as endangered by the World Conservation Union (IUCN) (Groombridge, 1993), and "Critically endangered", following the new IUCN threatened categories adopted in 1995 (Rylands *et al.*, 1995).

In 1994, we observed *L. flavicauda* frequently at one site in the Cordillera de Colán (site 1, above Comboca, see Fig. 1) from 2,220 to 2,650 m (the highest peak reached), but most often at 2,250-2,350 m, as shown in Table 1. The observations were made in very humid lower montane cloud forest (Holdridge *et al.* 1971) on

slopes of about 30-45°, at altitudes where there was little disturbance by man. The forest there was characterized by a canopy height of 20-25 m, and dense mid-storey and understorey. Moss and epiphytes were abundant, tree-ferns were common, and *Chusquea* bamboo clumps were in clearings caused by tree-falls and landslides.

Most of these observations are likely to refer to the same group, although the two records on 27 July at widely separated altitudes suggest that perhaps two groups were involved. The two large groups seen on 20 and 31 July both contained at least three presumed adult males. They were distinguishable by their larger size, greater bulk, and more prominent yellow genital tuft. Although Mittermeier *et al.* (1977) stated that, on the basis of a small sample of museum specimens, no definite statement could be made concerning sexual dimorphism of the pubic tuft, our observations suggest that the differences may be sufficiently distinct to permit field identification of the sexes.

The maximum group size observed was 10, as also found by Leo Luna (1980). However, Hendee reported a troop of 20 individuals in 1926 (Thomas 1927; Mittermeier *et al.* 1977). Such large groups must now occur infrequently given the current pressures on this monkey. On 20 July, two of the presumed males were seen carrying infants ventrally, and likewise one male was observed carrying an infant on 31 July. Parker and Barkley (1981) observed a female carrying an infant on her back.

The monkeys were seen feeding on lichen, a variety of fruits, and bromeliad leaf-bases. Piles of torn bromeliad leaves were often found scattered on the ground, at altitudes between 2,300 m and 2,650 m. However, these could not be taken as conclusive evidence of the presence of yellow-tailed woolly monkeys, as such signs are also left by brown capuchins, *Cebus apella* (pers. obs.), and similar, though often distinguishable, signs are left by spectacled bears, *Tremarctos ornatus* (see Peyton 1980; M. Leo Luna pers. comm. 1993).

Individuals were seen at heights ranging from 8 to 25 m above the ground, but most were in the canopy and sub-canopy. When moving rapidly, they would leap distances as great as 15 m. The monkeys were quite confiding, as was noted by Parker and Barkley (1981), and often approached as close 10 m. Males occasionally

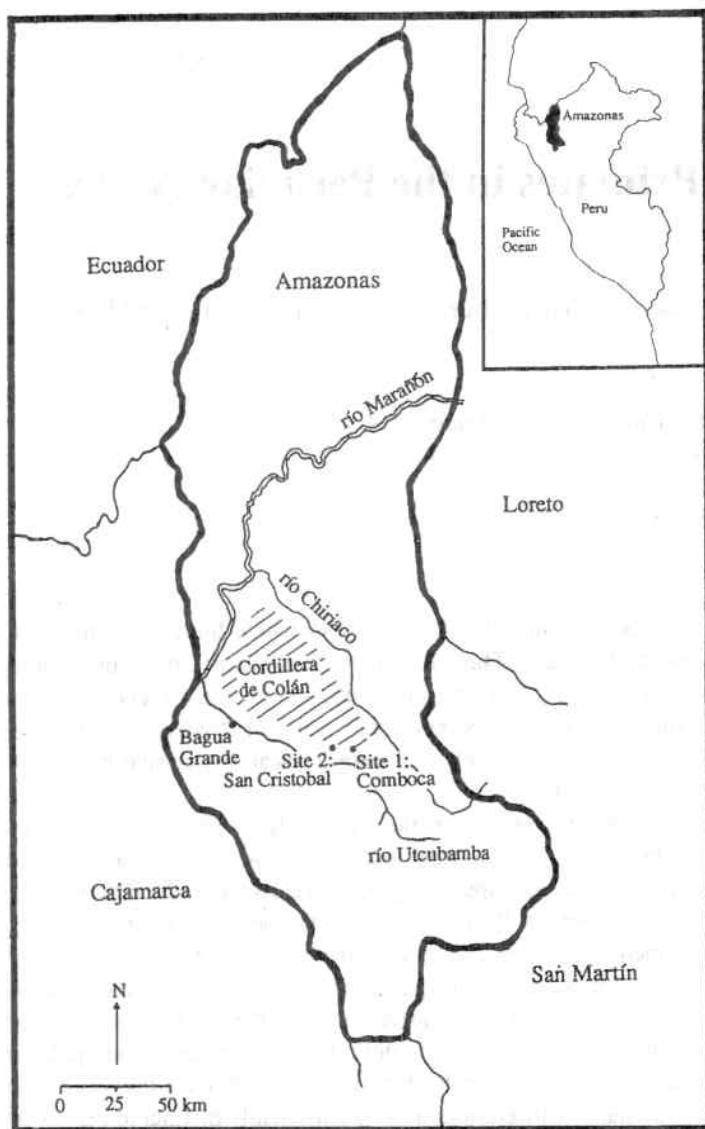


Fig. 1. Map showing the location of the study sites in the Cordillera de Colán, Peru.

performed aggressive displays, in which they would violently shake branches while calling loudly. The behavior was elicited on two occasions in response to imitations of their calls. Agitated individuals also responded to call imitations by defecating or urinating towards the observers beneath. Such behaviors were also recorded by Leo Luna (1980).

On 31 July, five minutes of continuous recordings were made of a group of eight yellow-tailed woolly monkeys at 2,320 m. These recordings have been placed in the British Library of Wildlife Sounds at the National Sound Archive. The recordings were mainly comprised of several series of yelping barks (described by Leo Luna 1980, as "puppy-like barks") given by one male in the group. The pitch and volume of these notes varied irregularly through the series, and the rate of delivery ranged from two to five notes per second. On two occasions the series of notes were introduced by a hoarse ascending squeal lasting about 0.3 seconds. The longest series of notes lasted 115 seconds, and included seven louder and faster bursts of notes, with each burst lasting about five seconds. Fig. 2 shows a sonogram of part of a series of barks.

Locals reported this species to be uncommon between 2,000 and 2,650 m in very humid lower montane forest at site 1. Previ-

Table 1. Yellow-tailed woolly monkey, *Lagothrix flavicauda*, contacts and observations. July-August, 1994.

Date	Time	Duration (minutes)	Altitude (m)	Minimum Group Size
18 July	14h00	10	2,300	5
19 July	12h30	2	2,220	1
20 July	14h05	55	2,300	10
22 July	14h30	15	2,300	3
23 July	09h30	2	2,450	2
24 July	14h00	3	2,600	1
25 July	10h00	60	2,300	2
27 July	10h15	1	2,250	1 heard
27 July	13h30	35	2,650	5
30 July	17h00	5	2,250	2 heard
31 July	16h30	60	2,320	8
1 August	10h45	1	2,350	1 heard
5 August	10h30	2	2,300	2 heard

Table 2. Andean night monkey, *Aotus Miconax*, contacts and observations. July-August 1994.

Date	Time	Duration (minutes)	Altitude (m)	Minimum Group Size
15 July	19h30	30	1,860	2
16 July	21h00	30	1,860	2
17 July	21h30	20	1,860	3
18 July	19h00	5	1,860	1 heard
19 July	19h00	10	1,860	1 heard
20 July	20h30	15	1,860	1 heard
21 July	20h00	5	1,860	1 heard
22 July	21h00	15	2,300	2
23 July	22h00	5	2,300	1 heard
16 August	19h30	10	1,730	2 heard
17 August	21h00	5	1,730	1 heard

ous observers have found this species as low as 1,800 m (Leo Luna 1980), but the suggestion by Mittermeier *et al.* (1975) that it may occur as low as 500 m seems unlikely given the altitudes of subsequent records and the extent of human disturbance at lower altitudes. It was not recorded from site 2 (above San Cristobal, see Fig. 1), despite the presence of apparently suitable habitat, probably because of the lower altitude of the forest there, and the higher levels of disturbance by man. It is hunted for food, and locals reported that at least two individuals from our study site had been shot in the preceding two months. The confiding behavior, conspicuousness, and large size of this species make it an easy and attractive target for hunters. Both hunting pressure and the very rapid rate of habitat destruction found on the Cordillera de Colán threaten this species.

When rediscovered in 1974, Mittermeier *et al.* (1975) recommended that a protected area should be established to ensure the survival of this rare, endemic primate. Graves and O'Neill (1980) concluded that if this species was not given protection, it would quickly become endangered. Parker and Barkley (1981) also recommended the establishment of a forest reserve. The first field study of the monkey in 1980 emphasized the urgent need for a protected refuge (Leo Luna 1980). Large-scale deforestation has occurred since these recommendations were made. Although the yellow-tailed woolly monkey occurs in the Río Abiseo National Park to the south of its range (Leo Luna, 1993), a protected area in the Cordillera de Colán would be a significant step to support the conservation of this and other important mammal species.

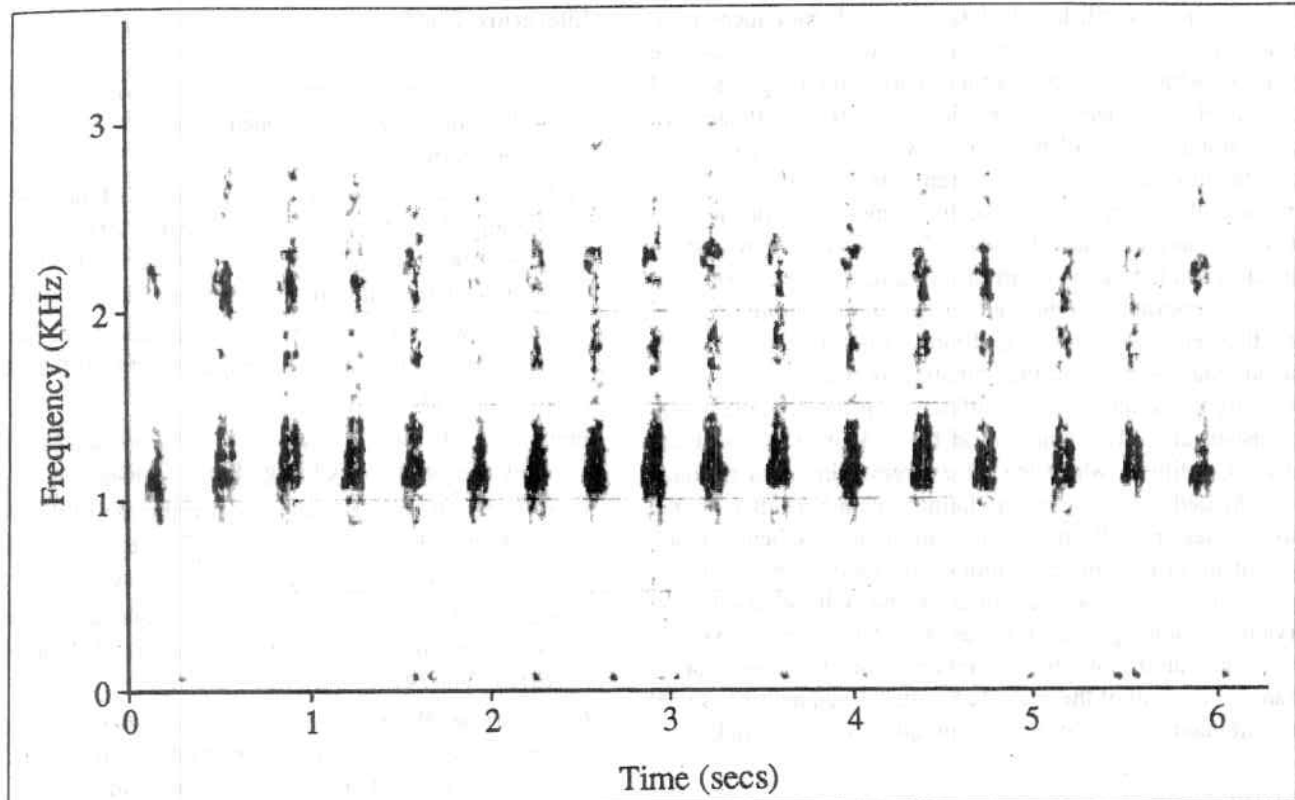


Fig. 2. Sonogram of calls of a male yellow-tailed woolly monkey, *Lagothrix flavicauda*.

The Andean Night Monkey, *Aotus miconax*

According to Hershkovitz (1983) and Ford (1994), the Andean night monkey, *Aotus miconax*, is the only night monkey found in the eastern Andes of Peru, south and east of the Río Marañón, and west of the Río Huallaga, where the Cordillera de Colán lies. This species was listed as vulnerable by IUCN (Groombridge 1993) and Rylands *et al.* (1995). Night monkeys were recorded at both sites visited in the Cordillera de Colán, and were found frequently at 1,860 m at site 1, and infrequently at two other altitudes (see Table 2). They were encountered in humid and very humid lower montane cloud forest in areas with little disturbance by man.

The series of observations at 1,860 m refer to repeated observations of the same group of night monkeys feeding approximately 15 m above the ground in the canopy of a fig tree, *Ficus*. Calls were heard frequently, particularly soon after dusk, and were described as loud, far-carrying, low-pitched hoots. These seemed to be given more frequently than the "series of whoopings" described for *Aotus* by Wright (1978), who only recorded such calls on three out of 34 nights.

Night monkeys appeared to be reasonably common in the areas of our study sites, and they are probably found at altitudes ranging from about 1,200 m to 2,300 m. They are reportedly not hunted for food, although an individual was being kept as a pet in the village of San Cristobal and had presumably been captured locally. The species is under threat primarily because of its restricted range and deforestation.

Other Species

A third species of primate, the brown capuchin, *Cebus apella*,

was found to be fairly common at both sites visited in the Cordillera de Colán. Eight observations of groups, numbering 2-15 individuals, were made at altitudes ranging from 1,550 to 2,350 m. It is interesting to note all these observations were above the altitudinal range given by Emmons and Feer (1990) for this species ("to 1,500 m"), and at these altitudes white-fronted capuchins, *Cebus albifrons*, might seem more likely, as they are found "to 2,000 m". However, good views were obtained frequently, and positive identifications were made by observers familiar with both species.

Local people informed of the presence of three other primate species not observed by the authors. They were the white-fronted capuchin, *Cebus albifrons* (a captive individual was seen in the village of San Cristobal), the red howling monkey, *Alouatta seniculus*, and the white-bellied spider monkey, *Ateles belzebuth*. These were reported to occur at lower altitudes, as would be expected from their known altitudinal preferences (up to 2,000 m; 1,200 m; and 1,800 m, respectively). The report of the latter species is interesting, as Emmons and Feer (1990) indicated that it is replaced by the black spider monkey, *Ateles chamek*, south of the Río Marañón. However, Mittermeier *et al.* (1975) reported finding a skin of *A. belzebuth* in the region, shot by a local hunter.

Another threatened mammal, the spectacled bear, *Tremarctos ornatus*, was found at site 1, with one observation at 1,550 m, one recently shot individual shown to us by a hunter, and numerous other signs of bears (trails, scats, and scratched tree trunks) in the area (Butchart *et al.* 1995).

Conservation of the Cordillera de Colán

Previous research in 1978 reported that the forest in the Cor-

dillera de Colán was still largely intact (T. S. Schulenberg pers. comm. in Collar *et al.* 1992). In contrast, we found large-scale deforestation, with areas in the northern part of the range reported to be completely degraded. Conservation action is urgently needed, as locals estimated that all the forests will be either cut or degraded in the next ten years at the current rate of destruction. The confirmation of the presence of the three species of primate reported here, including apparently healthy populations of two threatened species, and the likely occurrence of a further three primates, highlight the importance of the area. However, the limited amount of forest that remains, and the rapid rates of deforestation lead us to conclude that the conservation situation is critical.

We strongly recommend that an effectively protected area should be established urgently. This should be located in the southern part of the Cordillera, where the largest remaining area of intact forest is situated, and where populations of important mammal and bird species are still found. The conservation scheme should take advantage of current opportunities afforded to the improved security situation, and the local interest and willingness to help conserve the remaining forest (Davies *et al.* 1994). Effective prevention of the hunting of large mammals in the area should be an important component of the protected status. Such an area is vital for the continued survival of the yellow-tailed woolly monkey.

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A Survey of the Geographical Range, Habitats and Conservation of the Pygmy Chimpanzee (*Pan paniscus*): An Ecological Perspective

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This survey aims to outline the basic ecological conditions that determine the occurrence, abundance or rarity of the pygmy chimpanzee in its entire geographical range. Such a study is desirable for the following reasons:

(1) Nearly all field work has focused on only four sites within a relatively small area of the Central Zaïrean Basin: Lomako, Wamba, Yalosidi and Lilungu. All these four sites have approximately the same type of habitat.

(2) Most pygmy chimpanzee researchers cannot read the Belgian and Zaïrean geographical and botanical literature on the area in French and Flemish, and consequently ignore it. (For a translation of French technical terms compare Letouzey 1969 or 1982 with Letouzey 1986.) In fact, Zaïre is botanically the most extensively explored country of Africa except for South Africa (White 1983).

(3) These researchers had no access to unpublished data and other information available in Belgium which were collected during colonial times when guns were scarce among native hunters and the survival of the apes less threatened than nowadays.

This is a preliminary report because the collection of some data (including recent information from Zaïre and from satellite image interpretation) is still in progress. A comprehensive paper is being prepared. Publishing the preliminary results seems opportune because a better understanding of the basic factors involved in habitat ecology and affecting the vulnerability of the pygmy chimpanzee in its entire geographical range is important for its conservation.

Another reason for publication is to reduce the current confusion caused by the frequent incorrect use of technical terms by field workers on these apes. For instance, most of them call a seasonally inundated forest on clayish or sandy soil a "swamp forest". Properly speaking, a swamp has a predominantly organic soil and is by definition "a wet area that is normally covered by water all year" etc. (*Concise Oxford Dictionary of Ecology*, Allaby 1994). Furthermore, some authors call a rain forest on *terra firma* a "dry forest", a botanical term which refers to deciduous forests in the Sudanian and Zambezian vegetation belts. In addition, all authors with one exception consider the main type of forest in their study areas, the *Scorodophloeus* forest, as a "primary forest".

Actually it is in the central basin a centuries-old secondary forest, as is proven by the frequent presence of potsherds and charcoal in its soil, by its botanical composition and by its occurrence in the drier, subequatorial vegetation belt (Devred 1958; Evrard 1968; Lebrun & Gilbert 1954; Léonard 1952/55; Louis 1947). Only Sabater Pi & Veà (1994) among pygmy chimpanzee researchers have recognised the true nature of the *Scorodophloeus* forest. Finally, none of the primate field workers distinguishes the various botanical subtypes of the main types of vegetation in which their apes live. The developmental stages of an ecological succession — whether it is a swamp forest, a seasonally flooded forest, or a secondary forest — are usually not distinguished either. All this causes confusion when they try to compare different study sites. Unfortunately, vegetation experts have also contributed to the nomenclatural confusion. The latest example is the UNESCO-AETFAT-UNSO map (1981) and White's "memoir" to it (1983) in which the semi-deciduous rain forest (forêt semi-décidue, forêt mésophile) has been renamed as the "Guinéo-Congolian rain forest: drier types," and in French "forêt ombrophile planitiaire guinéo-congolaise: types relativement secs". Actually, in all the classical literature on tropical vegetation, "forêt ombrophile" or "forêt sempervirente" means evergreen rain forest as opposed to semi-deciduous rain forest. The renaming was founded on respectable phytogeographical and taxonomic grounds (White 1993). Basically, his classification distinguishes "regional centres of endemism", i.e. areas characterised by more than 50% endemic phanerogamic plant species totalling more than 1000 endemic species. This is, of course, all right in botany, but such a floristic concept contrasts with earlier ecological and physiognomic classifications based on the actual forms of life, e.g. types of forest, types of woodland, etc. Primatology requires primatomorphic concepts, even while using floristic concepts as research tools, e.g., in this paper. More generally, in zoology and conservation, we need clear-cut, non-confusing, descriptive terms. Regrettably, in a book published by IUCN, Doumenge (1990) has adopted White's terminology.

In the present paper I prefer the name "pygmy chimpanzee" rather than "bonobo" because it is the official term coined by Coolidge (1933) as a translation of its scientific species name "paniscus" (Schwarz 1929) which means little, lesser or pygmy chim-

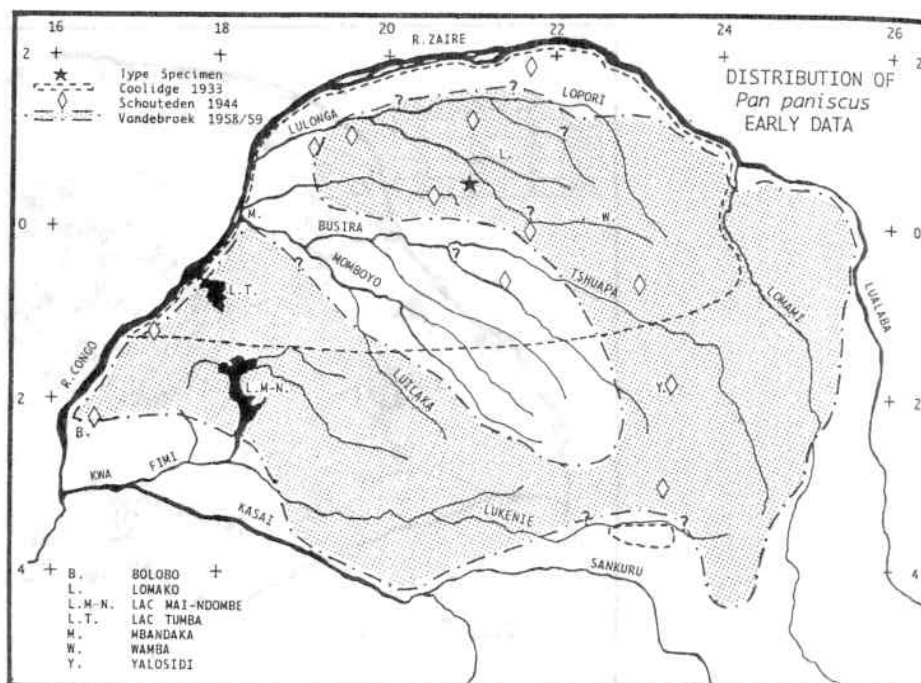
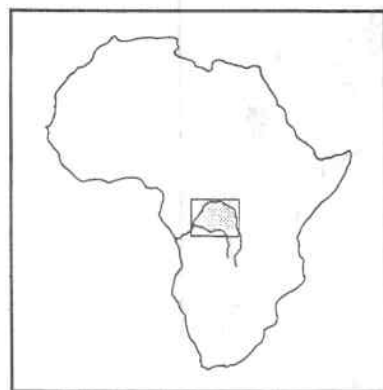


Fig. 1. Distribution of *Pan paniscus*. Early data.

panzee, furthermore because the names given by discoverers or first describers are generally retained in science, even if they are nonsensical (e.g. Greenland and even *Pan troglodytes*), thirdly because binomial names for primates are also current in vernacular language, fourthly because the species is indeed smaller on average than the common chimpanzee, and finally because the name refers to the "childish" (paedomorphic) anatomy of the species. It has a meaningful connotation. Schwarz himself summarised the six main anatomical features of the type specimen as follows (translated): "It is a definite pygmy [with] all characteristics of youth". "Bonobo" on the other hand is a nonsensical name, not a Zairean native word, and was proposed for obscure reasons as a new Latin genus name by Tratz & Heck (1954) to raise the taxonomic status of the species, but without bringing forward any taxonomical argument. It was a case of arrogance *vis à vis* taxonomy and against the leading American primatologist and conservationist H.J. Coolidge personally. Scientists should not endorse such bad science. Furthermore, trying to impose a new name by foreigners, without consulting with the authorities and zoologists in the host country (where the species is officially called "chimpanzé nain") also shows arrogance and a lack of courtesy that should not be endorsed by conservationists. Remarkably, a pygmy chimpanzee called Mafuka which lived in the Amsterdam Zoo from 1911 to 1916 had already been recognised as "a new geographical variety" and "probably a new species" by the then Animal Inspector of the zoo, A.F.J. Portielje (1913, 1916) but he did not give it a zoological name. (Further details in van Bree 1963.) With hindsight, the species should have been named "Portielje's chimpanzee (*Pan portieljei*)" by Schwarz and Coolidge, but they were not aware of the fact. The event seems never to have been recorded in any of the current literature on *Pan paniscus*, except by McHenry (1984). Renaming is now impossible according to the official rules of zoological nomenclature.

Available Data

The following sources have been used in compiling this review:

(1) Extensive geographical, zoological and botanical literature since 1936, in four languages, and maps and aerial photographs of the area.

(2) Unpublished extensive inquiries by Vandebroek in 1952-54 and his *carnet de chasse*, and unpublished records at the Musée Royal de l'Afrique Centrale, Tervuren. The Vandebroek data consist of 44 letters reporting the locations and observations of chimpanzees within the *Pan paniscus* area and a list of the locations of 27 specimens of this species that had been shot or otherwise col-

lected by or for him. A small part of his documentation has been lost.

(3) Recent inquiries by the present writer, N.M. Asquith and Dr. N.B. Bebwa, including 14 locality reports (excluding reports on current field work sites).

Of course, data collected by inquiries should always be interpreted with some caution. There is a statistical chance that a few reports are inaccurate or incorrect, but convergent evidence from several reports may be considered as reliable. Whenever possible, respondents should be interviewed personally. Unfortunately the two published regional field surveys on the presence or absence of pygmy chimpanzees have covered only relatively small areas of the total geographical range (Badrian & Badrian 1977; Kano 1984). They were not supplemented by botanical research. In the present paper an attempt is made to outline the ecology of the species by integrating all sources of data from the entire geographical range. The results are sometimes surprising.

Geographical Distribution

The geographical range of the pygmy chimpanzee is confined by two large river systems: the Congo-Zaire-Lualaba River and the Kwa-Kasai-Sankuru River (Fig. 1). They cannot cross these barriers because apes cannot swim. Within this area their distribution is, however, far from uniform:

(1) The semi-oval area in the central part of the Zaire basin where no pygmy chimpanzees were supposed to occur according to Vandebroek's (1958/59) map should have been drawn more to the south on his map, according to his own data as well as recent additional information (Figs. 1 and 2).

(2) The (apparent) absence or rarity of these apes in the southwest-central part and in the mid-eastern and southeastern part of their geographical range might, at least partly, be an artefact owing to the absence or scarcity of western informants in those areas,

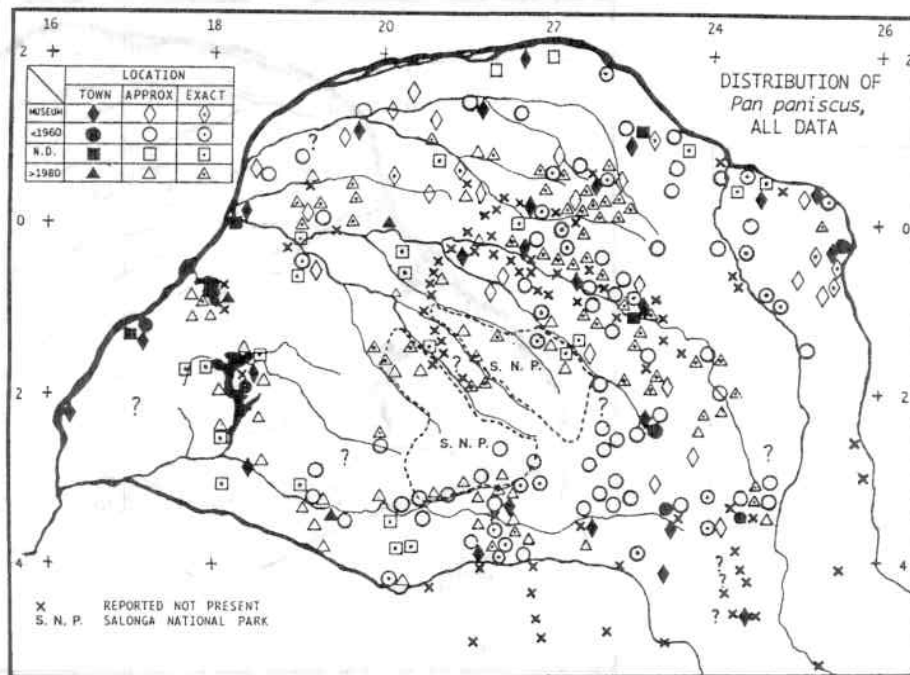


Fig. 2. Distribution of *Pan paniscus*. All data. About one half of the sites are imprecisely mapped, e. g. when the respondent wrote "observed (or shot) in the area of..." or "along the road from...to...". The dating was also sometimes uncertain. The unpublished IRSAC data mapped by Kano (1984, Fig. 1; 1992, Map 2) have been transferred to this map and are undated (N.D.) but are probably largely from before 1960 (U. Rahm, former Director, pers. comm.). The few data from 1961-1979 are included in N. D. The map has been revised and updated till January 1996 (see Postscript).

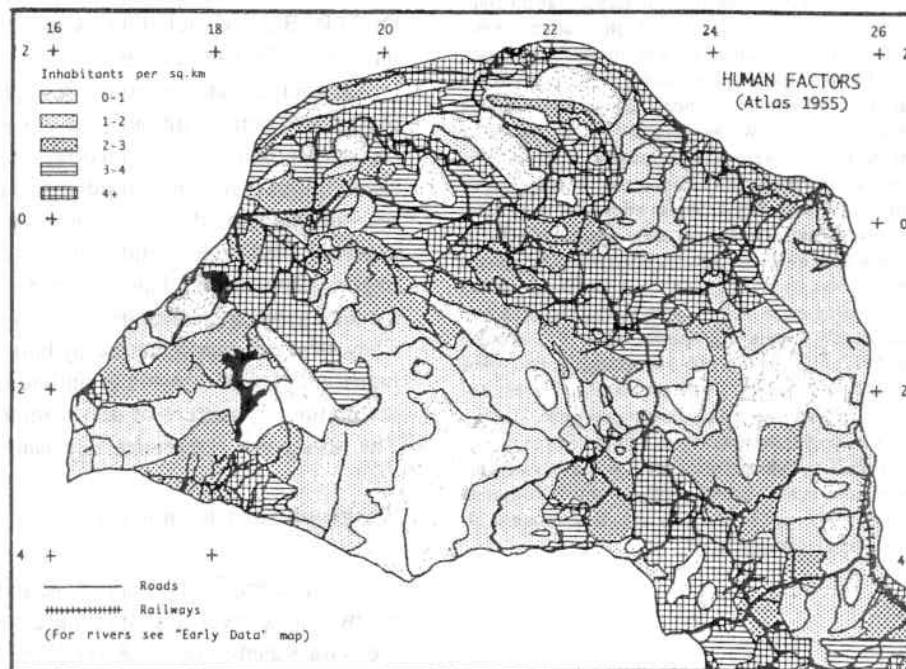


Fig. 3. Human factors. Rural inhabitants, roads and railways.

in the 1950s as well as today (Figs. 2 and 3).

(3) However, the (apparent) absence or rarity of the pygmy chimpanzee in the floodplain zones of the southwest-central part of the basin and between the Zaïre and Lulonga-Lopori rivers may be real, owing to occasional, abnormally high seasonal flooding (up to 2-3 m above normal high level) which would have killed many apes by drowning or starvation (Bouillenne *et al.* 1955; Savat 1973). In the southwest-central part the after-effect of intensive hunting before the sleeping sickness epidemic of 1895-1900

(Bouillenne *et al.* 1955) and during the heyday of the ivory trade (Anon. 1958) might possibly be an additional factor.

(4) The (apparent) absence or rarity in the SW corner of the range is probably real, owing to large-scale forest exploitation by the only industrial sawmill that already existed in the pygmy chimpanzee range in the 1950s (Anon. 1948-64).

(5) The (apparent) present-day rarity between the Lukenie and Kasai rivers is probably real in the zones bordering the rivers, owing to human hunting and trapping, as a serious decline of the

species along the river banks had already been reported in the 1950s (Vandebroek's inquiry reports). The same may apply to other navigable river routes. Away from the rivers the species may still be common.

(6) The high density of reported sites in the triangle between Boende, Yahuma and Ikela, both in the past and at present, is clearly correlated with a dense rural (native) population and a dense road network, i.e. probably a high density of western informants. It therefore does not necessarily indicate that the pygmy chimpanzee population outside this area should be less dense or even absent (Figs. 2 and 3). On the contrary, it is quite plausible that a similar or even higher population density of these apes occurred and may still occur in regions with a similar forest vegetation but with a sparser human population.

(7) In the past, the area between the Lomami and Lualaba rivers from 0°40'N to 1°S has always been known to harbour a dense pygmy chimpanzee population (Fig. 2 and hearsay). Ten of the 21 specimens collected (probably shot) by or for Vandebroek in 1955 came from that area (*Carnet de chasse*). Colyn and his students collected in 1980-84 during 35 months the skulls and skins of the small and medium-sized mammalian game (from rodents to apes) captured or killed mainly by terrestrial and arboreal snares, and subsequently consumed by the villagers of Ubilo, 60 km S of Kisangani on the railway to Ubundu. The collection consisted of 1501 mammals, including 290 primates among which were 20 pygmy chimpanzees, i.e. 1.33% of all mammals and 6.90% of all primates (Colyn *et al.* 1987). One may assume that the apes are still there because the area is sparsely populated. In the same way the authors collected in the village of Enano, 50 km E of Kisangani in the same type of environment on the opposite bank of the Zaïre River, the skulls and skins of 4775 mammals, including 1076 primates among which were 71 common chimpanzees, i.e. 1.49% of all mammals and 6.60% of all primates. Thus there seems to be no reason to believe that in this region the pygmy species is more rare or more threatened than its relative of the opposite bank.

(8) No data are available from the area west of the Lualaba between 24° and 26°E from 1° to 3°S because there were and are no roads and the area has remained virtually unexplored (Ndjélé 1988). One report to Vandebroek from Lokandu (2°34'S 25°44'E) on the west bank of the Lualaba river stated that chimpanzee calls were heard "every night" from the opposite bank (where *Pan troglodytes* lives) without mentioning the presence of chimpanzees on the west bank. This may, however, be attributed to the sound-damping acoustics of the forest. During my survey of the common chimpanzee I noticed such phenomena on forest edges.

(9) The (apparent) absence of the species in the southeast corner between the Sankuru and Lualaba rivers, south of 3°30' or 4°S is a mystery. On the one hand, vast tracts of rain forest still exist down to 5°30' and 6°S in parts of the area. On the other hand, a dense rural population and a dense road network in other parts would have ensured effective reporting (Figs. 2 and 3). (Data in items 2-9 from Anon. 1948-64; Anon. 1958; Gourou 1955; various maps). For comparison: the limit of the common chimpanzee east of the Lualaba river is, or was recently, at 7°30'S (Kortlandt 1983; Vandebroek's correspondence).

(10) The development of current ideas on the geographical distribution is almost a repetition of the development during 1929-1955. Coolidge (1933) drew the boundary approximately around

the northern half of the range, not beyond the Lomami river and with only one site at the Lukenie, because the remainder of the central basin was still almost *terra incognita*. Vandebroek (1958/59) discovered more or less the real range of the species. Newcomers since 1972, however, could not believe this, reproduced Coolidge's map even without the Lukenie site, ignored more recent maps, and/or supposed that the species hardly occurred, or not at all, in its southern range and east of the Lomami (e.g. Kano 1992). At present the true range is being rediscovered by D. Messinger and J.M. Thompson (pers. comm. and Thompson-Handler *et al.* 1995). Further exploration in an eastern and southeastern direction may yield some surprising results. It should be done.

Habitats

Very little is known about the ecological benefits of the various habitats where either common or pygmy chimpanzees occur. Comparative data from different types of habitat about the production of edible fruit in kg per hectare per month and about their nutritional value hardly exist, in spite of long botanical lists of foods eaten by these apes (see, however, Hladik 1973 and Hladik & Viroben 1974). One has to rely, therefore, on circumstantial evidence. Theoretically one would expect that forests with a K-type of reproduction, i.e. a slow growth, a long life and a low reproduction rate, would produce little chimpanzee food. Forests with an r-type of reproduction, i.e. with the opposite characteristics, should be excellent chimpanzee habitats (e.g. Bazzaz & Pickett 1980; see also for comparison van Schaik & Mirmanto 1985 and Djojosedharno & van Schaik 1992). One would also expect that forests with a relatively open stand of the tall trees, i.e. the semi-deciduous forests of the monsoon zone and forests that have been thinned out and rejuvenated by small-scale shifting cultivation, moderate selective logging and/or elephant action, would be the best chimpanzee habitats because these apes are mainly specialised to walk long distances on the ground and to climb isolated fruit-bearing tall trees. Conversely, undisturbed evergreen forests in the equatorial zone should be bad chimpanzee habitats because their dense, continuous canopies would be more advantageous to monkey competitors. Moreover, in such forests, there is little undergrowth and consequently no fall-back food source for a ground walker in times of food shortage at the canopy level (e.g. Tutin *et al.* 1991). Finally, of course, one expects fewer chimpanzees in habitats with less tall trees such as open woodlands, savannas and (true) swamp forests. These predictions apply to the common chimpanzee (Kortlandt 1965, 1968, 1972, 1983, 1984a, 1984b, with photographs of habitats and profiles of forest types; Thomas 1991). But do they also apply to the pygmy species? If not, or if there would be some minor difference, one would have a clue to their difference in ecological specialisation and evolutionary background. From a chimpomorphic point of view the following five main types of vegetation may be distinguished and their ecological merits specified (Table 1 and Fig. 4; see also Kortlandt 1983). The subtypes will be dealt with in a later paper (in prep.).

(1) Pygmy chimpanzees regularly forage in small swamp meadows on a very thin underlying peat layer. However, they seem never to have been observed in swamp meadows and swamp forests on deeper underlying peat along rivers and in ox-bows. (For

botanical descriptions of such true swamps see Bouillenne *et al.* 1955; Compère & Symoens 1987; Evrard 1968 and Lubini 1985; for physiographic descriptions Bouillenne *et al.* 1955; Kortlandt 1972; Lebrun 1936 and Léonard 1953.) The slender build, long legs and frequent bipedal gait of *Pan paniscus* might conceivably have evolved as a secondary adaptation to the watery and swampy environment in the deltaic western part of the Zaïrean basin. These features facilitate wading and they reduce the risk of being drowned when sinking through the vegetation mat because a quadruped walker or runner disappears head-first into the mud. Pygmy chimpanzees do indeed occasionally wade in shallow water with a solid bottom (Badrian & Badrian 1977). By means of tests in captivity

it should be possible to find out whether the species is more willing and better adapted than its relative to cross rivers by wading. Common chimpanzees have occasionally been observed in swamp meadows and forests in the Republic of Congo, eastern Zaïre and Uganda (Fay 1989 and pers. comm. Kortlandt 1972; Mitani 1992; photo 1). When necessary they jump bipedally like frogs from one tussock to the next. Perhaps the observers of pygmy chimpanzees have not yet ventured into such treacherous habitats. Or possibly the apes themselves are too shy to enter large open swamp meadows. For comparison, orang utans can thrive in Bornean true swamp forests (Galdikas 1978).

(2) The data on the occurrence of these apes in seasonally



Photo 1: A characteristic view of a subclimax swamp forest on peat soil, with scattered tall trees and an irregular lower layer of *Phoenix* palms. Two chimpanzee nests can be seen in the top of the tall (*Xylopia*) tree at left. (Kibona Swamp, Queen Elizabeth National Park, Uganda near the Zaïrean border, 0°13'S 30°02'E, © A. Kortlandt, No. 64-6-33.)

flooded forests on mineral soils are somewhat equivocal owing to the imprecise use of the term "swamp" and also because the subtypes of the botanical succession are not distinguished by the researchers. Botanical descriptions are provided by Bouillenne *et al.* (1955), Compère & Symoens (1987), Evrard (1968) and Lebrun & Gilbert (1954), a physiognomic description by MacKinnon (1978) and a photograph by Lebrun & Gilbert. Extensive lists of the foods eaten by pygmy chimpanzees have been published for the four main study sites. These sites contain both seasonally flooded and non-flooded forests. Surprisingly, the fruit mentioned in these lists include only one to four tree species considered to be botanically "characteristic" of seasonally flooded forests (Badrian & Malenky 1984; Idani *et al.* 1994; Kano & Mulavwa 1984; Sabater Pi & Veà 1994; botanical characterisation by Evrard 1968 and Lebrun & Gilbert 1954). This is remarkable because the seasonally flooded forests produce most fruit at a time when the fruit yield of the non-flooded forests is poor. Altogether the seasonally flooded forests do not seem to be good pygmy chimpanzee habitats (See also Horn 1980; Kano 1984).

(3) More favourable habitats for common as well as pygmy chimpanzees are the intermediate and older stages in the development of secondary forests. These forests are predominantly semi-deciduous, even in the evergreen vegetation belt around the equator, they have an r-type of reproduction, they produce mainly fleshy fruit adapted to dispersion by mammals and birds, their upper canopy is relatively open and irregular, and they have a substantial amount of undergrowth. Their age can be estimated from their botanical composition and from the trunk diameters of some characteristic tree species (e.g. Pierlot 1966). They are botanically heterogeneous from one site to another when they have been created by small-scale shifting cultivation by a sparse human population, and/or by nomadic elephant foraging, and/or by long-term low-intensity selective logging (Evrard 1968; Nanson & Gennart 1961; a profile in Bouillenne *et al.* 1955; and general literature on African forest vegetation, e.g. Letouzey 1986, Schnell 1970-77; photos 2a and b). A somewhat transitional type between the periodically flooded and the secondary forests has been described by Mosango & Lejoly (1990), with a profile. Mosaic forests are highly

favourable to long-distance walkers which are specialised to climb isolated tall trees. Their botanical diversity is particularly important, at least for the common chimpanzee (Kortlandt 1983, 1984a, 1986). In addition, the ground level vegetation provides food in times of scarcity in the canopy. These forests harbour the highest chimpanzee population densities when the apes are not hunted: 2 to 3 and even 4 per km² in the common chimpanzee area (Walikale, Beni, Budongo and Rabongo) and up to 3½ per km² in the pygmy chimpanzee area (Wamba and Lomako). Thus the ecological prediction based on botanical analysis, observations of tree architecture, and locomotion patterns is confirmed by the population densities. (See also Kortlandt 1965, 1983). This agrees with Kano's (1984) important conclusions that a "light degree of slash-and-burn agriculture diversifies the vegetation and works to the advantage more of the bonobo than of other nonhuman primates" and that "secondary vegetation works to the bonobo's advantage only where a vast primary forest is also available", provided that one translates Kano's incorrect term "primary forest" into "centuries-old secondary forest". Similarly, Thomas (1991) observed in the Ituri Forest (east of the central Zaïre basin) the highest population density of the common chimpanzee in remote old-secondary and "mixed" (mosaic) forests. Admittedly, Tutin & Fernandez (1984) and White (1992) obtained different results from their survey of chimpanzees in various habitat types in Gabon, but the secondary forests in their study area were at most only 25-50 years old. The current descriptions of foraging behaviour suggest that the older a secondary forest is the better it is as a food source for these apes (Kortlandt in prep.). It is indeed significant that the four main study sites of pygmy chimpanzees are all located in predominantly *Scorodophloeus* forests, i.e. in the last, most mature, and florally richest stage in the development of secondary forests in the central Zaïrean basin, or more briefly the *subclimax*. It is the pygmy chimpanzee's optimum habitat. It is also probably the most widespread type of forest in the central basin. This implies that the basin must have been fairly densely populated by shifting agriculturists since the arrival of the Bantu peoples some 2500-2000 years ago (Eggert 1992) until the outbreak of the sleeping sickness epidemic in 1895-1900. The extensive data published by



Photos 2a and b: In the Rabongo Forest a semi-deciduous *Cynometra-Holoptelea* lowland rain forest has been thinned out and rejuvenated (but not overbrowsed) mainly by elephants and additionally by buffalos and hippos. This has created a quite dense undergrowth which provides fall-back food in times of fruit scarcity in the trees. In 1964 the chimpanzee population density amounted to 2.7 (or more) per km² (J. M. Savidge, pers. comm., Murchison Falls National Park, NW Uganda, 2°04'N 31°52'E, ~1200mm annual rainfall, one physiologically dry month, © A. Kortlandt, Nos. 64-11-29 and 26).

Idani *et al.* (1994) suggest that a more penetrating analysis of the botanical diversity and of the successional aspects of the forest vegetation at the Wamba site should be possible. Such an analysis, in combination with food studies, might substantially clarify the ecological specialisation of the pygmy chimpanzee. It should be done. [Data on the *Scorodophloeus* forest in Devred (1958); Evrard (1968); Léonard (1952/55, 1953); Louis (1947) and Nanson & Gennart (1961); a profile in Léonard (1952/55, 1953) and Louis (1947); physiognomic description in MacKinnon (1976, 1978). Unfortunately MacKinnon causes confusion by generalising and incorrectly calling the (secondary) *Scorodophloeus* forest "the African rain forest", and then equally incorrectly contrasting it with "the Asian rain forest", i.e. the Malaysian (primary) Dipterocarp forest.]

(4) Two kinds of really primary forests, i.e. climax forests, have been described in the equatorial zone of the basin: the *Gilbertiodendron dewevrei* forest which occurs on relatively moist soils in valleys and the *Brachystegia laurentii* forest which occurs on the somewhat drier soils on plateaux. Both are by definition in a state of ecological and demographic equilibrium. Both are evergreen, both tend slowly to invade into and overwhelm the *Scorodophloeus* forest when they are bordering on it, and no potsherds or charcoal seem ever to have been found in their soil. That is, they are more than 2000 years old. Their canopy is homog-

enous, flat and very dense. Seen from the air they look like sheep huddled closely together (photo 3). Consequently there is little undergrowth. Their oblique branching systems are uncomfortable for chimpanzee locomotion. The fruit of the two dominant tree species and several others are woody and probably inedible to chimpanzees until germination is beginning. They are floristically poorer than the *Scorodophloeus* forest, even though they harbour more endemics which emphasises their evolutionary antiquity (Botanical descriptions in Devred 1958; Evrard 1968; Gérard 1960; Germain & Evrard 1956 and Nanson & Gennart 1961; profiles in Germain & Evrard 1956; Léonard 1952/55, 1953; Louis 1947; physiognomic description in Moffett 1993). Whether pygmy chimpanzees regularly live and forage in these forests is doubtful. According to the staff of the INEAC in Yangambi (who until 1960 conducted much agricultural and forestry research on both sides of the Congo-Zaire River) no "chimpanzees" occurred in *Gilbertiodendron* and *Brachystegia* forests (pers. comm. 1960), but it is not clear from my notes whether this referred only to the common species or to both species of ape. The Wamba study site includes an area of *Gilbertiodendron* forest, but only two tree species considered by botanists as characteristic of the (truly) primary forests have been reported from there as providing pygmy chimpanzee food (Kano & Mulavwa 1984). No common chimpanzees were spotted by Thomas (1991) in a large continuous area of



Photo 3: Central African evergreen (climax) lowland rain forests in the equatorial zone show a dense stand of the tall trees and a closed, dense and rather flat canopy. Consequently there is very little undergrowth (Réserve de Faune de Douala-Edéa, SW Cameroun, 3°55'N 9°40'E, ~4000 mm annual rainfall, no dry month, © A. Kortlandt, No. 64-15-18).

Gilbertiodendron forest in the Ituri Forest. Apparently the (truly) primary forests in the equatorial zone are the worst types of forest habitat for these apes. This raises two questions: Did their ancestors evolve during the Pleistocene in another climate with another vegetation than nowadays in the basin? Or were the primary forests in the Pleistocene regularly secondarised by foraging elephants and other large herbivores which have since been decimated by human hunters as a result of the invention of the spear? Whatever the case, the available evidence from forested habitats does not indicate any noticeable ecological difference between the two chimpanzee species, in spite of their conspicuous differences in locomotor abilities and social life.

(5) Devred's (1958) vegetation map shows that between the evergreen belt and the Kwa-Kasaï-Sankuru river there is a 100-200 km wide southern belt of primary semi-deciduous forests, together with a transitional zone along the evergreen belt, secondary forests and islands of savanna vegetation (Nos. 6-9 in Fig. 4, cf. Nos. II, IIIa and part of IIIb in Renier 1957, and Nos. 2 and 11a in UNESCO-AETFAT-UNSO 1981; see also Devred 1957, Duvigneaud 1949, 1955; Lebacqz & Dechamps 1967; Liben 1958; Lubini & Kusehuluka 1991; Mullenders 1954). Only relicts of the primary semi-deciduous forests remain in this belt. Their characteristics are much the same as those of old and centuries-old secondary forests in the evergreen belt: an irregular and somewhat open upper canopy, a relatively dense undergrowth, mainly fleshy fruit and predominantly an r-type of reproduction. Viewed obliquely from the air they resemble sheep of unequal size standing somewhat apart so that one can see the tree trunks as if these were the legs of the sheep (photo 4). One would expect in such primary and old secondary semi-deciduous forests in this belt a dense pygmy chimpanzee population because the common chimpanzee has its highest population densities in the primary and old secondarized semi-deciduous forests of eastern Guinea, eastern Zaïre and western Uganda (Kortlandt 1965, 1968, 1983, 1984a, 1986; R. Schnell pers. comm. 1965). A dense population of the pygmy species appears indeed to have occurred at least in the past in this semi-

deciduous belt. It seems even conceivable that this zone provides for them as good optimum habitats as the northern semi-deciduous belt does for the common species. Vandebroek's correspondence contains indeed many reports from the Lukeni-Sankuru region, in spite of the low density of potential respondents in this area (Fig. 2, compare with Fig. 3). They appear to have been particularly numerous in the region around Dekese (3°28'S 21°24'E). One respondent wrote that on the road between 20 km and 45 km south of Dekese "it rarely happened not to meet a group" (F.E. Torfs 1954, translated). Another reported that in 1946-48, when the old riverboat on the Lukenie anchored on the forest edge to spend the night between Watu and Bumbuli (between 20°03' and 20°31'E) "it frequently happened that the chimpanzees prevented the passengers to sleep", i.e. by their cries (W.J. Carels 1954, translated). Even nowadays the apes still seem to be fairly common in the area, judging from the animal trade. "Suppositions about bonobos becoming exterminated along the Kasaï river (but not yet the Lukenie) seem premature and presumptive. Around one half of the bonobos arriving in Kinshasa come from the southern range of the species" (D. Messinger pers. comm. 1992). A population in a mosaic habitat of forest, savanna and grassland near Yasa (3°49'S 21°21'E) is currently being studied by J.M. Thompson (pers. comm. and Thompson-Handler 1995). Thus the primary semi-deciduous forests of the southern belt may conceivably be as beneficial habitats as the old secondary *Scorodophloeus* forest. Whatever the case, any belief that the species may have disappeared in the southern part of its range (e.g., Kano 1992) is the worst possible viewpoint. Such ideas will seriously harm both research and conservation efforts.

(6) As mentioned, the apparent absence of the species in the SE corner of its geographical range beyond 3°40' or 4°S is a mystery. There are two uncertain (i.e. second-hand) reports about its presence, two museum specimens (which may have been killed elsewhere) and five negative reports from this area in the 1950s. Yet there were and still are extensive rain forests down to 5°30' and 6°S. (Fig. 4 from Devred's 1958 map which is based on information from 16 botanists in the former Belgian Congo and probably on topographic maps and aerial photography, and Fig. 5 from WCMC [1991] and Sayer *et al.* [1992], based on remote sensing but not very reliable). A survey aiming to determine the presence or absence of pygmy chimpanzees in these forests, nowadays and in the past, would be extremely important from an ecological viewpoint because this is the only area where the dispersal of the species is not blocked by river barriers. Such a survey should be carried out by interviewing the elderly local hunters in the local language while showing primate pictures, using a mountain bike or light moped to reach remote villages, and performed by an experienced botanist (accompanied by a translator, if necessary). The entire area between the Sankuru and the Lualaba from 4° to 8°S has been insufficiently explored botanically (Ndjélé 1988).

(7) Contrary to widespread belief, there is some good evidence, particularly from countries surrounding the Zaïrean basin, indicating that since about 1000-500 years ago the rain forest, when not cut or burnt, has expanded and still expands into the woodlands and savannas (Aubréville 1957; Bouillenne *et al.* 1955; Boulvert 1990; Deuse 1960; Elenga *et al.* 1994; de Foresta 1990; Lebrun 1936; Maley 1990; Schwartz *et al.* 1990; Vincens *et al.* 1994; White 1992 and references below; compare also the SE of



Photo 4: Semi-deciduous climax and subclimax lowland rain forests in the monsoon zone, as well as old mature and subclimax secondary lowland rain forests in the equatorial zone, have a more open stand of the tall trees and an irregular, relatively open canopy, so that one can see the tree trunks from the air. Consequently there is much more undergrowth than in the evergreen forest (Réserve Forestière de Berberati, SW Central African Republic, 4°13'N 15°47'E, ~1600 mm annual rainfall, two physiologically dry months, © A. Kortlandt, No. 65-14-17).

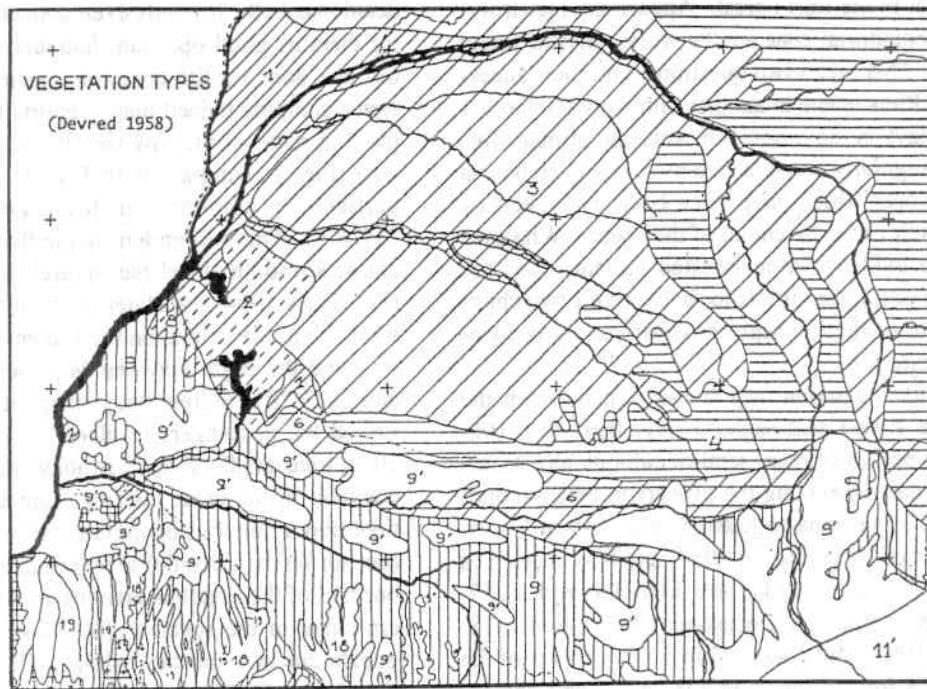


Fig. 4. Vegetation types (Devred 1958).

Table 1: Vegetation Types (Devred 1958)¹

1. Forêts édaphiques.
Forêts marécageuses et forêts périodiquement inondées pour plus de 80%, mélangées de formations herbeuses aquatiques, d'«esobe» et d'îlots de forêts sempervirentes de terre ferme.
2. Forêts édaphiques pour 50% mélangées de forêts denses humides sempervirentes.
3. Forêts denses humides sempervirentes et forêts denses humides semi-décidues de dégradation pour plus de 60% mélangées de forêts marécageuses et périodiquement inondées le long du réseau hydrographique.
4. Forêts denses humides sempervirentes et forêts denses humides semi-décidues de dégradation.
5. Forêts denses humides sempervirentes avec quelques essences forestières semi-décidues suborophiles.
6. Forêts denses humides sempervirentes mélangées de forêts denses humides semi-décidues subéquatoriales et guinéennes.
8. Forêts denses humides semi-décidues subéquatoriales et guinéennes mélangées de forêts marécageuses.
9. Forêts denses humides semi-décidues subéquatoriales et guinéennes et forêts denses secondaires avec îlots de savanes guinéennes (9').

¹The French technical terms have not been translated because they are more sharply defined than their English semi-equivalents used in other parts of Africa.

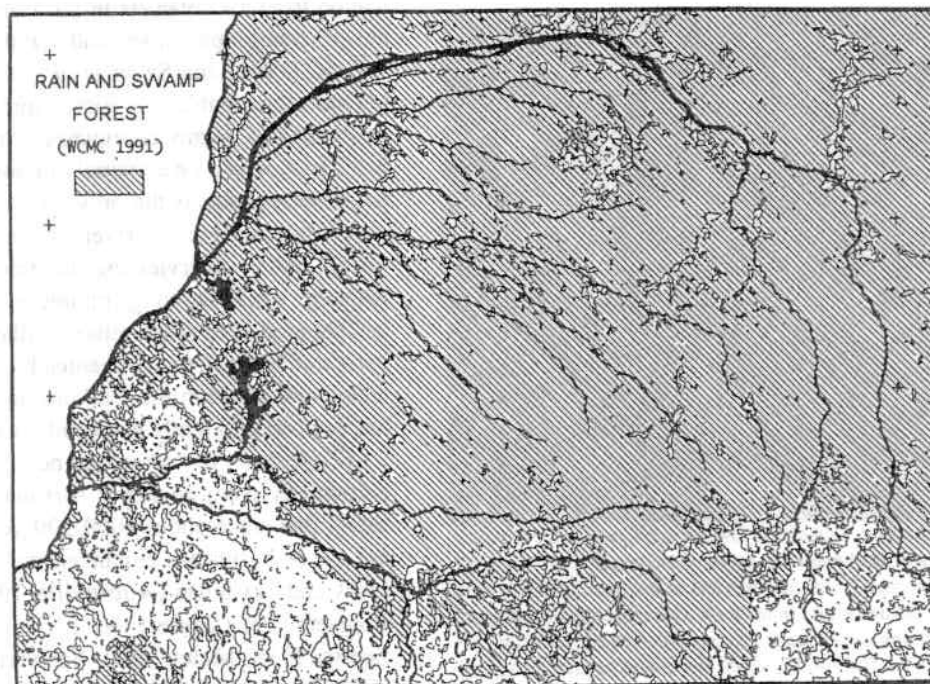


Fig. 5. Rain and swamp forest (WCMC 1991).

the basin in Figs. 4 and 5 in this paper). This might conceivably mean that many or most of the rain forests between 4° and 6°S are still relatively young secondary forests compared with the *Scorodophloeus* forest. Possibly the area was deforested in past centuries or millennia by a dense agricultural population who also used much wood in their iron-smelting furnaces, until this population was wiped out by the sleeping sickness epidemic in the 1890s. That is in fact what happened in the Lake Tumba area (Bouillenne *et al.* 1955) but we do not know the historical facts for the SE of the Zaïrean basin. The idea can be tested by analysing the present-day flora, the past flora buried in swamps, and the prehistoric finds, in combination with ¹⁴C dating. It should be done. On the other hand, it is equally possible that this unexplored area harbours some very old secondary and even primary forests inhabited by undiscovered (or recently exterminated) pygmy chimpanzees. This possibility should be investigated too. The new Methodist Patrice Lumumba University at Wembo-Nyama (4°14'S 24°27'E) may provide a practical base within the area. Relict forests containing many *Scorodophloeus zenkeri* trees, and locally some *Gilbertiodendron dewevrei* and *Brachystegia laurentii* trees, still occur (or occurred until recently) in belts 9 and 9' on Fig. 4 south of the Kasai-Sankuru river down to 6°S, with surfaces up to 240 km² (Devred 1957; Leback & Dechamps 1967; Lubini & Kusehuluka 1991; Mullenders 1954; Renier 1957). So why should similar forests inhabited by pygmy chimpanzees *a priori* be considered unthinkable in the corridor between the Sankuru and the Lualaba?

Impediments to Dispersal

(1) If indeed there are or were in the recent past no pygmy chimpanzees beyond 3°30' or 4°S in the southeast of their natural range, three possible explanations may be proposed:

(a) After the demise of the agricultural population as hypothesised above and the subsequent natural reforestation of the region, the pygmy chimpanzee may not yet have had enough time to regain its former natural range. This explanation, however, does not seem plausible because from field work on common chimpanzees we know that they are able to quite rapidly expand into neighbouring territory, even by "ethnic cleansing" of established conspecifics (Goodall 1986; Nishida *et al.* 1985). Still, the pygmy species may be different in this respect because it is much shyer.

(b) Owing to climatic fluctuations and/or the aftermath of agricultural developments, the more advanced types of secondary forest with their rich flora and predominance of fleshy fruit may not yet have recolonised the area south of 4°S. We know from the analysis of pollen in swamps and from old lake level marks in the area around the Zaïrean basin that the cool and quite dry climate during the latter part of the last Ice Age was followed by climatic fluctuations during the last millennia, perhaps with a cycle period of about 1300 years and presumably with increasing rainfall during the last several hundred years. These fluctuations are, however, obscured by the (partly apparent) aridification caused by the advent of the Iron Age and the following extension of agriculture into the forest belt, probably during the last two millennia (e.g. Eggert 1992; Jolly 1993; Moeyersons & Roche 1982; Muaka *et al.* 1984; van Neer 1990 and references above; see also de Foresta [1990] on Marantaceae and Zingiberaceae). We also know that

many tree species of old secondary forests and of primary forests have a slow rate of reproduction and dispersal (see above). These may often have been unable to follow the southward and northward oscillations of the vegetation belts and they will certainly not have reoccupied tracts of fallow land stretching over hundreds of miles after a sudden collapse of agriculture a century ago. The suggestion should be tested by a botanical survey and, if possible, be verified by subfossil wood research, pollen analysis and archaeological dating.

(c) The high sensitivity to disturbance and stress of the pygmy chimpanzee may have prevented it from reoccupying its former grounds after the demise of the agricultural invasion, even in areas which have now less than two human inhabitants per km². Several reports received by Vandebroek stated that these apes tended to stay away many hours walking distance from native villages, contrary to common chimpanzees. (Admittedly there were exceptions, including nowadays at Wamba.) Perhaps they are terrified by the sounds of guns and drums. During the bombardment of a German zoo in the last war, the three pygmy chimpanzees died from stress while the common ones survived (Tratz & Heck 1954). All 86 pygmy chimpanzees captured in the late 1950s by the Laboratoire Médical Provincial in Stanleyville (now Kisangani) for the American polio research programme died within three weeks, contrary to nearly all the common chimpanzees captured by them (Kortlandt 1976). All this indicates an extraordinary sensitivity to any kind of disturbance and stress. (See also Badrian 1977; Horn 1980; Kano 1980).

(2) This sensitivity may be related to the more arboreal way of life of the pygmy chimpanzee. Tree-dwelling primates are, as a rule, more relaxed and peaceful than ground-dwellers and semi-terrestrial species. Intraspecific bullying does not pay because the smaller individuals can always flee from the larger ones onto thinner branches. In the canopy there are fewer predators and food competitors around, and snakes can be more easily spotted. Thus one need not be surprised when the pygmy species is not adapted to cope with amounts of disturbance, danger and stress which were normal in the everyday life of many common chimpanzees in former times, when nearly one half of the latter's geographical range consisted of open woodlands and savannas. Conservationists, field workers and zoo personnel should keep this sensitivity in mind.

(3) Solving the mystery of the pygmy chimpanzee's ecological limits may also clarify the puzzle of its evolutionary origin. Is the species a primitive form, so to speak a living fossil more closely related to humans than the common chimpanzee, as proposed by Coolidge (1933) and still advocated by Zihlman (1984)? This may sound plausible because the Zaïre central basin was a Pleistocene faunal refuge (Colyn 1987) and also because the suggestion is supported by some anatomical and locomotor features. It is contradicted, however, by some other features, e.g. knuckle-walking on moderately thick branches when gripping the branch in the monkey and orang-utan way would be more appropriate. Or is the pygmy chimpanzee a secondarily "gibbonised", or more precisely "siamangised", adaptation to an exclusively forest habitat behind water barriers, as proposed by Kortlandt (1972) and MacKinnon (1978), perhaps at a time when the forests extended in the south-east to the large swamps in southern Shaba (Katanga) which might then have been a fairly effective barrier? But if so, where is the third chimpanzee species that should have survived in the large

forests south of the Zaïre-Kasai river in western Zaïre and Angola? Was it perhaps starved to death by the climatic drought from 25,000 to 12,000 BP? Its historic existence was erroneously claimed by Johnston (1905) but rectified by the same author in 1908. Or rather, is the pygmy species a case of secondary "insular dwarfism" behind the river barriers, similar to the dwarfism of mammals on isolated islands observed in palaeontology, as proposed by Johnson (1981)? The idea is not very plausible because the evolutionary root of such dwarfism, i.e. the absence of large predators (Sondaar 1976), does not apply to the Zaïre basin: there are leopards, crocodiles and large constrictor snakes.

(4) Whatever speculation one prefers, the fundamental questions are: Why are these apes smaller and more slender, why have they longer legs and why do they walk more often bipedally than their close relatives? Just one anomaly: long legs and bipedal gait are beneficial in watery and swampy habitats, but disadvantageous when climbing the thick and smooth tree trunks of the rain forest. On the other hand, the anatomical features may conceivably be advantageous in habitats in which trees with a relatively more or less horizontal architecture of their branch systems predominate (Pictures of trees in Letouzey 1969, 1982, 1988; Pieters 1977 and Tailfer 1989; see also the forest profiles in Bouillenne *et al.* 1955; Germain & Evrard 1956; Léonard 1952/55, 1953; Louis 1947; and Mosango & Lejoly 1990 and the general literature about tree architecture, e.g., Hallé *et al.* 1978). Of course, we all have learned that the pygmy chimpanzee is more arboreal in its behaviour than the common species, but that is not the full story. Compared with its relative, the pygmy chimpanzee is more arboreal horizontally, i.e. in the canopy, but it is less arboreal vertically, i.e. up and down thick tree trunks. One may even wonder whether its type of arboreality is an evolutionary cause, or an evolutionary consequence of its paedomorphic anatomy. Human Pygmy peoples have become smaller due to secondary adaptation to their rain forest habitat. They are also the mountaineers of the rain forest (Photographs in Kortlandt 1961/62). On the other hand, many large mammals have become larger due to secondary adaptation to open woodland, savanna and grassland habitats. Primary and secondary adaptation cannot be distinguished at first sight. The big question is: How, why, where and when did pygmy chimpanzee locomotor behaviour and its anatomical correlate evolve? Our present-day knowledge of habitats and foods provides no answer (This paper and in prep.). The ancestors of our contemporary African apes, subgenus *Proconsul*, were supposedly semi-arboreal, semi-terrestrial. Research on the interrelation between anatomy, locomotion, tree architecture, habitat types and foods of both species of chimpanzee has hardly started (e.g. Doran & Hunt 1994; MacKinnon 1978; Reynolds & Reynolds 1965; Susman 1984; Susman *et al.* 1980). No one among field workers on pygmy chimpanzees seems to have tried to correlate their observations on locomotion with a descriptive analysis of the architecture of food-producing trees and of various types of forest (cf. Kortlandt 1974/75, 1984, 1986). Behind all this looms the biggest question: With some exaggeration, are we humans descended from a dryland ape in a mosaic landscape, or from a wetland ape in a forested environment? These and similar problems may perhaps only be solved if and when we will know a lot more about the palaeoclimatology and palaeobotany, including the prehistory and archaeology of hominids in these regions, because they may have been the chimpanzee's main com-

petitors and predators in semi-open forests and open woodlands. Serious multidisciplinary research is badly needed. In the meantime, preservation of both chimpanzee species and *all* their natural environments should have the highest priority for conservationists, in order to enable us to better understand our own human ancestry.

Conservation

(1) Estimates of the surviving pygmy chimpanzee population have differed widely: from "rather arbitrarily in the order of magnitude of some 100,000-200,000" (Kortlandt 1976) to "may already number less than 5,000" (Thompson-Handler *et al.* 1995; see also Lee *et al.* 1988). The first, rather crude, estimate was based on a population density of 0.4 per km² and a geographical range of 350,000 km² but without being able to evaluate the patchy distribution. The second estimate ignored the non-surveyed areas of the range and is therefore obviously biased. In fact there cannot be a reliable estimate because there are no reliable figures of the surface areas of the different types of forest, nor of the population densities under different conditions of disturbance. Kano (1992) tentatively supposed that the pygmy chimpanzee had not reached and crossed the Lomami river (contrary to data published by Colyn 1987; Colyn *et al.* 1987; Fenart & Deblock 1973; Thys van den Audenaerde 1984; and Vandebroek 1958/59). He also assumed (incorrectly) that it was extinct or nearly extinct in its entire southern range. This resulted in an area estimate of 135,000 km². Postulating an average population density of 0.4 per km² (or less) the total population would be "at most about 50,000 individuals". Thompson-Handler *et al.* (1995), however, concluded from Kano (1984, p. 42) that he had made a decimal error in 1992 and that the surface was only 13,500 km², resulting in a population of only 5,400, which in their opinion might even have been reduced to one half in recent years. [Actually, p. 47 in Kano (1984) shows that "13,500" was a typing or printing error for 135,000.] Surprisingly, no one measured the range on Kano's map (No. 2, 1992). When I did just that the correct figure turned out to be 144,000 km² and consequently the estimate of the inhabiting ape population should be about 60,000 individuals. Thompson-Handler *et al.* also omitted in their population estimate the evidence of the presence of these apes between the Lomami and Lualaba rivers. Adding this area and the southern range to the measured surface, and estimating the same average density, would result in a total in the order of magnitude of 100,000 individuals.

(2) The major uncertain factor is, of course, the estimate of 0.4 individuals per km². We know nowadays that the distribution of the species within its geographical range is (and has apparently always been) quite patchy, even in regions relatively densely populated by them (e.g. Badrian 1977; Kano 1984, 1992; Vandebroek's correspondence). The cause of this should be investigated by an experienced botanist. If the gaps between areas inhabited by the apes outside Kano's survey area are larger than inside it, the calculated figure would be too high. However, we also know that, in many regions, these apes withdraw into the forest some hours of walking from villages (Vandebroek's correspondence). This shyness is their main protection. The villagers usually walk no further than about 5 or 6 km into the forest (Kano 1992). Interviewing people along the roadside may therefore be insufficient. [The

hunters of the Pygmy peoples range twice as far from agricultural villages (Bailey 1991) but they do not live south of the Zaïre river.] Nevertheless a comparison of Vandebroek's with Kano's data suggests a distinct decline in areas accessible via road or river. (See also MacKinnon 1987, Susman *et al.* 1980, Thompson-Handler *et al.* 1995).

(3) When in 1970 the Salonga National Park was established, the pygmy chimpanzee was intended to be its flagship. As it turned out, however, there were very few of them inside the Park and perhaps more just outside its SE boundaries (d'Huart 1988; UNESCO-IZCN-UICN 1987, Verschuren pers. comm. 1987, Fig. 3 in this paper). Some experts even incorrectly disclaimed its existence in the NW part and doubted its presence in the SE part of the Park (IUCN 1987; Nishida 1972). With hindsight the rarity could have been predicted: the NW part of the Park consists predominantly of seasonally flooded forests with on average 4 m water level fluctuations, and the SE part consists mainly of plateaux covered by *Gilbertiodendron dewevrei* and *Brachystegia laurentii* forests, while the areas of old secondary forests (including *Scorodophloeus* forest) are probably small (Davis *et al.* 1994; d'Huart 1988, Figs. 2, 4 and 5 in this paper).

(4) When one flies over the central basin in a medium- or low-altitude propeller plane one can see stretches of more than 100 km of forest without any signs of villages, agriculture or smoke (Kortlandt, obs. 1960-64; K. Ammann recent obs., pers. comm.). The human population is concentrated alongside the roads and rivers. The uninhabited areas might harbour tens of thousands of pygmy chimpanzees if the vegetation is favourable to them and if their population density is as high everywhere as locally at Wamba and Lomako. Such estimates would, however, be too high if the distribution is as patchy there as in the regions from where data are available. Fact-finding research in such remote areas should be recommended, though the job will be difficult. It should be done by an experienced botanist who should also be able to recognise the calls and nests of pygmy chimpanzees. Altogether the status of the pygmy chimpanzee is highly vulnerable in human-inhabited regions, but not threatened as long as the condition of the Zaïrean infrastructure remains as it is. Nevertheless the data and maps on logging concessions give rise to serious concern (Compère & Symoens 1987; Doumenge 1990; Lanjouw 1987). In addition, a new threat is the transportation of "bush meat" by plane (J. Kingdon pers. comm.).

(5) A survey in inaccessible regions may possibly find places similar to the recently discovered Nioko site in the Republic of Congo (e.g. in the large swamp areas from 3° to 3°50'S around 25°E and from 4° to 4°40'S around 25°40'E). As long as such surveys have not been undertaken, scientists should refrain from postulating that the apes do not occur in regions that have not yet been surveyed in our time, and from asserting that the species is "extremely vulnerable", or that "urgent actions are necessary to prevent the species from becoming critically endangered or extinct in the near future". Conservationists should be able to assess their priorities on the basis of unbiased data.

(6) In many tribal regions the apes are hunted and eaten but in many other regions they are protected by taboos and superstitions (Vandebroek's correspondence and data scattered in the literature). Reserves should, of course, preferably be established in the latter. Accidental killings caused by snares will nevertheless occur. Such

killings may even become the main cause of death. In the Budongo and Kibale Forests the numbers of common chimpanzees mutilated by snares has greatly increased in the last decades (V. Reynolds, pers. comm.). We do not know the numbers that have died by this cause, but the estimates of the population density of chimpanzees in the Budongo Forest have decreased from 4 to somewhere between 1 and 3 per km² (Reynolds & Reynolds 1965; Plumptre & Reynolds 1994). This decrease may, however, be (partly) due to different methodologies of counting. Gathering more information on this by questioning the locals and by experimenting with pseudo-traps on chimpanzee paths should be easy enough. In some cases chimpanzees appear to be able to recognise clearly visible pseudo-traps and will then avoid them (Kortlandt 1967). Pseudo-traps with a frightening device may perhaps even be used to train the apes to watch out and avoid genuine traps. Hunting by the villagers may be reduced by the promotion of goat keeping. Furthermore, to compensate for the ecological effect caused by the decimation or extermination of elephants, well-controlled small-scale tree-cutting in the reserves should be considered. This might also be a good public relations exercise but should be done only at moments when the apes are far away. At other times any noisy activities, particularly drumming, should be prevented.

(7) To protect an animal species as a form of life created by evolution — rather than as a safari species — one should protect it in a number of sample areas representing its *entire* ecological adaptive zone with all its diversity, including optimal as well as marginal habitats. To realise this for the pygmy chimpanzee we need first of all a botanical survey of its various vegetation types from a locomotor and food-producing viewpoint, combined with an ecosystem analysis of its food competitors, at sample sites chosen from satellite images and representing clue areas within its entire geographical range. That should be done. It is quite different from what current pygmy chimpanzee research is aiming at. Most of these scientists investigate mainly the social and sexual life of their animals in a poorly defined type of habitat and in a small part of the geographical range of the species. It is admirable work and the results are fascinating from a comparative anthropomorphic viewpoint, but it contributes hardly anything to conservation. Now is the time for explorers, ecosystem scientists and conservationists to contribute their multidisciplinary specialties to pygmy chimpanzee research. The two chimpanzee species are after all our closest relatives and therefore the most valuable animal species that exist, except for ourselves.

Postscript

When this paper went to press, a letter from Prof. M. Djamba and Prof. P. On'okoko of the Patrice Emery Lumumba University at Wembo-Nyama reported that two researchers from their university had recently made a *Pan paniscus* survey on bicycles in the area of the upper Tshuapa (as far as Elingampagnu) and the tributaries of the Lomami, pedaling more than 1000 km in difficult terrain. They found that the apes were "bel et bien présent" (alive and well) in the evergreen rain forests, even though they were occasionally killed in traps and eaten. Thirty-one location reports were also produced. Eighteen of these sites have been pinpointed

in Figure 2, but the others could not be found on available maps. Seven reports mentioned that fish in shallow water are regularly caught and eaten. The survey was undertaken on the initiative of Prof. J. Lejoly of the Free University of Brussels with a budget of US\$350. The results show how valuable such cooperation with native colleagues can be: a viewpoint of which current pygmy chimpanzee field researchers seem rarely to be aware.

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The Only Way to Determine the Conservation Status of The Pygmy Chimpanzee is to Conduct a Survey¹ in the Zaïre Basin: A Reply to Dr. Kortlandt

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Dr. Kortlandt raises a number of issues in his critique of the present state of knowledge of *Pan paniscus*. He also offers numerous criticisms of recent fieldwork. In his review, Dr. Kortlandt suggests that a better understanding of the natural history of pygmy chimpanzees will come from 1) a better characterization of the rainforest of the Zaïre Basin, 2) study of the field notes of hunters and collectors dating from the period of 1936-1954, and 3) anecdotes derived from correspondence with individuals presently or recently in Zaïre. In this response I will deal with the first two sources which constitute the main body of Dr. Kortlandt's review.

Dr. Kortlandt criticizes mammalogists, primatologists, botanists and other fieldworkers who, according to him, have incorrectly characterized the rainforest of the Zaïre Basin. He states, "...none of the primate field workers distinguish the various botanical subtypes of the main types of vegetation in which their apes live." Later, he states that there are two kinds of primary forest in the "equatorial zone". The fact is that we have recognized six types of forest habitats in the Lomako, two of which could be characterized as "primary" forest (e.g., White 1986).

Kortlandt is generally correct in his statement that the present field studies of bonobos are concentrated in a relatively restricted area within the larger range of the species. He should be aware, however, that the sites of Wamba, Lomako, Lilingu, and Yalosidi were selected as long-term study sites after extensive surveys of Equateur. It should be pointed out that there have been attempts to study the animals further toward the margins of their range, and these attempts have met with only modest success (e.g., Horn 1977). Kano's survey in the early 1970's resulted in the choice of Wamba, and later Yalosidi, as study sites (Kano 1983, 1984a). Only after a very long journey through central Africa in the mid-1970's was the Lomako Forest discovered as a place where bonobos could be studied under near pristine conditions (Badrian and Badrian 1977). This is significant because those who undertook field studies of bonobos did so in order to address questions appertaining to human evolution and paleoanthropology, to address the issues of ape evolution, and more recently to test behavioral-ecological hypotheses. Most of these questions require data from natu-

ral populations in undisturbed habitats rather than populations of animals or study sites that have been selected on the basis of some *a priori* ecological criterion.

Do all the present field sites where bonobos are being studied represent the same habitat? Kortlandt implies that this is the case. In fact, the Lomako and Wamba represent two very different settings within the *cuvette centrale* (see Susman 1984). Kano and his colleagues at Wamba, and we who have worked in the Lomako, have noted well the differences in the flora and fauna at the two sites. Wamba is characterized by a greater proportion of secondary forest and a fauna that lacks many of the mammals found in the Lomako, 160 km to the southeast. Wamba is devoid of leopards and elephants, and has a relatively impoverished monkey fauna. The Lomako, on the other hand, is characterized by a predominance of primary forest (including large stands of *Gilbertiodendron* forest in addition to the more polytypic primary forest which is characterized by, among other species, *Scorodophloeus zenkeri*). In fact, in the Lomako forest there are at least five different habitats that are recognized within the 25 km² of the study site, and bonobos frequently exploit all but the wettest swamp areas (White 1986), including the *Gilbertiodendron* forest. In the Lomako there are leopards, elephant, six species of monkeys, and a large complement of other mammals, reptiles (including forest monitors and crocodiles), and birds. Kortlandt further mis-characterizes what we and other fieldworkers have said about swamp forests. We do not suggest that swamp forest (or N'dele forest as it is known locally) is "seasonally inundated" as stated by Kortlandt. We subscribe to the definition he presents namely, that "...swamp forest is a wet area that is normally covered by water all year." In addition to floral and edaphic features swamp forest is characterized further by a unique complement of larger mammals (among other fauna), the combination of which is not observed in the *terra firma* forest. These include *Allenopithecus nigroviridis*, *Cercopithecus neglectus*, *Tragelaphus spekei*, and *Hyemoschus aquaticus*, among others.

Contrary to the representation by Kortlandt, my reading of the literature reveals a keen appreciation on the part of field workers for the different forest types at Wamba, Yalosidi, and in the Lomako. Not only has Kano described the different forest types at Wamba

¹ "Survey" here includes botanical inventory, focal animal census, and ethnological survey.

at Yalosidi, and elsewhere in Equateur, but he has noted further that it is in secondary forest where the greatest density of bonobos is found. Kano (1983) suggests that where there is extensive modification of the vegetation by human activity, but no hunting of chimpanzees, the density of pygmy chimpanzees is greater than in places such as the Lomako where undisturbed forest dominates. At Yalosidi, Kano recognized at least six types of forest and noted further the tree species that characterized each (Kano 1983).

The real weakness of Kortlandt's approach to botanical literature, however, lies in his suggestion that by identifying particular forest types one can predict the occurrence of free-ranging bonobos. Kortlandt does not indicate whether he is talking about identifying the existing *range* (or distribution) of *Pan paniscus* or whether he seeks to predict the *density* of the existing population. Nonetheless, the fact is that neither the present range nor the density of the present bonobo population in Zaïre can be reliably estimated from a forest survey, regardless of how detailed the forest inventory might be.

Experience suggests that it is human activity that is the key to understanding the conservation status of bonobos and other animals in central Zaïre. Normally, where there is human *habitation*², bonobos are absent³. In addition to human activity in general, it is the local village customs that result in bonobos being present in one area and absent from another.

Kano has noted that the density of bonobos at Wamba is greater than in the Lomako, where, in the latter case, there is a greater proportion of undisturbed forest. The common denominator for the presence of sizable bonobo populations at both of these sites is the fact that bonobos are protected from human depredation by local taboos and customs. At both sites, monkeys are hunted when shotgun shells are available, but there are strong proscriptions against hunting bonobos. Despite these taboos, roughly half the adult males and a large number of females in the E group at Wamba (Kano 1984b), and a smaller proportion of animals in the Lomako, have hand and foot injuries, largely from unintended (on the part of the trapper) encounters with wire snares. Thus, data indicate that it is first human activity (and customs) that determine the presence of bonobos, and second, ecological factors (including forest type, predators, and food competitors, and others) that determine the density of bonobos in an area.

If a broad overview of the equatorial rainforest will not yield information sufficient to enhance our knowledge of the conservation status of wild bonobos, can an ethnological survey alone provide useful data? Unfortunately, I think not. The problem with an anthropologically-oriented survey lies not only in the fact that there are four Bantu subgroups inhabiting central Zaïre, but also in the fact that the customs and hunting practices of the Mongo inhabitants (even within a single ethno-linguistic group) vary from village to village, and even from one age group to another within a village. One example of the varied nature of local taboos is observed in the area north of Boende. In the area south of the Maringa River, along the road from Boende to Samba, there is the village of Bolongo. In, and around, Bolongo there are few remaining primates and no bonobos due largely to local customs that do not

proscribe the killing and eating of primates, including pygmy chimpanzees. Proscriptions are most relaxed among the elders of Bolongo. However, many of the younger, French speaking, villagers say they do not eat bonobo meat. Eighty kilometers from Bolongo, north of the Maringa in the villages of Bokoli-Ikela and Lifengo, there are strong, ubiquitous proscriptions against eating bonobo meat. The Mongo villagers of Bokoli-Ikela consider it tantamount to cannibalism to eat bonobo meat. Kano has noted, based on the experience from his extensive surveys of Equateur beginning in the early 1970's, that where there are concentrations of people and activities such as hunting and shifting, root-crop agriculture, bonobos are normally pushed miles from these settlements (although Wamba is an exception). Again, it is not the presence or absence of forest in-and-of itself, that predicts the distribution or density of bonobos (or other animals). Rather, it is the local customs and specific patterns of human activity that determine where one will find bonobos.

Finally, Kortlandt laments that present students of bonobo natural history and evolution have ignored the field notes of collectors such as Vandebroek and correspondence by others such as Schouteden. Kortlandt suggests this shortcoming stems from an ignorance of the French and Flemish languages. I would point out that the issues raised by Kortlandt were addressed in large measure by Dr. Van den Audenaerde, Director of the Royal Central African Museum (Tervuren) Museum, in his review (Van den Audenaerde 1984). Dr. Van den Audenaerde is fluent in both Flemish and French and he has had access to the materials that Kortlandt refers to, many of which are housed at Tervuren. Van den Audenaerde has summarized the earlier contributions of Schouteden and Vandebroek and others, including a map of the area explored by Vandebroek. I would add that regardless of how systematic the data are in the field notes of Vandebroek and how accurate the correspondence of Schouteden is, the dates on this material span the period of 1936-1954. While these notes are of great historical interest, the usefulness of these data for understanding the present conservation status of the pygmy chimpanzee is limited.

The present status (population size, range, and density) of bonobos in Zaïre may surpass that of any of the extant apes. Ironically, the same factors that have thus far inhibited a systematic population survey within the *cuvette centrale*, namely the vastness of the Zaïre Basin, its remoteness and difficulty of travel due to the crumbling infrastructure (roads, bridges, ferries, airstrips, boats, etc.), have also served to protect much of the fauna. Nonetheless, negative changes are taking place. The rapid decline of numerous species can be seen on a local scale in many areas over the last twenty years. For example, elephants were present in the Lomako forest in the 1970's and early 1980's. Not only did we see, at that time, bones of animals killed by ivory poachers, but elephants were observed foraging in the study site. The last sighting, however, was in 1980. Since then elephant spoor has been observed only infrequently. The threats come from a number of sources. In addition to the subsistence economy of the indigenous people which impacts on the environment principally through shifting, root-crop agriculture (and often hunting), there are other pressures that loom from commercial logging, poaching, and occasionally, live animal trade. While a great many bonobos may still exist (see estimates of Kano 1984a; Anonymous 1991-1992), the

² *Habitation* refers to local settlements on land that has been cleared for dwellings and gardens. There are other places, such as areas where locals hunt, fish, and gather but do live permanently, that continue to support bonobos and other fauna.

³ Wamba, however, is a notable exception to this rule.

threats to the natural populations of free-ranging bonobos are real. Furthermore, if future studies of bonobos are going to continue providing insights into ape and early hominid evolution, or the relationships between behavior and ecology, then studies will have to continue under naturalistic conditions. Hopefully, at some point in the near future an effort will be made to conduct a systematic, comprehensive, "real-life" survey to accomplish the goals proposed by Dr. Kortlandt.

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Taxonomic Status of the Gorillas of the Bwindi-Impenetrable Forest, Uganda

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Based on their geographic proximity to the mountain gorillas, *Gorilla gorilla beringei*, of the Virunga Volcanoes (Fig. 1), the gorillas of the Bwindi-Impenetrable Forest were assumed to belong to the same subspecies (see Butynski 1984; Butynski and Kalina 1993; Groves and Stott 1979; Harcourt 1981; Pitman 1935; Schaller 1963). Although there was suspicion early on that the two populations of gorillas may be separate taxa (Akroyd 1934; Pitman 1935), behavioral, morphological and ecological data that refute or support the current taxonomic designation have never been presented.

Since we believe that we can identify, based on external appearance, which of the two populations any one gorilla comes from, we set out to test the claim that Bwindi and Virunga gorillas belong to the same subspecies. For this purpose, we examined and measured 30 skulls and 31 skeletons of Virunga gorillas and 12 skulls and three skeletons of Bwindi gorillas, and examined external features on cadavers and live individuals. We also compared the behavior and ecology of the two populations with the hope of relating these to the measured skeletal differences. By establishing such relationships, and testing for divergent adaptive trends, we sought to impart some biological objectivity to our measurements and interpretations.

We found that, in comparison to Virunga gorillas, Bwindi gorillas live at lower elevations, warmer temperatures, are much more arboreal, have longer day ranges, larger home ranges, and eat much more fruit and pith, and less bamboo and leaves. Notably, the measured morphological differences reflect the differences in ecology, habitat and behavior. Bwindi gorillas have smaller bodies, relatively longer limbs, hands and feet, shorter trunks, thumbs, big toes and tooth row lengths, and narrower trunks and orbital breadths than Virunga gorillas (Sarmiento *et al.* in press).

Theoretically, most of the differences between the two populations can be associated to a relatively higher intake of fruit and a higher frequency of arboreal behaviors in Bwindi gorillas relative to Virunga gorillas. In this regard, there are real ecological differences between the two populations, reflected in both their characteristic behavior and morphology. The close associations of their respective ecological and behavioral differences with their morphological differences, indicates that the two populations have re-

sponded to different selective forces and have developed divergent adaptations.

Our results show that Bwindi gorillas are not the same taxon as those in the Virungas. We are unable, however, to determine which taxon Bwindi gorillas belong to (i.e., Bwindi gorillas may merit a new taxon, or belong to the other recognized taxon of eastern gorilla, *G. g. graueri*), or to resolve the taxonomic level which the differences between Bwindi and Virunga gorillas correspond to (i.e., subspecies vs. species). Without the sympatric association of Virunga and Bwindi gorillas needed for testing reproductive isolation, there is some subjectivity as to what degree of difference distinguishes species from subspecies.

According to taxonomists not subscribing to the Biologic Species Concept (Cracraft 1987), the fact that any one individual gorilla from Bwindi and the Virungas can be identified as to its respective population is sufficient evidence to consider them two different species. That the differences distinguishing the two are nearly comparable in magnitude to those separating the two widely recognized species of chimpanzee (*Pan paniscus* and *Pan troglodytes*) (Table 1) would support this interpretation. Bwindi and Virunga gorillas, however, fit the classic definition of subspecies that is in agreement with the Biologic Species Concept (i.e., two allopatric populations with characteristic differences) (Mayr 1969; Simpson 1961). Presently, we favor this latter interpretation, but by no means do we have the data to refute the possibility that the two are different species.

In part, we will be able to further clarify the taxonomy of Bwindi gorillas by comparing them to all of the other eastern gorilla populations, and resolving how many subspecies, or possible species, of eastern gorillas exist. Grove's (1970) study indicates that Bwindi gorillas are most similar to those of the Itombwe Mts. where the type of *G. g. graueri* was collected (Fig. 2). We suspect *G. g. graueri* may have had a much greater distribution in the recent past. However, there also exists the strong possibility that the Bwindi population may represent an off-shoot subspecies of the Virunga gorillas or, less likely, of the gorilla populations to the west of Lake Edward (for example, Mt. Tshiaberimu). Although presently separated by the Rutshuru Plains, Bwindi is about 60 km from the historically known southern range of the Lake Edward

gorillas (Fig. 2). Intervening patches of forest may have once bridged this gap, particularly along the shores of Lake Edward and the banks of rivers (for example, the Ishasha and Semliki).

Two of us (TMB and EES) are presently studying both the habitat and morphology of the Lake Edward animals to see how they compare to the gorillas of the Virungas and Bwindi. We have already surveyed the Mt. Tshiaberimu population (Butynski and Sarmiento 1995) and will return in mid-1996 to examine other Lake Edward gorilla localities. Additionally, we have initiated a study of the Itombwe gorillas, since they seem to share strong morphological and habitat similarities with Bwindi. We hope to analyze genetic information from all the eastern populations to help grade the lability of morphological, behavioral and habitat differences, and further refine the taxonomic classification of these populations.

We are also preparing a paper on the musculature of the Bwindi gorilla foot. Notably, Bwindi gorillas share with Virunga gorillas some unique foot muscles which are rare in western lowland gorillas *G. g. gorilla*. On the whole, however, Bwindi gorilla foot musculature is different from mountain gorillas, showing struc-

Table 1. Probability values of "t" for differences in mean measurements in comparisons of *P. paniscus* vs. *P. troglodytes*^a and Virunga vs. Bwindi gorillas^b.

	<i>P. paniscus</i> vs. <i>P. troglodytes</i>	Virunga vs. Bwindi gorillas	
		Males	Females
1. Clavicle length	0.01	-	0.0005
2. Scapular length	0.01	-	-
3. Humerus length	n.s.	-	0.065
4. Radius length	n.s.	-	0.030
5. Ulna length	0.015	-	-
6. Os coxa length	0.01	-	0.13
7. Femur length	n.s.	0.56	0.0020
8. Tibia length	n.s.	0.86	0.093
9. Fibula length	n.s.	-	-
10. Scapular breadth	0.01	-	-
11. Humeral head diameter	0.01	-	-
12. Humeral biepicondylar breadth	0.01	-	-
13. Iliac breadth	0.01	-	-
14. Sacrum breadth	0.01	-	-
15. Acetabular diameter	0.01	-	-
16. Femoral head diameter	0.01	-	-
17. Femoral bicondylar breadth	n.s.	-	-
18. Talar trochlear breadth	n.s.	-	-
19. 1st Metatarsal	0.0001	-	0.084
20. 4th Metatarsal	0.1215	-	0.67
21. 4th Metatarsal foot length	0.0364	-	0.33
22. 4th Metatarsal lever length	0.0494	-	0.66
23. 1st Metacarpal	0.0221	-	0.16
24. 3rd Metacarpal	0.0213	-	0.57
25. Lumbar vertebral volume	0.0001	-	0.015
26. Palate length	0.0001	0.002	0.449
27. Premolar-molar length	0.0001	0.044	0.022
28. Incisor diameter	0.0001	0.63	0.36
29. Biorbital diameter	0.0001	0.018	0.0000
30. Interorbital diameter	0.0053	0.025	0.024
31. Molar area	0.0001	0.86	0.25

^a All p values presented from author's (EES) notes are corrected for sample size. Chimpanzee comparisons for most characters are based on 20 individuals of *P. paniscus* and 30 of *P. troglodytes*. The low sample size for Bwindi gorillas in some cases results in the comparatively higher p values of gorillas.

^b Comparisons of *P. paniscus* vs. *P. troglodytes* for characters 1-18 after Zihlman and Cramer (1978). Characters 19-31 from author's (EES) notes. Probability values for "t" higher than 0.05 are generally taken to be non-significant and are labelled 'n.s.' by Zihlman and Cramer (1978).

^c Comparison of Bwindi vs. Virunga gorillas after Sarmiento *et al.* (in press).

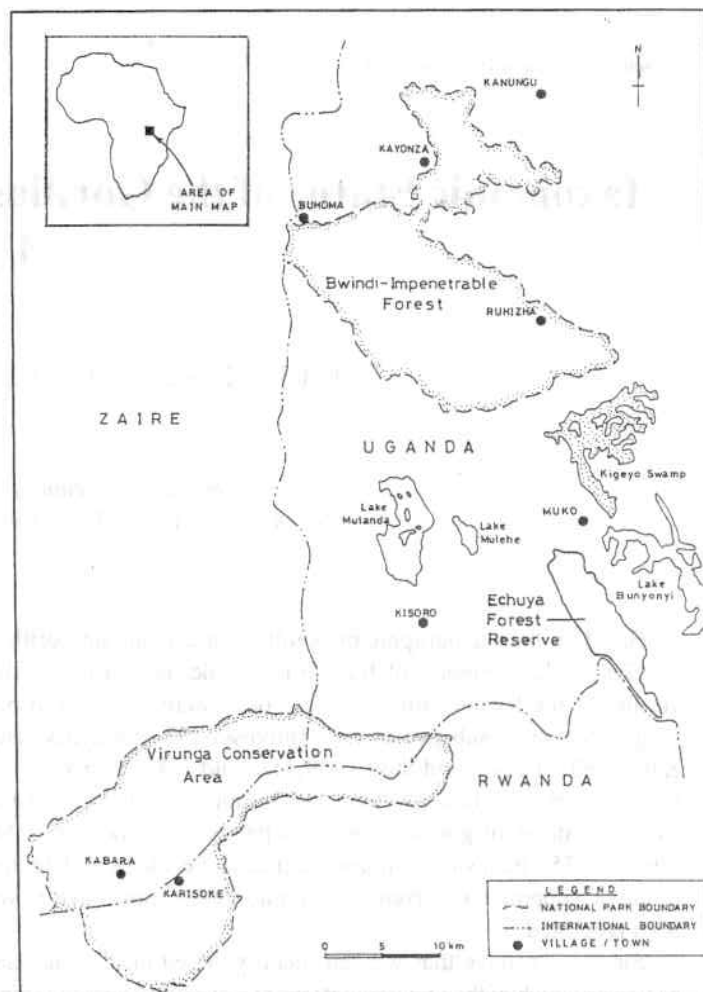


Fig. 1. Map of Bwindi Impenetrable Forest and the Virunga Volcanoes Conservation Area.

tural similarities to the more arboreal *G. g. gorilla*. Unfortunately, the foot musculature of the other eastern gorilla populations (e.g., Itombwe, Lake Edward, Kahuzi-Biega) is not well known. Ultimately, this knowledge will affect how we interpret the similarities and differences between Bwindi and Virunga gorillas. Nevertheless, because muscle attachment sites are fixed early in embryological development and do not change during the animal's ontogeny (Gilbert 1994; Wortham 1948) our study provides evidence of genetic difference between Virunga and Bwindi gorillas.

Garner and Ryder (1992a, 1992b) used mitochondrial DNA D-loop sequence analysis to evaluate phylogenetic relationships among the three currently recognized subspecies of gorillas. They found that, in spite of morphological differentiation between *G. g. beringei* and *G. g. graueri*, the *G. g. beringei* mitochondrial DNA lineage is not phylogenetically distinct from the *G. g. graueri* lineages. Based on the analyzed mitochondrial DNA region they concluded that Bwindi gorillas could not be distinguished from Virunga gorillas and must belong to the same subspecies. Given our findings, we interpret their results with some reservation. It is unclear whether those parts of the DNA which vary in eastern gorillas were analyzed for differences. Aside from Bwindi and Virunga gorillas, Garner and Ryder (1992a) sampled only one other population of eastern gorilla (Kahuzi-Biega) tentatively assigned to *G. g. graueri* (Groves and Stott 1979). Unfortunately, they were

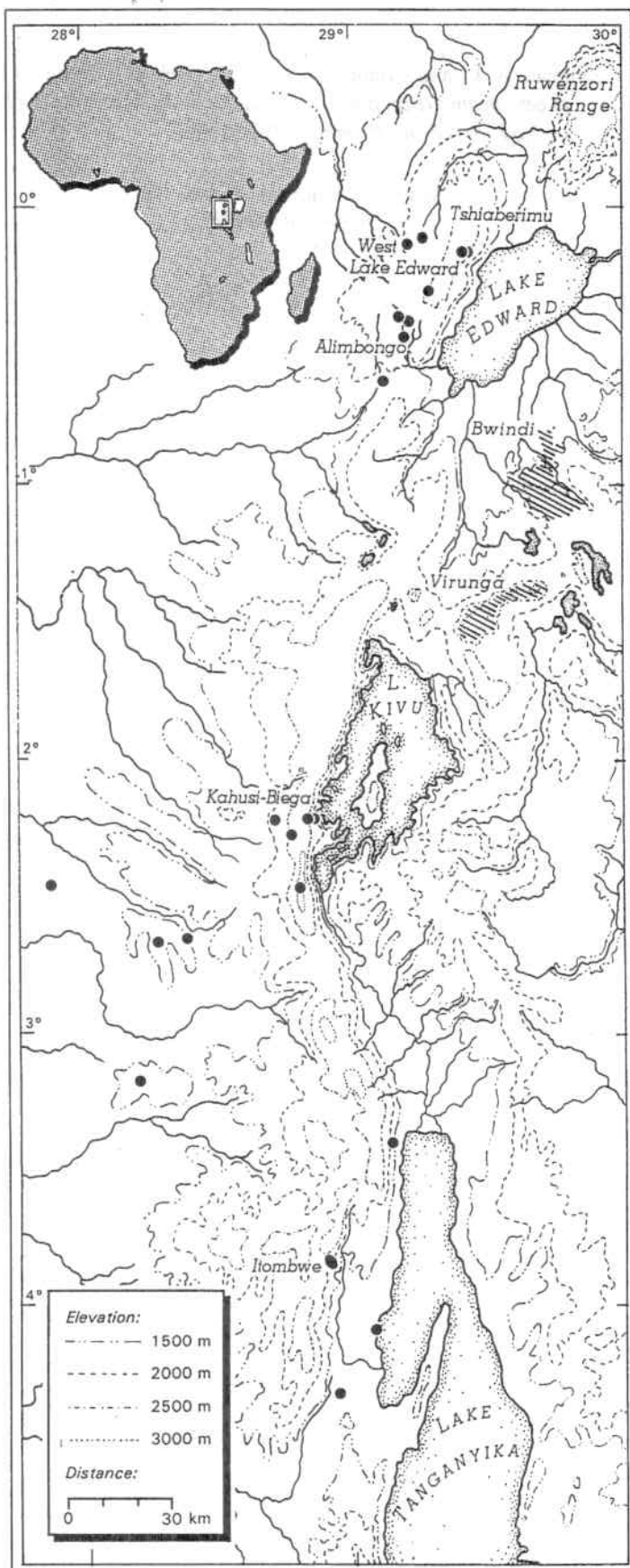


Fig. 2. Map of the Albertine Rift where at least five separate populations of eastern gorilla are found. Localities where gorilla specimens have been collected are represented by black dots. Aggregations of black dots represent gorilla populations. From north to south these are: Lake Edward, Bwindi Impenetrable Forest (stippled), Virunga (stippled), Kahuzi-Biega and Itombwe.

unable to show much variability between or within the three populations in the analyzed nucleotide sequence.

With knowledge as to which DNA sequences vary in eastern gorillas, and analysis of the appropriate sequences, we expect that characteristic differences between Bwindi and Virunga populations will emerge. The taxonomic significance of these differences, however, would remain a moot point. Since Garner and Ryder (1992a) do not associate magnitude of DNA differences to adaptive differences or isolating mechanisms, any taxonomic conclusions they make based on their data are 'biologically subjective'. Without such an association their taxonomy must depend on consistency as its guideline in order to attain some degree of objectivity. The magnitude of differences they choose to be diagnostic of any one taxonomic level within eastern gorillas must be consistent with that distinguishing corresponding taxonomic levels in other great apes. Before they can arrive at taxonomic conclusions, therefore, they must gauge the degree of DNA differences that exists among subspecies of living great apes. They can then test if these are greater or less than those they found between Bwindi and Virunga gorillas.

Our findings have a multitude of ramifications touching upon a wide range of topics from the biodiversity of the Western Rift and African ape adaptation, to conservation and ecotourism. Most importantly, they underscore the importance of effective research and conservation efforts. Principally, the number of mountain gorilla populations is reduced from two to one and the number of mountain gorillas from 620 to about 320 (Sholley 1990; Butynski and Kalina 1993). The possibility that Bwindi gorillas are also a unique taxon of but 300 individuals further emphasizes the need for serious conservation efforts on their behalf. Considering that the two gorilla populations exhibit characteristic differences in habitat, behavior and morphology, we strongly recommend that the concerned governments and conservation bodies recognize the two populations as different. Moreover, we urge that any conservation programs directed at these populations be tailored to account for these differences.

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Veterinary Evaluation of Ruffed Lemurs (*Varecia variegata*) in Madagascar

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The significance of infectious disease to reintroduction projects has become an increasingly important question. As captive propagation and management practices improve and remaining areas of natural habitat are secured, opportunities may develop for animals in captivity to be released into former ranges (reintroduction), new areas (translocation), or to supplement existing populations (restocking). The movement of animals is accompanied by the inherent risk of exposure to disease in a variety of scenarios. This report describes the rationale and application of a medical evaluation program for a potential restocking program of black-and-white ruffed lemurs (*Varecia variegata variegata*) in Madagascar.

Introduction

The opportunity for restocking of ruffed lemurs occurred due to ongoing projects supported by the Madagascar Fauna Group (MFG) of the American Zoo and Aquarium Association (AZA). Due in part to support by MFG, a forestry research station near Tamatave, on the east coast of Madagascar, has been converted into a small zoo. As a result of donations and government confiscations, the number of ruffed lemurs in the collection has grown beyond the carrying capacity, and is currently approximately 28 animals. This large population is pushing the limits of both the physical facility and the budget for animal care. An alternative for some of these animals would be desirable. At the same time, Reserve Naturelle Integrale No. 1, Betampona, is reasonably accessible and underused for research purposes. It is small enough to be well censused and monitored (5500 acres), and has the potential for holding more *Varecia* than are currently there. Population estimates from fieldwork carried out there indicate 20 to 45 animals. The reserve is 30 kilometers from Ivoloina, and is surrounded by degraded forest and agricultural land. This situation has resulted in an island population that is sure to suffer from loss of genetic diversity if new individuals are not introduced. The project proposed by the MFG advisors involves alleviating the overcrowding by releasing selected *Varecia* from the Ivoloina collection into the Betampona Reserve. Longterm monitoring of these animals, as well as the current population, would provide useful

information for future release projects.

An important and much discussed question regarding animal restocking and reintroduction projects involves the significance of infectious disease. In evaluating this question, many aspects must be considered. The animal species involved obviously defines disease susceptibility. Both the resident population and the introduced population must be evaluated. An assessment of the types of diseases to consider must be made, either based on known information or extrapolation. The effect of introduced diseases to the wild population is the most obvious concern, but the effect of introducing naive captive animals to diseases in the wild must also be addressed. The significance of each disease must be determined, and detailed statistical formulas are available to forecast the impact on the population. Depending on the species, availability of diagnostic technology may control the ability to monitor for health problems. In addition to the species involved in the project, other animal species in the area may be affected, either directly by disease, or indirectly by competition for resources.

For the Betampona Restocking Project, three populations were considered. Health assessments were to be done on each population, using comparisons between the populations to identify significant health issues. The populations were the potential release population at Ivoloina, the resident population at Betampona, and the North American captive population (useful for established normal values). To assess the wild population, samples were to be collected opportunistically during a radiotracking project conducted by a field researcher working in Betampona. In addition, samples were to be collected from the wild at a different location (Masoala Peninsula) during a separate radiotracking field project. Although those from Masoala were not part of the resident population at the release site (and in fact were a different subspecies, *V.v. rubra*), it was felt that they would be useful for comparative purposes.

Diagnostic evaluations were selected based on diseases felt to have potential for significant impact on the restocking project. Exposure to humans played a major part in determination of disease testing. The assumption was made that the captive population had been exposed to many human diseases to which the wild population had not.

Health Profile

Complete health profiles were completed on all lemurs in the study. This consisted of 18 *Varecia variegata variegata* held in captivity at Parc Ivoloina and four *Varecia variegata rubra* from the Masoala Peninsula. No animals were captured in the reserve at Betampona. Health profiles were designed to assess the physical health of the animals, as well as to detect exposure to disease. The type of test and location were determined based on need, availability, and reliability. Some tests were, by necessity, done on location (physical examinations, complete blood counts, TB tests). For others, samples were preserved for later examination for convenience (fecal samples) or reliability (serum profiles, viral serology, cultures).

Each animal was physically (captive) or chemically (wild) restrained. Chemical immobilization was achieved via remote injection of a tiletamine / zolazepam combination anesthetic (Telazol). A complete physical examination was performed. Each captive animal received an intradermal tuberculin test (0.1 cc Cooper's old tuberculin, upper palpebra). Whole blood was collected for a complete blood cell count (CBC) and hemoparasite examination, and preserved for genetic evaluation. Blood was collected, separated, and serum saved frozen for serum biochemical profile and viral serology. Fecal samples were collected and preserved in 10% formalin for microscopic examination for endoparasites. Rectal swabs were collected in transport media for enteric pathogen culture. Hair samples and pelage color pattern descriptions were collected for genetic research.

Test Results

Physical Examinations

Ivoloina - All examined animals were found to be in good condition. Body weights and composition seemed appropriate. Hair coats appeared dry and slightly dull. The animals were reproducing, but many adults of appropriate reproductive age were not bearing young. A single newly donated animal (donated less than one week previously) had a much thicker, more lustrous coat. No evidence of external parasites, injuries, or other medical problems were detected on physical examination.

Betampona - Although no animals were captured, several were visually examined at close distances. All animals observed appeared in good health, and all had dense, lustrous hair coats. All were active, and no evidence of compromised health (gait abnormalities, wounds, ocular or nasal discharges, etc.) were detected. Infants were seen on one occasion and heard in a nest on another, indicating that reproduction is occurring.

Masoala - All examined animals were found to be in good health. No evidence of compromised health were detected. External parasites, as yet unidentified but thought to be mites, were present in the ear canals of all four lemurs. It was felt that these parasites did not present a clinically significant health concern.

Tuberculin Testing

All of the captive *Varecia* were negative on intradermal tuberculin tests at 72 hours.

Table 1: Serum biochemical analyses

	Mean-wild	Mean-Malagasay (captive)	Mean-ISIS*
Calcium (mg/dl)	9.4	10.25	10.2
Phosphorous (mg/dl)	5.4	6.98	8.0
Sodium (Meq/l)	143.3	143.06	141
Potassium (Meq/l)	4.6	5.25	4.6
Chloride (Meq/l)	106.8	103.44	103
Cholesterol (mg/dl)	60	54.28	85.7
Triglycerides (mg/dl)	40.5	49.89	
LDH (IU/l)	726	460.39	340
AST (IU/l)	58.8	38.28	48.6
Total bilirubin (mg/dl)	0.3	0.34	0.5
GGT (IU/l)	16.8	11.83	
ALT (IU/l)	29.8	64.22	66.5
SAP (IU/L)	530.5	275.5	432
Total protein (IU/l)	6.2	7.42	8.0
Globulin (g/dl)	2.0	2.22	2.1
Albumin (g/dl)	4.2	5.21	5.8
Albumin/globulin ratio	2.12	2.41	2.76
Blood urea nitrogen (mg/dl)	3.8	7.83	24.1
Creatinine (mg/dl)	0.78	0.81	0.9
BUN/creat ratio	4.25	9.28	26.8
Uric acid (mg/dl)	0.05	0.01	0.4
Glucose (mg/dl)	112.5	96.83	104

Hematology

Results of complete blood counts and biochemical profiles are shown in tables 1 and 2. Mean values are compared, and although this does not reflect the same rigorous analysis as statistical evaluation, it does suggest basic trends. Briefly, with the exception of blood urea nitrogen (BUN), blood values of captive and wild animals fall within normal ranges as established for the captive North American population. Two parameters, lactate dehydrogenase (LDH) and serum alkaline phosphatase (SAP), were near the upper end of normal range in the wild lemurs. Both of these parameters may be artifacts of chemical immobilization and small sample size.

BUN levels in wild (3.8 mg/dl) and Malagasy captive lemurs (7.83 mg/dl) are below the normal range for North American captive ruffed lemurs (mean \pm 2SD = 8.3 - 39.9 mg/dl). There are several possibilities to explain this result. One is that the North American captive population, from which the ISIS normal values are determined, are receiving excessive amounts of dietary protein, resulting in a higher average BUN (a reflection of nitrogenous wastes, the breakdown products of protein metabolism). Both the Malagasy captive and the wild ruffed lemurs are significantly lower than the ISIS values, the wild animals being roughly half of the Ivoloina animals. Although these two groups are different subspecies, it is unlikely that it is a taxonomic difference. A possibility for this difference may be diet, but this would suggest that the wild animals eat a diet even lower in protein than that fed at Ivoloina. The small sample size might be introducing an artefact into the comparison, however the trend is certainly interesting. This finding should be further investigated as more blood samples became available from Madagascar, and should be taken into consideration when reviewing and formulating diets.

No abnormalities were detected for captive animals at Ivoloina that would suggest specific health abnormalities or nutritional deficiencies. No hemoparasites were detected in any blood smear.

Viral Serology

Serological assays were done for the following viral diseases:

Table 2: Complete blood count comparisons

Population	Total WB Ccount ($\times 10^3$)	segmented neutrophils (%)	band neutrophils (%)	lymphocytes (%)	monocytes (%)	eosinophils (%)	basophils (%)
North American (ISIS)	8.2	47.34	0.27	51.38	0.41	0.30	0.30
Captive - Ivoloina	10.51	39	2	54.2	4.11	0.5	0.06
Wild - Masoala	9.6	54.5	0.5	41.8	2.3	0.5	0.5

hepatitis A (HEP A), hepatitis B (HBsAb), herpes simplex 1 (HSV-1), cytomegalovirus (CMV), Epstein Barr virus (EBV), measles, and simian immunodeficiency virus (SIV). These diseases were selected based on several criteria. They are present in the human population of Madagascar. They all have a carrier state, such that they could be maintained latent in a host and shed at a later date. They all have potential to produce significant disease, either by direct mortality or reduced reproduction. The exception is simian immunodeficiency virus. Immunodeficiency viruses are being discovered in a variety of species, including nonhuman primates. Although no immunodeficiency diseases have been documented in lemurs, samples were surveyed for evidence of infection. None of the 22 Malagasy animals tested positive for any of the viral diseases tested for.

Fecal Flotations

Saline flotation of formalin - fixed feces was done for detection of parasite ova. None of the captive lemurs showed evidence of internal parasites. These animals are routinely treated with ivermectin (every four months), so the results are not surprising. One of the wild *Varecia* had a single nematode ova detected in the flotation. Attempts are being made to identify the species of parasite that produced the egg.

Fecal Cultures

An enteric pathogen screen was performed on the fecal culture swabs. Each sample was cultured for *Salmonella*, *Shigella*, *Campylobacter*, and *Yersinia*. These organisms all cause disease syndromes in humans and a variety of animal species, and have the potential of persisting in a carrier state. All 22 *Varecia* sampled were negative for enteric pathogens.

Conclusions

Ivoloina - Excess animals present a variety of problems for this collection. Budget constraints limit the ability to provide further cage space and may affect provision of a proper diet. Current diets are functional, but may be lacking in trace vitamins or minerals, or lack adequate levels of basic nutrients. The possibility of a marginal diet is evidenced by the dry, dull hair coats of the animals examined, as well as the decreased reproductive rate. Complete bloodwork does not indicate any specific nutritional deficiencies. Of most significance is the fact that no evidence of infectious disease exist in this captive population that would restrict their inclusion in release projects. Although these animals were held as pets by private individuals, no transmissible diseases that occur in the human population in Madagascar were detected in the animals.

Betampona - No specific medical conclusions may be made for the ruffed lemurs in Betampona. In general, the animals appeared in good health.

Masoala - Although not germane to this project, the examination of samples collected from the red ruffed lemurs in the Masawala area provides some useful information. Although the subspecies and location differ from the ruffed lemurs of Betampona, basic health parameters may be used for comparison. Examination of the animals and evaluation of the blood and fecal samples suggest that this group of wild lemurs does not harbor any of the potentially serious infectious diseases surveyed.

Recommendations

Initial review of this medical evaluation is favorable. No significant health problems were identified in the captive, potential release animals nor (at least indirectly) wild ruffed lemurs. Obviously, direct examination and biomedical sampling of the Betampona resident *Varecia* is necessary to make a firm conclusions. Although in generally good condition, the animals at Ivoloina are probably not in prime condition. As discussed previously, poor hair coat and lack of reproduction suggest a suboptimal diet.

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Past and Present Lemur Fauna at Ankarana, North Madagascar

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Over the centuries, the forests of the Ankarana Massif in the extreme north of Madagascar have been home to at least 18 species of lemurs. Fifteen of these species (six extinct and nine extant) are known from subfossil remains in the caves of the Massif. This makes Ankarana one of the two richest lemur subfossil locations in Madagascar. Unlike the other site, Ampasambazimba, which today is devoid of lemurs, Ankarana's forests have remained sufficiently intact for at least ten lemur species to survive until the present day. These include seven of the nine extant species represented in the subfossil deposits, and three additional species whose remains have not yet been found in the caves. Even the surviving remnant fauna is unusually rich: it comprises one of the greatest number of primate species for any forest habitat worldwide, and the dominant species occur in amongst the highest primate population densities known. This reflects the remarkable diversity of habitats which occur within Ankarana's small area.

Habitat

Ankarana is a 300 m high outcrop of Jurassic limestone which lies about 100 km south of the northern tip of Madagascar (Fig. 1). The region receives about 2000 mm of rain annually, most of which falls between October and March. Perennial rivers originating in higher rainfall regions, flow through the massif. These support luxuriant forest in collapsed caves within the massif, and outside on the savanna there are bands of forest along surface streams and over underground rivers. Ankarana's vegetation types are unusually diverse: xerophytes grow on the limestone, sparse shrubs sprout wherever there is a little soil, and there is semi-evergreen canopy forest where the limestone cliffs give shelter from drying winds and the cave rivers provide water. Further away from the subterranean rivers, the soil is dry and the vegetation sparse. Hence some forest within and around the massif remains green whilst vegetation of the surrounding Western Shrubby Sa-

vannah-with-Palms (Koechlin 1972) becomes parched. This explains why Ankarana can support a much richer and diverse fauna than is typical of the Western Zone of Madagascar. A description of the habitat is given by Wilson *et al.* (1988), Fowler *et al.* (1989) and Wilson (1990).

History of Research at Ankarana

Ankarana's ecological wealth was formally recognized in 1956 when it was designated a special reserve, but it was not until the 1980s that much serious scientific work began. Jean Radofilao was responsible for Ankarana's rediscovery by the scientific community. In the 1960s he began exploring and meticulously mapping the complex systems in tropical Africa (Radofilao 1977), and attracted the attention of a team of five cave-zoologists from Southampton University, U.K., who in 1981 documented the fauna of the longest (11 km) cave system (Wilson 1985). They collected the first lemur subfossils from the region (see Vuillaume-Randriamanantena *et al.* 1985), and identified the forests around the cave entrances as an important habitat for *Eulemur coronatus* and *Eulemur fulvus sanfordi* (Wilson 1987a)¹.

This reconnaissance expedition was followed, in 1986, by a larger Anglo-Malagasy expedition comprising cavers (including Radofilao), zoologists, a paleontologist and a botanist (Wilson *et al.* 1988). This team established the endangered status of *Eulemur coronatus* and Ankarana as a critical refuge for this and other extant primates (Wilson *et al.* 1989). They identified Ankarana as an important formation for subfossil sites (Vuillaume-Randriamanantena and Ralaivison-Raharizelina 1990), and also mapped a few more kilometers of caves, bringing to 98 km the total of subterranean passages that had been surveyed at Ankarana

¹ One of us (ELS) has recently placed *Lemur coronatus* and *Lemur fulvus* in the genus *Eulemur* to distinguish these and other species of the genus *Lemur* from *Lemur catta*, which appears to be closely related to *Haplorhina* (Simons and Rumpler 1988).

(Wilson 1987b).

These results stimulated two expeditions the following year. One continued the zoological research (Hawkins *et al.* 1990). The other marked the beginning of paleontological research at Ankarana, a program which involved scientists from the University of Antananarivo and from the USA (Duke University, the University of Massachusetts at Amherst, and the State University of New York at Stony Brook) (Simons *et al.* 1990).

Subfossil Discoveries

Paleontological exploration of the Ankarana during the years 1986-1992 has yielded thousands of bones of extinct and extant lemurs. The extinct lemurs represented there include one new genus which is related to the living indris and sifakas (Godfrey *et al.* 1990; Jungers *et al.* 1991; Simons *et al.* 1992). This new lemur was given the generic name *Babakotia* after the Betsimisaraka name for the indri, the "babakoto," and the specific name *radofilai* to honor Jean Radofilao.

The giant extinct lemurs of Madagascar have only recently vanished, like the other large Malagasy herbivores (pygmy hippopotamus, elephant bird, and gigantic tortoise) which disappeared with them from Madagascar's forests. The cave deposits at Ankarana contain bones of some of these large nonprimates (for example, *Aepyornis*, the gigantic flightless elephant bird), as well as those of bats, rodents, insectivores, suids and viverrids (primitive carnivores). However, over 90% of the subfossils found at Ankarana are primates.

Knowledge of the lemurs that lived in northern Madagascar a few millennia ago has greatly increased over the past decade. In 1983, a spectacular skeleton of the giant extinct lemur, *Palaeopropithecus*, was found in a cave on the Mahajanga plateau in northwestern Madagascar (MacPhee *et al.* 1984). Further fieldwork in this region yielded new remains of two more giant lemurs: *Megaladapis* and *Archaeolemur*. It also led to the first discovery of *Hapalemur simus* at Anjohibe (Vuillaume-Randriamanantena *et al.* 1985; Godfrey and Vuillaume-Randriamanantena 1986).

The paleontological expeditions to Ankarana, which began in 1986, yielded remains of these same taxa, and more. Indeed, six

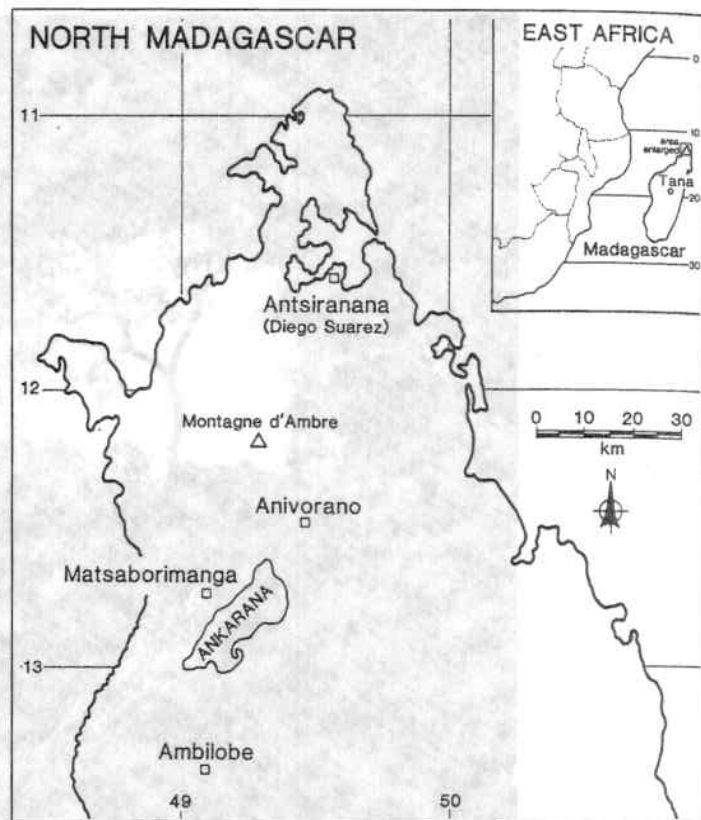


Fig. 1. Map of Northern Madagascar showing the Ankarana Range and nearby villages.

of the eight extinct lemur genera known from Madagascar, have now been found at Ankarana. The bones of these animals occur in many of the caves of Ankarana, alongside those of extant species. To date, a total of 15 primate species have been recovered, including nine living and six extinct taxa (Table 1). Most of the extant lemurs whose bones have been recovered in the caves still live in this area, with two striking exceptions: *Hapalemur simus* and *Indri indri* (Jungers *et al.* 1995). *Hapalemur simus* lives today only in southeast Madagascar (Wright 1988, 1989). *Indri indri* currently has a broader range than *Hapalemur simus*, but it has never before been reported in the far north. It is noteworthy that no bones of

Table 1. Lemurs at Ankarana: subfossils and living species.

Species	Current Status at Ankarana	Conservation status ¹	Represented as subfossils
<i>Pachylemur</i> sp.	-	extinct	yes
<i>Megaladapis</i> cf. <i>grandidieri</i>	-	extinct	yes
<i>Mesopropithecus</i> sp.	-	extinct	yes
<i>Palaeopropithecus</i> cf. <i>ingens</i>	-	extinct	yes
<i>Archaeolemur</i> cf. <i>edwardsi</i>	-	extinct	yes
<i>Babakotia radofilai</i>	-	extinct	yes
<i>Indri indri</i>	locally extinct	endangered	yes
<i>Hapalemur simus</i>	locally extinct	endangered	yes
<i>Hapalemur griseus</i> (maybe <i>occidentalis</i>)	scarce	vulnerable	yes
<i>Eulemur fulvus sanfordi</i>	common	vulnerable	yes
<i>Eulemur coronatus</i>	common	endangered	yes
<i>Lepilemur septentrionalis</i>	common	vulnerable	yes
<i>Microcebus</i> sp. (maybe <i>rufus</i>)	common	abundant	no
<i>Cheirogaleus</i> sp. (maybe <i>medius</i>)	scarce	abundant	no
<i>Phaner furcifer</i>	scarce	rare	no
<i>Avahi laniger</i>	scarce	vulnerable	yes
<i>Propithecus diadema perrieri</i>	very scarce	endangered	yes
<i>Daubentonina madagascariensis</i>	rarely seen	endangered	yes

¹IUCN assigns conservation status as follows: extinct; endangered (in danger of extinction); vulnerable (likely to become endangered in the near future); rare (small global population but not yet vulnerable or endangered); abundant (not presently threatened) (see Harcourt and Thornback, 1990).

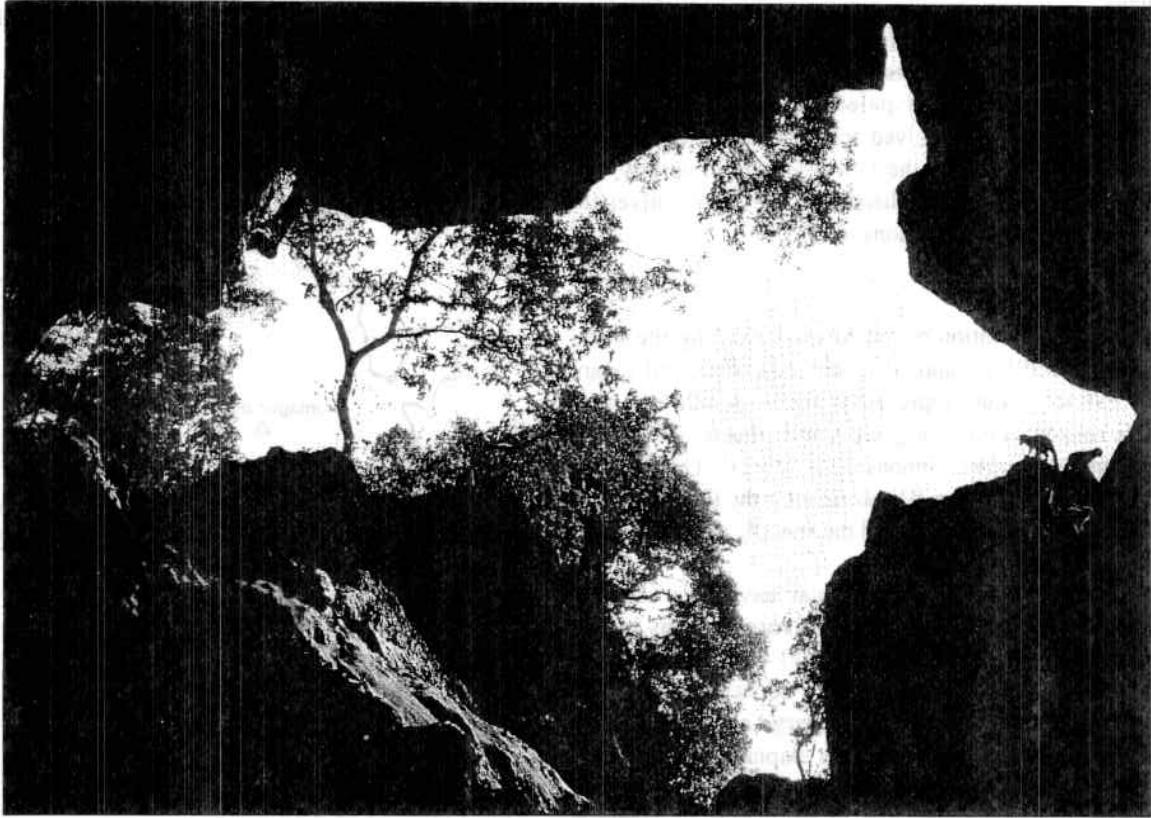


Fig. 2. *Eulemur coronatus* at the entrance to the Second River Cave. Photograph by Jane Wilson.

the smallest extant lemur species (i.e., *Microcebus*, *Cheirogaleus*, and *Phaner*) have been found in the cave deposits at Ankarana. Very small-bodied species are typically absent from fossil deposits. However, several specimens of the slightly larger *Lepilemur septentrionalis* and *Hapalemur griseus* have been recovered within the caves.

All known extinct lemurs of Madagascar were heavier than the largest of the living lemurs. *Palaeopropithecus* and *Megaladapis* were as large as chimpanzees and orangutans (Jungers 1990; Godfrey 1991), and smaller only than *Archaeoindris fontoynontii*, a poorly known species (found only at Ampasambazimba) which may have weighed as much as a gorilla (Vuillaume-Randriamanantena, 1988; Godfrey, 1991).

Many of the extinct primates at Ankarana were folivorous browsers. Several of these were slow-moving climbers and hangers with long, curved hands and feet and forward facing eyes. These unusual species, including the newly described *Babakotia radofilai* and the chimpanzee-sized *Palaeopropithecus*, belong to a group recently termed the "sloth lemurs" due to their remarkable convergence with South American sloths (Simons *et al.* 1992).

The most common extinct lemur in the deposits at Ankarana is *Archaeolemur*. This baboon-sized animal moved predominately along the ground. It had a relatively wide and heavy trunk; short, stubby hands and feet; a short muzzle with large and human-like, rather vertically implanted, central upper incisors. Far less common was *Megaladapis*, a giant leaf-eating climber with eyes that faced laterally and a narrow projecting muzzle which is thought to have sported a soft proboscis (Tattersall, 1982). Only one extinct Ankarana primate, *Pachylemur*, resembled living lemurs (particularly *Varecia*), although it too was larger and slower in gait. In all,

the giant lemurs of Ankarana formed a magnificent and diverse array of bizarre primates, unlike any alive today.

Given the interdependence of many species of plants and animals, it may well be that, even without further deforestation, the long-term effects of Holocene extinctions in Madagascar are not yet fully completed. Some of the plants that are endangered may be keystone mutualists for extant lemurs. For example, two of Madagascar's seven endemic baobabs, *Adansonia grandidieri* and *A. suarezensis*, are highly endangered with limited geographic distributions: the former has a limited distribution in the southwest and the latter exists only on the Montagne des Français and Cap d'Ambre (at the northern tip of Madagascar). Both have fruit with fragile pericarps, highly palatable and nutritious pulp, and tough seeds which are adaptations for animal, rather than water, dispersal. Yet, Baum (1995) notes that neither of these species has known extant animal dispersers, a fact that could account for their current limited distribution. It is possible that some of the extinct megafauna of Madagascar, such as *Archaeolemur* or *Aepyornis*, were the main dispersers of nonwater-dispersed baobab seeds, and their extinction will have inevitable effects on the survival of other animals that depend on them for food. Indeed, both *Adansonia grandidieri* and *Adansonia suarezensis* are apparently mammal (rather than insect or bird) pollinated; *Phaner furcifer* is a likely pollinator of the former (Baum 1995; see also Sussman and Raven 1978).

The lemurs known from Ankarana, both from subfossil evidence and from sightings of living animals, are listed in Table 1. Details of the conservation status of the extant species are also given.



Fig. 3. Male crowned lemur emerging from the Second River Cave water hole. Photograph by Jane Wilson.

Extant lemurs

Ten lemur species have been reported for the forests of Ankarana (records by Wilson *et al.* 1989, confirmed by Hawkins *et al.* 1990). Three of these are endangered and four are vulnerable. *Eulemur coronatus* is the commonest day-active lemur in intact canopy forest. Sympatric with this and also in populations of several hundred per square kilometer are *Eulemur fulvus sanfordi* and the nocturnal *Lepilemur septentrionalis ankarensis*. Ankarana is an important refuge for the dwindling populations of this *Lepilemur*.

The semi-evergreen forests provide dry season foraging for lemurs. In September, just before the rains recommence, *Eulemur coronatus* alone reaches a density of 1-5 per hectare in small pockets of canopy forest. The habitat at Ankarana is so heterogeneous that estimates of total population are difficult, and calculations of lemur biomass at this season are misleading: they cannot reflect the forest's carrying capacity. However, they emphasize the importance of small pockets of forests and help explain Ankarana's role as a refuge for so many lemur species. In canopy forest where, throughout the dry season, fruiting *Strychnos* lianas provide food for both *Eulemur* species, and there is abundant foliage for *Lepilemur*, total lemur biomass reaches a maximum of 37 kg/ha. This approaches one of the highest primate densities known (Wilson *et al.* 1989; Hawkins *et al.* 1990). Once the rains begin, xerophytic plants (including *Ficus* spp.) on the limestone come into leaf and fruit enables the lemurs to expand their ranges widely, and population densities fall. A tiny area of forest is responsible for maintaining large numbers of lemurs through the dry season, which, as a result, means that logging of even relatively small areas of forest will have disastrous effects on the lemurs.

Water holes in cave entrances attract *Eulemur* troops from wide areas because, during the six-month dry season, there is little or no surface water elsewhere. It may be that cave water holes enticed many of the large extinct species inside to drink, as do the smaller species today. In any case, it is clear from the abundance of their bony remains in the caves that extinct lemurs frequented the sunken forests near the cave entrances and that, just like the extant lemurs, they climbed over the cliffs of the Ankarana.

Threats

Ankarana has been a special reserve since 1956, and work is underway to upgrade its reserve status. Four wardens have been employed there, and yet protection of this region is still inadequate since access to many parts of the reserve is easy: there are many roads; it has a large periphery; and patrolling across the area is impossible. Despite its reserve status and the presence of wardens, it is still threatened directly by illegal logging. In addition, felling in the forest upstream of Ankarana may compromise the perennial flow of the rivers. Hence a critical refuge of three endangered and four vulnerable lemur taxa could disappear entirely.

The apparent rapid decimation of a much richer fauna in the recent past bears testimony to the fact that, despite its wealth, the current primate fauna of the Ankarana is not an ecologically intact community. Recently dated bony materials submitted for dating should help to establish a chronology for the local extinctions (Simons *et al.* 1995). Given the endangered status of three of the surviving lemur species and subspecies at Ankarana, as well as the encroachment of brush fires and selective and more extensive felling, it is clear that without conservation efforts, the remnant fauna may suffer the fate of many of the earlier lemur inhabitants of this region.

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A Study on the Management and Conservation of Small Mammals in Fragmented Rain Forests in the Western Ghats, South India: A Preliminary Report

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Introduction

Tropical rain forests are the centers of biodiversity. These forests, which cover about 6% of the land surface of the world, harbor more than 50% of the extant species (McNeely *et al.* 1990). Extensive removal of these forests is therefore a matter of global concern. Of equal concern is the progressive loss of species from the fragmented and isolated remnant forests. Unlike habitat loss, however, the effects of fragmentation are manifested over a long period of time. For many species, in fact, fragmentation could ultimately have the same consequence as extinction (Cutler 1991). Wilcox and Murphy (1987) stated that "habitat fragmentation is the most serious threat to biological diversity and is the primary cause of the present extinction crisis". At the current rate of loss and fragmentation of tropical rain forest, the survival of a significant component of biological diversity would depend on the retention and management of a network of fragmented forests (Saunders *et al.*, 1987).

The south Indian rain forests, confined to the Western Ghats mountain ranges, have a very high biodiversity, particularly flora (Nair and Daniel 1986), herpetofauna (Inger and Dutta 1986) and small mammals (Prater 1980). Nearly a century of human activities in this area have removed vast areas of rain forest. That remaining exists as a number of isolated small fragments which differ in their size, shape, isolation and type of ownership. Loss of rain forest has now been more or less stemmed and a significant proportion of the remnant patches come under the protected areas network. The very existence of remaining rain forest as isolated fragments, however, poses a serious threat to the long-term survival of the rich and endemic flora and fauna. An assessment of the conservation value of the remnant patches and of the management options to retain these values is, therefore, urgently needed. The project reported here proposes to make such an assessment, and to suggest a management strategy for small mammals, consisting of arboreal squirrels and primates, rodents and small carnivores.

This project was funded by Ministry of Environment and Forest, Government of India, in November 1993. The major objectives are:

1. to assess the nature and extent of loss of small mammals from fragmented rain forests in the Western Ghats, South India;
2. to identify the factors which govern such a species loss;
3. to assess the efficacy of the existing protected area network in conserving fauna endemic to the rain forests of Western Ghats; and
4. to suggest measures which would enhance the efficacy of existing protected area network.

The Indira Gandhi Wildlife Sanctuary in the Anamalai Hills was selected as the main study site, taking into consideration the high degree of fragmentation of the rain forest in the area. This report presents the findings of a survey of the status of 25 patches of rain forest and the presence/absence of three arboreal mammals: lion-tailed macaque (*Macaca silenus*), Nilgiri langur (*Presbytis johni*), and giant squirrel (*Ratufa indica*).

Study Area

The Indira Gandhi WLS (Tamil Nadu) in the Anamalai Hills (76° 49.3' - 77° 21.4' E and 10° 13.2' - 10° 33.3' N) is one of the largest sanctuaries in south India, covering an area of about 1000 km², in an altitudinal range of about 350 m to 2600 m. The western slopes of the sanctuary receive up to 500 cm of annual rain fall whereas the eastern rain shadow areas receive less than 100 cm. The vegetation reflects the rain fall and altitudinal variation in the sanctuary, and ranges from scrub forest on the eastern foot hills to the rain forest in high rainfall areas, and montane grass lands at the higher elevations. The Anamalai Hills probably had the largest area of contiguous rain forests in the not too distant past. Large areas were lost to tea, coffee, cinchona and teak plantations, and a series of hydroelectric projects. Most of the remaining rain forest is included in the Indira Gandhi WLS in Tamil Nadu, and the Parambikulam WLS in Kerala. The total area of rain forest in the Indira Gandhi WLS is probably about 130 km², most of which occurs as small fragments from less than 10 ha to 2000 ha. Many of these fragments are privately owned and many are under-planted with cardamom. Most of the fragments are surrounded by tea and

coffee estates, or eucalyptus and teak plantations or secondary forests. Many are near human settlements and roads. Most of the fragments are confined either to slopes or hill tops.

The Valparai area, where most of the studies are being carried out, is at an average elevation of 1100 m. Valparai is a small town with about 50,000 people, mostly tea and coffee estate workers. Most of the fragments selected for study are within 15 km radius of Valparai, but up to 30 km by road.

Methods

From March to end of May 1994, we surveyed all of the 25 fragments that we had identified in the Indira Gandhi WLS. The survey was limited to the arboreal mammals; the lion-tailed macaque, Nilgiri langur, and giant squirrel. Data on landscape and habitat parameters were recorded for each fragment. We also recorded habitat degradation parameters such as cattle grazing, logging, wood-cutting and firewood collection.

The survey of arboreal mammals was carried out on foot along existing tracks in the forests. The survey team consisted of 2-4 people who walked at a speed of about 2 km per hour. The length of the transect varied from 500 m to about 4 km. The sighting angle and sighting distance were recorded for all sightings of the

three species. This data can be used to estimate relative abundance and absolute densities. One to three surveys have been carried out in each fragment to date.

For each fragment, the following landscape parameters were recorded: area, altitude, nearest village and distance to it, distance from road, connectivity (that is, whether the patch is connected to other natural forests), vegetation around the patch, nature of undergrowth (planted or natural), location (in valley, slope or hill top), time since isolation, ownership, and water source.

Data on habitat parameters were collected at sampling points at intervals of 300 strides. Canopy height, canopy cover, slope, and soil type were recorded at the sampling point, while tree species, girth at breast height (GBH), shrub cover, and litter cover were recorded from a 5 m radius plot, centred on the point. Canopy cover was estimated using a gridded rear view mirror of a motor cycle. Canopy height (in meters), shrub cover (percentage), litter cover (percentage), slope (in three categories), and soil type were all visually estimated. Since the length of the transect was proportional to the area of the patch, the number of sample points increased with the area of the fragment.

Results

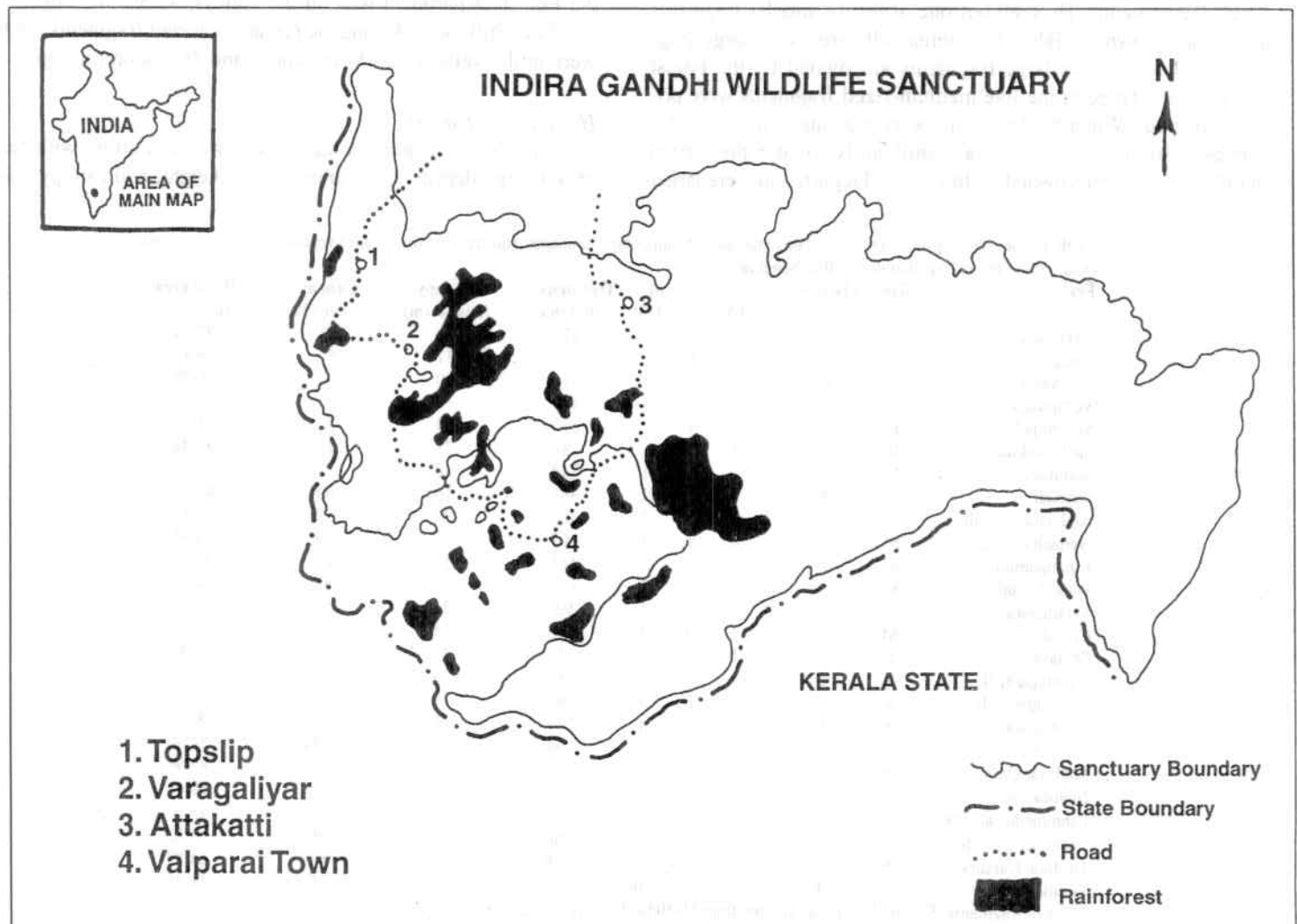


Fig. 1: Map of the Indira Gandhi Wildlife Sanctuary showing the patches of rain forests.

A preliminary survey of the arboreal mammals in all 25 rain forest fragments has been completed. We also carried out vegetation studies in each fragment. Since estimation of abundance of arboreal mammals requires a large sample size which will be collected only in the coming year, for the interim report the analysis is based on their presence/absence. The fragments are first compared with reference to the landscape parameters, followed by habitat parameters and the presence/absence of arboreal mammals.

Landscape Parameters

Area and Ownership. Since the precise area of each fragment remains to be estimated, the 25 fragments were grouped into four area classes (Table 1): small (<10 ha), medium (11-50 ha), large (51-200 ha) and very large (> 200 ha). Eleven small, five medium, six large and three very large fragments were surveyed. Of the three very large fragments Varagaliyar shola, including the Banathiyar shola, is the largest (c. 1500 ha) followed by Akkamalai shola (c. 1000 ha) and Kuruvampali shola (c. 500 ha).

Eleven of the fragments are owned by the Forest Department, and are part of the Indira Gandhi Wildlife Sanctuary, while 14 fragments are privately owned, either by large tea estates (such as Tata Tea Ltd.) or by small cardamom estates. There was a definite relationship between area and ownership, with the smaller fragments being privately owned and the larger ones owned by the Forest Department. Thus, all but one of the 11 smaller fragments are privately-owned (Table 1) whereas all three very large fragments and four of six large fragments are owned by the Forest Department. Three of the five medium-sized fragments were privately-owned. When the fragments were regrouped into two size classes (<50 ha and >50 ha), a significantly greater proportion (63.6%) of fragments owned by the Forest Department were larger

in area ($\chi^2 = 6.5$, $df = 1$, $p < 0.05$) compared to those privately-owned (14.3%).

Altitude. The altitude of the fragment was grouped into three categories, low (600-900 m) medium (901-1200 m) and high (1201-1500 m). Low and high altitudes each contained five fragments, whereas 15 were in the medium altitude. Most of the privately-owned fragments were in the medium altitude (78.6%), while fragments owned by the Forest Department were almost equally distributed among the three altitude classes. Most of the smaller fragments (<50 ha) were in the medium elevation (nearly 80%, $n = 16$) whereas most of the larger fragments (>50 ha) were either in high (44%) or low altitude (33%).

Connectivity. Of the 25 fragments, only 11 had connectivity or canopy contiguity with other rain forests. Nearly 90% of the larger fragments (>50 ha) had connectivity compared to 18% of the smaller fragments. As expected, fragments owned by the Forest Department had greater connectivity (82%, $n = 11$) than privately-owned fragments (nearly 15%, $n = 14$).

Location. The location of each fragment was classified as being primarily in valley, hill slope or hill top. Of the 25 fragments, eight were in valleys, ten on slopes, and seven on hill tops. One of the very large fragments (Varagaliyar) was primarily in the valley, whereas the other two fragments were primarily on hill tops at high elevations. A total of 36.4% of the fragments belonging to the Forest Department were in the valleys, 45.5% on slopes and 18.2% on hill tops. Among the privately-owned fragments, 28.6% were in the valleys, 35.7% on slopes and 35.7% on hill tops.

Habitat Parameters

Status of vegetation in the patches was quantified with reference to tree density, basal area, canopy height, and canopy cover.

Table 1: The presence/absence of lion-tailed macaque, Nilgiri langur, and giant squirrel, and the status of vegetation in 25 rain forest fragments in the Indira Gandhi Wildlife Sanctuary.

Fragment	Size ¹	Owner ²	Presence of			Tree density ind./ha	Canopy height (m)	Canopy cover (%)	Basal area (m ² /ha)
			LTM	NL	GS ³				
Akkamalai	VL	F	1	1	1	879	19	67	97.54
Varagaliyar	VL	F	1	1	1	455	31	57	49.81
Kuruvampali	VL	F	1	1	1	410	30	55	58.73
Vellaimalai Top	L	F	0	1	1	323	13	33	33.71
Monopoly	L	F	1	1	1	347	23	52	55.46
Sankarankudi	L	F	1	1	1	184	21	33	37.48
Surlimalai	L	P	1	1	1	244	36	52	75.18
Iyerpadi	L	P	0	1	1	441	16	60	85.86
Andiparai W. Falls	L	F	1	1	1	357	22	77	29.41
Iyerpadi Church	M	F	0	1	1	403	17	59	43.90
Kurangumudi	M	P	1	1	1	161	17	23	37.82
Puthuthottum	M	P	1	0	1	128	19	62	67.23
Varattuparai-I	M	P	1	1	1	93	25	56	11.01
Cinnakallar	M	F	1	1	1	336	18	56	39.53
Sholayar P. House	S	P	0	1	1	244	13	27	31.41
Varattuparai-II	S	P	0	1	1	233	18	42	51.59
Varattuparai-III	S	P	0	1	1	182	10	21	20.29
Varattuparai-IV	S	P	0	1	1	127	9	18	8.01
Nirar Dam	S	F	0	1	1	164	8	75	6.54
Sholayar Dam	S	P	0	1	1	370	17	55	85.96
Monica Estate	S	P	0	0	0	127	20	5	18.48
Pannimedu Fac. div.	S	P	0	0	0	216	15	44	43.70
Pannimedu Ist. div.	S	P	0	0	0	306	14	48	42.82
Urulikal Nursery	S	P	0	0	0	178	16	36	61.87
Urulikal	S	P	0	0	0	111	9	35	19.28

¹ Size of fragments: S = small <10 ha, M = medium 11-50 ha, L = large 51-200 ha, VL = very large >200 ha.

² Ownership of fragments: F = Forest Department, P = private estate.

³ Presence of arboreal mammals: LTM = lion-tailed macaque, NL = Nilgiri langur, GS = giant squirrel; 1 = present, 0 = absent.

Table 2. Comparison of habitat parameters with reference to landscape variables.

Landscape variables	N	Tree density ind./ha	Basal area m ² /ha	Canopy height (m)	Canopy cover (%)
Location					
Top	7	282.0	43.79	15.57	46.00
Slope	10	272.1	46.32	21.30	46.50
Valley	8	290.5	42.86	16.75	44.75
M-W test		n.s.	n.s.	n.s.	n.s.
Connectivity					
No	14	204.64	34.86	15.07	40.50
Yes	11	377.64	56.78	22.27	52.55
M-W test		<0.01	<0.05	<0.05	n.s.
Altitude (m)					
600-900	5	309.80	41.28	24.40	49.40
900-1200	15	204.45	41.05	16.47	40.13
1201-1500	5	480.60	58.08	17.40	59.20
M-W test		<0.01	n.s.	n.s.	n.s.
Area					
<10	11	205.27	35.45	13.55	36.91
11-50	5	231.80	48.29	19.00	50.80
51-200	6	309.67	45.86	22.06	51.00
>200	3	581.33	68.69	26.67	59.67
M-W test		n.s.	n.s.	n.s.	n.s.
Ownership					
Forest Dept.	11	364.27	46.67	19.09	54.55
Private	14	215.14	42.81	17.57	38.93
M-W test		n.s.	n.s.	n.s.	n.s.

All these parameters varied considerably among the 25 fragments (Table 1). The major landscape variables affecting vegetation parameters are the area of the fragment and ownership. Tree density, basal area, canopy height, and canopy cover all seemed to increase with increasing area of the fragment (Table 2). The difference was statistically significant only in the case of tree density and canopy height, however (Table 2). Similarly, among the two kinds of ownership, tree density, basal area, canopy height, and canopy cover were greater in the fragments owned by the Forest Department (Table 2), although significantly so only in the case of tree density and canopy cover (Table 4).

There was however a significant connection between area and ownership, as mentioned earlier, with the fragments owned by the Forest Department being larger, and most of the small fragments being privately owned. The effect of area was therefore examined within each ownership category and vice versa, wherever data permitted (Table 3). Thus, among the fragments owned by the Forest Department, the very large fragments had greater tree density, canopy height, canopy cover and basal area, although only tree density was significantly greater. Among the privately owned fragments, the larger fragments (11-200 ha) had a greater tree density, canopy height, canopy cover and basal area compared to small fragments (<10 ha). The difference was significantly greater only

for canopy height, but nearly so for canopy cover. It is evident, therefore, that within each category of ownership, degradation is greater in the small fragments than in the larger.

Among fragments of similar area (<50 ha), there was a significant difference between private and forest department-owned fragments only in tree density, the latter being greater. Canopy height, canopy cover and basal area were more or less similar between the two kinds of ownership. Although it appears that privately-owned fragments are more degraded, the effect is largely because they are often smaller in area compared to fragments owned by the Forest Department.

The status of the vegetation was also examined with reference to other landscape variables. There was no difference between the three categories of location (Table 2). Patches with connectivity, however, had greater tree density, basal area and canopy height. There was no difference among the three altitude categories except in tree density. However, the mid-altitude (900-1200 m) had the lowest values in all the parameters.

Arboreal Mammals

Between March and the end of May 1994, a preliminary survey of all 25 fragments was carried out to assess the presence or absence of diurnal arboreal mammals (Nilgiri langur, lion-tailed macaque, and giant squirrel). Presence/absence was determined on the basis of at least one transect in the fragment and reliable local information. The transect surveys were carried to estimate abundance of the arboreal mammals, but in the absence of adequate sample size the data is not analyzed here. For the present, fragments are compared only with reference to the presence or absence of three species of arboreal mammals.

Of the 25 fragments surveyed, ten had all three species, nine had Nilgiri langur and giant squirrel, one had lion-tailed macaque and giant squirrel, two had only giant squirrel and two had none of the three species. The fragments with and without each species were compared with regard to the landscape variables - area, ownership, location, altitude, and connectivity (Table 4). To carry out a χ^2 test, the fragments were regrouped into two size classes (<50 ha and >50 ha) in order to meet sample size requirements. A significantly larger proportion (77.8%) of the larger fragments had lion-tailed macaque than the small fragments (18.8%). This was also true for Nilgiri langur, with all the larger fragments having the species compared to only 62.5% of the small fragments. There was no significant difference between the small (81.3%) and large fragments (100%) for the presence of giant squirrel.

There was no significant difference between Forest Department-owned and privately-owned fragments in the presence of any of three species (Table 4), although in all cases a greater proportion

Table 3. Comparison of habitat parameters, area within ownership and ownership within area.

Size (ha)	Ownership	N	Tree density ind./ha	Basal area m ² /ha	Canopy height (m)	Canopy cover (%)
<10	Private	9	220.33	40.60	14.67	32.89
>10		5	205.80	47.03	22.80	49.80
M - W test significance			n.s.	n.s.	n.s.	n.s.
50-200	Forest Department	4	302.75	39.01	19.75	48.75
>200		3	581.33	68.69	26.67	59.67
M - W test significance			n.s.	n.s.	n.s.	n.s.
50-200	Forest Department	6	331.33	46.90	18.83	51.83
	Private	5	205.80	47.03	22.80	49.80
M - W test significance			n.s.	n.s.	n.s.	n.s.

Table 4. Percentage of fragments with lion-tailed macaque, Nilgiri langur and giant squirrel with reference to various landscape variables.

Landscape variables	N	<i>Macaca silenus</i>	<i>Presbytis johni</i>	<i>Ratufa indica</i>
Area				
Small	11	0	54.5	72.5
Medium	5	60.0	80.0	100.7
Large	6	66.7	100.0	100.0
Very large	3	100.0	100.0	100.0
χ^2 test		8.4	4.4	1.9
Significance		<0.01	<0.05	n.s.
Location				
Valley	8	50.0	75.0	87.5
Slope	10	50.0	80.0	90.0
Top	7	14.3	71.4	85.7
χ^2 test		2.8	0.17	0.07
Significance		n.s.	n.s.	n.s.
Altitude (m)				
Low (600-900)	5	80.0	100.0	100.0
Medium (901-1200)	15	26.7	60.0	80.0
High (1201-1500)	5	40.0	100.0	100.0
χ^2 test		4.4	5.3	2.3
Significance		n.s.	n.s.	n.s.
Ownership				
Forest	11	54.5	90.9	100.0
Private	14	28.6	64.3	78.6
χ^2 test		1.7	2.4	2.7
Significance		n.s.	n.s.	n.s.
Connectivity				
No	14	21.4	64.3	78.6
Yes	11	63.6	90.9	100.0

of the Forest Department-owned fragments contained them. Location of the fragment in valley, slope or hill top seemed to have no effect (Table 4). Connectivity with other forests was important only for the lion-tailed macaque, with a greater proportion (63.6%) of such fragments having the species compared to fragments without connectivity (21.4%).

The vegetation parameters, tree density, basal area, canopy height and canopy cover, were compared between fragments with and without the three species (Table 5). Tree density, basal area, canopy height and canopy cover were all greater in the fragments with a species for all three species. The difference was, however, statistically significant only for canopy height in the case of the lion-tailed macaque, and for tree density in the case of the Nilgiri langur.

Discussion

The preliminary data reveal that the status of the rain forest fragments is largely dictated by their area, those which are larger being better, with greater tree density, basal area, canopy cover and canopy height. The apparent effect of ownership (the fragments owned by the Forest Department being better) is probably an artefact of most of the larger fragments being owned by Forest Department and the smaller fragments being privately owned.

Most of the fragments support at least one of the three species, even fragments of less than 10 ha. However, the three species show considerable differences in their tolerance to fragmentation, with the giant squirrel being found in most of the fragments, and the lion-tailed macaque being found only in the larger fragments. The Nilgiri langur also disappears from the smaller fragments. This area effect perhaps largely accounts for a higher percentage of the fragments owned by the Forest Department having the Nilgiri

Table 5. Comparison of habitat parameters between patches with and without lion-tailed macaque, Nilgiri langur and giant squirrel.

Species Name	N	Tree density ind./ha	Basal area m ² /ha	Canopy height (m)	Canopy cover (%)
<i>Macaca silenus</i>					
Absent	15	250.73	39.5	14.2	40.9
Present	10	325.80	51.9	24.3	53.1
M-W test		n.s.	n.s.	<0.001	n.s.
<i>Presbytis johni</i>					
Absent	6	177.67	42.2	15.5	38.3
Present	19	313.32	45.2	19.1	48.2
M-W test		<0.05	n.s.	n.s.	n.s.
<i>Ratufa indica</i>					
Absent	3	216.33	35.0	16.3	32.3
Present	22	289.55	45.8	18.5	47.6
M-W test		n.s.	n.s.	n.s.	n.s.

langur and lion-tailed macaque. The fragments with any of the three species also had greater tree density, basal area, canopy height and canopy cover.

This preliminary study revealed, therefore, the overriding effect of area on the status of the forest as well as the presence or absence of three species of arboreal mammals. Among the three species, the effect is most pronounced on the lion-tailed macaque and least on the giant squirrel. The effect of ownership is largely due to its effect on area of the fragment.

Results of practical importance

The presence of arboreal mammals even in fragments as small as 10 ha demonstrates the conservation value of rain forest fragments. The total population of lion-tailed macaques in the Anamalai Hills is estimated at about 800 animals. Nearly 40% of this population is in forest fragments of less than 200 ha. The situation might also be similar for the Nilgiri langur. The loss of species, especially the two which are endemic (lion-tailed macaque and Nilgiri langur), as the fragments become smaller or more degraded is, therefore, a matter of serious concern. Most of the fragments also serve as temporary refuges for many other terrestrial mammals and birds, while they move from one part of the sanctuary to another. As such, the fragments have other biodiversity values, and are essential for the maintenance of the integrity of the Sanctuary as a whole.

Two conservation measures obviously required include: (a) the prevention of any further reduction in area of the rain forest fragments; and (b) the prevention of any further degradation. The success of the above two measures is, however, intricately linked to the ownership of the fragments. While the larger fragments owned by the Forest Department are not very degraded and are far from human settlements, the smaller fragments are mostly privately owned and near human settlements. The privately-owned fragments are subject to two major pressures which cause habitat degradation and loss. Firstly, most of them are underplanted with cardamom, which prevents any forest regeneration. Secondly, and more importantly, these forests are often subjected to selective logging, either to meet shade requirements for cardamom or to meet fuel wood requirements for cardamom curing and labor. The Forest Department seems to have little control over this. Apart from habitat degradation, selective logging can also lead to immediate mortality due to various factors. The recent bout of selective log-

ging in one of the cardamom estates, and the resulting reduction in the population of lion-tailed macaques from 43 to 34 is a typical example.

One major finding of this study so far which is of practical value is that the retention of a significant component of the biodiversity in Anamalai Hills would depend on our ability to manage fragmented rain forests which differ in size, connectivity, and ownership. The most critical factor is the conflicting interests in managing the privately owned fragments.

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Survey of Primates in Mizoram, North-East India

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North-east India, widely regarded as one of India's biodiversity hot-spots, is also the region where the country's primate community reaches its greatest diversity (Rodgers and Panwar 1988; Choudhury 1988). Some sanctuaries, such as Gumti in the state of Tripura, have seven of the nine species of primates reported from north-east India (Gupta and Kumar 1993). Today, the diverse fauna of the region is threatened by logging, shifting cultivation, and hunting by local human communities (Johnsingh 1985; Choudhury 1987; Rodgers and Panwar 1988; Katti 1992). However, ecological information that can lead to comprehensive conservation measures is severely lacking for most of the hilly regions of north-east India.

Recently we carried out a survey of primates in three protected areas in the hill state of Mizoram in north-east India (Mishra *et al.* 1994; Fig. 1). The areas surveyed and the duration of the surveys were as follows:

Dampa Tiger Reserve	24 December 1993 to 04 January 1994
Murlen National Park	07 January 1994 to 10 January 1994
Phawngpui Wildlife Sanctuary	13 January 1994 to 18 January 1994

Mizoram (area - 21,087 km²) is a hilly state in the southern tip of north-east India. The parallel ranges of the Mizo or Lushai hills run in a north-south direction along the Burmese arc of the Himalayan mountain chain. The hills range in altitude from 200 to 1200 m above sea level in the west to 1500-1800 m a.s.l. in the east. The terrain is highly dissected with numerous streams and rivers. Dampa Tiger Reserve, where most of our observations were made, occupies an area of 500 km² on the western border of Mizoram. Murlen National Park (200 km²) and Phawngpui Wildlife Sanctuary (50 km²) are on the eastern border of the state. The highest peak in Mizoram (Blue Mountain, 2157 m above sea level) is in Phawngpui.

Mizoram receives a heavy annual rainfall of about 2500 mm during the south-west monsoon between June and September. The vegetation grades from tropical evergreen forests in the west (Dampa) to semi-evergreen in the east (Murlen and Phawngpui). Moist bamboo brakes dominated by *Melocanna bambusoides* (Vern. *Mautak*) occur extensively as secondary formations in Dampa. The

two higher altitude eastern sites are characterized by the presence of *Quercus* spp. in the primary forests and *Rhododendron arboreum* in the secondary scrub, steep, and grassy slopes (Champion and Seth 1968; Anon. 1989).

Shifting cultivation or *jhum* is the main form of land use and the occupation of the majority of the population (Ray 1993). As in much of the north-east India, the *jhum* cycle or fallow period is believed to have decreased from 15-20 years in the past to just 3-5 years today. This, besides being energetically and ecologically unstable, has created large tracts of an arrested successional vegetation dominated by weeds or bamboo, and problems such as soil erosion and desertification (Ramakrishnan 1992). In the sanctuaries we visited, three successional stages created by *jhum* could be clearly distinguished: almost pure bamboo forests (c. 5-15 years old); secondary forests of various ages (with trees older than 15 years); and primary evergreen forests (which have not been subjected to *jhum*). In addition, the areas had long chains of cliffs (>3 km in length). A narrow belt of vegetation along these cliffs was richer in grass cover, and had a lower tree density than the surrounding areas (steep slope vegetation, Fig. 1).

All field observations were carried out on foot, and distances were measured using a pedometer. The distance covered in the Dampa Tiger Reserve, where most of the observations were made, was 39.5 km. For each primate sighting, the species, number, height in the trees, and successional vegetation type were noted. We also made inquiries with the local people and forest guards about wildlife. For gibbons, listening posts on prominent locations were used to detect their presence by their loud calls (Brockelman and Ali 1987). We prepared rough vegetation maps for Dampa and Phawngpui. This could not be done for Murlen due to the short time spent there.

Five species of primates were seen during the survey, and at least seven probably occur in the state. The information obtained on the local primates is given below.

Hylobates hoolock

Extensive habitat for gibbons is available in Dampa in the primary evergreen forests. Three mornings were devoted exclusively to listening for hoolock loud calls from a watchtower at a promi-

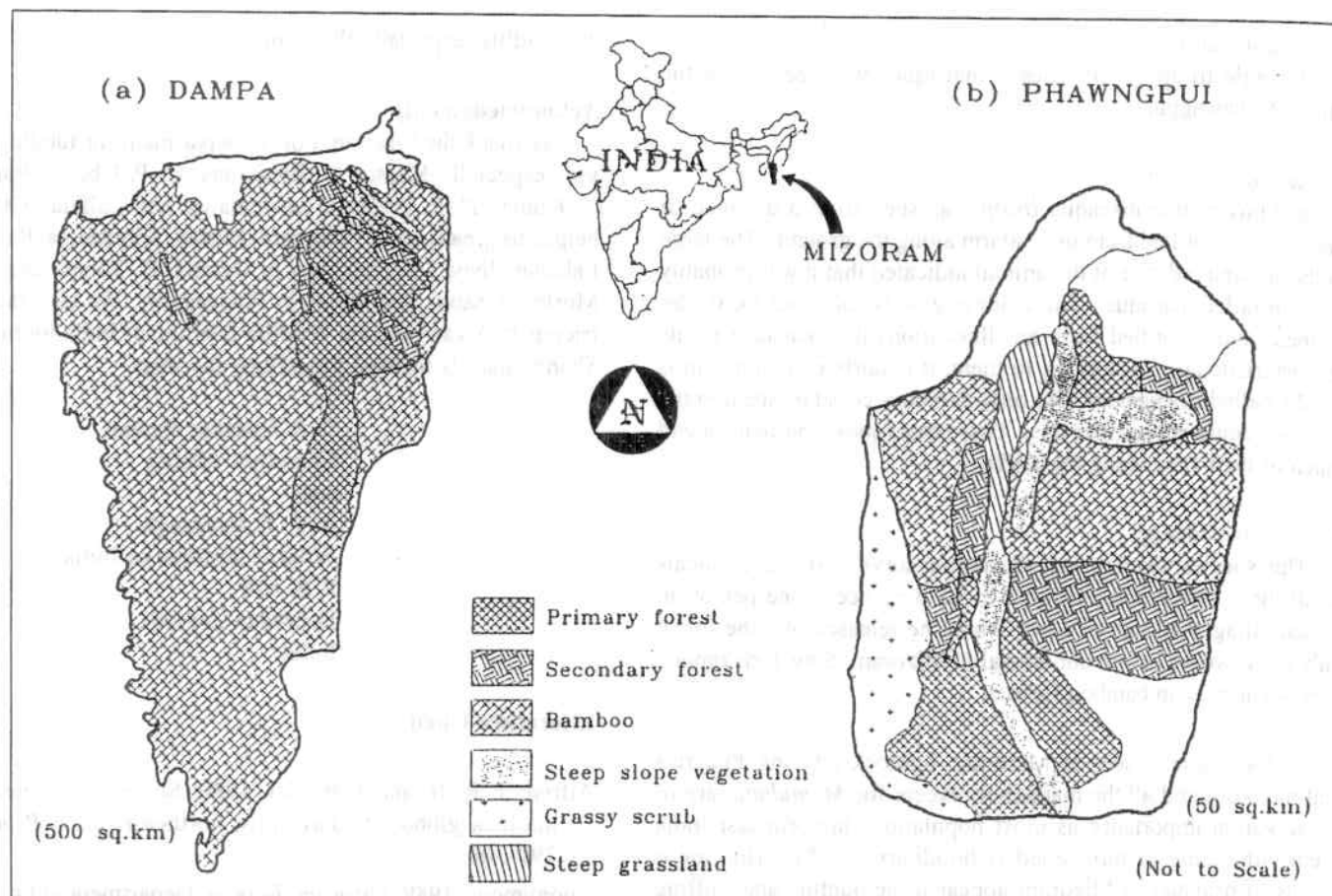


Fig. 1. Vegetation maps for (a) Dampa Tiger Reserve and (b) Phawngpui Wildlife Sanctuary, Mizoram, North-East India.

nent ridge top (Dampatlang). Six groups of gibbons were heard calling in an area of about 6 km² along the Tuichar river valley and eastern slopes of the Chawrpialtlang ridge. A possible seventh group could not be confirmed. This minimum density of one group/km² is low compared to some other areas (Gittins and Tilson 1984; Alfred and Sati 1990). Attempts were made to locate only one group due to time constraints. This group comprised one adult female, one adult male, one subadult, and an infant. The mean group size of hoolock gibbons is usually about 3-4 animals (Choudhury 1990). This being the case, the Dampatlang-Chawrpialtlang area in Dampa has at least 18-24 gibbons in contiguous primary forest. If, however, the entire area of Dampa is considered, there has been extensive habitat loss for gibbons (Fig. 1a). As the figure shows, most of the area is covered by stands of bamboo.

In Murlen, two hoolock groups (one with at least three individuals) were heard calling from the vicinity of Chamdur camp in the core area of the Park. Most of the forest seen was oak-dominated, low-canopied, and relatively open, unlikely to be suitable habitat for hoolocks. Primary forest in Phawngpui occurs in two isolated patches in the north-east and south-west corners of this small sanctuary (Fig. 1b). Hoolock gibbons were heard from these areas. As the isolated patches are small, the population of hoolocks in Phawngpui is unlikely to be sizable.

Presbytis pileatus

Five troops of capped langurs were encountered in Dampa,

giving an encounter rate of 0.13 troops per km (onward and return sightings along the trails). All sightings were in primary (or late-successional secondary) forests. The troop size was 10-15. Infants were seen in two of the troops. In Murlen, one troop of about 20 individuals was sighted, also in primary forest. The animals, detecting our presence, fled through the canopy in alarm. We did not see capped langurs in Phawngpui, but locals informed that they do occur there.

Presbytis phayrei

This species has been reported only from Tripura, Cachar (Assam), and Mizoram in India (Gupta and Kumar 1993; Rai and Johnsingh 1993). Phayre's leaf monkey was seen only in Dampa. In 39.7 km of trails covered, only one troop was seen, in secondary forest along a rocky ravine. Another troop was seen in dense bamboo with few, scattered trees, near Teirei Rest House, with about 15 individuals.

Macaca assamensis

Six troops of assamese macaque were seen in Dampa, five of which were along cliffs with primary vegetation. One sighting was in primary forest near a ravine close to the cliff face. This species was also seen in Phawngpui (troop sizes 4 and 12-13, including five infants), again on cliff faces. They were quite vocal, making harsh and squealing noises, as they searched under stones for food.

Macaca mulatta

A single troop of >10 rhesus macaques was seen along the cliffs of Phawngpui.

Macaca arctoides (?)

In Murlen, one macaque troop was seen from a distance of about 50 m as it fled from us in alarm along the ground. The large body size and red face of the animal indicated that it was probably a stump-tailed macaque. The wildlife guards and other locals described (and identified from an illustration) this macaque by its characteristic tail. According to them, it is fairly common, and is locally called *zawngmawt*. As only two days could be spent in the field, we could not confirm this. These macaques reportedly spend much of their time along the cliffs.

Nycticebus coucang

This species was not seen during the survey. However, locals in all three survey sites attested to its presence. One person in Lallen village had one as a pet, which he released into the forest only a few weeks before our arrival in Mizoram. Slow loris reportedly occur even in bamboo forests.

Of the primates seen in Mizoram, hoolock gibbons, Phayre's leaf monkeys and all the macaques, except for *M. mulatta*, are of conservation importance as most populations in north-east India seem vulnerable or threatened (Choudhury, 1988). The major threats to primates in Mizoram appear to be hunting and shifting cultivation. All the primates seen were very shy of humans, fleeing immediately on seeing us. Many huts in the villages we visited had their walls adorned with skulls of mammals such as gaur (*Bos gaurus*), bears, deer, serow (*Capricornis sumatrensis*), rodents, clouded leopard (*Neofelis nebulosa*), and primates. Macaque skulls comprised nearly all of more than 50 primate skulls examined. Hunters claimed to have shot all the primates, including hoolock gibbons. Practically all these animals are eaten. Hunting is part of the local traditions, and its exact impact on primates is unknown. Slow-breeding species such as gibbons are probably the most affected.

Shifting cultivation, or *jhum*, causes dramatic changes in the vegetation. *Jhum* cycles of 15-20 years create successional forests which may be able to support species such as Phayre's leaf monkey (Gupta and Kumar, 1993). However reduced *jhum* cycles have created large areas of monotypic bamboo vegetation (Figure 1a, 1b), which is unlikely to be suitable habitat for many primates. The survival of hoolock gibbons probably hinges on the existence of tracts of undisturbed, primary, evergreen forests. The demographic and genetic viability of the small populations in many sanctuaries of north-east India needs to be studied.

The conservation outlook, however, is positive. The Mizoram Forest Department has taken commendable steps towards conserving wildlife in the state. About 7.5% of the total land area is under protected forests, and an additional 6,400 km² are in Reserve Forests (Anon. 1989). In Dampa, eleven villages were amicably relocated outside the sanctuary, and *jhum* is now disallowed within. Similar efforts are being made in Murlen and Phawngpui. The regeneration of bamboo forests into later successional stages, and protection from poaching are likely to have beneficial effects on

the wildlife, especially the primates.

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Population Survey of the Crested Black Macaque (*Macaca nigra*) at Manembonembo Nature Reserve in North Sulawesi, Indonesia

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The crested black macaque (*Macaca nigra*) is one of the seven (Fooden 1969; Kawamoto *et al.* 1982; Hamada *et al.* 1988) to eight (if *M. togianus* is accepted, as proposed by J. W. Froehlich [1994]) endemic species of macaques that allopatrically occupy the island of Sulawesi and Togian Island off the central-east coast of Sulawesi, Indonesia. Presently, *M. nigra* is restricted to a few isolated patches of forests along North Sulawesi (Fig. 1). Since the earliest population surveys of *M. nigra* by John and Kathy Mackinnon (1980), recent surveys by Sugardjito *et al.* (1989), Ashmore-DeClue and DeClue (J. Erwin pers. comm.), and Rosenbaum *et al.* (1994) have shown a precipitous population decline. Here, I report on preliminary findings from a population survey conducted from June through July of 1994 at the Manembonembo Nature Reserve in North Sulawesi, Indonesia.

I used the population estimates by Sugardjito *et al.* (1989) from surveys during 1987-1988 as a baseline for population abundance and density for Manembonembo Nature Reserve. According to Sugardjito *et al.* next to the Tangkoko Nature Reserve (which encompasses the three contiguous Tangkoko-Batuangus-Duasaudara Reserves), the highest density and abundance was seen at Manembonembo. To monitor the continued viability of natural populations, therefore, I chose to conduct a population survey in Manembonembo.

Although habitat disturbance was attributed by Sugardjito *et al.* (1989) as the primary factor in population decline, hunting remains pervasive and intensive. In addition to forest surveys, village, roadside, and market surveys were conducted to assess the impact of hunting.

Manembonembo is a 6,500 ha nature reserve located southwest of Manado in North Sulawesi (1°23' - 1°18' N, 1°34' - 1°39' E) (Fig. 1). The topography is characterized by steep mountains consisting of mostly clayish soils. Elevation ranges from 50 m above sea level to approximately 650 m. The reserve itself is made up of patches of plantations, along-alang grass fields (*Imperata cylindrica*) along the edges, and, within central parts of the reserve, dense ratans (*Calamus* sp.), abundant woka palms (*Livistona rotundifolia*), and mature forests can be found. The reserve has experienced very little protection. A very rough estimate that I have derived by sampling vegetation/habitat types along transects

shows that more than 25% of the reserve is in the form of intensively used gardens/plantations that produce coconuts, cloves, and corn. As the soil is comprised mostly of clay, the productivity in the reserve is relatively low. Other wildlife, many endemic and threatened from hunting and habitat disturbance, include: anoa, the mountain buffalo (*Bubalus depressicornis*), babirusa (*Babirusa babirusa*), dwarf and bear cuscus (*Phalanger celebensis*, *P. ursinus*), redknobbed hornbills (*Rhyticeros cassidix*) among others.

Forest surveys used the line-transect sampling method (Anderson *et al.* 1979) entailing systematic walks on transects following a compass bearing. Four trails, each 5 km long (total 20 km), were walked from 0600 to 1800, at the rate of 1 km/hour. Observers were required to walk slowly, stopping every five minutes to listen for sounds. Data collected included: weather, location, time, path-to-animal distance, observer-to-animal distance, height of animal, mode of detection, number of animals, age/sex composition, and habitat type. Censuses were repeated six times.

The effective strip width (37 m) was determined after detection distances were noted, based on perpendicular distance. A total of 4.44 km² were surveyed. On the average, 3.83 groups were seen per census, with an average group size of 8.83 animals. The density was 22.8/km², amounting to a total population estimate of 1486 individuals.

Comparing this with the estimate of 38.5 individuals/km², and abundance of 2502 individuals by Sugardjito *et al.* (1989), my figures indicate an overall decrease by 40.6% in six years. The density estimate of 22.8 individuals/km² at Manembonembo corresponds to the density figures for hunted areas in other parts of North Sulawesi (22.9 individuals/km² at the Duasaudara Nature Reserve [Rosenbaum *et al.* 1994] and 22 individuals/km² at the Batuangus Nature Reserve [Sugardjito *et al.* 1989]). Densities of these areas are significantly lower than the density within the fully protected area of the Tangkoko Nature Reserve (67.7 individuals/km² [Rosenbaum *et al.* 1994]).

Although habitat disturbance has been shown to have serious repercussions for the survival of natural primate populations (Wilson and Wilson 1975; Terborgh and Winter 1980; Johns 1983), differences in density figures for *M. nigra* between central versus

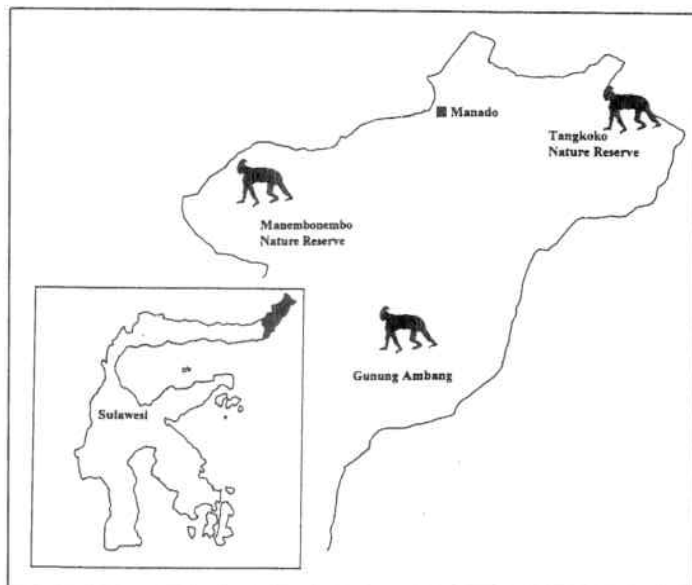


Fig. 1. A map of sites within North Sulawesi, Indonesia, occupied by the crested black macaque (*Macaca nigra*) (map provided by author)

peripheral areas can be explained as a function of hunting pressure. Interviews with residents on the peripheries of Manemboembo corroborate findings from forest surveys that hunting is by far the highest threat to the survival of *M. nigra*. Information concerning consumption rates and location of catch indicate that nearly all of the monkeys caught in Manemboembo were caught by using snares close to gardens which are located 1-2 km from the village. Significantly, most of the monkey groups detected during the population survey were located in central areas (71%) of the reserve rather than on the periphery. Although there are those who hunt on a full-time basis and venture into the central areas of the reserve, the majority of hunting comes from subsistence farmers who hunt on the side.

Even though the crested black macaques are fully protected under Indonesian law (UURI No. 5, Chapter 5 Paragraph 21), they are eaten throughout much of their geographic range. Subsistence hunting of "yaki" has been traditionally important in North Sulawesi. In addition, hunting of monkeys is highly profitable, in an energetic and economic sense, in that: 1) due to the large number of monkeys in a social unit, one hunting trip will provide several carcasses; 2) hunting costs are very low as there are few expenses involved; 3) due to their large body size, there is a relatively high amount of protein per carcass; and 4) infants can be captured to be sold as pets (Fig. 2). In the market economy, the meat of *M. nigra* is considered a delicacy, and there is, therefore, a demand throughout the year.

Given the lack of funding and personnel of government conservation agencies, natural resource management policies should consider the most important steps that will have an immediate impact on the conservation of threatened species. Unless a management program to ensure the continued survival of the crested black macaque includes the cessation of all hunting activities immediately, the program will surely fail. Once a sustainable population is established, other programs such as conservation education should be implemented.



Fig. 2. A pet juvenile crested black macaque (*Macaca nigra*) (photo provided by author).

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Remarks on The Occurrence of Gibbons in Central Java

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In the 1990 issue of *Primate Conservation*, Seitre and Seitre (1990) report on sightings of the two endemic Javan leaf monkeys *Presbytis comata* and *Trachypithecus auratus* on the southern slopes of Gunung Slamet [109° 13'E, 7° 19'S] in the western half of Central Java. In addition to these monkeys they also observed a single gibbon *Hylobates moloch*. Of this latter species, Seitre and Seitre (1990) state that "10 years ago, [this species] was only known to survive in central Java, in a 10 km² area of forest on Gunung Lawu." No reference for this is given.

Besides Seitre and Seitre, M. Riffel and C. Saleh (1994) in a preliminary project proposal also mention the occurrence of gibbons on Gunung Lawu, referring, however, to Kappeler (1984). In 1978, Kappeler (1984) conducted a survey on Javan gibbons and apart from a few individuals he found on Gunung Slamet, the only place in Central Java where the species seemed to be present in reasonable numbers was in a small forest block of 10 km² on Gunung Lawét [109° 30'E, 7° 15'S]. This was at the same time the easternmost record for the species.

It would seem that there is some confusion between Gunung Lawét and Gunung Lawu. Apart from Kappeler's papers I have not seen any reports which mention the name Gunung Lawét, nor have I seen any map with this name. Inhabitants of the region, however, are familiar with the name, and I therefore assume it is a local name only. Gunung Lawu [111° 11'E, 7° 40'S], in contrast, is a well known volcano on the border of Central and East Java, almost 200 km east of the former site. The impression could arise that Javan gibbon indeed occur on Gunung Lawu, but to the best of my knowledge there is no documentation about this whatsoever.

Given the confusion between Gunung Lawu and Gunung Lawét, and since it is almost 20 years after Kappeler's survey, it is perhaps important to give a brief update of our knowledge on the status and distribution of gibbons in Central Java.

The Javan gibbon is among the rarest and most endangered species of the genus (Eudey 1987). It is confined to closed canopy forest in the lowlands and mountains up to c. 1600 m, and only occurs in isolated pockets scattered throughout the western half of Java. The species' distribution corresponds with areas of the highest rainfall (Kappeler 1984), i.e., with the wettest vegetation types.

Java shows a striking contrast between the very wet climates in the west and the more seasonal, dry east; Central Java forms the climatic transition zone. Although most of the larger gibbon populations can be found in the western province, some still survive in the central province (Nijman and Sözer 1995). The most recent population estimate ranged from 386 (direct observations) to 1,957 individuals (estimated from the available habitat) (Supriatna *et al.* 1994), although none of the Central Javan populations were taken in account in these estimations.

Ten months of surveys by the author, together with R. Sözer and B. van Balen, in March-October 1994 and June-July 1995, in almost all larger forest tracts from Gunung Sawal [108° 16'E, 7° 12'S] in the eastern part of West Java to Gunung Liman-Wilis [111° 46'E, 7° 48'S] in the western part of East Java, revealed the presence of gibbons in three localities: The southern slopes of Gunung Segara [108° 48'E, 7° 07'S], the southern slopes of Gunung Slamet, and the western parts of Pegunungan Dieng [109° 37'E, 7° 05'S to 109° 43'E, 7° 10'S].

Gunung Segara is a small mountain situated in the north-eastern part of the Pembarisan mountains. Pegunungan Pembarisan consists of moderately disturbed lowland and hill forests ranging from c. 300 to 1351 m. Part of the area, c. 130 km², has been proposed as a nature reserve, and the entire area is considered by Mackinnon *et al.* (1982) to be of great value for conservation purposes. Gibbons may be present in the north-eastern part of the area only, as Kappeler (1984) reported the species to be absent from Gunung Pojok [108° 40'E, 7° 10'S] in the central part, although he did not actually survey the area.

Gibbons were observed frequently on the southern slopes of Gunung Slamet. The natural forests on this part of the mountain descend to altitudes of c. 700 m, and Seitre and Seitre (1990) rightly consider the area to be high priority for research on, and the conservation of, endangered primates.

However, the forests on Pegunungan Dieng are even more valuable. Gibbons were observed throughout the western half of this large forested area of c. 225 km². The observations of gibbons in the area extended the known range of the species (Nijman and Sözer 1995). Records were established from 300 to 1,300 m and, on the basis of the available habitat, the area probably harbors the

single largest population of gibbon on Java after the Halimun National Park in West Java (Nijman and van Balen unpubl. data).

None of the above forested areas are protected, although Mackinnon *et al.* (1982) has recommended that (parts of) all three areas should be. Pressure on the remaining forests on Java, and especially the lowland forests, remains high. The last forest remnants are still being destroyed. The establishment of protected areas in one, or preferably all three, forested areas is of prime importance for the survival of the eastern populations of the Javan gibbon. Especially important is the protection of the lowland forests of Pegunungan Dieng; a measure which is long overdue due to the fact that it harbors a significant proportion of the total world population of one of Indonesia's most endangered primates, and large parts in the westernmost part of the area are planned for conversion into rubber, pine or damar plantations.

We have not visited the isolated forest patch on Gunung Lawét, but local informants living in the north-western part of Pegunungan Dieng, confirmed the continued existence of forests on this mountain. Whether or not gibbons still occur there is not known. We did visit the southern and south-eastern slopes of Gunung Lawu on several occasions but no gibbons were found.

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Presbytis fredericae (Sody, 1930), An Endangered Colobine Species Endemic to Central Java, Indonesia

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Sody (1930b) announced that cranial characters and pelage quality had enabled him to detect a new subspecies of sureli, *Pithecus aygula fredericae* from Gunung Slamet, central Java, Indonesia. It differed sharply in pelage color from its nearest relative, the paler west Javan sureli, and more closely resembled the ebony leaf monkey (*Semnopithecus auratus*). Dorsally it was black, except for a small amount of white on the thumbs, and middle and sometimes the distal phalanges of the digits. At least at their tips, the guard hairs were a climatically induced ashy brown. A few were entirely white. The chin and throat were a fairly pale grey, bordered by a black collar on the upper part of the chest. This was succeeded by a greyish white transverse pectoral band; a relatively broad, blackish grey sternal region; and a pure white lower abdomen. A white tract on the inside of the limbs and underside of the tail attained a significant width only on the inner thigh, where it coalesced with the white of the lower abdomen.

Natives at Gunung Slamet were unaware of its existence, and used the name "lutung" for both it and the ebony leaf monkey (Sody, 1930a, 1930b). Bartels' (1937) father had observed it in 1910-1912 in the vicinity of the "Kaligoea" plantation, c.1500 m altitude, on the southern slope of Gunung Slamet. Its call readily identified it as a sureli. In early 1990, Seitre and Seitre (1994) saw two pairs and a troop of five or six in a large Forestry Department plantation of introduced *Araucaria* sp. below 1500 m, near Baturaden which adjoins Tegalsari [7°19' S 109°14' E] where four specimens have been collected (see Table 1). In April 1994, Linsley and Nawimar (1994) heard surelis 2.5 km north of Baturaden at c. 1380 m. During their surveys in the Pancoran tuju area, 2 km WNW of Baturaden, only one group was recorded. This group, of four adults and an infant, was present on at least four days in the forest surrounding the hotwater springs tourist site, and was habituated to human presence. In May 1994, on Gunung Cupu/Simembut [7°14' S 109°26' E], Linsley and Nawimar (1994) recorded one group at the Hutan Cupu/Simembut Complex, c.350-1000m. One to two groups were also found in a fragment of natural forest apparently entirely surrounded by pine plantations or open ground (thus restricting, if not preventing emigration), on the steep western slope of the river Tamba valley, south of the river Arus confluence and a small area on the eastern side, c.375-

700 m. Local people and forestry personnel were aware of the presence of four primate species, but used the name "lutung" for both leaf monkey and sureli.

In 1936, Bartels (1937) received three specimens collected for him in the "Pagilaran" plantation [7°07' S 109°51' E], c.1300-1500 m by K. Landberg, manager of this central Javan plantation on the northwestern side of the Diyeng mountains. The sureli was known locally as "rekrekan" (pronounced rackrackan), from its call. On several occasions, Landberg (in Bartels 1937) had observed a small troop which associated with a fairly large band of *Semnopithecus auratus*. The surelis frequented a ravine of dense secondary forest with small scattered patches of undisturbed primary rainforest. When aware they were being pursued, they dropped to the forest floor and attempted to escape through dense undergrowth, probably partly along the ground.

Pocock (1935) reserved judgement on the systematic position of *Pithecus aygula fredericae*, implying he suspected the syntypes were leaf monkey skins with sureli skulls. The ebony leaf monkey sometimes had whitish grey on the throat or chest, and the females always had a white patch on "the inguinal region, which might be regarded as part of the abdomen". That Pocock (1935) had not consulted Sody (1930a), is evident from his repetition of the erroneous publication date, "1913" ascribed to it by Kloss (1930). Pocock's (1935) expression of doubt that "a Javan race of *aygula*" could lose all trace of the generically characteristic whiteness on the inner aspect of the leg "retained in such black forms...as *femoralis*, *sumatrana*, and *chrysomelas*", demonstrates he had not seen Sody (1930b). Sody (1937) corrected Pocock's (1935) errors. Chasen (1940) considered that specimens he had examined confirmed the validity of the subspecies.

For this study, six skins (see Table 1) and five skulls were examined at the National Museum of Natural History, Leiden. LM14612 is apparently a skin only. Had Bartels (1937) obtained specimens from Gunung Lawu, he would almost certainly have recorded the fact. It is therefore likely that LM14614 (which is implicitly, but not categorically from that locality) is the, otherwise unaccounted for, third specimen from Pagilaran. It is the sole basis for the alleged occurrence of the sureli on Gunung Lawu. C. P. Groves has kindly supplied notes on four specimens at the

Museum Zoologicum Bogoriense, Indonesia.

The hair of the frontal region radiates mainly caudally, from a whorl immediately behind the facial margin. A crown whorl was reportedly absent in the Bogor skins. This head hair direction is disrupted by the erect hairs of the vertex. The dorsal hair is predominantly blackish brown. The nuchal and back hairs are longer and coarser than elsewhere and very sparsely intermingled with pale hairs, most noticeably in LM146c. The roots of the dorsal hairs at the distal end of the tail, and the entire hairs at the tail tip are whitish. Wholly pale hairs are scattered throughout the distal half of the tail in the lectotype. The roots of the hairs on the outer surface of the thigh in LM14612 are whitish, and externally discernible posterior to the external midline of the thigh. This may represent the last vestiges of the neonatal pelage color.

Ventral pelage coloration is very similar in all Leiden specimens. The chest is brownish, darkest in LM 14608. The neck and "bib" are more blackish. The lectotype and LM146c have most white on the throat; the paralectotype and LM14612 an intermediate amount; and LM14614 and especially LM14608 very little. LM146c not only has the sagittally broadest transverse whitish pectoral band, but also the most conspicuously white sternal midline, and the furthest incursion of whitish into the long hairs anterior to the navel. In other specimens whitish is most prominent at the hair roots of the pectoral band. In the paralectotype, LM14608 and LM14614, intermingled blackish hairs almost completely encircle the leg just below the knee. The whitish ventral tail color dissipates about 70-120 mm short of its tip in most specimens, but faintly persists throughout in the lectotype and LM 14608.

There seems to be more ventral pelage color variation in Bogor specimens. In MZB167, the limbs are apparently wholly dark brown. In MZB2993, ventral whitish includes the brachium and thigh. In MZB2994, it extends along the forearm and shank, albeit heavily suffused there with dark brown. In MZB2995, the venter is a buffy-white which extends along the underside of the tail and to the flank and paws, where it envelops the digits.

If the digits are numbered I-V, where I represents the thumb or big toe, and p and m the proximal and middle phalanx respectively, the hairs of the hand are blackish brown with the following exceptions. In the lectotype they are intermingled with yellowish white ones on II(m) and V(m). On III-IV(m) they are intermingled proximally, and sparsely intermingled distally with yellowish white ones; and yellowish white only at their roots on II-V(p). The hairs of phalanges I(p-m) are totally yellowish white. The paralectotype is similar, but the distal part of the hair shaft is more saturated with blackish brown, especially on digit III. In LM146c there are

intermingled yellowish white hairs on I-V(m); sparsely intermingled ones on V(p); and only the extreme hair roots are yellowish white on I-IV(p). Whitish, rather than yellowish white hairs, are similarly distributed in LM14608. In LM14612 yellowish white hairs pervade I-V(m) and V(p); are sparsely intermingled on I-IV(p); and only the extreme hair roots are yellowish white on right III(p). In LM14614 whitish is sparsely intermingled on II(m), V(m) and left I(m); present as small central patches on III and IV(m); and virtually absent elsewhere.

Whitish on the foot is concentrated at the base of the hairs at the joint between the proximal and middle phalanges. It is readily discernible only on phalanx V(m) where all specimens have only a small minority of blackish brown hairs, except LM14614 whose foot is almost wholly blackish brown. In the lectotype, more so in LM146c and especially in LM14612, there is a conspicuous extension of whitish onto V(p). The lectotype and LM14612 have the most whitish on digits I-V, extending onto the metatarsus between digits I and II.

With the possibility eliminated of mismatched skins and skulls, *Pithecius aygula fredericae* Sody, 1930 stands indisputably as a valid taxon. As intimated by Brandon-Jones (in Eudey 1987), this raises the question of whether its taxonomic status has been underrated.

Miller (1934, 1942) described new subspecies for the Bornean and the Sumatran populations respectively of *Presbytis comata*. These are satisfactory subspecies, but are patently less distinct from their sister subspecies than is the central Javan *sureli* from the west Javan form. Conversely, the chromatic relationship between the latter shows a remarkable parallel to that between the Sumatran *P. comata thomasi* and *P. femoralis*, and to that between the Bornean *P. comata sabana* and *P. frontata* (Brandon-Jones in press). In all three instances, a dorsally brown population replaces a dorsally gray population, with no evidence of initial reproductive isolation. At the *P. c. thomasi/P. femoralis* faunal boundary near Bohorok, north Sumatra, M. Borner (in litt. 1976) saw one group in which some members were positively *P. c. thomasi* with white underside and white facial markings, and other members were uniformly gray (similar to the animals at Torgamba, further south) with uniformly gray infants. The continuity of this population is demonstrated by the fact that blackish brown does not become the dominant dorsal pelage color until considerably south of Torgamba.

In Java and Sumatra, these populations are allopatric. In Borneo, however, *P. comata* and *P. femoralis* are partially sympatric, as they are with the endemics of equivalent morphological distinctiveness, *P. frontata* and *P. rubicunda*. This sympatry in

Table 1- Study specimens of *Presbytis fredericae* with collector's measurements

Locality	Accession No.	Collector	Coll. No.	Collection Date	Age	H & B (mm)	Tail (mm)	HF (mm)	Ear (mm)
Male									
Gunung Slamet, Tegalsari, 800m.	LM	H.J.V.Sody	146C	? Oct 1929	A	474	686	175	32
Gunung Slamet, Tegalsari	MZB2994	V.Balgooy		28 May 1931	A				
Gunung Slamet, Tegalsari	MZB 2995	V.Balgooy		28 May 1931	I				
Gunung Slamet, Tjoeroegilang	LM(lectotype)	H.J.V.Sody	9c	28 Sep 1929	A	485	665	170	33
Gunung Slamet, Tjoeroegilang	LM(paralectotype)	H.J.V.Sody	19c	30 Sep 1929	A	450	575	155	32
[Pagilaran]	LM14614	M.Bartels, Jr.	1969	228 Jun 1936	A			179	32
Pagilaran	LM14608	M.Bartels, Jr.	1684	30 Aug 1935	S			171	27.5
Pagilaran	LM14612	M.Bartels, Jr.	1819	30 May 1936	[J]	254	430	125	26
Female									
Gunung Slamet, Kaligoca, 1400m.	MZB167	Denin		nd Feb 1917	A				
Gunung Slamet, Tegalsari	MZB2993	V.Balgooy		27 May 1931	A				

Borneo thus establishes the threshold for specific status to be applied consistently throughout the genus. On this basis, *Presbytis fredericae* (Sody 1930) clearly warrants specific status. The species is known only from the slopes of three volcanoes, Gunung Slamet, Gunung Cupu, and Diyeng within the confines, 7°05' - 7°15' S and 109°10' - 109°50' E. It appears to be able to cope with some degree of habitat disturbance, but if this is a true reflection of its actual distribution, then it must be considered an endangered species deserving conservation priority.

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Soulé, M. E. (ed.). 1987. *Viable Populations for Conservation*. Cambridge University Press, Cambridge.

Example - dissertation:

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