

PRIMATE CONSERVATION

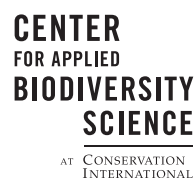
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Front cover. Although Sri Lankan red lorises are far from cryptic, this flowering bush makes a scenic hiding place for this adult female *Loris tardigradus tardigradus* from Pitigala, Galle District. Photograph by K. A. I. Nekaris.

A Word from the Chairman

This, the 19th issue of *Primate Conservation*, has suffered a long delay in publication, arising to some extent from the increasingly significant role of the IUCN/SSC Primate Specialist Group newsletters (*African Primates*, *Asian Primates*, *Lemur News* and *Neotropical Primates*), which are themselves evolving into journals in their own right, but also related to uncertainty as to its future. Its production is informal, and each issue requires funding in direct competition with the newsletters. *Primate Conservation* has played a key role in allowing for the publication of highly significant conservation-related research, most especially distribution and status surveys, which were difficult to publish elsewhere, and with the added advantage of it being distributed for free. Today, however, the more formal subscription journals, notably the *International Journal of Primatology*, the official journal of the International Primatological Society (IPS), increasingly publish conservation-related research (note *IJP*'s earmarking of the aye-aye with its "Vivamus" sign). *Folia Primatologica* (journal of the European Federation of Primatology), the *American Journal of Primatology* (American Society of Primatologists) and *IJP*, have made commendable efforts to increase accessibility to researchers and field workers by reducing subscriptions and linking them to the membership of the respective societies. *Primate Conservation* has its costs (its distribution worldwide is significantly more expensive than its actual printing), but it is, however, no easy decision to let a journal such as this lapse, and we have avoided taking it! We believe it still has a strong role to play as a venue for the lengthier articles and, for example, with extra funding provided, in allowing for the publication of color images, as is the case here in the article by Robert Sussman and his colleagues on their survey of the range and habitats of ringtailed lemurs in southern Madagascar. Longer monographs, workshop results and symposium proceedings can be accommodated by *Primate Conservation*, but not so easily the PSG newsletters.

That said, this issue has some excellent articles. Five are from the Neotropics, all of them dealing with highly threatened species – two concern status surveys (Trinidad and Costa Rica), one an evaluation of the status of Colombian primates, and the last discussing preliminary attempts to translocate black lion tamarin, and an evaluation of its potential in the management of the few and isolated populations remaining. The Madagascar section is given over to the remarkably detailed survey of *Lemur catta* mentioned above. For Africa, two articles deal with gorillas (aspects of coprophagy and the implications for tourism and field research, and a second on the status and distribution of the Cross River gorilla in Nigeria and Cameroon), and a third gives an overview of the primates of a little known country, Guinea-Bissau. Lastly the Asian section includes articles on the status of pig-tailed macaques in India and Assamese macaques in Nepal, a review of the taxonomy, distributions and status of lorises in Sri Lanka, and some observations on the status of the Nilgiri langur in the Silent Valley National Park in the Western Ghats, India. We sincerely thank the authors for their contributions and, for many, most especially their patience and understanding considering the delay in publishing their studies.

Russell A. Mittermeier
Chair – IUCN/SSC Primate Specialist Group

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New Data on the Distribution and Abundance of *Saimiri oerstedii citrinellus*

Claudine Sierra, I. Jiménez, M. Altrichter, M. Fernández, G. Gómez, J. González,
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Introduction

The Central American squirrel monkey, *Saimiri oerstedii* (Reinhardt, 1872), found in Costa Rica and Panama, is represented by two geographically isolated subspecies: *S. o. oerstedii* and *S. o. citrinellus* (Thomas, 1904) (see Hershkovitz 1984). The latter is endemic to Costa Rica and listed by IUCN (2002) as “Critically Endangered” (assessed using the IUCN [1994] criteria) (Hilton-Taylor 2002). The last, optimistic (*sic*) estimate of the population of *S. o. citrinellus* was of 1,500 individuals (Boinski *et al.* 1998).

The northeastern limit of the range of *S. o. citrinellus* is marked by the Herradura (9°40'N, 84°35'W) and Dota Mountains (9°37'N, 84°35'W). The southern limit is marked by the Río Grande de Térraba (8°25'N, 84°25'W) (Arauz 1993) (Fig. 1). This is also the historical distribution, although the habitat is now extremely fragmented (Alfaro 1987). *S. oerstedii* is diurnal, and Baldwin (1985) reported it lives in troops of up to about 30 individuals, with two or so adult males and 6-7 adult females. They feed mainly on fruits and insects, especially orthopterans in forests in different states of succession, mangroves, African oil palm (*Elaia guineensis*) plantations and fruit plantations (Boinski 1987; Wong 1990; Arauz 1993). Baldwin and Baldwin (1981) reviewed the ecology and behavior of the species.

The second *Squirrel Monkey Population and Habitat Viability Assessment Workshop (PHVA)* took place in Costa Rica in June 1995. Its primary recommendation was to “verify *in situ* the localities where [*S. oerstedii*] has been recorded, to obtain counts of the number of troops and individuals, along with data on forest size, its characteristics and status (Matamoros *et al.* 1996, p.12). Referring to *S. o. citrinellus*, Boinski and Sirot (1997) stated that “an immediate priority is a detailed survey that identifies the specific locations, and estimates the size of remaining squirrel monkey populations.” Following these recommendations we carried out an intensive survey to assess the presence of the subspecies, number of monkeys, troop size and composition in every forest fragment

in the central area of the squirrel monkey’s total distribution range (Figs. 1 and 2).

Study area

The study area was in the Costa Rican Central and South Pacific lowlands, from 0 to 350 m above sea level, between the western margins of Ríos Parrita and Naranjo (Figs. 1 and 2). The center and 35% of the range of *S. o. citrinellus* lies within this area, it includes Manuel Antonio National Park (MANP) reported to hold the single largest population of this primate (Boinski 1987; Wong 1990; Arauz 1993). The annual mean temperature is 26°C and the precipitation approximately 3000 mm per year (Coen 1991). MANP (683 ha) is the only National Park in the area (Figs. 1 and 2).

The original forest cover was very humid tropical forest, humid tropical forest, and transition to premontane humid tropical forest (Tosi 1969). During the 1950s, logging and cattle ranching were encouraged, and large areas were planted with African oil palm and rice (Mattey 1992). At present the study area consists mainly of rural areas, pastures, crops, wood, African oil palm and fruit plantations (Arauz 1993; Savitsky *et al.* 1995). There are scattered forest fragments, coastal mangroves and large remnants of forest in MANP and a northern fringe of uninterrupted forest that extends above 1000 m above sea level (hereafter “the foothills”) (Fig. 2).

Methods

Within our study area, we identified every forest fragment below 350 m above sea level detectable on 1:35.000 and 1:60.000 aerial photographs. We excluded MANP and surroundings because surveys of *S. o. citrinellus* have already been carried out there (Wong 1990). During April 1995 our team of 14 biologists divided into four to five subgroups to carry out surveys and interviews which totaled 1220 hours-person effort, and a 400 hours-team effort. Forest fragments,

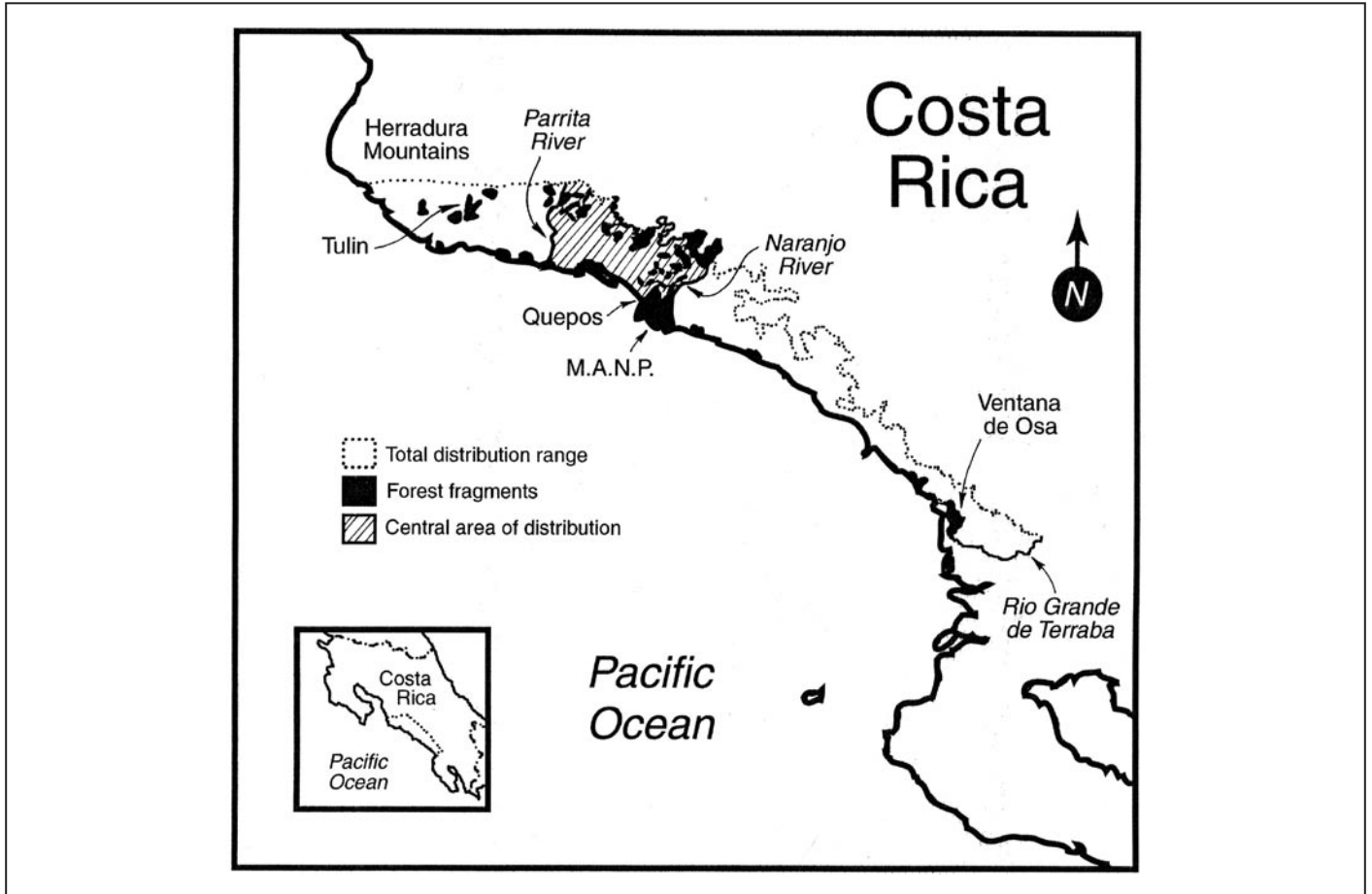


Figure 1. Map showing the total distribution range and the central area of distribution of *Saimiri oerstedii citrinellus*. Map by Stephen D. Nash.

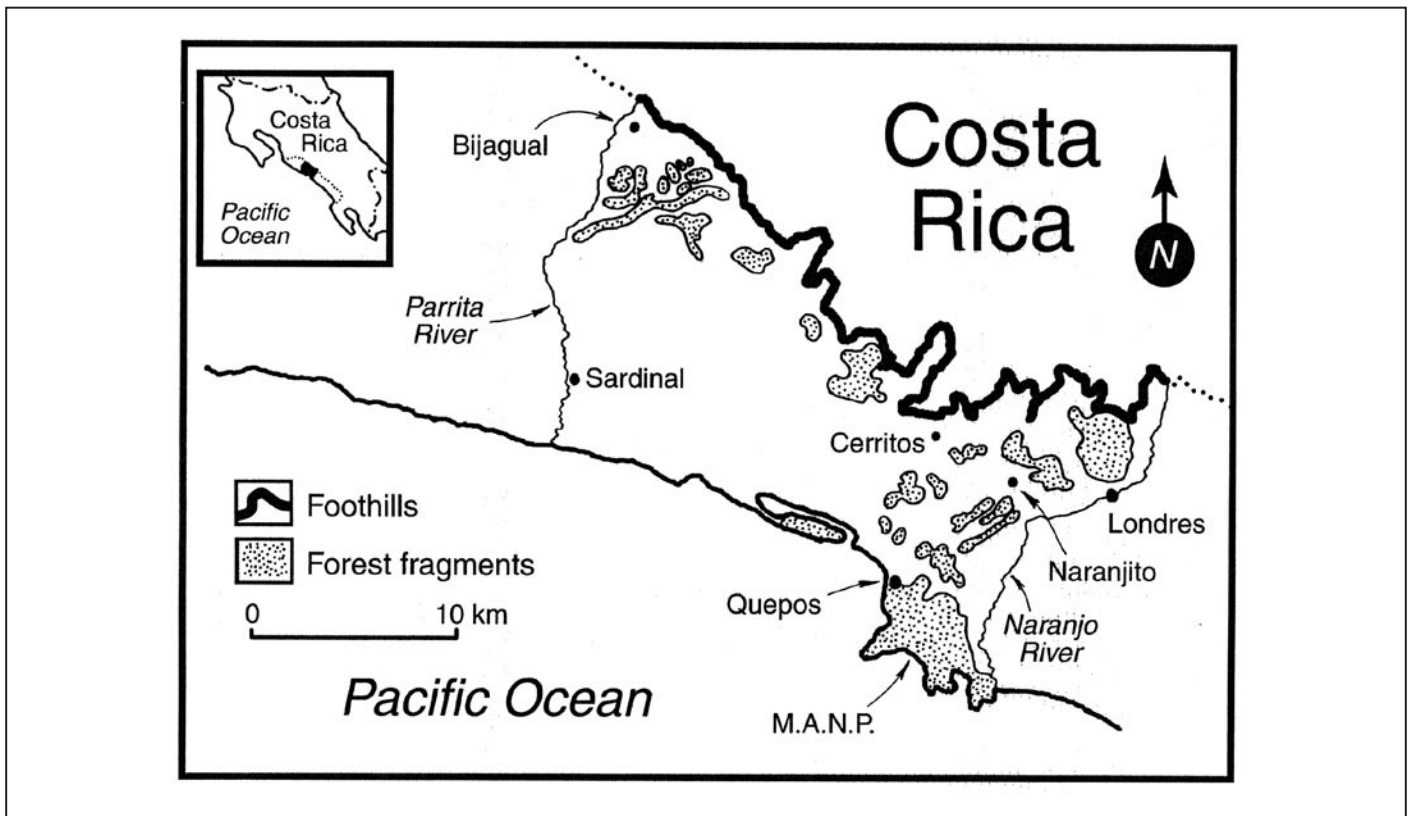


Figure 2. Map showing the study area and the forest fragments where *Saimiri oerstedii citrinellus* was sighted. Map by Stephen D. Nash.

African oil palm, fruit and silviculture plantations were surveyed.

Each forest fragment identified was traversed along a line as close to its center as possible. Whenever we found squirrel monkeys we registered troop size, sex and age composition. We interviewed local farmers and ranch owners near every fragment, totaling 124 interviews. Each informant was asked about the presence of squirrel monkeys in the neighboring forest fragments. We used photographs of the four primates found in the region (*Ateles geoffroyi*, *Alouatta palliata*, *Cebus capucinus* and *Saimiri oerstedii*) to verify that the informer could identify squirrel monkeys from other primates.

The squirrel monkey was considered as being present in a fragment either when sighted or when there was convincing confirmation among all the informers about the monkey's presence there. The foothill forests were not considered as a fragment because of their extent, covering 30 km² rising from

400 m and reaching 1000 m above sea level. We surveyed these foothills and conducted interviews below 700 m above sea level.

Results and Discussion

We surveyed 45 fragments that ranged from 10 to 200 ha, with a mean of 60 ha. The total number of squirrel monkeys sighted was 445 (Tables 1 and 2). Troop sizes ranged from 15 to 80 individuals, with a mean of 32. We recorded 48 infants with an average of three infants per troop, ranging from 9% to 25% of infants per troop. We saw squirrel monkeys in 13 fragments (at six locations the presence of squirrel monkeys had never been reported before) and another 17 fragments (12 unreported locations) were considered to hold troops after interviews. This gives a total of 18 new locations for *S. o. citrinellus*. Two of these locations were

Table 1. Locations with squirrel monkey's sightings in the central area of the range of *Saimiri oerstedii citrinellus*, Costa Rica.

No.	Location	Coordinates	Minimum # (adults+infants)	Comments
1*	Camino a Paso Real	9°2'9N, 84°06'W	17 + 33 14 + 1	Troops were 1 km apart from each other.
2*	Isla Damas	9°30'N, 84°15'W	30	Feeding in fruit plantation.
3*	Bambú (property of C. Gamboa)	9°37'N, 84°16'W	50 + 5	
4	Close to Finca Cerros	9°32'N, 84°11'W	16	
5	2 km north of Cerritos, Fila del Nene, Quebrada Guacalillo, foothill forest	9°31'N, 84°08'W	20	Many troops reported by interviews.
6	Rubbish dump, Quepos	9°28'N, 84°09'W	31 + 3	Monkeys on trees bordering the highway
7	2 km east of Quepos, on highway 22 (Property of Delgado)	9°26'N, 84°09'W	31 + 4	Monkeys sighted at Hotel Rancho Casa Grande, troop with many juveniles. Hotel employees reported 100 monkeys for 1996.
8	Villanueva, 4 km east of Naranjito de Quepos, foothill forest (Alvarado Machado family)	9°29'N, 84°04'W	15 + 5	Monkeys feeding on pink apples, banana and palms. Troop with many juveniles. Interviews reported 400 monkeys.
9*	La Managua	9°27'N, 84°08'W	27 + 4	Riparian forest fragment surrounded by pasture.
10	La Vasconia (Valverde family)	9°38'N, 84°19'W	41 + 17	Monkeys cross the highway to travel from Vasconia to San Gerardo.
11	1.5 km north of Surubres (Godine family)	9°37'N, 84°21'W	70 + 10	
12*	Pirris	9°36'N, 84°19'W	12 + 3	In a riparian forest. Interviews reported that this troops joins another troop.
13*	Las Cuevas	9°31'N, 84°11'W	23 + 3	In a riparian forest.

* New locations

Table 2. New squirrel monkey localities confirmed after interviews in the central area of the range of *Saimiri oerstedii citrinellus*, Costa Rica.

No.	Location	Coordinates	Comments
14	Quebrada Guapil and Guapinol	9°27'N, 84°07'W	A natural bridge that connected two sides of the highway was destroyed by a hurricane in 1992.
15	Quebrada Suya	9°27'N, 84°10'W	
16	Quintero's property	9°29'N, 84°07'W	Connected with Delgado's property.
17	Quebrada Salas	9°27'N, 84°07'W	Connected by secondary growth forest, oil palm and passion fruit trees to Delgado's property.
18	San Rafael Norte	9°35'N, 84°14'W	
19	Surubres (Property of Ortega)	9°36'N, 84°16'W	Monkeys feed on guavas.
20	Property of R. Gamboa	9°37'N, 84°15'W	
21	Property R. Prieto	9°32'N, 84°14'W	Monkeys cross a river and a fence to get to this property.
22	Property of Angulo	9°32'N, 84°15'W	Monkeys travel through a riparian forest to get to this property and feed on fruits.
23	San Antonio (Property of Hernandez)	9°12'N, 84°33'W	Interviewees reported many troops in the San Antonio foothills that come down to feed on bananas in this property.
24	San Antonio between Quebrada La Reina and Valeria river (Property of Camacho)	9°32'N, 84°13'W	The owner frequently saw a troop and reported a recent shooting.
25	Settlement of the Institute of Agriculture	9°31'N, 84°12'W	Monkeys feeding on "biscoyol" palms.

in the foothills (#5 and 8 in Table 1) where we saw squirrel monkeys. Although Boinski and Sirot (1997) concluded that *S. oerstedii* troops are unlikely to be present in forest patches smaller than 30 ha, we found troops with 34, 55 and 58 monkeys in 14, 20 and 33 ha forest fragments (Table 1), connected with other fragments by fruit plantations or creeks.

Fifty six percent of the fragments located between the Ríos Parrita and Naranjo were connected by riparian forests, fruit, silvicultural, and African oil palm plantations. During our field work we saw troops traveling along hedgerows, plantations, and electric wires which were rarely insulated, and we also obtained reports of squirrel monkeys crossing highways and pastures between forest strips. We observed troops feeding in natural forests, fruit plantations of guava (*Inga* sp.), banana (*Musa acuminata*), and pink apple (*Eugenia jambos*), and on the outskirts of villages. Surprisingly one of the palm plantations where we saw them (Finca Cerros, Table 1) had no forest in the immediate vicinity.

The squirrel monkey was known by 98% of the interviewees who informed that it is common in the region. Interviews confirm that squirrel monkeys move through African oil palm, fruit and wood plantations. Those carried out in the foothills also confirmed the monkey's presence in the area. There were no reports of squirrel monkeys above 400 m above sea level.

The study area has three zones containing squirrel monkeys: the foothills, the forest fragments and Manuel Antonio National Park (MANP). In the foothill forests, we estimated around 750 individuals (based on the lowest density estimate of 25 individuals/km² [Wong (1990)]). In the forest fragments we saw 445 individuals. There are two population estimates for the MANP based on different methodologies: 1) 105 individuals after a brief survey by Boinski *et al.* (1998) and 2) 581 individuals after a nine-month census (Wong 1990).

With this information and not including the 12 new localities where the monkey's presence was confirmed through interviews, we conservatively estimate that there are at least 1300-1780 squirrel monkeys living in the study area. These numbers surpass those reported for the subspecies within its entire distribution (Boinski *et al.* 1998). Taking into account that some areas such as Tulin (Arauz 1993), Londres and Ventana de Osa (Arauz 1993, Boinski *et al.* 1998) where the monkey occurs have not been included in our study and not included in our estimate, we indicate that the total population size reported for *S. o. citrinellus* is significantly larger than has been previously estimated.

Acknowledgments

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Conservation Priorities for Colombian Primates

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Introduction

Colombia is recognized as one of the most primate-rich countries in the world (Mittermeier and Oates 1985; Hernández-Camacho and Defler 1985, 1989; Mast *et al.* 1993; Defler 1994, in press). While we are uncertain exactly how many species exist in Colombia, there are at least 42 taxa of primates representing 28 confirmed species with 30 subspecies (but see Note 11 of Table 1, below). In the future it is almost certain that these numbers will change due to taxonomic rearrangements and the discovery of additional taxa within the country's borders. Recent reclassifications of various genera (such as for *Callicebus*, Van Roosmalen *et al.* 2002) using the phylogenetic species concept would raise the number of species listed here to 42, the number of taxa recognized by us for the country, but we continue using the traditional biological species concept, as discussed by Mayr and Ashlock (1991).

Based on the most recent classification of Colombia's primate taxa and using the new IUCN (2001) Mace-Lande categories, the threatened taxa found within the country, those which are "Vulnerable" (VU), "Endangered" (EN) and "Critically Endangered" (CR), are listed in Table 1 (Defler, 1996a, 1996b, Rodríguez-M. *et al.*, in preparation), along with those evaluated as "Near Threatened" (NT) and "Least Concern" (LC).

Top Conservation Priorities

Hooded spider monkey, Ateles geoffroyi griseescens – DD

Although this subspecies was included in Hernández-Camacho and Cooper's (1976) discussion of Colombian primate fauna (see note 1, above), there is no recent information

regarding its presence or otherwise along the Panamanian border. Observations of *A. f. rufiventris* in the middle Baudó would indicate that if *A. g. griseescens* occurs there, it is limited to the immediate portion of the Sierra de Baudó abutting Panamá, and not the entire range. If found in Colombia *A. g. griseescens* would certainly be the most endangered form of spider monkey in the country. Confirmation of a population would require the immediate formulation and execution of a management plan. The area is sparsely populated and as such there would be opportunities for their protection. Confirmation in the field, however, is dangerous due to Colombian insurgents.

Variiegated spider monkey, Ateles hybridus – CR

Both *Ateles hybridus hybridus* and *Ateles hybridus brunneus* are considered to be at extreme risk in Colombia, and they are classified as "Critically Endangered". Although not formerly recognized as a species – Kellogg and Goldman (1944) placed it as a subspecies of *Ateles belzebuth*, and Froehlich *et al.* (1993) as a subspecies of *Ateles geoffroyi* – J. Froehlich (pers. comm. 1995) agreed that it is very probably a "good" species; a view strongly supported by his cladogram of the *Ateles* species (Froehlich *et al.* 1993). Further work by Collins and Dubach (1999) confirmed that it is a separate species. It is important to underline the precarious condition of these two taxa, one of which (*A. h. brunneus*) has not been widely recognized by many and is a Colombian endemic from a recognized dispersal center (the Nechí). Censuses are required for a better understanding of the status of *Ateles hybridus*, and local populations need to be clearly identified and actively managed; a situation that does not exist at this time, even in the protected areas where *A. h. hybridus*

†We inform the primatological community of the death, on September 15, 2001, of our friend and colleague, Professor Jorge Ignacio Hernández Camacho. Jorge had a vast intellectual influence on the professional formation of the other two authors Defler and Rodríguez, and his immense knowledge of the Colombian biota was placed at the disposition of all who were interested. His human qualities were a part of his charm and contributed to the great esteem with which he was regarded by so many. We shall miss him sorely in the future.

Table 1. Conservation priorities of Colombian primates, based on the IUCN Red List threat categories (IUCN, 1994; Rylands *et al.*, 1995) and the most recent (IUCN 2001) categories (Rodríguez-M. *et al.*, in prep.). Also shown is the portion of the geographic range of each taxon which extends into Colombia.

Taxa	IUCN (1994) (Rylands <i>et al.</i> 1995)	Colombia (IUCN, 2001) (Rodríguez <i>et al.</i> in prep.)	% of total distribution represented by the Colombian population	Notes (see text)
Data Deficient				
<i>Ateles geoffroyi grisescens</i>	EN/DD	DD	9	(1)
Critically Endangered				
<i>Ateles hybridus hybridus</i>	EN	CR A3 a,c,d	40	(1)
<i>Ateles hybridus brunneus</i>	EN	CR A3 a,c,d	100	(1)
Endangered				
<i>Ateles geoffroyi rufiventris</i>	VU	EN A2 a,d	90	(1)
Vulnerable				
<i>Alouatta palliata aequatorialis</i>	LR	VU A2a,c,d	50?	
<i>Aotus brumbacki</i>	VU	VU A2c	100?	(2)
<i>Aotus griseimembra</i>	EN	VU C1	70	(3)
<i>Aotus zonalis</i>	VU	VU C1	80	(4)
<i>Aotus lemurinus</i> (= <i>A. herskovitzi</i>)	VU	VU C1	70?	(5)
<i>Ateles belzebuth belzebuth</i>	VU	VU A2a,c,d	10-15	
<i>Callicebus cupreus ornatus</i>	VU	VU B1b(iii)	100	
<i>Callicebus cupreus discolor</i>	LR	VU B1b(iii)	5	
<i>Callimico goeldii</i>	VU	VU D2	20?	
<i>Lagothrix lagothricha lugens</i>	CR	VU A2a,c,d	95-100	(6, 8)
<i>Pithecia monachus milleri</i>	VU	VU A2c	100	
<i>Saguinus leucopus</i>	VU	VU A2c	100	
<i>Saguinus oedipus</i>	EN	VU B1a,c	100	(7)
Near Threatened				
<i>Cacajao melanocephalus ouakary</i>	LR	NT	35	
<i>Cebus albifrons cesarae</i>	LR	NT	100	
<i>Cebus albifrons malitiosus</i>	LR	NT	100	
<i>Cebus albifrons versicolor</i>	LR	NT	80 ?	
<i>Cebus albifrons yuracus</i>	DD	NT	10?	
<i>Lagothrix lagothricha lagothricha</i>	VU	NT	50	
Least Concern				
<i>Alouatta seniculus seniculus</i>	LR	LC	20	
<i>Aotus vociferans</i>	LR	LC	50?	
<i>Callicebus torquatus lucifer</i>	LR	LC	40	
<i>Callicebus torquatus lugens</i>	LR	LC	40	
<i>Callicebus torquatus medemi</i>	VU	LC	100	(8)
<i>Cebuella pygmaea</i>	LR	LC	20	
<i>Cebus albifrons albifrons</i>	LR	LC	30	
<i>Cebus apella apella</i>	LR	LC	?	
<i>Cebus capucinus</i>	LR	LC	45	(9)
<i>Pithecia monachus monachus</i>	LR	LC	15	
<i>Saguinus fuscicollis fuscus</i>	LR	LC	90?	
<i>Saguinus nigricollis nigricollis</i>	LR	LC	20	
<i>Saguinus nigricollis graellsii</i>	LR	LC	20	(10)
<i>Saguinus nigricollis hernandezii</i>	LR	LC	100	
<i>Saguinus geoffroyi</i>	LR	LC	40	
<i>Saguinus inustus</i>	LR	LC	50	
<i>Saimiri sciureus albigena</i>	LR	LC	100?	
<i>Saimiri sciureus cassiquiarensis</i>	LR	LC	40?	
<i>Saimiri sciureus macrodon</i>	LR	LC	60?	
Other possible species in Colombia				(11)

Notes on Table 1 (see column 5)

(1) In agreement with the cladogram drawn by Froehlich *et al.* (1993) using morphometrics, his personal comments, Collins and Dubach's (2000a) phylogenetic analysis of mitochondrial and nuclear DNA, and the results of Collins' (1999), this paper recognizes *Ateles hybridus* as a separate species containing the subspecies *A. h. hybridus* and *A. h. brunneus*, and considers all *Ateles* west of the Río Cauca to belong to *Ateles geoffroyi* (see DeFler in press). There is no confirmation of the presence of *A. g. grisescens* in Colombia. Both Kellogg and

Goldman (1944) and Hernández-Camacho and Cooper (1976) have suggested it may exist. Hernández-Camacho and Cooper (1976, p.66) state that "...[it] is known only from the vicinity of Juradó very near the Panamanian border on the Pacific coast. It is undoubtedly restricted by the Baudó Mountains to a narrow coastal strip that may extend as far south as Cabo Corrientes." There are, however, no specimens or observations to prove this assertion. If they do occur in this region, the population would be small and extremely endangered. Comments

is known to occur. The habitat of *A. h. hybridus* is extremely fragmented as well, and there may be few populations of an adequate size to be viable in the mid-to long-term.

Ateles h. brunneus does not occur in a protected area, and its total population size is undoubtedly much smaller than that of *A. h. hybridus*, which at least is widely distributed in small, localized populations in both Colombia and Venezuela. The only stronghold of *Ateles h. brunneus* is in the Serranía de San Lucas in southern Bolívar, which has been identified

Notes on Table 1 (continued)

made by colonists near the northern parts of the Serranía de Baudó region talk of two “types” of *Ateles*, one in the lowlands (definitely *A. g. rufiventris*) and another, different form above 500–600 m altitude (J. V. Rodríguez-M. unpubl. data). This is the only real suggestion that this taxon might actually be present in Colombia.

(2) In our judgement, *Aotus brumbacki* cannot be a subspecies of *Aotus lemurinus*, as listed by Groves (2001), because of considerable chromosome differences between them. Chromosome evidence must take priority over taxonomic decisions made using phenotype. This taxon is undoubtedly reproductively isolated prezygotically.

(3) Because of chromosome differences, this taxon may best be considered a separate species from *A. lemurinus* (Defler, Bueno and Hernández-Camacho 2001; Defler and Bueno 2003).

(4) As in the other *Aotus lemurinus* subspecies listed by Groves (2001), we consider the form *zonalis* to be distinct at the species level (Defler, Bueno and Hernández-Camacho 2001; Defler and Bueno 2003).

(5) Defler, Bueno and Hernández-Camacho (2001) have demonstrated that *Aotus hershkovitzii* is a synonym for *Aotus lemurinus*, which we restrict to the Andean highlands. *Aotus lemurinus* is a separate species from the forms *griseimembra*, *zonalis*, and *brumbacki* because of pronounced chromosome differences (Defler and Bueno 2003).

(6) Defler (1996b) evaluated the threatened status of *Lagothrix lagothricha lugens* and demonstrated that it should be classified as “VU” and not “CR”, contra Rylands *et al.* (1995), who in turn had followed a previous classification by Defler (1994) before the latest reassessment.

(7) A Colombian national mammal committee was formed in 2000 in order to classify all Colombian mammals using the latest IUCN (2001) criteria. This was particularly appropriate, since the authors of the IUCN criteria suggested that classifications using the same international criteria should be made on national and regional levels. The new, upgraded IUCN (2001) classification uses additional species characteristics such as the capacity to adapt to new habitats or to degraded or disturbed habitats, among others. At the last meeting our national mammal committee discussed the need to re-classify 15 taxa of primates, elevating the category of 10 and lowering the category of 5. Among those lowered was *S. oedipus*, formerly “EN” and now “VU”, based on the observations of J. V. Rodríguez-M. (unpubl. data) and J. I. Hernández-Camacho, as well as considerations and evidence in northern Colombia that the populations of wild *S. oedipus* do not meet the population criteria for “EN” and that it is more appropriately a “VU” species. Here we reclassify *S. oedipus* “VU”, due to its improved population numbers over the past twenty years, and the species’ failure to qualify for the “EN” under the IUCN (2001) criteria. This change is not yet an official classification as mandated by IUCN (2001), although documentation in the form of a reassessment has been submitted (Defler and Rodríguez-M. unpublished).

(8) Groves (2001) classified the form *medemi* as a full species, but we feel that this is unjustified. Groves (2001) also elevated the following Colombian monkeys to full species: *Callicebus ornatus*, *Callicebus discolor*, *Lagothrix lugens*, *Saguinus graellsii*. He considered *Cebus albifrons cesarae* and *Cebus albifrons malitiosus*

as an important site for the establishment of a national park. There is also a completely unassessed population in northern Antioquia. A park in the Serranía San Lucas would protect a number of species endemic to this dispersal center (or refugium); but the region has been a source of civil unrest for years, and census work there would be hazardous, since guerrilla groups have placed anti-personnel mines in some parts of the mountain range.

be synonyms of *Cebus albifrons versicolor* in central and northern Colombia; *Cebus capucinus* to be monotypic in agreement with Hershkovitz (1949) and Hernández-Camacho and Cooper (1976); placed *Aotus brumbacki* as a subspecies of *Aotus lemurinus*; and listed *Aotus hershkovitzii*. Van Roosmalen *et al.* (2002) also considered all *Callicebus* variants in Colombia as species, a view that we find problematic. Our preference, for want of any new convincing evidence (and due to our use of the biological species concept rather than a phylogenetic species concept), is to follow Hershkovitz (1990) for all Colombian *Callicebus*.

(9) Hershkovitz (1949), Hernández-Camacho and Cooper (1976) and Groves (2001) all agreed that there is insufficient variation in this species to merit the distinction of subspecies, so it appears monotypic here.

(10) Hernández-Camacho and Cooper (1976) and Rylands *et al.* (2000) classified this taxon as a separate species, but such a designation requires proof that it is sympatric with some other population of *Saguinus nigricollis*. This is lacking, and we leave it here as a subspecies of *S. nigricollis*. A collection of *S. nigricollis nigricollis*, deposited in the Instituto de Ciencias Naturales de la Universidad Nacional de Colombia, has no specific collection data and the supposition that it is from the left bank of the Río Putumayo may be an error (Hershkovitz 1977).

(11) *Aotus nancymai* and *Aotus nigriceps* observed in captivity by P. Hershkovitz and J. I. Hernández-Camacho in Leticia, and reported in Defler (1994), have never been confirmed in the wild for Colombia. There is some traffic in *Aotus* in Leticia, with animals being taken from the other side of the Río Amazonas to Colombia for sale to the local primate laboratory. There they are erroneously treated as being from Colombia (since it is illegal to purchase fauna from either Brazil or from Peru). It is most probable that the specimens examined by Hershkovitz and Hernández-Camacho were purchased animals from the other side of the river. *Aotus trivirgatus* listed in Defler (1994) is probable but not confirmed for Colombia; three *Aotus* from widely separate sites in the eastern Colombian Amazon, examined by Defler, and confirmed by P. Hershkovitz, have phenotypes agreeing with the description for *A. trivirgatus* (Hershkovitz 1983; Hershkovitz pers. comm.). Karyotypes still urgently need to be determined for this phenotype and for *Aotus trivirgatus*. *Saguinus labiatus* and *Saguinus tripartitus* reported in Rodríguez *et al.* (1995) may extend into Colombia judging from their known or supposed geographic ranges, but this has yet to be confirmed in the field. Hernández-Camacho and Cooper (1976) accept *Saguinus graellsii* as a valid species, but the validity of this position must be confirmed through field studies. *Cacajao calvus* is known in Brazil, not far from the border with Colombia and may have historically been present in Colombia in Caño Uacarí upriver from Leticia, but there are no recent observations. If all the above were to be confirmed as Colombian species the total number would go up to 35 species of primates in Colombia. Should some of these species be confirmed in the near future, it is likely that they would be classified as threatened within the country, due to very small populations (especially *A. nancymai*, *A. nigriceps*, *S. tripartitus*, *S. labiatus* and *Cacajao calvus*).

Colombian black spider monkey, *Ateles geoffroyi rufiventris* (= *A. fusciceps robustus*) – EN

We consider all *Ateles* west of the Río Cauca to be *Ateles geoffroyi*. All Colombian taxa belonging to this genus are considered to be threatened in Colombia, due in part to habitat fragmentation and destruction but also greatly due to the desirability of these animals as game. National Parks such as Katios and Orquideas are believed to have very few spider monkeys because of indigenous hunting pressure (N. Vargas pers. comm.; H. Rubio pers. comm.) and the population density of *Ateles* may be decreasing in Los Katios (Director del Parque Los Katios, D. Pintor pers. comm.). These primates are not easy to observe in the wild, apparently due to a continuing decline in numbers exacerbated by very low population replacement.

Widespread censuses of *Ateles* are vitally needed, especially in national parks, so that we have some idea of densities. Problems of hunting need to be identified and countered in parks, and the indigenous right to continue hunting endangered taxa needs to be reconsidered, especially with respect to endangered species.

This species is heavily hunted and its populations are fragmented. Its situation seems precarious at best. Most censuses of fauna do not even find them, even in national parks. *Ateles geoffroyi* may be one of the first taxa to go extinct in Colombia (along with *A. hybridus*) because of hunting, since Colombian law allows continued hunting by the two main minority groups found in the species' range. All insurgent groups may contribute to the hunting problem, although information is lacking.

Basically neither hunting prohibitions nor educational efforts are easily implemented in the isolated areas where *Ateles* are to be found. The fact that the genus is considered fair game by many rural Colombians and indigenous people is definitely the heaviest pressure after habitat loss. Action is urgently needed, yet the places where such action should be implemented are usually closed to officials and conservationists. The continued violence in rural areas is probably directly affecting every species. As a genus, *Ateles* is by far the most threatened genus in Colombia because of targeting it for food, habitat loss and very low reproductive rate.

Cotton-top tamarin, *Saguinus oedipus* – VU

Saguinus oedipus is a good example of a partial success story of conservation efforts for an endangered species. Large numbers of animals were exported during the late 1960s and early 1970's for biomedical research (Mast *et al.* 1993), and numerous colonies were established overseas. Export was prohibited in 1973, and the situation of the species has improved accordingly, even though a considerable portion of the species' habitat has been modified by agriculture and the cattle industry (Defler and Rodríguez-M. 2003). Forest destruction is considerable and ongoing throughout the range of *S. oedipus*, but there are still large sections of secondary forest in the Valle del Magdalena, the Montes de María and areas towards the Cordillera, which maintain healthy popu-

lations. Today we can be certain that most of the traffic in *Saguinus oedipus* has stopped, not only because of its prohibition but also because of the various campaigns that were carried out by the government agency INDERENA (now replaced by the Ministry of the Environment). The species is able to survive in isolated forest fragments, and they are able to withstand considerable weight loss during the dry season (Rodríguez-M. pers. obs.). Cotton-top tamarins are able to colonize new habitats when introduced, as demonstrated by populations established outside of their historic range in the Yotoco forest (Chocó), in small forested areas around Cali, and in the Tayrona National Natural Park. These populations arose through the liberation of captive specimens by their owners or by government officials freeing confiscated animals. Ironically the present activities of the guerilla and the paramilitary have left extensive areas of small-holdings in Sucre, Córdoba and Bolívar without their owners, who have been converted into refugees or worse, but this national disaster has had positive effects on Colombian fauna, including *Saguinus oedipus* (Rodríguez-M. in prep.; Wood *et al.* 1992). A captive population is maintained and registered by studbook in North America, Great Britain and Europe (Mast and Fajardo 1988; Mast *et al.* 1993).

Some surveys for this species were undertaken in 1987 by Barbosa *et al.* (1988) in Sucre, Bolívar, Atlántico, Córdoba, Antioquia, del Valle, and Chocó. They were able to demarcate the northern extent of the range, but to the south, the range limits are still poorly known. Barbosa *et al.* (1988) reported considerable forest destruction, and many areas where *S. oedipus* had evidently been extirpated. A major research and conservation program, Proyecto Tití, which includes education programs and the development of economic alternatives, including an agricultural training program for local communities and the training of primate field researchers, was set up for the cotton-top tamarins at the Colosó (Sucre) primate facility in the Montes de María Reserve, Bolívar in 1987 (Savage 1988; Savage and Giraldo 1990; Savage *et al.* 1990, 1996a, 1997). Unfortunately the facility was closed to researchers because of civil unrest caused by guerillas and paramilitary groups two years ago. Since 1998, Anne Savage, Humberto Giraldo and their collaborators have continued the program in the dry forests of the Hacienda el Ceibal, Santa Catalina, Bolívar. Comparison of the population dynamics and social organization of the cotton-top tamarins at the two sites will allow for a better understanding of the capacity of cotton-top tamarins to adapt to degraded forests, increasingly the only remaining habitat for them, and the Proyecto Tití team are also carrying out surveys, with the use of satellite images, to examine patterns and rates of forest loss and fragmentation throughout the range of *S. oedipus*.

Recommendations for Conservation Action

A review by Mast *et al.* (1993) suggested a number of measures for a more aggressive conservation effort for *S. oedipus*. These are listed below with commentary and could apply equally well to the very endangered *Ateles* taxa.

(1) *Identification of key sites, creation of public and private reserves.* Some censuses have been carried out, but wide areas of the putative geographic distribution have yet to be investigated for the presence of this and other primates. Important areas include the upper Río San Jorge and in and around the Paramillo National Park, which has the largest single remaining primary forest within the species' range, although anecdotal evidence suggests that the species is able to exist in higher densities in secondary forest. The southern and southwestern limits to its range are poorly defined, although *Saguinus geoffroyi* was recently observed to the east of the Río Atrato (Vargas 1994). Isolated populations throughout the species' range need to be mapped.

J. V. Rodríguez-M. (unpubl.) found an evidently healthy population along the left bank of the Río Magdalena between Carmen de Bolívar and the Zambrano region (Bolívar). Populations such as this should be given special protection from and by the local communities, but the positive indications mentioned above have led J. V. Rodríguez-M. to argue that the species should now be classified as "Vulnerable". Conservation efforts initiated either through government or private interests have generated excellent results which should be continued for this and for other species which at this date are more threatened than *Saguinus oedipus*. Nevertheless, we need good inventories of the known populations in order to document the situation better. Populations located in municipal watersheds or other forests (including private forests) could be touted as special resources to be proudly protected, since this is a unique Colombian species. The Ministry of the Environment and local semi-autonomous corporations should become more involved in the preservation of this endemic species and its conservation via the establishment of appropriate reserves and conservation programs.

(2) *Environmental education.* Educational efforts must be made on both the national and local level for this species' conservation. Proyecto Tití has demonstrated well the enormous potential for success through education and capacity building to improve the well-being of local communities while promoting the conservation of wildlife and *S. oedipus* in particular (Savage 1988, 1993, 1995, 1996, 1997; Savage and Giraldo 1990; Savage *et al.* 1990, 1996a, 1996b, 1997, 2001). Local people can be convinced that it is not acceptable to trap or buy these primates as pets. Conservation education ought to be included in school curricula, and communities close to wild populations of *S. oedipus* must be made aware and proud of the importance of their local population. Local populations could be made into tourist attractions in this way. Local conservation or wildlife clubs should participate in this effort. Publications, videos and workshops for local people should be made available.

(3) *Law enforcement.* Local authorities often fail to apply national laws when their importance is not emphasized. They must be informed of the national conservation programs, and local police need to be given the instruction and wherewithal to enforce environmental legislation.

(4) *Forest restoration.* Forest regeneration is incipient in Colombia. The role of forests in the conservation of water resources should underlie a major campaign for forest preservation and restoration, targeting local communities and even private landowners, and which could contribute significantly to the survival of local populations of *S. oedipus* and other primates.

(5) *Efforts for developing wildlife and ecotourism.* Development of wildlife tourism with local communities, an increasingly successful model throughout South America, can contribute significantly to the value given to primates such as the cotton-top tamarin, and the preservation of their forests. Local communities benefit through employment, eco-guides and the increased business in local stores, hotels and restaurants.

Gray-legged night monkey, Aotus griseimembra – VU

This night monkey is evidently highly threatened in Colombia, in part due to habitat loss but also because of its capture in the past as an important model for malaria research. Censuses carried out by Struhsaker *et al.* (1976) found it to be very scarce, while Green (1976) identified populations in the Sierra San Lucas. This area remains unprotected and could easily be destroyed, should the local problems of civil unrest be solved, allowing for colonization. Populations recognized as *A. griseimembra* are genetically heterogenous and we consider to be a species complex, with distinct lowland and highland forms.

The systematics of the entire genus is complex and controversial. Hershkovitz' (1983) and a number of other systematists and geneticists have made major contributions to our understanding of the diversity of night monkeys, but further studies are urgently needed to help us to recognize important differences in these populations. Ford's (1994) studies of their morphology have been interpreted by her that *Aotus* in northern and Andean regions of Colombia could be just one clinal species. This view is not accepted by Defler *et al.* (2001) mainly on the basis of karyological differences. There is a real danger that karyologically and genetically distinct populations of *Aotus* may actually be unrecognized sibling species in danger of becoming extinct, even before we understand their systematic relationships.

Defler, Bueno and Hernández-Camacho (2001) have argued that the subspecies of *Aotus lemurinus* (see Groves, 2001) should be elevated to full species, that *Aotus hershkovitzi* is a synonym of *Aotus lemurinus*, and that *A. lemurinus* is limited to the Andean highlands (Colombia and Ecuador), with the Chocó being inhabited by *Aotus zonalis*. Studies are necessary even to understand the geographical distribution of the Colombian species such as *Aotus lemurinus*, *A. brumbacki*, and *A. vociferans*. Analyses of *Aotus* karyotypes north of the Rio Amazonas ("grey-necked" *Aotus*) that have been carried out up to now convince us that the various karyomorphs are separate species (*Aotus zonalis*, *Aotus griseimembra*, *Aotus lemurinus*, *Aotus brumbacki*, *Aotus vociferans*, *Aotus trivirgatus* and probably an as yet undescribed species)

(Defler *et al.* 2001; Defler and Bueno 2003; Defler and Bueno in prep.).

Most urgent is the protection of any forests that provide habitat for populations in northern Colombia. There should be a national ban on the collection of the decimated *A. griseimembra* for research in malaria; other non-endangered populations from the Amazon basin have also been shown to be adequate models.

Brumback's night monkey, Aotus brumbacki – VU

Except for the region around Villavicencio, Meta, the distribution of this species remains unknown, and classification of “Data Deficient” (DD) may be more appropriate. The known part of this taxon’s geographic range is congruent with much human activity, but may extend south to the Rio Guayabero, where there would be healthy populations protected by one or two large national parks.

Lemurine night monkey, Aotus lemurinus – VU

Much of the habitat of this night monkey is congruent with human disturbance and they are classified as “Vulnerable” (VU). Censuses of populations and habitat are needed to better assess its status, since these taxa might possibly be reassigned to the “Near Threatened” classification.

Goeldi's monkey, Callimico goeldii – VU

Because of naturally sparse populations throughout its geographic range, this species has been registered from only six sites in the Colombian Amazon. Two sites are in national parks, although one locale in the Cahuinari National Park (reported to Hershkovitz [1975] by the Colombian herpetologist Federico Medem), has never been precisely located. A first step for the conservation and management of Goeldi’s monkey is a detailed knowledge of the precise locus of all known populations, so that each can be protected. Since four of the six populations are found in generally undisturbed primary forest, the pressures upon them are not considered to be severe. Nevertheless, the apparently special habitat requirements needed by this primate may mean that any site is fundamentally at risk for one reason or another, if the habitat proves to be attractive for development and colonization.

Silvery brown bare-face or white-footed tamarin, Saguinus leucopus – VU

This small endemic primate is not yet protected in any unit of the national park system, although it occurs in an area of intensive colonization and forest loss. A basic conservation program for this species must include detailed ecological field studies, widespread censuses, and the establishment of adequate reserves (Vargas and Solano 1996). Municipal watersheds would be ideal local reserves, as long as populations are protected from trapping. The trapping of this small monkey to sell as pets must be strictly prohibited and the law enforced. Local educational campaigns should convince that this beautiful small Colombian mammal should be strictly protected in as many populations as possible. Finally, the establishment

of an eventual Sierra de San Lucas National Park needs to be supported so that populations of this, as well as of *Ateles hybridus brunneus* and other endangered organisms of the Nechí refugium may be conserved for the future.

The ornate titi monkey, Callicebus cupreus ornatus – VU

This small endemic subspecies is found congruent to heavy colonization and destruction of its habitat. A trend that continues to destroy local wood lots and forests must be reversed, so that some of the smaller faunal elements in this part of Meta Department can be conserved. Local educational efforts are required to accomplish this. Perhaps the best populations are located in and adjacent to La Macarena National Park, so there is some hope that populations there and in Tinigua National Park can support a safe nucleus. However, habitat destruction is widespread in this part of La Macarena and enforcement of national laws is very difficult, especially since there is civil unrest and heavy insurgent activity.

Careful censuses and local educational campaigns are probably the best tools at the moment to ensure this subspecies’ conservation. Convincing local farm and ranch owners of the importance of protecting a portion of their forests and woodlots would go a long way towards protecting this primate. *C. cupreus ornatus* is endemic to Colombia. Groves (2001) and Van Roosmalen *et al.* (2002) regard this taxon to be a full species, but we believe that further research is needed to establish if this is the correct taxonomic status.

Titi monkey, Callicebus cupreus discolor – VU

Although not considered to be threatened throughout most of its Ecuadorian and Peruvian range, the Colombian portion of its range is very small and at risk, due to multiple activities of agriculture, colonization, petroleum exploration, drug activities and guerilla presence. The Colombian Amazon between the Ecuadorian border and the Río Guamués is part of the “Napo Refugium” and the most biodiverse region within the country, but unfortunately it is very difficult to carry out fieldwork there.

The Colombian government recognizes that there is an urgent need for a national park in the south-west of Putumayo, but any government activity in the region would be opposed by insurgents and coca growers. There is no defined colonization front in the region, only widespread, isolated, and illegal coca farms, which leave no part of the forest intact. Recent attempts by the government to eradicate these farms have led to confrontation with the farmers ensuring that any conservation attempts on a national scale will be even more difficult. Pressure from the United States government is resulting in widespread herbicidal spraying in a vain effort to eradicate the illegal coca, but the consequences are only further environmental degradation and damage to the natural ecosystems surrounding these fields.

Surveys are needed to investigate tentative evidence that populations of this or other subspecies of *Callicebus cupreus* may be found in other parts of Putumayo Department and the

southern part of the Caquetá Department. Moynihan (1976) described one of these populations in southern Caquetá, between the Ríos Ortegaza and Caquetá. Hershkovitz (1977) overlooked Moynihan's observations and no qualified observations have confirmed his published description since.

Miller's monk saki, Pithecia monachus milleri – VU

Much of the known distribution of this monk saki is congruent with colonization. Fortunately La Paya National Park should help to protect a healthy population, and it may eventually also be found between the Ríos Caguan and Yarí. Hopefully future surveys may eventually establish its range and a better understanding of its status.

White-bellied spider monkey, Ateles belzebuth — VU

This is probably the most threatened taxon in the Colombian Amazon (Defler 1989, 1994). Published geographic ranges by Hill (1962), Hernández-Camacho and Cooper (1976) and Konstant *et al.* (1985) greatly overestimate its occurrence in Colombia, which is mainly congruent with heavy colonization in the lowlands and the piedmont forest to the north. Although it is known to occur in at least three national parks (La Macarena, Tinigua and Picachos), widespread colonization around them makes it necessary to control hunting, but unfortunately park management in this region is greatly complicated by the presence of insurgents. Another large block of forest between the colonized portions of the Ríos Caguán and Yarí to the east evidently has a good population of this primate. Only the comparative isolation of this forest will keep this population intact for the near future, but any development which facilitates the movement of colonists into the region will quickly endanger the spider monkeys there.

Colombian woolly monkey, Lagothrix lagothricha lugens – VU

Of the woolly monkeys, only *L. l. lagothricha* seems to have widespread and healthy populations. Although classified in the past as “Critically Endangered” (Rylands *et al.* 1995), *L. l. lugens* is best characterized as “Vulnerable”, since fairly extensive piedmont forest still remains where this subspecies is found (Defler 1996b). However, conservation efforts in Colombia should be concentrated on *L. l. lugens*, since all populations are threatened by nearby human settlements. Although it is known to occur in 6-7 national parks, the extent of the populations is not known. Censuses are urgent, and local threats need to be evaluated. Because it may be a Colombian endemic (it possibly extends into a small part of Venezuela), it is important to emphasize the responsibility of Colombian conservationists in carrying out an effective conservation program for this subspecies. The establishment of the proposed San Lucas National Park would hopefully protect the northernmost island deme of this primate (apparently isolated from other populations of *L. l. lugens* and potentially a new subspecies), but preliminary work on this project has not yet begun, partly because of problems explained above

for *Ateles hybridus brunneus*. Groves (2001) suggested that this taxon and the other two subspecies are separate species from *Lagothrix lagothricha*, based on his belief that “the four taxa are sharply distinct, with no intermediates between them” and Ruiz and Alvarez (2003) found different haplotypes of mtDNA for each taxon and so agreed with Groves' (2001) assessment. However, neither the differences noted by Groves for *lugens* and *lagothricha* are so distinct, nor are they so sharp, and some genetic differences between the two taxa are to be expected. Whether the differences are enough to justify species status remains unclear. Further research is needed on this genus.

South Pacific blackish howling monkey, Alouatta palliata aequatorialis – VU

Although not considered threatened globally, in Colombia this howling monkey is “Vulnerable”, because of widespread hunting by Afro-Colombian and indigenous people. There are no evaluations of the population status of this in Colombia, but recent faunal surveys in Utria National Park found them to be extremely rare, in areas where they were much more common in years past (H. Rubio pers. comm.). Widespread hunting for meat and forest destruction in the Chocó region is a serious threat.

General Comments and Discussion

Wildlife inventories and population assessments of endemic and threatened species are needed, and most especially for the primates listed here as “Critically Endangered” and “Data Deficient”. Populations occurring within protected areas should receive special attention from the national park's division of the Colombian government, underlining the need to protect these animals in particular. The priorities discussed here should be included in the Instituto von Humboldt's national research plan. Educational campaigns are fundamental in any conservation program, and human communities near populations of threatened primates need to be convinced of the importance of their participation in such programs and the rich biological heritage that is theirs in Colombia. The conservation of threatened species should be included in the ongoing talks with the guerilla groups, since so many parts of Colombia are off limits to researchers and conservationists. These people say that they are interested in preserving the natural Colombian ecosystems, and it behooves conservationists to get the conservation message to all groups, insurgents or not, since in many cases they may be the local authority. Because of the widespread presence of armed groups in many areas where primates are to be found, it is necessary to publicize conservation priorities (perhaps directly with each group when possible) in an effort to convince these guerilla bands to accept field workers in their area and to support conservation efforts.

More Colombians need to be involved in the study and conservation of primates; there are too few data to allow for the proper conservation and management decisions, and the

generation of this information should be made a top priority. Because most Colombian university biology students are obliged to write a Bachelor's thesis as part of their graduation requirements, an effort could be made to convince universities and students to consider basic surveys and censuses as a worthy subject of study.

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Distribution and Conservation Status of the Primates of Trinidad

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Introduction

The Republic of Trinidad and Tobago is the most southerly Caribbean country, located on the continental shelf of northeastern Venezuela. Trinidad is 11 km from the mainland, Tobago another 35. These islands have probably been separated from Venezuela's Paria Peninsula since the end of the Pleistocene (Vuilleumier 1972), and thus share many geological, floral and faunal features with northeastern South America. While there is no record of primates on the island of Tobago, two non-human primates are endemic to Trinidad: the red howler monkey (*Alouatta seniculus insulanus*) and the white-fronted capuchin monkey (*Cebus albifrons trinitatis*) (Neville 1976). The subspecies classification of these primates suggests that they may show important behavioral and genetic differences from their mainland conspecifics. However, Trinidad's primates have been little studied, and consequently are not well known. During the last 30 years only population surveys have been completed (Agoramoorthy and Hsu 1995; Neville 1976). Hunting, logging, and agricultural development have greatly reduced these monkey populations so that today they persist only in three national sanctuaries (Bush Bush, Trinity Hills, and Central Range [Agoramoorthy and Hsu 1995; Rylands *et al.* 1997]) and a few isolated, unprotected areas (Phillips unpubl. data). Under the IUCN's Mace-Lande criteria, the red howlers are listed as "Vulnerable" and the white-fronted capuchins are listed as "Critically Endangered" (Hilton-Taylor 2002).

In 1996, we began intensive efforts to study the behavioral ecology of white-fronted capuchins. At the request of Trinidad's Wildlife Section, we also surveyed both *Alouatta* and *Cebus* throughout the various habitats on the island. In this paper we present data on population status, density, and forest use of these primates in Trinidad. We focused our efforts on three sanctuaries, Bush Bush, Trinity Hills, and Central Range, where both species have been reported, and in unprotected areas in between these sanctuaries.

Areas Surveyed

The Forests Act of 1989 established three protected areas in Trinidad. These wildlife sanctuaries, Central Range (CRWS), Bush Bush (BBWS), and Trinity Hills (THWS) encompass three distinct ecosystems (see Fig. 1). The CRWS is a 2,153 ha. sanctuary of tropical dry evergreen forest. *Carapa guianensis*, *Eschweilera subglandulosa* and *Sabal glaucescens* dominate the canopy. The CRWS has a history of logging. Teak planting began in 1953, as a response to non-regeneration of the forest due to overexploitation. The teak plantation now occupies approximately 40% of the sanctuary. While the teak plantation has been recognized as 'regrettable,' it does provide browse for some animals, and also is regarded by the Ministry of Agriculture as a profitable and feasible restoration policy (Bacon and French 1972).

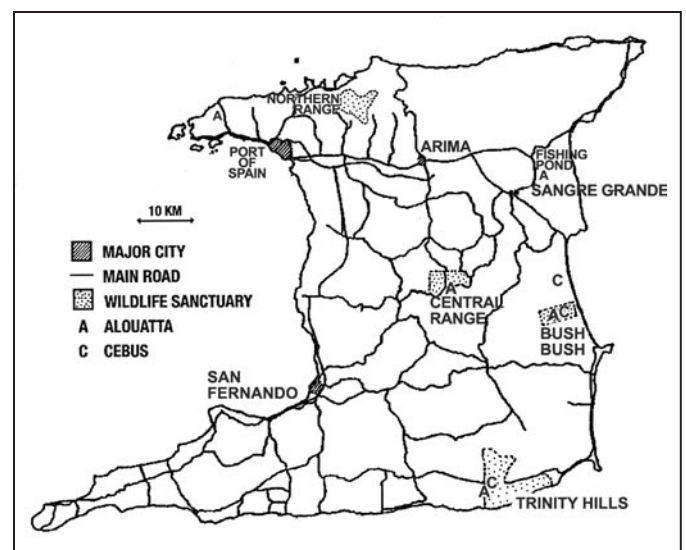


Figure 1. Locations of populations of howler monkeys (*Alouatta seniculus insulanus*) and capuchin monkeys (*Cebus albifrons trinitatis*) in Trinidad. Map redrawn from Neville (1976).

Trinity Hills Wildlife Sanctuary, at 6,483 ha, is the largest strictly protected area in Trinidad. This seasonal evergreen forest, characterized by *Pentaclethra macroloba*, *Spondias mombin*, *Eschweilera* sp. and *Carapa* sp., is located in the southeastern corner of Trinidad. Since at least 1965, the sanctuary has been under a mining lease for oil. Although the oil company does provide some security for the sanctuary, hunting is allowed in some adjacent areas, and hunting camps were established near the border of the sanctuary. During 1998 and 1999 these camps were still active, though the extent of incursions into the sanctuary *per se* is unknown (Phillips pers. obs.).

Nariva Swamp is a 24,000 ha wetland located in eastern Trinidad. The Central Range borders Nariva to the west and north, and rolling hills characterize the areas to the south. The Bush Bush Wildlife Sanctuary (BBWS), a 1,500 ha seasonally evergreen forest, is located within Nariva and is the only protected area of the swamp. Nariva is characterized by a mosaic of plant communities, which include swamp wood, morichal, roystonea, rain forest, mangrove and roseau (Bacon, 1990). BBWS was originally founded in 1968 as a game preserve and was managed by the Trinidad Regional Virus Laboratory and the New York Zoological Society until the government resumed management control in 1971. In 1992 the Convention on Wetlands designated Nariva Swamp as an internationally important wetland area.

One additional sanctuary, Northern Range (NRWS), has been mentioned as another site where one or both primate species might occur (Rylands *et al.* 1997). This 937 ha reserve is characterized by steep slopes supporting lower montane and montane rain forest. No primates have been reported in Northern Range since at least 1972 (Bacon and French 1972). However, we included this sanctuary in our surveys since there has been a history of primates inhabiting it.

Areas outside of these sanctuaries were also surveyed. In particular, we investigated appropriate habitat near Fishing Pond community and in the vicinity of Nariva Swamp (see Figure 1).

Methods

Primate censuses were conducted during January 1997, June-August 1997, and November-December 1997. In all areas we slowly walked trails and off-trails daily during mornings (06:00-09:00) and afternoons (13:00-17:30). When

primates were encountered, we recorded the number of individuals and the level of forest they were using.

Interspecific differences in the use of forest strata and type were analyzed using a two-sample Kolmogorov-Smirnov test (Siegel and Castellan 1989). Actual *versus* expected sighting frequencies in forest strata use were compared using a chi-square test. Significance was set at $p = 0.05$ for analyses and tests were two-tailed.

Results

Observations per site are summarized in Table 1. Howler monkeys were observed in all areas surveyed except NRWS and have the wider species distribution in Trinidad. Capuchin monkeys were found in only two sanctuaries (THWS and BBWS) and one unprotected area (vicinity of Nariva Swamp).

Both species occurred throughout BBWS, and howlers were also found in an area of red mangrove swamp just outside of the sanctuary. Within BBWS, we identified five troops of howlers totaling 34 individuals and three capuchin troops totaling 31 individuals. Two howler troops (seven individuals in all) and two capuchin troops (18 individuals in all) were observed in the surrounding Nariva Swamp.

Both howlers and capuchins were reported to inhabit the Central Range (Bacon and French 1972). However, we observed only howlers (one troop with six individuals) during our surveys. Interviews with local people gave no indication that capuchins were present in the CRWS, which strongly suggests that they no longer exist there.

In Trinity Hills, we observed one capuchin troop with 12 individuals and two howler troops totaling 9 individuals. One additional howler troop was vocally identified but could not be visually located. All were found deep within the sanctuary; no howlers or capuchins were located in forested areas adjacent to the sanctuary.

The Fishing Pond community is located in rural eastern Trinidad. We surveyed this area because the Wildlife Section sponsors a successful marine turtle monitoring and nesting program there. In the forested areas surrounding this community we identified three troops of howlers, totaling 23 individuals. This area had not been surveyed previously, so these data add information to the overall population numbers and habitats of howlers in Trinidad.

Analysis of interspecific differences in the use of forest strata reveals that *Alouatta* routinely use medium and

Table 1. Both *Cebus* and *Alouatta* are found in a variety of ecosystem types on the island of Trinidad. *Alouatta* has a more widespread distribution than *Cebus* and occurs in more sanctuaries and protected areas.

Location	<i>Cebus</i> present?	Troops	Individuals	<i>Alouatta</i> present?	Troops	Individuals
Central Range WS	No	n/a	n/a	Yes	1	6
Bush Bush WS	Yes	3	31	Yes	5	34
Northern Range WS	No	n/a	n/a	No	n/a	n/a
Trinity Hills WS	Yes	1	12	Yes	2	9
Fishing Pond	No	n/a	n/a	Yes	3	23
Nariva Swamp	Yes	2	18	Yes	2	7

Table 2. Observed frequency of use different forest strata by *Cebus* and *Alouatta*.

Canopy height	<i>Cebus</i>	<i>Alouatta</i>
High (> 30 m)	12	15
Medium (20-30 m)	37	12
Low (< 20 m)	21	2

$\chi^2 (2) = 14.28, p < 0.01$.

high levels of the forest, whereas *Cebus* are concentrated in the lower and medium strata. This pattern of use was observed in all forest types. Table 2 summarizes the statistical results.

Comparing our troop size and range data to those reported in other studies of *Alouatta seniculus* and *Cebus albifrons* produces some interesting patterns (Table 3). Overall, our howler troop sizes and range sizes were comparable to those reported at other sites. Home ranges of our capuchin troops were also comparable to those of capuchins at other sites. Capuchin troop sizes, on the other hand, were smaller than average troop sizes reported for other areas.

Discussion

Our data on population numbers and distribution of howlers in Trinidad are similar to that reported by Agoramorthy and Hsu (1995) and Neville (1976). Neither the density nor the distribution of these monkeys has changed appreciably over the past 20 years, which indicates that these primate populations are quite stable for now. Howler monkeys are adaptable and can survive in small patches of forest, as is clearly the case in Trinidad.

Our results for capuchin numbers are more interesting. Like Agoramorthy and Hsu (1995) we identified no capuchins in CRWS; similarly, we found no capuchins in NRWS. However, we observed them in BBWS, in THWS, and in unprotected areas within and around Nariva Swamp. Our data for BBWS triple the numbers of capuchins reported by Agoramorthy and Hsu (1995), who found only one troop with eight individuals inhabiting this sanctuary. Differences in numbers of capuchins reported at Bush Bush may be

attributable to differences in sampling effort or to the monkeys' often inconspicuous nature. The capuchins in BBWS have densities comparable to those reported in more protected and ecologically diverse sites on the South American mainland. While our data show higher population numbers of capuchins in Bush-Bush, our surveys suggest reduced levels of capuchin troops in Trinity Hills. While numbers may have actually declined at Trinity Hills, it is also possible that we under-sampled capuchins in this sanctuary. Continued hunting in the area has likely resulted in increased wariness among both capuchins and howlers. Overall, white-fronted capuchins in Trinidad are limited to only three areas: THWS, BBWS and an unprotected area in the Nariva Swamp. Compared to howlers, these primates need larger ranges (>80 ha.) and thus are not as likely to exist outside of large tracts of forest.

One important factor for the long-term survival of capuchins and howlers on Trinidad would be their capacity for dispersal among protected areas. Obvious dispersal corridors do not presently exist; however, we plan eventually to conduct a more formal investigation into this matter.

Jernvall and Wright (1998) recently concluded that, given the roles primates play in maintaining ecosystems (e.g., dispersing seeds, pollinating plants and serving as prey items), the loss of primate species could have deep impacts on ecosystem health. In many areas in Trinidad, including the sanctuaries surveyed, many large mammalian species—including deer, paca, agouti and peccaries—have already been extirpated. Thus Trinidad's primate populations may be fulfilling system-roles for which few other occupants remain, and the protection of these monkeys could be important for general ecosystem health.

Because we have observed no evidence of forest cats or large raptors, we assume that predation pressure on these monkeys is minimal (although individuals may be occasionally taken by boid snakes). Therefore, primary short-term threats to howlers and capuchins in Trinidad are probably hunting and habitat destruction (particularly further fragmentation of forests and perhaps human harvest of important plant species within and near protected areas). Many important habitat areas already enjoy *de jure* protection; Trinidad has 13 legal sanctuaries or reserves, comprising about 3.4% of the total land area. However, these areas are not in fact adequately protected from hunting, plant harvest, or even agricultural encroachment. Without intensive enforcement efforts, such illegal activities will continue to occur within the sanctuaries. It should also be remembered that some monkeys persist in unprotected areas, and it is likely that protection of these populations may be particularly difficult. If these wildlife-protection issues are adequately addressed, then the future of our study populations is probably not in immediate jeopardy. In the long term, however, establishment of mechanisms for dispersal amongst Trinidad's fragmented forests may be critical for the survival of the island's non-human primate species.

Table 3. Density and home range comparisons of *Cebus albifrons* and *Alouatta seniculus*.

Location	Density (km ²)	Home range (ha)	Av. Group Size	Reference
<i>Cebus</i>				
Cocha Cashu, Peru	24	>150	15	Terborgh 1983
Colombia	-	115	35	Defler 1979
Trinidad	13.5	>84	10	This study
<i>Alouatta</i>				
Suriname	17	6-11	4.3	Mittermeier, in Wolfheim 1983
Venezuela	<36-53	4-25 6-8	5.9-10.5	Crockett 1984, 1985; Neville 1976
Trinidad	19.3		5	This study

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Translocation as a Metapopulation Management Tool for the Black Lion Tamarin, *Leontopithecus chrysopygus*

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Introduction

The four lion tamarins are amongst the most seriously threatened species of New World primates. All have restricted and fragmented distributions and are endemic to the Atlantic Forest of Brazil (Coimbra-Filho and Mittermeier 1973). Three of them, the golden lion tamarin (*Leontopithecus rosalia*), the golden-headed lion tamarin (*Leontopithecus chrysomelas*), and the black-faced lion tamarin (*Leontopithecus caissara*), occur in coastal regions in the states of Rio de Janeiro, Bahia and Paraná/São Paulo, respectively. The fourth species, the black lion tamarin (*Leontopithecus chrysopygus*), is endemic to the forests of the interior of the state of São Paulo.

The black lion tamarin was first discovered in 1822 by Johann Natterer who collected eight specimens from the Fazenda Ipanema, Sorocaba. Johann C. Mikan described it in 1823. In 1902, Ernst Garbe, then Director of the Zoology Museum of São Paulo, collected three animals in Botucatu, São Paulo, and in 1905, O. Hume obtained another from Bauru, São Paulo (Coimbra-Filho 1970). From that time, the black lion tamarin languished in obscurity, and was even thought to be extinct due to the subsequent widespread devastation of forests where it occurs during the 1950's and 1960's. In 1970, however, Ademar Coimbra-Filho found two stuffed animals in the town of Presidente Venceslau, São Paulo, which inspired him to carry out expeditions in the forests near Presidente Epitácio and Teodoro Sampaio. On 14 May 1970, he observed three individuals in the then State Reserve of Morro do Diabo, the first sighting in 65 years (Coimbra-Filho 1970). In July 1986, the Morro do Diabo forest was decreed a State Park, and in that same year, the Forestry Institute of São Paulo State created an International Committee for the Preservation and Management of the Black Lion Tamarin. In 1976, Olav Mielke, an entomologist of the University of Paraná, photographed *L. chrysopygus* in an isolated forest fragment in the Fazenda Paraíso, Gália, São Paulo (Coimbra-Filho 1976b). This resulted in the protection of the forest, first

as the Gália State Reserve, and then in 1987, as the Caetetús Ecological Station.

Between 1984 and 1989, Valladares-Pádua carried out ecological, behavioral and genetic studies of the population in the Morro do Diabo State Park (Valladares-Pádua 1993), and from 1988, first Keuroghlian (1990), then Passos, likewise, studied the behavioral ecology of the black lion tamarins in the Caetetús Ecological Station (Passos 1999; Passos and Alho 2001). In the early 1990's, surveys of remaining forests in the west of the state located a further five small populations on private lands (Valladares-Pádua and Cullen Jr. 1994), and resulted in an estimate of about 1,000 black lion tamarins remaining in the wild, as follows: Morro do Diabo (34,441 ha) - 820; Caetetús (2,179 ha) - 69; Fazenda Ponte Branca (1,305 ha) - 28; Fazenda Rosanella (400 ha) - 28; Fazenda Tucano (1,400 ha) - 14 (these three Fazendas in the region known as the Pontal do Paranapanema); and Fazenda Rio Claro (1,324 ha) - 44, in the municipality of Lençóis Paulista. Four new small populations have been discovered since then: in 1993 in the Fazenda Santa Maria (511 ha); in 1997 in the Fazenda Santa Mônica (486 ha), both in Pontal do Paranapanema; in 1999 in a small forest in Buri, in the east of the state, and in 2001 in the Angatuba Ecological Station, São Paulo (A. Santos, pers. comm.). As such, there are 11 scattered and isolated known populations; with the large majority in the Morro do Diabo State Park (Rylands *et al.* 2002; Valladares-Pádua *et al.* 2002).

The captive population is rather more than 112, maintained in 11 zoos and breeding centers: in Brazil in the Rio de Janeiro Primate Center (CPRJ) and the zoos of São Paulo, Bauru and Brasília, and in five zoos in Europe, one in North America, and one in Australia (Valladares-Pádua and Martins 1996; Ballou *et al.* 2002).

The information obtained on ecology, behavior and demographics, and the results of *Population and Habitat Viability Assessment* (PHVA) workshops held in 1990 and 1997 with the IUCN/SSC Conservation Breeding Specialist

Group (CBSG) (Seal *et al.* 1991; Rylands 1993/1994; Ballou *et al.* 1998) provided the basis for a conservation management plan for the species (Valladares-Pádua and Martins 1996). The 1990 PHVA showed that the survival of the black lion tamarin was threatened in the mid- to long-term. Genetic homogeneity and deleterious inbreeding was identified as a particularly major threat (Foose 1991; Forman *et al.* 1986; Valladares-Pádua 1987). Metapopulation management of the wild and captive populations was recommended as an urgent step for their preservation (Levins 1969, 1970), being seen as the only way to diminish the threat posed by the fragmentation and small size of the populations.

Valladares-Pádua (1993) investigated extinction probabilities and the loss of genetic diversity in each of the sub-populations with different scenarios of metapopulation management through simulations using the VORTEX software. All, with the exception of the Morro do Diabo population, had more than a 50% probability of going extinct within 100 years. The results also showed, however, that, with due management, there was a good probability that the sub-populations and the remaining forests were sufficient for the maintenance of a metapopulation through translocations, reintroductions of captive-born animals, and managed dispersals.

The IUCN *Position Statement on the Translocation of Living Organisms* (1987) defined translocation as the release of animals into the wild to establish, re-establish, or increase the size of a population. Konstant and Mittermeier (1982) defined it as the transfer of wild-born animals from one place to another within their natural area of occurrence, with a minimum of time spent in captivity. The objectives of a translocation can include the recovery of a population locally extirpated through hunting (Kleiman 1990), to increase genetic heterogeneity, to establish satellite populations to reduce the risk of extinction through catastrophes (e.g., epidemics, hurricanes or fires) (Conant 1988), resolution of overpopulation, and the removal of locally threatened animals or re-population in protected areas (Konstant and Mittermeier 1982).

Key issues regarding the use of translocation as a management tool relate to the costs, resource use, acquisition of permits, capture, transport, release, rehabilitation, carrying capacity of the area, hunting, and long-term protection (Caldecott and Kavanagh 1988). Common causes of fatality of the animals being translocated include wounding during capture, stress during confinement and handling, dispersal outside of the release area, predation, and competition with residents (Fritts 1984), the collapse or disruption of social groups, and the transmission of diseases to the resident population (Caldecott and Kavanagh 1983). Other factors that have to be considered include the potential for unexpected ecological effects (Conant 1988) and for speciation (Boag and Grant 1981).

Translocation has been used as a management tool for a number of primate species. Examples include the rescue of red howling monkeys, *Alouatta seniculus*, from areas flooded by the Guri dam, Venezuela, (Konstant and Mittermeier 1982); red howlers, weeper capuchins, *Cebus oli-*

vaceus, and Midas tamarins, *Saguinus midas*, likewise from the inundation area of the Afokaba dam, Suriname (Walsh and Gannon 1967); the translocation of troublesome Rhesus macaques, *Macaca mulatta*, from the suburbs of Delhi, India (Malik and Johnson 1994); black howling monkeys, *Alouatta pigra*, taken from a tourist area to repopulate the Cockscomb Reserve in Belize (Ostro *et al.* 2000); and the translocation of Kirk's red colobus, *Procolobus kirkii*, from threatened forests to protected areas in Africa (Struhsaker and Siex 1998). Translocation was the very successful solution to rescue small, isolated and threatened groups of golden lion tamarins, *Leontopithecus rosalia*, identified during a two-year population survey throughout their range in the state of Rio de Janeiro (Kierulff and Rylands 2003). The release site was a 2,400 ha forest which lacked any resident population and was given full protection as the União Biological Reserve in 1998 (Kierulff *et al.* 2002).

Although intensive monitoring is required to evaluate the success of a translocation (Stanley-Price 1989; Griffith *et al.* 1989; IUCN/SSC 1995), it is often lacking or superficial, most especially in the case of large-scale faunal rescues from forests to be flooded by dams. The lack of monitoring makes it difficult to improve the techniques used through scientific evaluation of the efficacy of the procedures and protocols involved (Konstant and Mittermeier 1982; Kierulff *et al.* 2002). The increasing species extinction rates and impending reduction in overall biological diversity demand an intensive management of species and their remaining habitats (Conway 1989; Foose 1991) and suggest that, in the near future, translocation may become an increasingly important conservation and management tool for endangered species.

Griffith *et al.* (1989) noted that the key factor to guarantee the success of a translocation is the selection of an adequate release site. Release in an unpropitious habitat may result in higher rates of dispersal or even death of translocated animals. Translocation programs should be considered only where the habitat at the release site is intact, where adequate protective measures are in effect, and where the species in question has disappeared locally for reasons unrelated to habitat suitability (Konstant and Mittermeier 1982).

In 1995, IPÊ - Instituto de Pesquisas Ecológicas (Institute for Ecological Research), under the coordination of Cláudio Valladares-Pádua, took the initial steps in establishing a metapopulation management program for the conservation of black lion tamarins. The planning process was based on previous experiences with translocations, results from IPÊ's previous research on the species, and on discussions with the International Committee for the Preservation and Management of the Black Lion Tamarin. The first experimental translocation was carried out in May 1995. An entire group was taken from the Fazenda Rio Claro, Lençóis Paulista, and released in the Fazenda Mosquito, Narandiba, both in the state of São Paulo.

The aim of the translocation was to increase the area available for black lion tamarins at the Fazenda Rio Claro, and establish a new population at the Fazenda Mosquito.

The translocation had no genetic basis, as at the time there was insufficient information. There was also an experimental aspect of the study in establishing the feasibility of using translocation as a metapopulation management tool for black lion tamarins, and we were particularly attentive to their capabilities in finding the necessary food resources and shelters, and capacity to adapt to the new habitat and survive long enough to reproduce. Valladares-Pádua (1993) concluded that *L. chrysopygus* is a highly flexible species, capable of adapting to significantly different habitats, but this needed confirmation through actual management. We evaluated the patterns of reproduction and group composition before and after the translocation.

Study Areas

Fazenda Rio Claro, Lençóis Paulista, São Paulo

The Fazenda Rio Claro is located in the municipality of Lençóis Paulista, in the central region of the state of São Paulo (22°48'S, 48°55'W). The geology of the area is characterized by sedimentary formations and the soils are from sandstone and clay (Morelli 1988). According to the Köppen classification, the climate of the region is Cwa, with temperatures in the hottest months (October to March) averaging 22°C, and in the coldest months (April to September) 18°C (Setzer 1976). The Fazenda Rio Claro is the property of Duratex Florestal S.A., and the forest there (1,324 ha), is characterized by secondary growth riparian forests following the course of two medium-sized rivers - Claro and Palmital - which form corridors (Mamede 1997). The area where the black lion tamarin group was studied before translocation was 165 ha in one of these corridors along the Rio Claro.

Fazenda Mosquito, Narandiba, São Paulo

Fazenda Mosquito is located in the municipality of Narandiba, São Paulo (22°24'S, 51°31'W). The geology is characterized by sandstone, carbonated nodules and decomposing eruptive formations. The soils are sandy, with low fertility and low capacity for water retention (Almeida 1981). According to the Köppen classification, the climate of the region is between Cfa and Cwa, with temperatures in the hottest months (October to March) averaging 22°C, and in the coldest months (April to September) 18°C. Mean annual rainfall is 1,131 mm (Setzer 1976). Fazenda Mosquito is the property of Brascan do Brasil, and the forest there, of 2,344 ha, is mesophytic, semi-deciduous (Rizzini 1963), typical of the inland Atlantic Forest, once covering a large part of the state of São Paulo.

Methods

Selection of the site for the capture of the group to be translocated, and the release area

The Fazenda Rio Claro population had been under study since 1990, which provided a baseline to compare the behavior of the animals once released. The group chosen for trans-

location had already been studied systematically. Fazenda Mosquito lies within the natural area of occurrence of the species, and a vegetation survey indicated that the forest was suitable in terms of size, habitat availability, the absence of a resident lion tamarin population, and its protected status.

Capture and release

Prior to translocation, the group was composed of an adult female, an adult male, a juvenile male and a six-month old female. On 14 May 1995, the group was captured, the adults were equipped with radio-collars (Telonics™), and the animals were transported (overnight, to avoid the heat of the day) in individual *Tomahawk* traps. On arrival at Fazenda Mosquito, they were transferred to a larger cage (90 x 90 cm) previously set up in the forest to allow them to recover from the stress of the journey. On the following morning, water and wild fruits were offered and accepted. They were maintained in the cage for a further 24 hours, and were closely observed for any possible problems. The animals were released at dawn on 16 May 1995. At the beginning, the group was followed from a distance so as not to alarm them while exploring the new area. No food or shelter was provided after the release. Foraging and exploration were evident from the first day in the new forest, and they found a hollow where to sleep on the first night.

Data collection

Fieldwork involved 21 months of data collection at the Fazenda Rio Claro (January, March to September, November and December 1993, and January to July, September and December 1994) and 30 months at Fazenda Mosquito (May to July, October 1995, January to December 1996, January to December 1997, and January and February 1998). The group was recaptured every five months to replace the radio-transmitters. The same sampling methodology was used before and after the translocation. The group was habituated to the presence of the field team and it was possible to identify each individual through observation of size, pelage, and the presence of radio-collars or color collars.

With few exceptions, the group was followed for five days per month, from the moment when they left their tree hollow in the morning to the moment when the last individual entered a hollow again at the end of the day. The observation method was *focal animal sampling*; recording the behavior of each individual of the group separately during determined sample periods (Altmann 1974). Sample periods and intervals were 10 minutes, and the behavior of the focal animal was recorded at the end of each minute (instantaneous sampling). The order in which the members of the group were sampled every day was randomly chosen before visualizing the group in the morning. Although all members of the group were sampled, only adults were included in the analysis. Group composition (births, deaths, immigrations and emigrations) and reproduction (mating periods, births) were monitored closely before and after the translocation.

Results

Group composition - Fazenda Rio Claro

At the Fazenda Rio Claro, group size fluctuated from two to eight animals. There were at least two other groups living in the periphery of the home range of the study group. Three emigration events were observed: two adult males in October 1993, one juvenile female in April 1994, and two females, one adult and one juvenile, in August 1994. A juvenile male immigrated in November 1994. There were two deaths: one adult male in May 1993 and a 3-month old male in April 1994. Births occurred in December 1993 (a male that died two months later) and December 1994 (a female that was translocated with the group to the Fazenda Mosquito). In both cases, it was possible that two infants had been born but only one survived (Table 1).

Group composition - Fazenda Mosquito

After translocation to the Fazenda Mosquito the group remained together, but the number of individuals fluctuated from two to six. The infant female died in October 1995, five months after the translocation. The adult female and dominant adult male were seen mating in June 1995, and two male infants were born in December 1995. One died two months later. In June 1996, the adult female and adult male were again seen mating, and two male infants were born in November 1996. Again, one of the infants died two months later. In February 1997, the adult dominant male disappeared. The field team had captured the group to replace the radio collars three months before, and observed that the adult male's teeth were considerably worn, and that it was certainly the oldest member of the group. With his disappearance, the other adult male in the group took over as dominant male, and was seen mating with the adult female in June 1997.

The third birth, of a single female infant, was in November 1997. Once again, it is possible that two infants were born but only one survived. In March 1998, the group was composed of five animals: the adult female and adult male translocated from Fazenda Rio Claro, two young adult males (one born in Fazenda Mosquito in December 1995 and the other in November 1996), and the infant female born in November 1997. In July 1998, the adult female and two adult males were found dead. The female was in a hollow, the males were on

the forest floor, and the three animals had a number of wounds on their limbs. They were taken to the Veterinary Department of the São Paulo Zoo and autopsied. The probable cause of death identified was predation by ocelot or bird of prey. The remaining sub adult male (born in 1996) and female (born in 1997) were seen again only in June 2000 (Table 2).

A second translocation

To reinforce the population, a year later (July 1999) a second group of six black lion tamarins was taken from the Fazenda Rio Claro and translocated to the Fazenda Mosquito. The group was composed of four adult males and two adult females and was released in the same area occupied by the resident pair. There was little evident interaction, however, until June 2000, when a subadult male emigrated, and joined the pair remaining from the first translocation. This second group was accompanied and studied from July 1999 to July 2002 by Cristiana Saddy Martins (in prep.). It has maintained its size at six individuals, and has evidently adapted well to the new area and has been reproducing normally.

Translocation as a Management Tool

A translocation is successful if the animals stay on the release site, find the necessary food resources and shelters, and survive long enough to reproduce, resulting in the establishment of a self-sustaining population (Wilson *et al.* 1992). Another important parameter for the evaluation of a translocation program is the maintenance of group composition and social structure (Konstant and Mittermeier 1982). Many reintroduced or translocated groups of primates have been observed to break up upon release or shortly after (Konstant and Mittermeier 1982).

The translocation described in this article involved the relocation of an entire group of black lion tamarins. Group members were captured, transported and released in the new area at the same time, in the hopes of maximizing their chances of survival, permanence in the area and reproductive success. The group stayed together when released at the Fazenda Mosquito. Group size fluctuated between two and six (averaging 4.5 individuals), quite within the range typical of the species (two to eight individuals, with three to four being the most common; Coimbra-Filho 1976a). Average

Table 1. Composition of the group in the Fazenda Rio Claro. January 1993 to May 1995.

Year	Month	Group Composition			Births	Deaths	Emigration	Immigration	Nº. Ind.
		Adults	Juveniles	Infants					
1993	Jan	4M (M-A/b/c/d) 2F (a/FE)	2F (c/d)						8
	May	3M (M-A/c/d) 2F (a/FE)	2F (c/d)			1M (b)			7
	Oct	1M (M-A) 2F (a/FE)	2F (c/d)				2M (c/d)		5
	Dec	1M (M-A) 2F (a/FE)	2F (c/d)	1M (e)	1M (e)				6
1994	Apr	1M (M-A) 2F (a/FE)	1F (d)			1M (e)	1F (c)		4
	Jul	1M (M-A) 2F (a/FE)	1F (d)						4
	Aug	1M (M-A) 1F (FE)					2F (a/d)		2
	Nov	1M (M-A) 1F (FE)	1M (M-SA)					1M (M-SA)	3
	Dec	1M (M-A) 1F (FE)	1M (M-SA)	1F (R1)	1F (R1)				4
1995	May	Translocation of the group to Fazenda Mosquito							

Table 2. Composition of the group in the Fazenda Mosquito. May 1995 to April 2001.

Year	Month	Group composition			Births	Deaths	Emigration	Immigration	No. Ind
		Adults	Juveniles	Infants					
1995	May	1M (M-A) 1F (FE)	1M (M-SA)	1F (R1)					4
	Jun	FE e M-A seen mating (16 June 1995)							
	Oct	1M (M-A) 1F (FE)	1M (M-SA)			1F (R1)			3
	Dec	1M (M-A) 1F (FE)	1M (M-SA)	2M (R2a/R2b)	2M (R2a/R2b)				5
1996	Feb	1M (M-A) 1F (FE)	1M (M-SA)	1M (R2a)		1M (R2b)			4
	Jun	FE & M-A seen mating (11 June 1996)							
	Nov	1M (M-A) 1F (FE)	2M (M-SA/R2a)	2M (R3a/R3b)	2M (R3a/R3b)				6
1997	Jan	2M (M-A/M-SA) 1F (FE)	1M (R2a)	1M (R3a)		1M (R3b)			5
	Feb	1M (M-SA) 1F (FE)	1M (R2a)	1M (R3a)		1M (M-A)			4
	Jun	FE e M-SA seen mating (25 June 1997 and 27 June 1997)							
	Nov	2M (M-SA/R2a) 1F (FE)	1M (R3a)	1F (R4)	1F (R4)				5
1998	Feb	2M (M-SA/R2a) 1F (FE)	1M (R3a)	1F (R4)					5
	Jul	1M (R3a)		1F (R4)		2M (M-SA/R2a) 1F (FE)			2
1999	Jul	Translocation of a new group from the Fazenda Rio Claro to the Fazenda Mosquito							
		Composition of new group: 4 adult males and 2 adult females							
2000	Jun	G1: 1M (R3a) 1F (R4)							2
		G2: 4M (A,B,C,D) 2F (E,F)							6
	Jul	G1: 1M (R3a) 1F (R4)							2
		G2: 4M (A,B,C,D) 1F (E)				1F (F)			5
	Sep	G1: 2M (R3a/D) 1F (R4)						1M (D)	3
		G2: 3M (A,B,C) 1F (E)					1M (D)		4
	Nov	G1: 1M (D) 1F (R4)				1M (R3a)			2
		G2: 3M (A,B,C) 1F (E)							4
2001	Mar	G1: 1M (D) 1F (R4)		1X (R5)	1X (R5)				3
		G2: 3M (A,B,C) 1F (E)							4
	Apr	G1: 1M (D) 1F (R4)		1X (R5)					3
		G2: 3M (A,B,C) 1F (E)							4

group size in the Morro do Diabo State Park is 4.75 individuals (Valladares-Pádua 1993), and for *L. rosalia* in Rio de Janeiro is 5.4 ± 2.05 (Dietz and Baker 1993).

The first mortality occurred five months after the translocation, when the infant female disappeared. This may have been related to the translocation process, but there is no evidence either way. The dominant male disappeared two years after the translocation, probably due to old age, and three years after the translocation, the adult female and the two adult males were killed by a predator, resulting in a drastic reduction in the number of individuals in the group. Once again, there was no evidence that the deaths were related to the translocation given that they had already been exposed to the predators in the Fazenda Rio Claro for a considerable time (L. Cullen Jr. pers. comm.).

The first birth was seven months after the translocation, and the group reproduced annually from then on. The *L. rosalia* group translocated by Pinder (1986) showed sexual activity on several occasions, but did not reproduce in the first year, probably due to a hormonal dysfunction already observed in captivity. Mating was observed in June (dry season) and births occurred between November and December, in the wet season. Coimbra-Filho and Mittermeier (1973) observed that the birth peak for *L. chrysopygus* was between September and February, a seasonality which coincides with periods of higher availability of resources in the wet season (Valladares-Pádua 1993; see also Dietz and Baker 1993; Dietz *et al.* 1994).

Two offspring were born in the first two births (1995 and 1996), and a singleton in the third. Of 128 births documented

for *L. rosalia* by Dietz *et al.* (1994), 27 were singletons, 100 twins and one of triplets. In the first two births, and probably also in the third, only one of the infants survived, the deaths occurring in the first few weeks. However, there is no reason to believe that the mortality rate is abnormal or directly related to the translocation. Average survival rate for *L. rosalia* in Poço das Antas has been estimated at $0.83 \pm 1.04\%$ (Dietz and Baker 1993). Higher infant survival is expected in periods of higher resource availability (Dietz *et al.* 1994), and it is possible that the group's foraging success was lower in their new home range. The time it takes for a group to reach complete familiarity with the food resources available is not known.

Between 1984 and 2000, 146 captive-born and one confiscated golden lion tamarin were reintroduced in the Poço das Antas Ecological Station and 21 private forest fragments (total of 3,200 ha). In December 2000, seventeen years after the beginning of the program, the reintroduced population was of 359 lion tamarins - 36% of the total estimated population of 1,000 animals still surviving in the wild, and 19% of the total habitat occupied by the species (Kierulff *et al.* 2002). From the total of 359 lion tamarins (50 groups), 5% were reintroduced animals and 95% were wild-born (Kierulff *et al.* 2002). The loss of reintroduced animals was high in the first year (70%), but in the subsequent years similar to indices found for wild population. Major causes of death were diseases (viral) and vandalism, or causes related to feeding, locomotion, orientation and anti-predator behavior deficiencies (Beck *et al.* 1991, 1994). Wild-born infants were less affected by these deficiencies and an annual survival

rate of 65% was observed. Around 28% of the infant deaths occurred in the first month of life, 68% survived up to six months, 45% survived up to one year, and 45% survived up to two years (Beck *et al.* 1991).

Kierulff (1993) conducted a major survey all over the probable *L. rosalia* distribution area and located 60 tamarins in 12 groups living in small and isolated secondary forest fragments. Since 1994, six groups were rescued and translocated to the forest of Fazenda União (3,200 ha), considered to be adequate for the establishment of a new population. In December 2000, the translocated population was of 120 tamarins - 12% of the total estimated population in the wild, and 19% of the total habitat occupied by the species. From the total of 120 tamarins, 23 were translocated and 97 were born in Fazenda União. The survival rate of translocated animals was 81.5% and main causes of death were injuries during group encounters and predation. A total of 107 infants were born after the translocations. Around 81% of the infants survived longer than six months, 78% longer than a year, and 74% longer than two years (Kierulff *et al.* 2002). Twelve years were necessary for the reintroduced population to exceed the number of reintroduced animals, while for the translocation this period was of only three years.

Griffith *et al.* (1989) associated translocation success with the establishment of a self-sustaining population. However, for most of the species this objective is long-term, and the time required for the assessment of the biological success of a given management intervention makes it complicated to use this criteria. In the case of lion tamarins, viable populations will only be achieved through a long-term metapopulation management program. The translocation of a second group, also removed from the Fazenda Rio Claro, in 1999 was fundamental for the maintenance and reproduction of the first translocated group. The forest of the Fazenda Mosquito has a carrying capacity for about four more groups, or 18-20 tamarins (Medici 2001), which corresponds to 2% of the total estimated population of 1,000 individuals still surviving in the wild (Valladares-Pádua and Cullen Jr. 1994). It is possible, however, that the presence of a second translocated group, and other groups to be translocated in the future, will reduce the size of the black lion tamarin home range in the Fazenda Mosquito, increasing our estimate of the carrying capacity of the forest. Kierulff (1993) observed that the low density of *L. rosalia* in Fazenda União, unoccupied before the translocations, allowed the groups to use areas considerably larger than normally described for the species. The home range size decreased with the increase of population density.

The 11 known wild populations of black lion tamarin, including the Fazenda Mosquito, cover an area of 43,366 ha of forest: 38,543 ha in the Pontal do Paranapanema region and 4,823 ha in other regions of the state. As such, the Fazenda Mosquito forest corresponds to 3% of the total habitat occupied by the species. The forests of Buri and Angatuba are not included in this estimate. The IPÊ - Instituto de Pesquisas Ecológicas estimates that there are still 26,000 ha of

habitat available for black lion tamarins inside the original distribution of the species. From this total, 7,000 ha are in the Pontal region (nine forest fragments with sizes between 400 and 1,828 ha) and 19,000 ha in other regions of the state. The available habitat would have a carrying capacity for 79 groups or 355 black lion tamarins (Medici 2001), although it should be remembered that the habitats are different for a number of variables (Ditt 2000) and may have specific carrying capacities.

Following the first translocations to the Fazenda Mosquito, IPÊ - Instituto de Pesquisas Ecológicas has continued its actions in terms of the metapopulation management of the species. Two reintroductions (captive-born tamarins from Jersey Zoo in England and the Rio de Janeiro Primate Center), and a managed dispersal of two males were conducted in Morro do Diabo State Park. The aim was to test the different options for the metapopulation management plan, analyzing the success, advantages and disadvantages, and establish protocols and actions to maximize their success and contribute to the conservation of the species through increasing their population and genetic diversity in the wild.

Any conclusions as to the best management strategy are still premature, but it is safe to affirm that translocation follows a simpler protocol and is significantly less expensive than reintroduction. Reintroduction of captive-born animals requires extensive and intensive management, and is very expensive (Kleiman *et al.* 1991), involving captive management, ecological and behavioral field studies, and a considerable administrative infrastructure. Kleiman *et al.* (1991) estimated a cost of about US\$22,000 for each golden lion tamarin surviving after the reintroduction. Considering only the direct expenses in Brazil, Kierulff (2001) estimated that each reintroduced golden lion tamarin costed US\$7,000, while a translocated tamarin costed US\$4,600, including expenses with capture and monitoring. Translocation requires less infrastructure and personnel, does not demand training, acclimatization, habituation or previous preparation of the animals, and does not require posterior management or provision of additional food; factors extremely important for reintroduction and managed dispersal. Additionally, as observed by Kierulff (2000) for *L. rosalia*, translocation, when compared with reintroduction and managed dispersal, seems to result in lower mortality and higher rates of reproduction and infant survival.

One of the greatest benefits of translocation is the maintenance of the forests involved in the process, indirectly as such promoting habitat protection (Caldecott and Kavanagh 1988; Griffith *et al.* 1989; Kleiman *et al.* 1991). The establishment of the translocation program in the Fazenda Mosquito attracted the attention of the local community, and landowners became interested in the conservation of the species and its habitat. Today, there is a firm possibility of turning the Fazenda Mosquito into a protected area. After the translocation, and due to the IPÊ's presence in the area, greater attention is being given to the forest. Farm owners are using their resources and

employees to put up fences to prevent cattle grazing in the forest, and maintain contact with the local representatives of IBAMA, reporting any cases of poaching in the area. Another important aspect is educational, given that researchers can use the translocation of threatened species as a chance to educate the local community and promote conservation.

Conclusions

The results of this translocation experiment showed that the black lion tamarin is able to adapt to different habitats, which vary in the availability and seasonality of resources. The translocated animals reproduced with some success in the new area, and overall we believe that translocation is a feasible tool for the metapopulation management of the species. An understanding of this first translocation experience was fundamental for the application of this technique for the management of black lion tamarins and other primates. The translocation of only one group was obviously no guarantee for the establishment of the species at the Fazenda Mosquito, and a series of translocations are necessary to establish a viable population. Further research is necessary to monitor the population dynamics and possible changes in the carrying capacity of the forest with the increase in population density, besides examining the expediency of a mixed management strategy, which would include reintroduction and managed dispersal. Intensive management is necessary for species such as the black lion tamarin with such reduced and fragmented populations, and translocation will become increasingly important as a management tool as forest destruction continues and populations are increasingly confined to the small and widely-spaced protected areas which remain.

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A Survey of the Habitat of *Lemur catta* in Southwestern and Southern Madagascar

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Introduction

Madagascar is one of the world's most "threatened hotspots" for terrestrial biodiversity and a priority for conservation action (Mittermeier *et al.* 1992, 1994, 1999). However, development of a realistic conservation action plan is dependant on accurate and up-to-date data. For example, although the ringtailed lemur, *Lemur catta*, was listed as a "high priority" species in the IUCN/SSC *Lemur Action Plan* (Mittermeier *et al.* 1992), the ranking was based in part on the flagship nature of the species. Later, the Tropical Field Guide series volume *Lemurs of Madagascar* ranked it as "Vulnerable" (Mittermeier *et al.* 1994). This reclassification caused some NGOs to consider that *Lemur catta* was not in need of any immediate and intensive conservation action. However, its habitat may be undergoing much more rapid deforestation and deterioration than most others on the island.

Green and Sussman (1990) used maps generated from aerial photographs and satellite images to study the history of deforestation of the rain forests of eastern Madagascar. They were able to show that, in 1985 (Fig. 1a), only 34% of the estimated original rain forest remained and that it was being cleared at a rate of 110,000 ha/year. Their data also showed that deforestation was most rapid in areas of low topographic relief and high population density. Observations of the dry and deciduous forests of southeastern and southern Madagascar suggest that they are being reduced at a similar or even faster rate than the tropical wet forests in the east (Sussman *et al.* 1994; Smith 1997; Smith *et al.* 1997).

The dry forests of the south and west are unique and are inhabited by many plants and animals found nowhere else on Earth. Although much attention has been directed to deforestation in the east, the unique semi-arid habitat of southern Madagascar (Fig. 1a), containing more endemic plant families than elsewhere on the island (Fig. 1b shows *Alluaudia procera* trees of the endemic Didiereaceae family), is even more vulnerable to human disturbance. Furthermore, these forests mostly cover areas of low topographic relief and,

unlike the remaining eastern rain forest that are afforded some inherent protection by steep slopes, the lack of topographic relief in the south leaves this unique habitat more vulnerable to clearing. For example, western primary forest cover declined from 12.5% in 1950 to 2.8% in 1990, relative to an average cover of 11% in all of Madagascar in 1990 (Nelson and Horning 1993; Smith 1997; Smith *et al.* 1997). Disturbingly, once cut much of the natural vegetation of the south regenerates slowly, if at all.

Although rain forests have received a great deal of research attention from conservation and development organizations, there has been less focus on dry forests. There is some indication that dry forests are among the most endangered habitats worldwide. For example, Janzen (1988) states: "the rain forest is not the most threatened of the major tropical forest types. The tropical dry forests hold this honor." He calculated that by the late 1980's less than 2% of the original dry forest on the Pacific Coast of Mesoamerica was relatively intact. Similar patterns of loss are exhibited in other tropical regions, such as parts of Mexico, Central and South America, and Southeast Asia, Australia, and Madagascar (Janzen 1988; Kramer 1997; Smith 1997; Cabido and Zak 1999; Trejo and Dirzo 2000; Dirzo and Sussman 2002). Concerning Madagascar, Smith (1997, p.441) states: "seasonally dry...forests have declined more severely, and are under greater threat, than tropical wet forests...leaving western dry forests relatively ignored and underprotected." Protected areas cover only around 2% of the total remaining forest in the dry forest areas of Madagascar compared with approximately 5.3% for lowland evergreen forest (Du Puy and Moat 1996). Recently, the spiny forest of southern Madagascar has been listed as one of the 200 most important ecological regions of the world (Olson and Dinerstein 1998). Thus, there is great urgency to document the deforestation as well as to determine the rate and patterns of habitat loss in southern and southwestern Madagascar.

Given these facts, we have begun to survey the habitat of *Lemur catta* (Fig. 1c) using satellite mapping. We employ scenes from six contiguous Landsat footprint locations

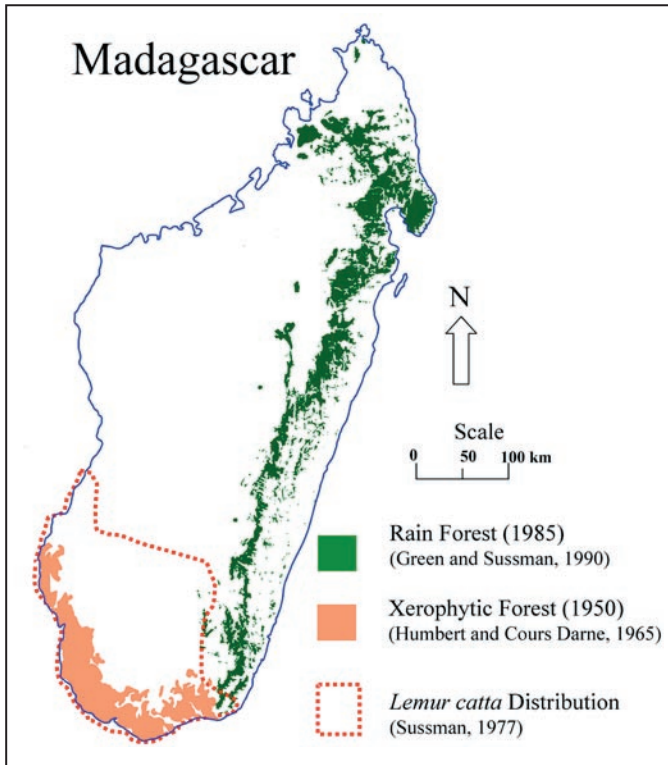


Figure 1a. Map of Madagascar showing the distribution of rain forest (Green and Sussman 1990) and xerophytic forest (Humbert and Cours Darne 1965), together with the general distribution of *Lemur catta* (Sussman 1977).



Figure 1b. Stand of *Alluaudia procera* trees of the endemic plant family Didiereaceae, on the road between Betioky and the Beza-Mahafaly Special Reserve. Photo taken by Green in 1987.



Figure 1c. Group of ringtailed lemur (*Lemur catta*) at the Beza-Mahafaly Special Reserve (Parcel 1). Photo taken by Green in 1987.

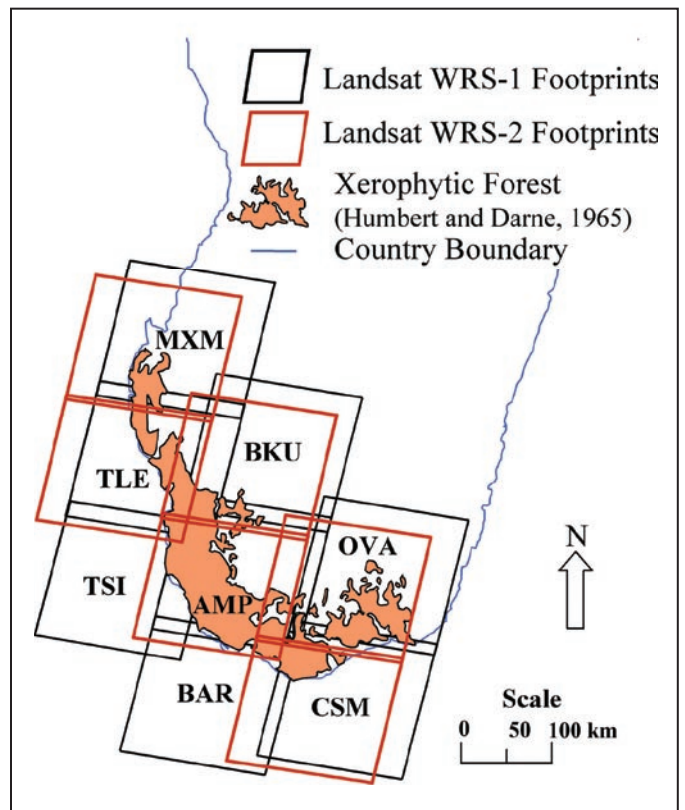


Figure 2. Map showing the distribution of xerophytic forest (Humbert and Cours Darne 1965) in southern Madagascar, together with the Landsat image footprints used in this study. Two coordinate systems (World Reference Systems) are used to identify the position of Landsat images: WRS-1 and WRS-2. WRS-1 is used for Landsat 1, 2, and 3, while WRS-2 is used for Landsat 4, 5, and 7. This map shows WRS-1 footprints in black and WRS-2 footprints in red. We use the term *location* to refer to the overlap between images from these two coordinate systems. For convenience we have also identified these locations by unique 3-letter codes (from the international airport code) from the airport in the largest city contained within that location. All the images used in this study and their locations are listed in Appendix 1.



Figure 3. Map showing the field route used by the authors in 2001. The route traveled is shown in red. The background image is a mosaic of multi-spectral color composites of the 1999/2000 Landsat 7 ETM+ images. Bands 3, 4, and 5 are colored as blue, green, and red, respectively.

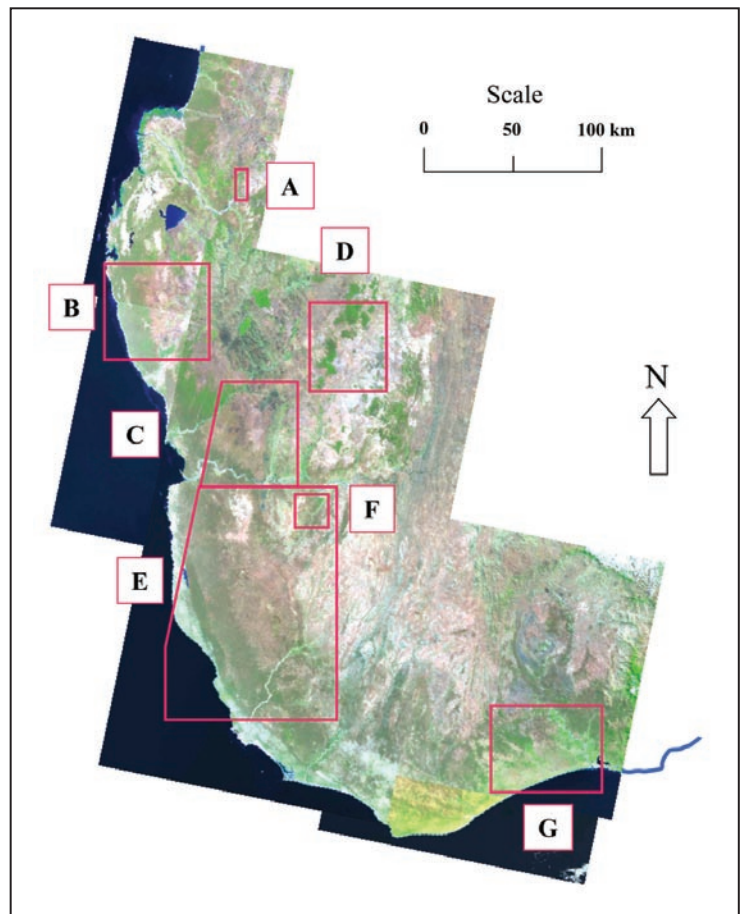


Figure 4. Map showing seven areas (A through G) that mark the boundaries of the multi-temporal color composite image figures shown in this paper. The background image is a mosaic of multi-spectral color composites of the 1999/2000 Landsat 7 ETM+ images. Bands 3, 4, and 5 are colored as blue, green, and red, respectively.

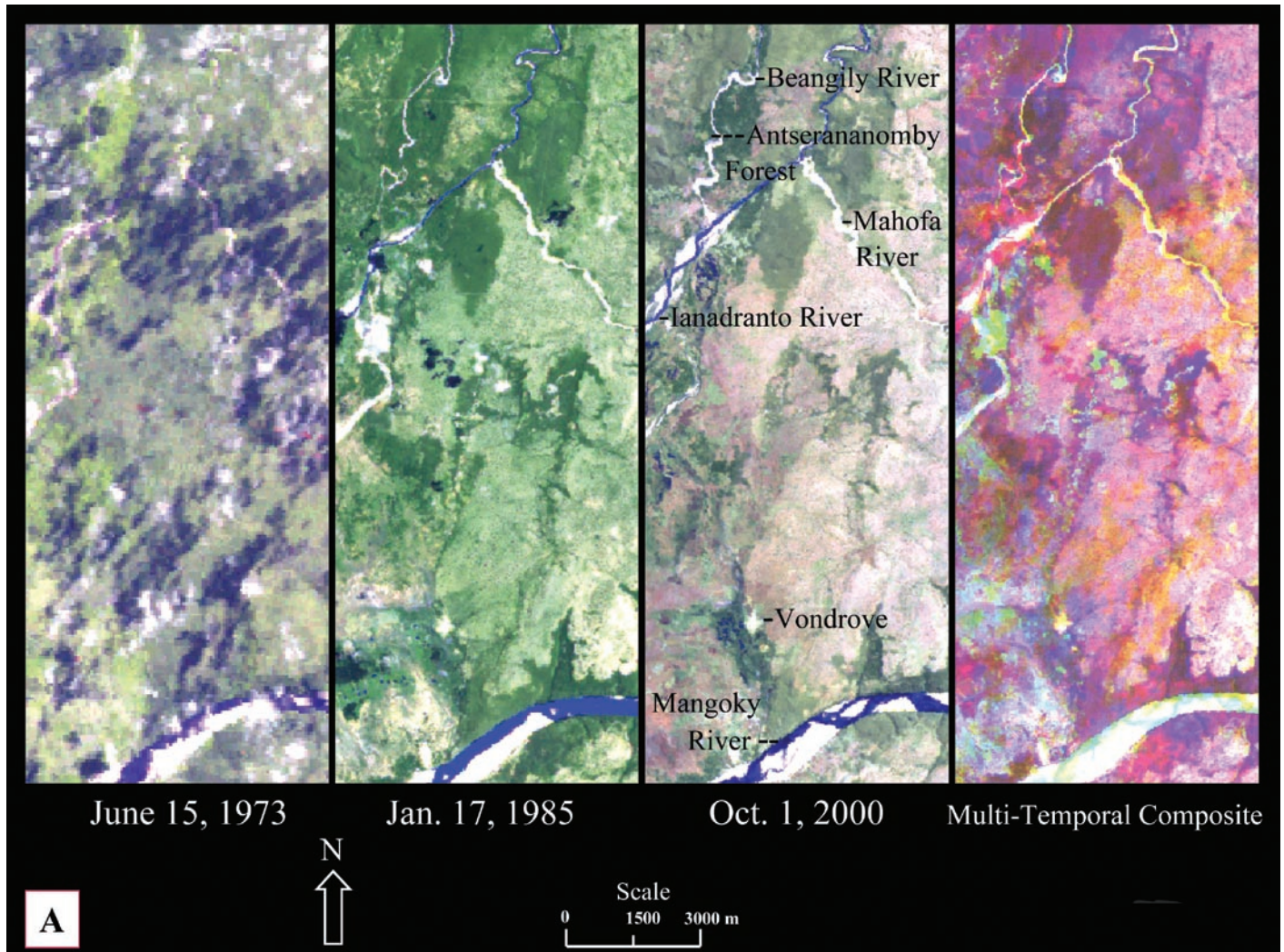


Figure 5. Three different dates of Landsat images are used in this study for the area labeled A in figure 4. The June 15, 1973 MSS multi-spectral color composite uses bands 1, 2, and 4 as blue, red, and green, respectively. The Jan. 17, 1985 TM multi-spectral color composite uses bands 3, 5, and 7 as blue, green, and red, respectively. The Oct. 1, 2000 ETM+ multi-spectral color composite uses bands 3, 5, and 7 as blue, green, and red, respectively. In each of these multi-spectral color composites, dense tree covered areas are shown as green colors, rivers are blue, and river sandbars and clouds are white. There are more clouds (and shadows) in the 1973 scene.

The multi-temporal color composite uses one band (of the red wavelengths) from all three dates. The 1973 MSS band 2 is colored as blue, the 1985 TM band 3 is colored as green, and the 2000 ETM+ band 3 is colored as red. See the text for an explanation of the resulting colors. Figures 6, 8, 10, 13, 14, and 15 (areas B, C, D, E, F, and G respectively) also depict multi-temporal color composites generated in the same way.

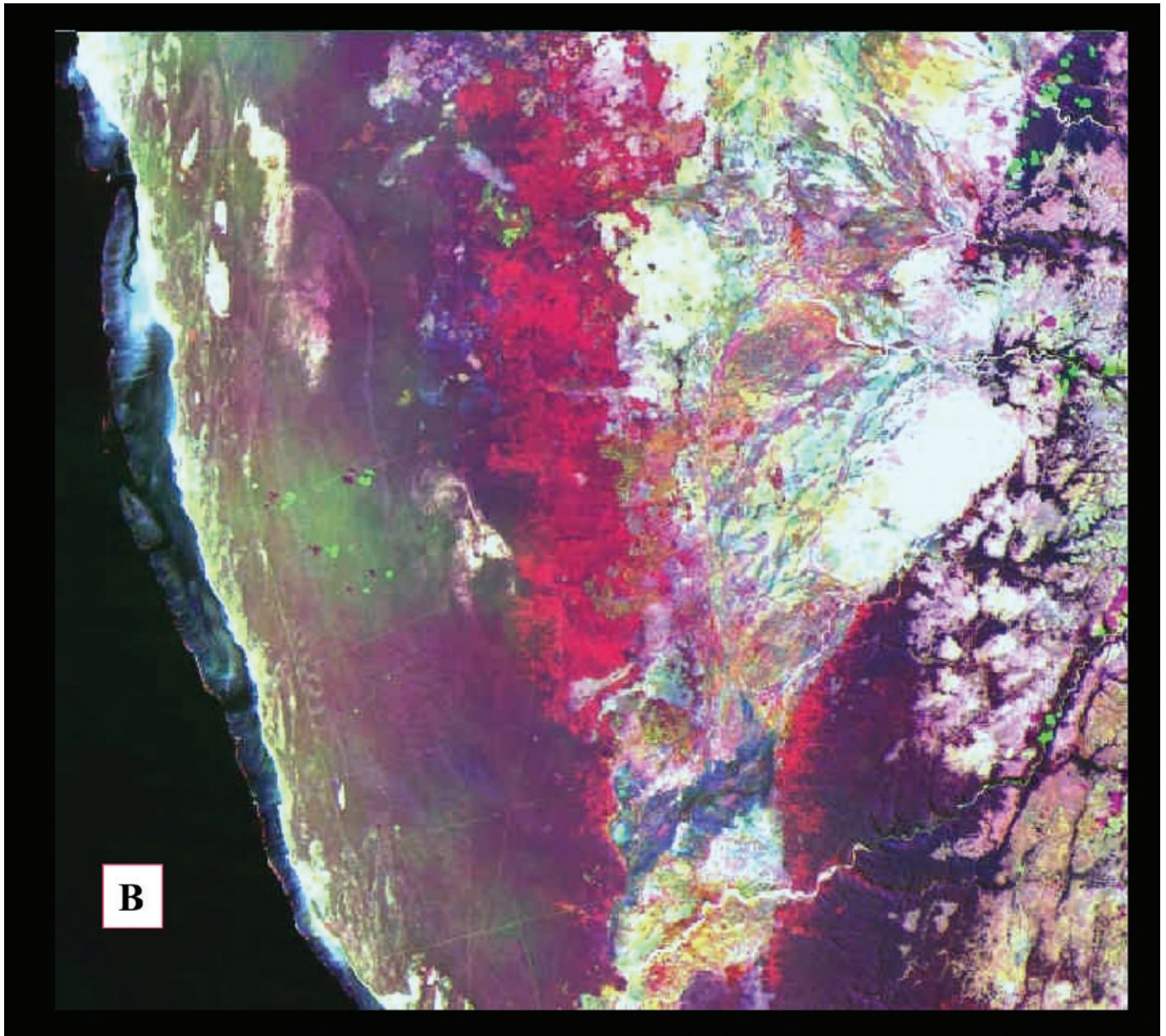


Figure 6. A multi-temporal color composite for area B (see Fig. 4). This area is approximately 60 km wide. Black or dark gray colors represents forests that have remained largely unchanged from 1973 to 2000. Light colored (white) areas are non-forest areas, generally savannahs dominated by grasses, which have undergone little change between 1973 and 2000. Forest cut between 1973 and 1985 that did not re-grow significantly is colored yellow, while forest cleared between 1985 and 2000, which did not re-grow, is bright red in this multi-temporal composite. The vertically oriented red swath that runs down the center of the image depicts forests cleared recently using swidden agriculture techniques for commercial corn production destined for export from the port of Toliara just to the south.



Figure 7a. Photo of an area where corn is bought from local swidden farmers, bagged and loaded onto large trucks. The corn is then hauled by truck to the nearby port of Toliara for export.



Figure 7b. Photo of the Mikea Forest in an area previously cleared of all but the baobabs, farmed for corn production for several years using swidden techniques and then abandoned. Photos taken by Nathan Vogt.

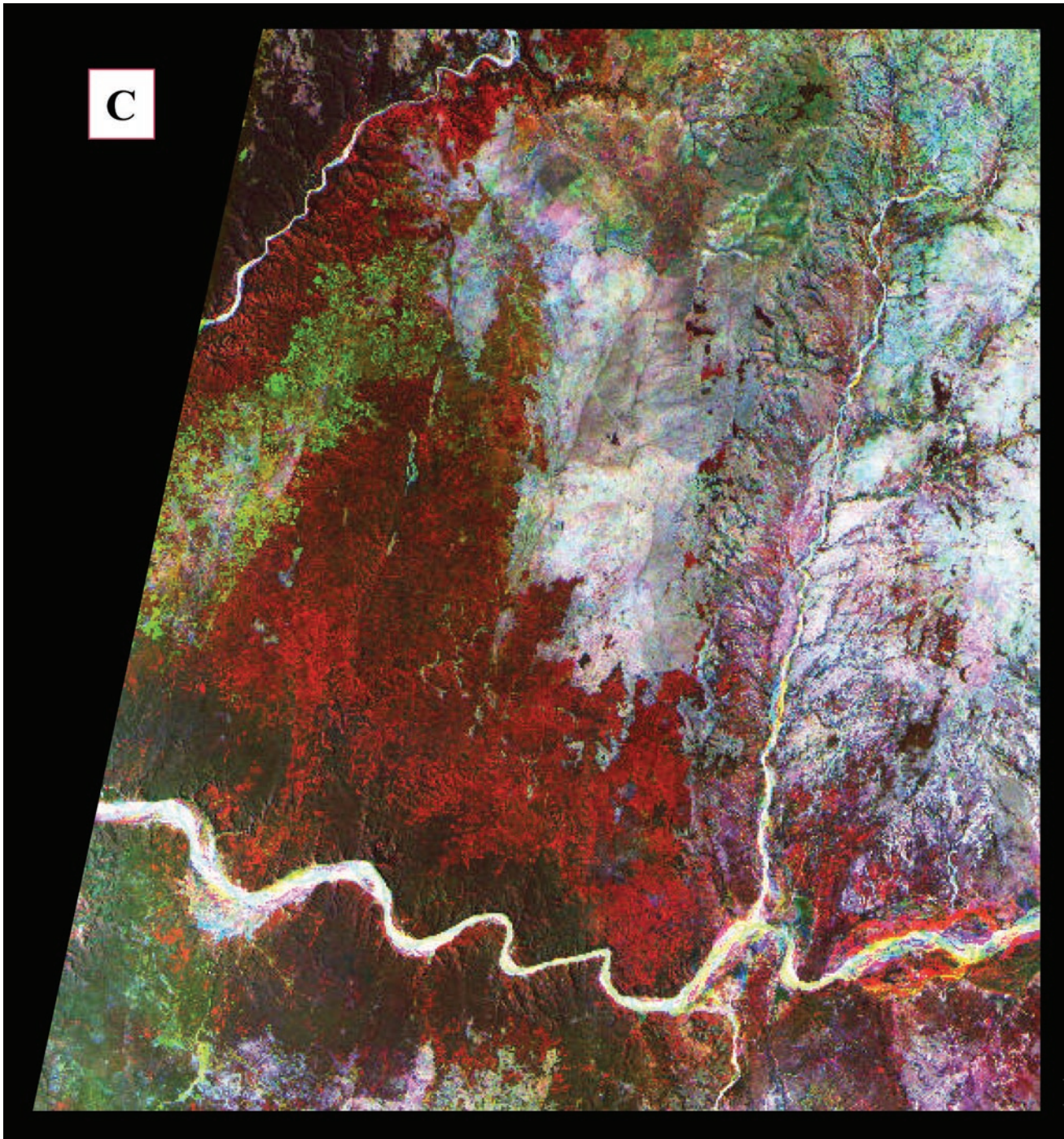


Figure 8. A multi-temporal color composite for area C (see Fig. 4). This area is approximately 50 km wide. Deforestation associated with commercial charcoal production to be sold in Toliara for cooking fuel is shown in this figure. Forest was first cut along Route Nationale #7 between 1973 and 1985. These areas have not re-grown significantly and are colored yellow or yellow green. The red areas depict more recent cutting between 1985 and 2000, in an area bounded by the Fiherenana and the Onilahy rivers to the north and south respectively, and by natural savannah to the east.



Figure 9a. Photo shows a young Malagasy man standing along side bagged charcoal next to the edge of a road south of Andranovory, a small town on Route Nationale #7 east of Toliara.



Figure 9b. Photo shows land adjacent to Route Nationale #7 east of Toliara which was cleared for charcoal prior to 1987. Little re-growth of woody plants in the subsequent 14 years is evident. The practice of cutting forest to produce charcoal has resulted in a large and expanding zone devoid of many woody plants to the northeast of the city. Much formerly forested land present along Route Nationale #7 until the late 1960s is now characterized by abundant bare limestone rock exposures. Photos taken by Green in 1987.

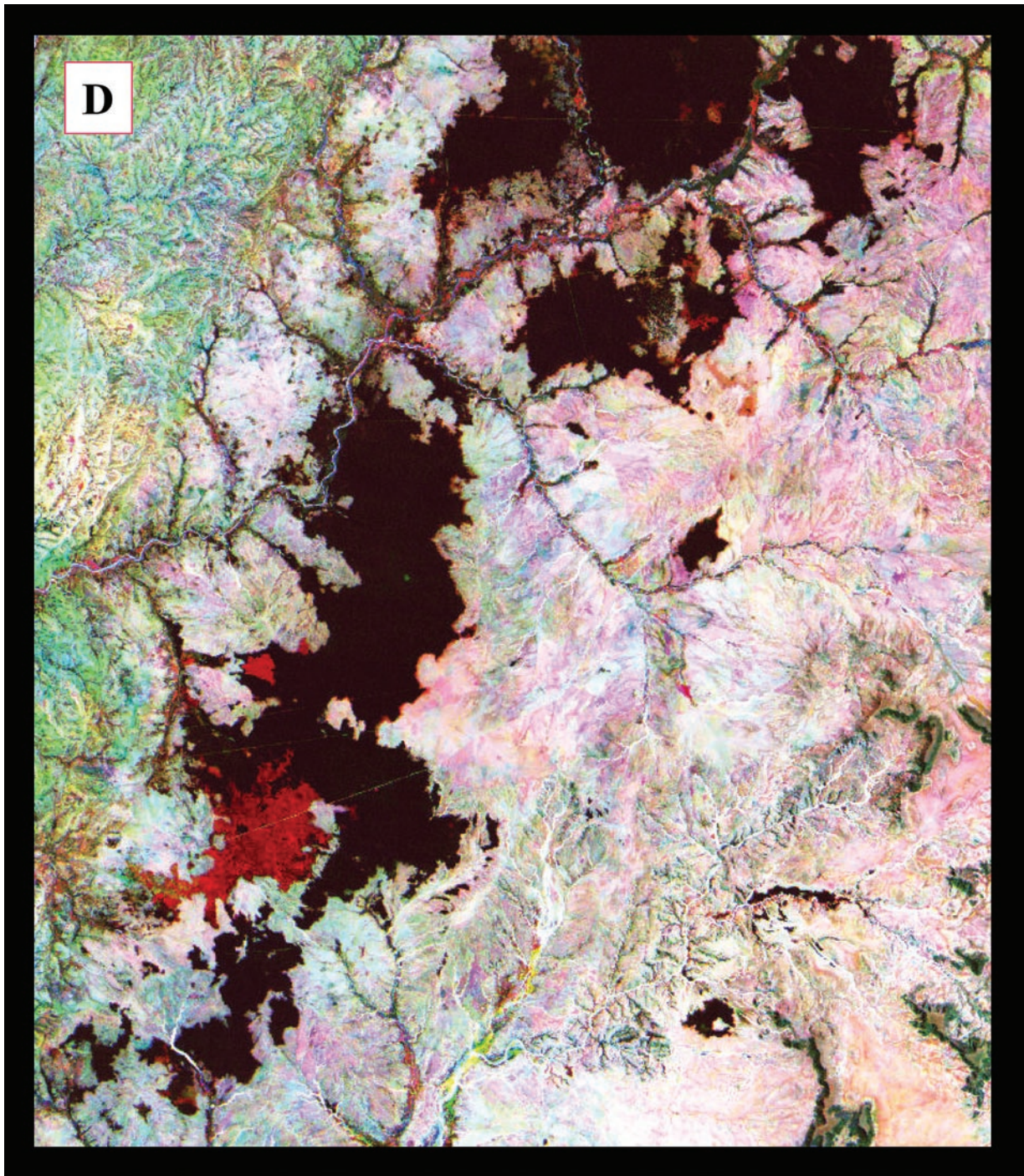


Figure 10. A multi-temporal color composite for area D (see Fig. 4). This area is approximately 40 km wide. The figure shows that the Zombitsy forest has remained largely intact from 1973 to 2000. The red area in the multi-temporal composite (in the southwestern portion of the forest) was cut in the early 1990s during a period of severe drought. Since 1997 much of the remaining forest has been designated as a National Reserve, and little cutting has been observed recently.



Figure 11a. Photo shows portion of Zombitsy forest along Route Nationale #7 just east of Sakaraha in 1987.



Figure 11b. Photo shows same area as 11a in 2001. Migrants from the Mahafaly Plateau region, fleeing a severe drought, settled along this highway in the early 1990s. This photo shows that the forest has been cleared for subsistence farming. Now only the baobab remains from the original forest. Photos taken by Green in 1987 and 2001, respectively.



Figure 12a. Photo of a grass-dominated savannah from the center portion of area C. There is some disagreement as to whether the savannah of this region is natural or the result of earlier deforestation events.



Figure 12b. Photo shows what may at first glance appear to be a remnant forest patch isolated by the cutting of surrounding forests.



Figure 12c. Photo shows that on closer inspection this forest patch is underlain by an isolated outcrop of calcareous rock which is surrounded by red lateritic clay-rich soils derived from an upper Cretaceous sandstone unit.



Figure 12d. Photo shows that the contrasting geological formations that underlay forest and savannah at this location probably account for the different vegetation each unit supports. George Schatz of the Missouri Botanical Garden stands on the shores of this lithologic island which supports woody growth. Photos taken by Green in 1987.

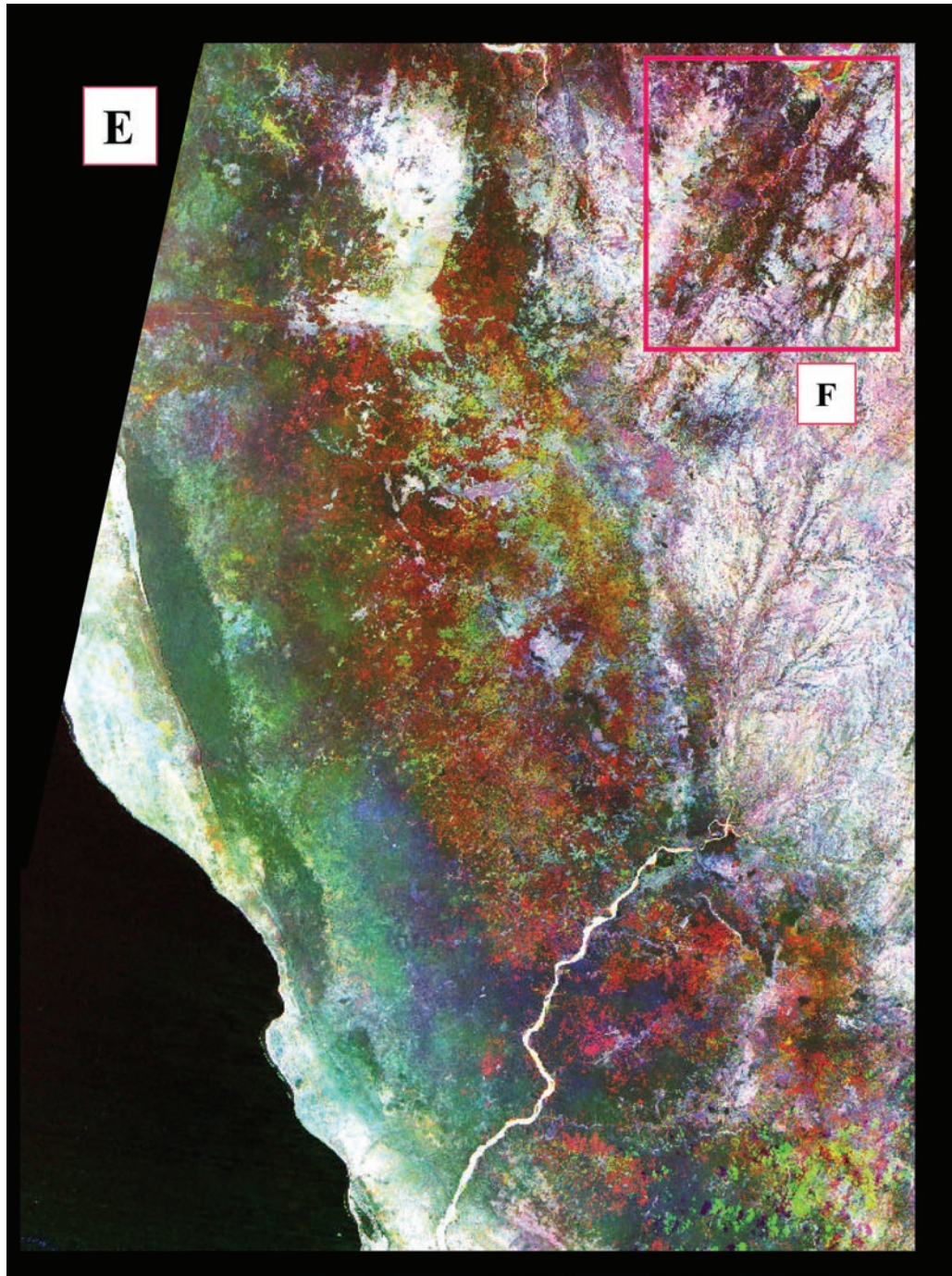


Figure 13. A multi-temporal color composite for area E, with area F also shown (see Fig. 4). This area, which covers much of the Mahafaly Plateau, is approximately 90 km wide. This multi-temporal color composite shows that much of the Mahafaly Plateau has undergone extensive clearing since 1973. Cutting between 1973 and 1985 is shown as yellow, while areas cleared between 1985 and 2000 are red. Clearing for subsistence agriculture has generally advanced from east to west. Cutting has progressed from the high-biomass, eastern forests of the Mahafaly Plateau toward the more western dry forests having progressively lower biomass. While the dark region close to the coast in this figure may appear at first to be intact, higher-biomass forest, field observations reveal it to be very low biomass open canopy shrubland, in which dark gray limestone rocks are abundantly exposed between small trees and shrubs.

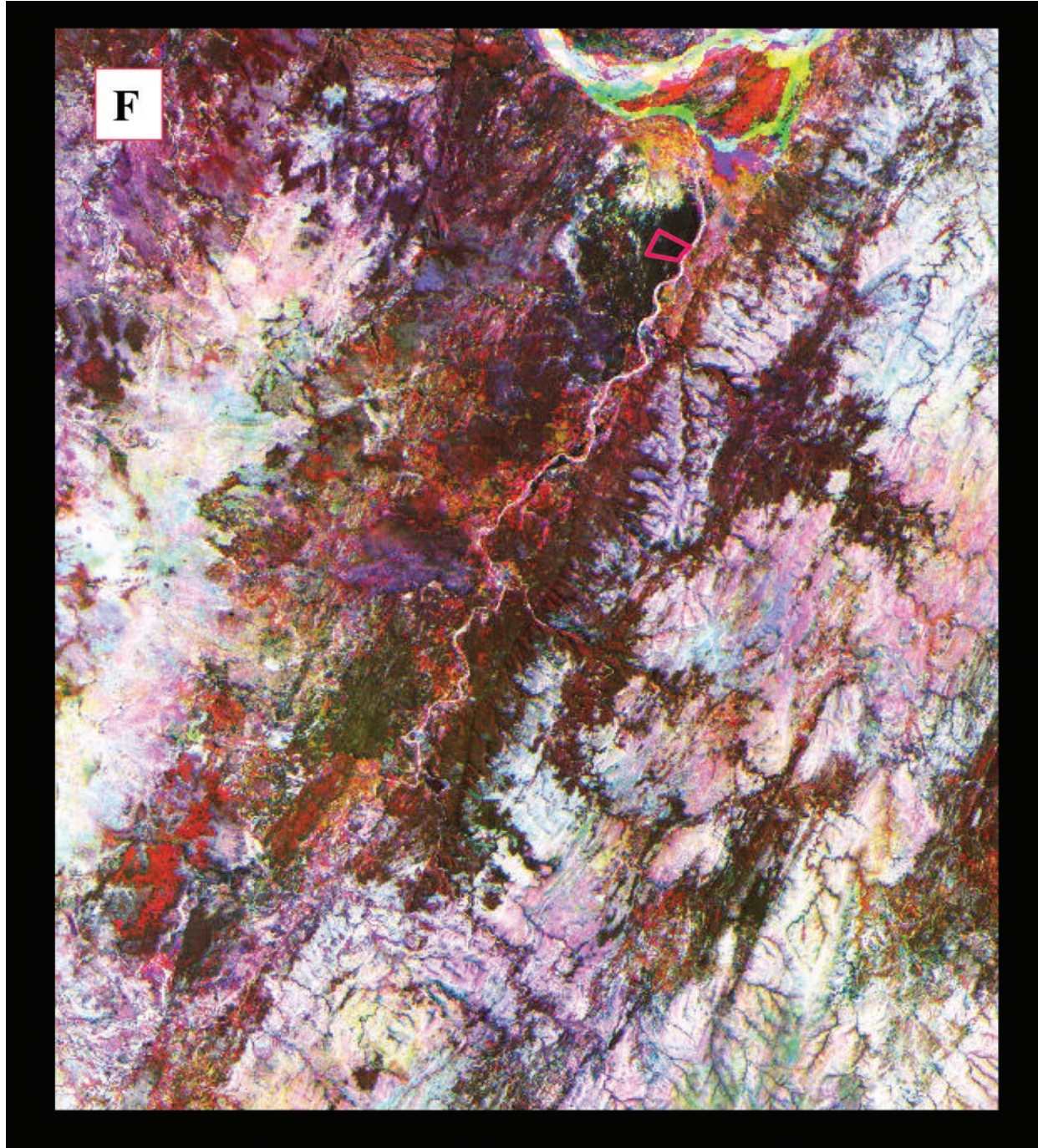


Figure 14. A multi-temporal color composite for area F (see Fig. 4). This area along the Sakamena River east of Betioky is approximately 15 km wide. Forest cut between 1985 and 2000, which have not re-grown are shown as red. Parcel 1 of the Beza-Mahafaly Special Reserve is outlined in pink. This reserve sits in one of the few remaining large stands of gallery forest.

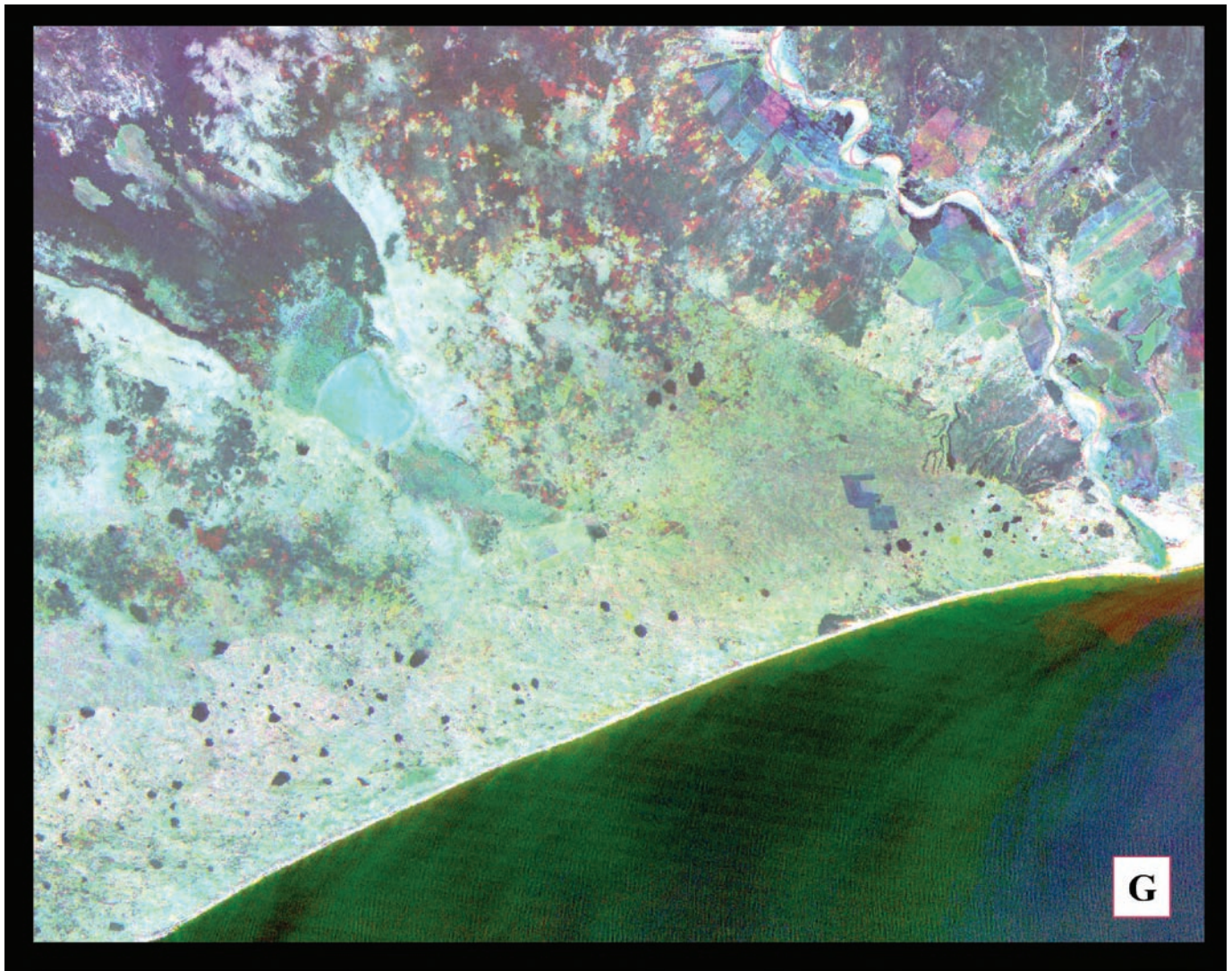


Figure 15. A multi-temporal color composite for area G (see Fig. 4). This area is approximately 60 km wide. Small dark circular patches in the southern portion of this figure are “islands” of forest vegetation which do not appear to be associated with lithologic boundaries. This multi-temporal color composite reveals that many of these stands have not experienced significant change since 1973. According to maps based on aerial photographs taken around 1950, the boundaries of these remnant patches have also remained virtually unchanged over the past 50 years.



Figure 16. Photo shows one of the forest stands (of approximately 300 x 300m) shown in Figure 15. These stands are forest remnants now surrounded by agricultural fields and fallows. They appear to be protected by local human institutions. We talked to local villagers and were told that we could not enter many of the forests because they protected tombs. We observed lemurs in this forest, which were generally absent from the surrounding agricultural terrain. Photo taken by Green in 2001.

acquired at three different dates (and satellites): 1973 (from Landsat 1), 1985 (from Landsat 5), and 1999/2000 (from Landsat 7). A total of 20 scenes were purchased and geometrically registered to 1:100,000 scale topographic maps. These topographic maps were generated from photo-interpretation of aerial photos acquired around 1950 and differentiate broad vegetation habitat types. Figure 2 shows where these Landsat scenes are located as well as their relation to the dry forests of the south (Humbert and Cours Darne 1965).

The geographical range of the ringtailed lemur corresponds with the distribution of dry forests in this region (Fig. 1a), and our ultimate goal is to compare and correlate it with the distribution and density of various habitat types over the past 50 years. With these data, we will be able to compare the rates of forest loss for different habitats with the density of ringtailed lemurs in each. This will result in a map and estimate of the current extent of various dry forest types in southwest Madagascar and the historical rates of deforestation for each habitat. It also will allow us to highlight “hotspots” of rapid current or exceptional habitat loss. Further, we will be able to determine the effects of habitat loss on the distribution and density of ringtailed lemur populations in Madagascar. Few studies have tied the history of deforestation to that of the population of a primate species over its entire geographical range.

Research on the ecology of *Lemur catta* at several sites (Jolly 1966; Budnitz and Dainis 1975; O'Connor 1987; Sussman 1991, 1992; Koyama *et al.* 2001; Jolly *et al.* 2002; Gould *et al.* 2003) has demonstrated that ringtailed lemur density is directly related to habitat quality. O'Connor (1987) found that a population of ringtailed lemurs, originally reduced due to hunting, was unable to recover to its former size in a degraded habitat. We know that riparian forests, the habitat that sustains the highest densities of ringtailed lemurs, are being cut at a rapid rate (Sussman *et al.* 1994). We also suspect that fragmented habitats may lead to a loss of gene flow and that small populations are highly vulnerable to the effects of stochastic events (Gould *et al.* 1999). The habitat and distribution of ringtailed lemurs in southern Madagascar has not been surveyed for over 30 years and estimates of population densities of this species are based on little more than guesswork. Documentation of the environmental status of the xerophytic forests of southern Madagascar and its most famous inhabitant, the ringtailed lemur, will be of great utility for the Government of Madagascar and conservation organizations to better protect this habitat and its inhabitants in the future.

In June-July, 2001, we traveled approximately 3000 km of roads in southern and southwestern Madagascar (see Fig. 3) guided by multi-spectral and multi-temporal composite map products based on satellite images from 1973, 1985 and 1999/2000. In this paper, we describe the results of this survey. Data were collected on the following: 1) habitat type in relation to features on the composite satellite image map products; 2) distribution, extent, and patterns of cutting in recently deforested areas; 3) reasons for recent extensive deforestation in particular areas; 4) the presence or absence,

and general density of ringtailed lemurs in particular habitat types; and 5) the reasons why some forest boundaries have been stable for the past 50 years even though surrounding forest has largely disappeared.

Methods

Multiple methodologies were required because each of the protocols collects information at particular scales of space and time. A combination of several datasets at various scales is necessary to map the distribution of the lemurs. For example, our Landsat data set has a spatial extent covering the entire southern and southwestern portion of Madagascar, a resampled spatial resolution of 30 m (for the TM and ETM+ images) and 60 m (for the MSS images), as well as a temporal duration of 27 years and temporal time-steps of 12 (between 1973 and 1985) and 15 (between 1985 and 2000) years. These scales provide useful information on landcover change over broad scales of space and time, yet are not at sufficient spatial resolution to identify and map *Lemur catta* directly. On the other hand, field observations, measurements, and interviews can acquire data at high enough spatial resolution to identify particular species but are much more limited in their spatial extent. These limits are imposed mostly because of the high cost of fieldwork per unit area.

In surveying the habitat of *Lemur catta*, therefore, we employed a strategy that leveraged broad scale data sets, such as satellite images, to determine advantageous sites for the collection of more costly fine-scale datasets, such as direct observations of the lemurs, interviews and vegetation plots. Thus, we prepared the topographic maps and Landsat-derived products first. This gave us a broad land cover change perspective in both space (parts of six contiguous Landsat footprint locations @ 185 x 170 km each) and time (50 years). Examination of these products before our field component allowed us to focus our field resources in a more productive and representative manner.

Map products

We used three map products to help direct our field studies: 1:100,000 scale published topographic maps, which were made using *c.* 1950 aerial photographs, plus two map products which we produced derived from Landsat satellite images.

1) The topographic maps show topographic relief, roads and trails, plus the names of towns and forests. They also contain photo-interpretations from *c.* 1950 aerial photographs, which depict basic land cover types recorded in the form of coded class polygons. While a detailed description of the species composition and physiognomic character of these cover type classes is largely lacking, many forest boundaries depicted on these maps appear to be distinct and accurately determined. Thus, these topographic maps give us very useful information on the distribution of vegetation cover 50 years ago.

2) Multi-temporal color composite map products of scale 1:100,000 were produced from Landsat images from 1973,

1985, and 1999/2000. The images were first geometrically registered to a digital (scanned) version of the 1:100,000 scale paper topographic maps using the Laborde coordinate system and the Tananarive 1925 datum. The multi-temporal image composites were constructed using the red wavelength bands from three different dates: band 2 from the 1973 MultiSpectral Scanner (MSS) scenes, band 3 from the 1985 Thematic Mapper (TM) scenes, and band 3 from the 1999/2000 Enhanced Thematic Mapper Plus (ETM+) scenes. For the multi-temporal Landsat-derived map products the 1973 image brightness was set to the color blue, the 1985 image brightness was set to green, and the 1999/2000 image brightness was set to red.

Constructed in this way the resulting color of the composite can be used to detect land cover change between the three dates. In these multi-temporal products land cover that does not change appreciably between the three dates appears black, white or a shade of gray, depending on its inherent brightness at red wavelengths (0.6 to 0.7 micrometers). At these wavelengths forested terrain is generally dark, while savannah, cleared land and riverbank sands are bright. Thus, stable forest (between 1973 and 1999/2000) is depicted as black or dark gray in the multi-temporal composites, and unchanging savannah is generally bright gray or white. On the other hand, areas which experience land cover change between the three dates exhibit different image brightness in the 1973, 1985 or 1999/2000 scenes and this imparts a color to the multi-temporal composite map product. Thus, areas that experience land cover change can be identified in these products by their color. The particular color gives the particular sequence of those changes. For example, if forest, stable between 1973 and 1985, is subsequently cleared between 1985 and 1999/2000 the resulting composite would be dark in the 1973 scene (blue), dark in the 1985 scene (green), but bright in the 1999/2000 scene (red), which results in a red color in the multi-temporal color composite. Forest that was cut between 1973 and 1985 and had not regenerated by 1999/2000 would be dark in the 1973 scene (blue) but bright in both the 1985 (green) and 1999/2000 scenes (red). Thus, those areas of forest cleared between the first and second date of our sequence are depicted as yellow (green plus red produces the color yellow).

These simple color rules are complicated by the fact that processes other than land cover change can also alter the reflectance of land cover and impart color to the multi-temporal composite. For example, if a savannah has burnt just prior to image acquisition it may appear darker for that date than for the other two even though no land cover change has taken place: burned and unburned savannahs are still savannahs. Thus, savannahs can often appear as a mosaic of different pastel colors in these multi-temporal composites. Similarly, agricultural land also can be quite variable in brightness from year to year depending on the particular history of harvesting and fallow, yet it is all still cropland. Variability in seasonal climate and year-to-year variability in rainfall can also influence reflectance and thus influence the color of the multi-temporal color composite. These non-land cover effects can

usually be distinguished as such by examining their spatial patterns. For example, a resultant color pattern associated with a fire scar on a savannah will most probably be distributed like that of a fire, i.e., controlled by the prevailing wind and other factors that affect fire propagation, and can thus be distinguished from forest cutting which typically has a different pattern.

3) We also used 1:100,000 scale map products produced from three different wavelengths (bands) from just the most recently acquired Landsat images (1999/2000). These multi-spectral color composites are generated from three separate spectral bands from one image: band 4 brightness of the TM scene (near infrared wavelengths) was set to the color red, band 5 (mid infrared) was set to green, and band 7 (mid infrared) was set to blue. Brightness variations recorded by the Landsat instruments between these three different wavelengths can be used to distinguish different land cover types. The infrared wavelengths are used because they typically contain more spectral variability than visible wavelengths (useful in distinguishing cover types) and are less affected by the atmosphere (which preferentially decreases the image contrast at shorter wavelengths). Thus, these "All-Infrared" multi-spectral image products provide a near current depiction of the distribution of various dry forest habitats throughout southern Madagascar. They are useful in choosing field sites to examine in person as well as providing information (in conjunction with field ground truth data) on the amount and distribution of different habitat types currently existing.

Ringtailed lemur surveys

After the satellite-derived map products were produced and examined, a survey procedure was developed to maximize and standardize the information to be gathered within the survey area. Because we were covering a large geographic area in a relatively short period of time, broad survey methods and interviews were used (NRC 1981; Sussman and Phillips-Conroy 1995). Broad survey methods have been used in a number of studies and are described in detail in NRC (1981). They "provide a useful technique for obtaining information on the presence and relative numbers of a species population in particular areas. Their advantages are the relatively short time involved in collecting comparative data at several sites and the relatively low cost" (Muckenhirn *et al.* 1975, p.34). Areas both at the extremes and within the middle of the geographic range of *Lemur catta* were surveyed (see Fig. 3). Specifically, methods used in our survey were as follows.

1) Surveys were carried out by Sussman, Green, Porton and Andrianasolondraibe. Our driver was Felix Ramiamanana, who also assisted in interviews. Satellite-derived products helped to identify areas of potential interest for on-the-ground surveys, and assisted in identifying types of habitat and areas of habitat disturbance (see section on ground truth methods).

2) Throughout the road survey, interviews were conducted with local inhabitants in each area. The Malagasy personnel conducted the interviews. Interviewees were asked to identify local lemurs from photographs and specify exact

localities in which ringtailed lemurs could be found in their area. Local inhabitants were also asked to give information on the general density of the lemur population. Comparing the results of these interviews from village to village allowed an accurate overview of the distribution of ringtailed lemurs for each region. A hand-held Global Positioning System (GPS) unit was used to determine the exact positions of specific forest localities or villages.

3) In many regions we conducted foot surveys of forests identified on the satellite images or noted by local inhabitants. We recorded the location, date, starting time, weather, and participating personnel. Lemur species identified were noted and a general estimate of the population density of ringtailed lemurs was made using the broad survey methods mentioned above. During the surveys we were accompanied by local inhabitants who were familiar with the animals and terrain.

4) The composite satellite maps enabled us to identify recent hotspots of deforestation, and the local inhabitants were asked questions concerning the context of recent habitat modification.

Ground truth methods

To maximize the amount of ground truth information acquired per unit time we used a methodology based on point-quarter vegetation quadrats. We sampled selected vegetation canopies to characterize the relationship between Landsat image reflectance and vegetation structure. At each corner point of a 30 x 30 m quadrat (a comparable size to the TM and ETM+ resampled image pixel) the nearest woody-stemmed plants were measured in each of four quarters (NE, SE, SW, NW). The effective sampling size of the quadrat depended, therefore, on the structural scale or stature of the forest (areas with larger trees typically use longer distances). Four woody plants were measured at each corner point for each of several stem diameter classes (16 plants per diameter class). This quadrat method was designed to gather comparable vegetation data (in accord with the Landsat sensor characteristics) across the widely varying (in structure and density) habitats of southern Madagascar. We collected structural and cover information, as well as taxonomic data. Numerous structural measures were taken from each woody plant sampled, such as height, dbh, distance to the corner point (measured with a sonic ranging instrument), canopy thickness, crown diameter, and the position of the plant relative to the general forest canopy.

Vegetation quadrats provided the following: 1) information to establish the relationship between Landsat-derived reflectance measures and specific physiognomic characteristics of the forest directly measurable in the field; 2) taxonomic, density and distribution data on plant species within the quadrat, all locatable to within 30 m using GPS technologies; 3) sufficient ecologically significant physiognomic and biophysical parameters to allow a broad ecological and functional characterization of the forest; and 4) a framework for the lemur field surveys. The diverse canopy structures and leaf morphologies present in the xerophytic forest habitats of southwestern Madagascar provide sufficient spectral dif-

ferences (detectable in Landsat images and with field instruments) to enable us to map their extents and evaluate their potential as lemur habitat. We incorporated diverse technologies for our vegetation fieldwork such as field spectrometers, 35 mm hemispherical photography (to estimate canopy cover and Leaf Area Index: LAI), as well as more traditional vegetation biometry. When integrated these datasets provide the necessary ground truth data to build a robust yet extensive monitoring system of *Lemur catta* habitat.

General logistics

The region was divided into a number of focal areas, and a base was set up in each. Our bases were Manja, Toliara, Betsioky, Ampanihy, Faux Cap, Taolanaro (Fort Dauphin), Berenty and Ihosy. From each of these bases we made road trips (Fig. 3), guided by topographic maps and image products to determine the particular areas to survey. It was impossible to cover all areas due to time restrictions and inaccessibility. Thus, representative areas were chosen based on satellite-derived spectral and temporal change characteristics as well as location and distance to road. Areas identified on the image products as potential ringtailed lemur habitat which were distant from the national highways were visited whenever possible. Using the satellite images in this way often allowed us to identify lemur habitats that would not have been found otherwise. Furthermore, because of the land cover and change features observable on the composite satellite maps, specific questions concerning particular and unique aspects of the local region could be addressed in each area.

The area covered in our survey was divided into a number of regions, both for logistic reasons and because each presented some general conformity within and differences between one another. Our findings are presented for each. They were as follows: north of the Mangoky River; between the Mangoky River and Toliara; east of Toliara along Route Nationale #7; between Route Nationale #7 and the Onilahy River; between the Onilahy River and Ampanihy; between Ampanihy and Faux Cap; between Faux Cap and the Mandrare River; between the Mandrare River and Taolanaro; and along Route Nationale #7 between Isalo and Ambalavao. Figure 4 shows a Landsat TM mosaic of multi-spectral composite images acquired in 1999/2000, which contains illustrative areas of contrasting land cover change we identified in the Landsat products and visited in the field (labeled A through G).

Results

North of the Mangoky River

This region is bordered by the Morondava River to the north and by the Mangoky River to the south. These rivers are usually impassable during the rainy season and there are few roads approaching from the east, making the region generally inaccessible for many months each year. There are no protected areas within the region. It is occupied mainly by the Sakalava people and characterized by scattered subsistence farming. Although large plantations

(especially rice) existed there before the late 1960s, we observed no major commercial agriculture in this region. There are, however, many forest clearings for local swidden farming (manioc, corn, beans), and some large areas of former wetlands used for irrigated rice production, apparently for local consumption only. Some large manioc fields (surrounded by mango trees) are found near villages in former savannah. Livestock, mainly cattle (zebu) and pigs, are also economically important. The natural vegetation in flatter areas is savannah (dense savannah woodland to low-density palm savannah in the west). Rocky uplands of sandstone and limestone are covered by closed-canopy deciduous forest of *Commiphora* species and others of similar physiognomy. Denser forest can support scattered baobabs (*Adansonia*). Non-inundated land near streams supports gallery forests of *Tamarindus indica* and other species. While the savannahs are largely intact, forests near villages are often cut and now may support secondary bushlands of *Acacia* species, euphorbs and others.

Gallery forest remains along the Mangoky River and its tributaries, but there has also been clearing of the relatively few remaining patches of this forest type over the past 20 years for subsistence farming. However, we believe that Antserananomby, one of the forests most densely populated by lemurs in Madagascar (Sussman 1972), is still largely intact. This forest contains five nocturnal genera of lemurs (*Mirza*, *Phaner*, *Lepilemur*, *Cheirogaleus*, and at least one species of *Microcebus*) and three diurnal species (*Lemur catta*, *Eulemur fulvus*, and *Propithecus verreauxi*) and has the highest population density recorded for some of these species. Tongobato, a similar forest nearby, on the other hand, appears to have been cleared for swidden agriculture (*tavy*) within the last 15 years.

Figure 5 shows Landsat image products for an area north of the Mangoky River, which includes the Antserananomby Forest (see Fig. 4 Area A for its geographic location). This figure includes three multi-spectral composites from 1973 (MSS bands 1, 2, and 4 as blue, red, and green respectively), 1985 (TM bands 3, 5, and 7 as blue, green and red), and 2000 (ETM+ bands 3, 5, and 7 as blue, green and red) Landsat images, as well as a multi-temporal composite made from the red wavelength bands (MSS band 2, TM band 3, and ETM+ band 3) from the 1973, 1985 and 2000 images which control the blue, green, and red colors respectively in the multi-temporal composite. In the multi-spectral composites water in the Mangoky and Ianadranto Rivers is blue, river sands are white, dense forest is green and savannah is light green or tan. Clouds and their shadows are white and black respectively in these composites. The local names of rivers surrounding the Antserananomby Forest are included in Figure 5 (on the 2000 composite). In the 2000 multi-spectral composite, dense closed-canopy gallery forest of the Antserananomby Forest and those surrounding the Beangily River are dark green, and can be distinguished from the closed-canopy upland forests on the north bank of the Mangoky River southeast of Vondrove (depicted as a green color).

The multi-temporal composite in Figure 5 shows (as red) several areas of dense forest that have been cleared between 1985 and 2000. We observed several of these recently cleared areas: those on the north and south banks of the Mangoky to the southeast of Vondrove. We also were told of forest clearing north of Vondrove and along the Ianadranto River south of the Antserananomby Forest. Stable gallery forest of the Antserananomby Forest appears as black in the multi-temporal composite in Figure 5. These black areas extend from the Antserananomby Forest north along the Beangily River and suggest that this gallery forest may be significantly larger than previously documented (Sussman 1972).

An important factor is that the human population has decreased in some areas since the 1970s, which are now much more isolated than in the past. For example, the village of Vondrove, once a large and economically important town bordering the Mangoky River, is now extremely difficult to reach due to bad roads. In the 1960's-early 1970's it took approximately an hour to travel the 50 km from Manja south to Vondrove. In the present survey, it took over 3.5 hours. The road, and much of the area, is now covered with dense grass and secondary bush. There is still a good deal of natural vegetation in the area, predominantly savannah. Large cultivated fields containing crops (rice, manioc, and beans) for local consumption are also present.

This region marks the northern limit of the geographical range of ringtailed lemur (Sussman 1977; Mittermeier *et al.* 1994). However, the precise limits were not verified during this survey. From our interviews and surveys, it appears that *Lemur catta* is limited to the western portion, north of the Mangoky River, as reported by Sussman (1977). The eastern limit along the Mangoky River is unknown, and its range along the upper reaches of the Mangoky may be a very important factor in explaining the species distribution into Isalo and the southern limits of the Central Plateau.

We surveyed the region between Bevoay and Manja, and then south to Vondrove, east to Beravy, and northwest to Antevamena, covering approximately 250 km of roads.

Between the Mangoky River and Toliara

The people in this region classify themselves as Vezo, Mikea and Masikoro. The Veso inhabit coastal areas and are mainly fisherman, though they practice some cultivation and livestock rearing along forest edges. The Masikoro are farmers and cattle herders and live in inland areas south of the Mangoky River and east of the Mikea Forest. The Mikea are mainly gatherers and hunters, but they also participate extensively in agriculture and rear livestock. There are also a significant number of Antandroy and Mahafaly immigrants from the south who live in the region (Seddon *et al.* 2000).

Traveling along Route Nationale #9, between Toliara and Bevoay, one sees the results of extensive deforestation north of the Manombo River, both to the east and west. To the west, from the road to the coast, is the Mikea Forest that originally formed a coastal strip 200 km long and 30-60 km wide between the Mangoky and the Fiherenana Rivers.

The forest has a rich flora and fauna with numerous locally endemic taxa that do not extend to the drier forests to the south. It comprises a dense, highly xerophytic flora attaining a maximum height of 6 m towards the coast and 8-12 m further inland. The original forest consists of Didiereaceae (*Didierea madagascariensis* in particular), woody euphorbs, baobabs (mainly *Adansonia fady*), and several species of *Commiphora* among other species. Within 2 km of the coast the vegetation becomes more sparse and scrub-like (Seddon *et al.* 2000).

Much of the higher biomass, closed-canopy forest of the Mikea Forest has been cut, leaving only a narrow strip of shorter and less dense vegetation remaining to the west. The land has been cleared within the last 15 years for swidden-based corn production (*hatsake*). Apparently, these upland forest soils (on limestone and sandstone) are quickly depleted of nutrients, because each year new areas are cleared and old fields are abandoned after, at most, four years of production. There is little to no regrowth of forest indicated in the satellite multi-temporal composites and most of these areas are now bare or covered with bushes. However, Tucker (pers. comm.), a human ecologist who is studying subsistence strategies in the Mikea Forest, has seen places with some regeneration where forest cleared for cultivation 30 years ago is now full of young hardwoods.

Recently, Antandroy migrants have tended to cultivate larger areas than did the Mikea in the past (10 ha plots per annum compared to 1-3 ha plots). This was still mainly for local consumption (Seddon *et al.* 2000). However, during our survey, we observed that large tracts are being cultivated by commercial agriculturalists from Toliara, and much of the corn is evidently exported to Europe, Africa, Reunion and the Seychelles for cattle feed (Seddon *et al.* 2000).

Recent cutting (mostly since 1985) has eliminated much of the higher biomass, more mesic, eastern portion of the Mikea Forest, home to the last hunter/gatherer people existing in Madagascar. A Landsat-derived multi-temporal color composite for Area B of Figure 4 is shown in Figure 6. Forest generally exhibits low reflectance at visible wavelengths because chlorophyll absorbs light in the visible. The multi-temporal composites are generated with the red bands from the 1973, 1985, and 2000 images (which drive the blue, green, and red colors of Figure 6 respectively). In Figure 6, black or dark gray represents forests that have remained largely unchanged. Areas of recently cut forest generally exhibit higher reflectances at visible wavelengths in Landsat images because less chlorophyll is present and more soil (which is bright) is exposed. While areas of little change are shades of black and white, areas in which the forest was cut are various colors in the multi-temporal color composite. If a forest is cut between 1985 and 2000 and does not re-grow significantly, the red wavelength bands of Landsat images exhibit dark reflectance, in both the 1973 and 1985 images, but bright reflectance in the 2000 scene. Since the 2000 image drives the red color, cleared area comes out bright red in the multi-temporal composite.

A large, red, vertically-oriented swath in Figure 6 depicts those forests cleared between 1985 and 2000. During our field observations, we observed clearings in this area using swidden agriculture techniques for commercial corn production as described above (Fig. 7a). The corn is bought from local farmers, bagged and loaded onto large trucks. The corn is then hauled to the nearby port of Toliara where it is shipped out. Once cleared of all but the baobabs and farmed for up to 4 years, the land is apparently abandoned and used only as low value rangeland (Fig. 7b). The western portion of the Mikea Forest is less suitable for corn cultivation (Tucker pers. comm.). However, as the eastern portion is cleared it opens corridors for charcoal production destined for Toliara and the few remaining hardwoods left in the western Mikea are thus more vulnerable.

The species of lemur reported to exist in this forest are *Lemur catta*, *Propithecus verreauxi*, *Lepilemur mustelinus*, *Cheirogaleus major*, and *Microcebus murinus*. All except possibly the mouse lemur (*Microcebus*) are found in very low densities in the forest (Yount, Tucker pers. comm.). Besides losing much of their forest habitat, these species are all hunted by the Mikea. However, because of their low density, in 19 months of study Tucker only saw six *Microcebus*, and one each of *Lepilemur* and *Cheirogaleus* captured and eaten by these hunters. He reports that *Propithecus* and *Lemur catta* are not preferred items in the Mikea diet and are considered tough meat (*hena mahery*). However, Yount (pers. comm.), who conducted an ethnographic study of the Mikea, observed recently captured young ringtailed lemurs being kept as pets. Unlike the lemurs, tenrecs are a major part of the diet and are an important commodity in the rural markets here and throughout the south.

Nearer Route Nationale #9 and east from the road, savannah woodland is being converted to commercial cotton fields (and manioc), and former wetlands and savannah have been converted to irrigated rice cultivation. Some tractors are used in cotton production, and large trucks bring the cotton to Toliara. Further east, the closed-canopy forest on the western slopes of the Mikoboka plateau remains largely intact except near the Manombo River, where the forest has been similarly cleared for corn (Fig. 6). The clearing here is also extensive and has occurred within the last 15 years. Further northeast, along the Sakamavaka River, a southern tributary of the Mangoky in a more isolated area, it appears from the satellite images that the vegetation may be similar to that found just north of the Mangoky River, including some gallery forest near the river. Much of this forest has been cleared since 1985. South of the Manombo the vegetation, which includes dense stands of Didiereaceae, also becomes more dense and widespread until just north of Toliara and east of Route Nationale #9. This spiny forest is largely intact except for the removal of scattered hardwood trees that are charcoaled for the Toliara market and clearing for homes and small plots close to the road. The charcoal is produced by the Masikoro people. Recently, in some villages, 40% of the people were employed in the production of charcoal and only 30% was

being consumed locally, the remainder being transported by road to Toliara (Seddon *et al.* 2000). Some mangrove forests on the coast have been cut as well.

Ringtailed lemurs are present throughout this region, except in savannah and cultivated areas, though they do not appear to be successful in spreading into deforested areas recolonized with secondary bush growth. However, even in the habitats where they are found, they occur in very low density. For example, they were very rarely observed in the Mikea Forest even before the recent massive cutting occurred. It is interesting to note also that *Eulemur fulvus rufus* is not reported to occur in this forest although it is found further south in the Zombitsy Forest, the southern limit of its distribution. Higher densities of ringtailed lemurs are only likely to occur in the very few remaining gallery forest patches along the tributaries of the Mangoky River mentioned above. However, most of this area is very difficult to access and remains to be surveyed. With all of the habitat transformation along Nationale #9 in this region, it appears that the remaining ringtailed lemur population in the Mikea Forest now may be more isolated than in the past from populations to the east.

In this region, we surveyed along Route Nationale #9 between Toliara and the ferry at Bavoay, making detours along dirt roads both to the east and west of the main road. We covered approximately 250 km.

Toliara to Sakaraha along Route Nationale #7, and south to the Onilahy River along Route Nationale #10

This region was once covered with dense, closed-canopy deciduous forest on the limestone uplands, some to the east reaching more than 10 m tall. Most of this forest is now cut. The biomass of this vegetation decreases (due to decreasing precipitation) as one moves east and descends to lower elevations near the coast. Near the coast near Toliara the forest has been replaced by a natural open shrubland less than 2 m high. Hardwoods have been cut intensively since the early 1970s to supply charcoal to the coastal city of Toliara (used primarily for cooking fuel). This cutting began immediately adjacent to Route Nationale #7, the main road between Toliara and Antananarivo. However, by 2000, deforestation had spread over a very wide swathe and most of the higher biomass forest between the Fiherenana and Onilahy Rivers is already gone. Some small areas are protected by their isolation. North of the Fiherenana River there is less cutting because the area cannot be reached by truck.

Deforestation associated with this commercial charcoaling is shown in Figure 8 (Fig. 4 Area C). The red areas in this multi-temporal color composite show those areas of forest cleared between 1985 and 2000. Figure 8 reveals that recent cutting is, in general, bounded by the Fiherenana and the Onilahy rivers, to the north and south respectively, and by natural savannah to the east. Dark grey or black areas on the image are predominantly forested and have experienced little change. Toliara, the largest city in the southwest of Madagascar, is located on the coast just to the northwest of the region shown in Figure 8.

The yellow/green swathe in Figure 8 (oriented southwest to northeast) running from the middle of the left side of the figure to the savannah edge, parallels Route Nationale #7. These areas were cleared between 1973 and 1985 for commercial charcoal production. Charcoal is produced by local inhabitants, right where trees are felled. It is then transported by ox-cart to a location along the highway accessible by large truck. Along the road this bagged charcoal is then sold to distributors (Fig. 9a). The charcoal is then transported to Toliara where it is sold in the public markets. Currently most residents of Toliara cook all their food (mostly rice) with charcoal. In 2000, one large sack of charcoal (100 kg), containing on average about 30 boles from mature trees, would be valued at around \$1.00 (Seddon *et al.* 2000).

When this forest is cleared nearly all the woody vegetation greater than 3-4 cm dbh is cut, charcoaled locally, and removed. Subsistence swidden agriculture, typically of corn, is practiced on the deforested lands for 1-3 years before abandonment. During these farming periods, the remaining vegetation is burned to release its nutrients into the soil. These deforested areas are often colonized by tall grasses, which subsequently burn. The practice of cutting forest to produce charcoal for Toliara has resulted in a large and expanding zone devoid of many woody plants to the northeast of the city. Much formerly forested land present along Route Nationale #7 until the late 1960s is now characterized by abundant bare limestone rock exposures (Fig. 9b). Observations of land cleared for charcoal prior to 1987 reveal little re-growth of woody plants in the subsequent 14 years.

In the early 1970s, gallery forest could be found on the borders of the Fiherenana River, but less exists there today. East along Route Nationale #7, around 130 km from Toliara, is Sakaraha and the Zombitsy and Vohibasia Forests. These forests represent the largest intact seasonal closed canopy forest in the region and contain a diverse mix of species, with some trees over 15 m. Unlike forest to the west, it grows on sandy soils in more mesic areas of the Fiherenana's upper watershed.

Figure 10 (Area D in Fig. 4) shows that the Zombitsy forest has remained largely intact from 1973 to 2000. However, the red area in the multi-temporal composite (in the southwestern portion of the forest) was cut in the early 1990s during a period of severe drought. At this time, approximately 1000 people immigrated into the eastern Sakaraha area from around Ejeda and Ampanihy (WWF personnel: Raymond Rasary pers. comm.). These migrants settled along the national highway that runs through the forest and an area of around 25 km² was cut for subsistence farming. Since 1997 much of the remaining forest has been designated as a national reserve, and little cutting has been observed recently. Fig. 11a and b were taken in 1987 and 2001, respectively, and document these recent land cover changes (only the baobab remains). The only other significant cutting here is a much smaller area in the northeast portion of Figure 10. These smaller clearings also occurred between 1985 and 2000. We were told they were the result of timber being cut by local people and destined for the Toliara market.

Figure 10 also reveals that the annual burning of the savannah may not be a significant factor in forest loss in southern Madagascar. In general, forest savannah boundaries in this multi-temporal composite are not ringed with color, which would reveal progressive forest loss due to burning. An examination of forest boundaries on topographic maps derived from aerial photos taken in 1950 show that the vast majority of forest/savannah boundaries of this area have been stable for the last 50 years. We have also acquired ground photos, which document the general stability of the forest/savannah edge between 1987 and 2001 (14 years). The conclusion one draws from these observations is that burning of the savannah is not a significant threat to the forests of this area. This conclusion is similar to that made by Philippe Morat (1973) based on his analysis of aerial photos and field observations of the area from the 1950s and 1960s.

There is some disagreement as to whether the savannah of this region (Fig. 12a) is natural or the result of earlier deforestation events. However, since the borders of this habitat type often correspond directly with lithologic contacts in the underlying geology and corresponding changes in soil patterns, and given that these boundaries have generally been stable for the last 50 years, we believe that most savannah is natural.

Much of the northeast portion of Figure 8 exhibits a bright tone indicative of the presence of a predominantly treeless savannah between 1973 and 2000. Aerial photography from c. 1950 reveals that much of the area was also treeless then. Figure 8 shows that many forest boundaries were quite distinct and conform to current boundaries. Field observations and the examination of geological maps show that many of the forest boundaries in 1950 correspond to lithologic contacts. Geological maps of the region show that Eocene and Paleocene limestone and dolomite underlie nearly all of those areas of Figure 8 still forested in 1950. The contrasting geological formations that underlie forest and savannah probably account for the different vegetation each unit supports. Many of the savannahs are found on red lateritic clay-rich soils derived from an upper Cretaceous sandstone unit (Fig. 12a). What may at first appear to be remnant forest patches isolated by the cutting of surrounding forests (Fig. 12b) are actually forest stands underlain by isolated outcrops of calcareous rock (Fig. 12c and d). A time series of Landsat images can help distinguish forest boundaries produced by recent cutting for charcoal from those forest boundaries controlled by contrasting soils derived from differing geological units. Without the temporal perspective of a Landsat image sequence, however, contemporary deforestation can obscure these natural forest/savannah boundaries.

Ringtailed lemurs are now extremely sparse in the remaining remnants of limestone forest in this region. They do occupy the Zombitsy Forest but, for the most part, this forest is drier than western gallery forests and does not support tamarind trees, even along watercourses. Where we surveyed, *Lemur catta* densities were quite low and it has been hunted in this forest in the past. As mentioned above, the Zombitsy

Forest represents the southern limit of *Eulemur fulvus rufus*. Other species found in this region are *Propithecus verreauxi*, *Lepilemur mustelinus*, *Microcebus murinus*, *Cheirogaleus medius* and *Mirza coquereli*.

The natural habitat to the south of Route Nationale #9, between the Fiherenana and Onilahy Rivers also includes dense, deciduous closed-canopy forest on limestone and low-density savannah woodland on clay-rich red lateritic soils. Almost all of the higher biomass forest of the region west of Sakaraha has been cut for commercial charcoal production. Probably more than 75% of the original woody plant biomass between the Fiherenana and Onilahy Rivers west of Sakaraha is now gone. Low biomass, open-canopy natural shrublands remain nearer the coast, extending to around 15 km inland to the east. There are currently few gallery forests along the Onilahy River and there may never have been many, possibly because this large river frequently meanders, leaving only large sandy flood plains along its banks. We believe that lemurs are now generally absent from the area (between Route #7 and the Onilahy River along Route Nationale #10). We covered approximately 250 km in this region.

From Betsioky to Ampanihy and the Menarandra River

This region contains a great variety of natural habitat types, including savannah, dense dry forest and shrubland. It is dominated by the extensive limestone massif of the Mahafaly Plateau, which was formerly covered by dense deciduous closed-canopy dry forest. As one approaches the coast these dry forests exhibit lower biomass, are shorter in height and take on the structure of an open canopy shrubland dominated by Didiereaceae species (mainly *Alluaudia ascendens* and *A. procurea*). The region also contains numerous edge habitats and secondary bushlands of *Acacia* and euphorbs. Along the banks of the Sakamena, Linta and Menarandra Rivers there is more *Tamarindus indica* dominated gallery forest remaining in the region than anywhere else in the southwest or south.

While the western portion of this region is underlain by Paleozoic sedimentary rocks, the eastern portion is mainly underlain by PreCambrian metamorphic rocks. The metamorphic-derived soils are typically poor in nutrients and support grass or low biomass bush vegetation. Bordering Lake Tsimanampetsotsa there is marsh vegetation, but immediately to the east of the lake, along the talus slope of the bordering escarpment, there is a 20-meter-wide strip, approximately 50 km long, containing small patches of *Tamarindus* forest. Along the flat lying coastal plain there is an open shrubland on stabilized sand dunes.

The human population of the region is made up mainly of Mahafaly, but also Antandroy and Tanala (Ratsirarson *et al.* 2001). Throughout, there is scattered, subsistence farming of swidden fields of various sizes. Many of the highest biomass hardwood forests, including the gallery forests, have already been cleared over the past 50 years. In 1985, there were still large patches of the various types of natural vegetation throughout the area. Unfortunately, within the past 15 years, large tracts of the remaining natural vegetation

have been cut down, again mainly for swidden-based, subsistence agriculture.

Landsat images reveal that, unlike the Zombitsy, many of the dry forests on the much larger Mahafaly Plateau have undergone extensive clearing since 1973. This cutting is shown in Figure 13 (Area E of Fig. 4) as yellow areas - cleared between 1973 and 1985 - and as red areas - cleared between 1985 and 2000. This clearing has greatly accelerated over the last 50 years and has generally advanced from east to west. It appears to not be directly associated with major roads, unlike the clearing associated with charcoal production to the north. Clearing for subsistence agriculture appears to be responsible for this widespread forest loss in these more populated areas of southern Madagascar. It has progressed from the high-biomass, eastern forests of the Mahafaly Plateau toward the more western dry forests of progressively lower biomass as one drops down in elevation toward the coast (down the moisture gradient). Clearing for swidden agriculture appears to stop in a certain transition zone, probably due to forests that are not worth farming because of poor soils and a lack of woody biomass. While the dark region close to the coast in Figure 13 may appear to be intact, higher-biomass forest, field observations reveal it to be very low biomass open canopy shrubland, in which dark gray limestone rocks are abundantly exposed between small trees and shrubs. These dark rocks produce a similar reflectance to higher-biomass forest.

Some large areas seem to be in constant production. For example, there are large agricultural fields along Route Nationale #10 near Betsioky, as well as in the southern portions of the Sakamena Valley. A large new road has recently been opened between Betsioky and Route Nationale #13 to the east, which is surrounded by very large, recently planted, manioc fields. Along the road to Lake Tsimanampetsotsa, a forest of 10 km², with numerous *Adansonia*, has been almost completely cleared within the last 15 years. While manioc is now being grown on a portion of the remaining fallow fields, most are bare or covered with secondary grass.

Between 1988 and 1993, the populations of villages surrounding the Beza Mahafaly Reserve shown as a pink outline in Figure 14 (Area F in Figs. 4 and 13) grew by 52% (Sussman *et al.* 1994). In the late 1980's, it was estimated that the human population in the general region of Betsioky was growing at a rate of between 3 and 4% per year (Ratsirarson *et al.* 2001). We believe that much of the recent expansion of agriculture is driven by this population growth and by the need for protection against the periodic droughts that devastate the area. Agriculture (mainly corn, manioc, and sweet potatoes) and raising livestock (cattle, sheep, and goats), mainly for local consumption, constitute the principal economic activities of the local people (Ratsirarson *et al.* 2001). Most of the exploitation of the remaining forest products is sustainable. However, with the growing population, some hardwoods used for construction, such as *Cedrelopsis grevei* (*katrafay*), may be becoming overexploited (Sussman *et al.* 1994). From our preliminary examination of satellite images, we believe that around 50% of the extent of natural forest of this region has

already been cut, more in terms of biomass, since the more mesic, higher-biomass forests are often cleared first.

Even with all of the past and current forest clearance, *Lemur catta* is found in a number of areas and different vegetation types throughout this region. In the drier habitats, ringtailed lemurs are widely present but scarce. They are not found in the savannahs or Dideariaceae shrublands, except along the edges. As elsewhere, the highest densities are in the remaining patches of gallery forest. We found small but good patches of gallery forest in the following locations. 1) Along the banks of the Sakamena River, a tributary of the Onilahy River. The Beza-Mahafaly Special Reserve is located in this forest (Fig. 14). However, the reserve and the forest surrounding it (around 500 ha) is the largest remaining patch there. The black areas of Figure 14 show the remaining gallery forest along the Sakamena River. 2) The long thin strip at the base of the western escarpment of the Mahafaly Plateau bordering Lake Tsimanampetsotsa. These forests contain small areas of *Tamarindus* forest. 3) Finally, some remaining small patches of gallery forest bordering the Linta and Menarandra Rivers, though most of them have been cut (as have those on the eastern flood plain of the Sakamena River), apparently because this habitat provides richer soils for agriculture. We found the highest densities of *Lemur catta* in these forests. Besides a high density of ringtailed lemurs in one of the small gallery forests bordering the Menarandra River, we observed the largest colony and roosting site of fruit bats, *Pteropus rufus*, that any of us had ever seen. Other lemur species in this region are *Propithecus verreauxi*, *Lepilemur mustelinus*, *Microcebus murinus*, and *Microcebus griseorufus*.

It is interesting to note that most of the forests containing higher densities of *Lemur catta* of this sort that we visited in this region were protected because they are either part of a government reserve (for example, Lake Tsimanampetsotsa and Beza Mahafaly) or are considered sacred forests by the local Malagasy. In fact, the local name for the Beza Mahafaly forest is *Analafaly* or "sacred forest". We return to this point later. We covered approximately 520 km in this region.

Between the Menarandra River, Tsihombe and Faux Cap

Central southern Madagascar, between the Menarandra River to the west and the Mandrare and Mananara Rivers to the east is home to the Antandroy people and is often referred to as the Androy region or Ifotaka. In general, the Antandroy rely on livestock (cattle, goats, and sheep) and four major crops - maize, cassava, sweet potato, and beans. There are two National Forest Reserves (Andohahela National Park and Cap Sainte Marie Special Reserve) and two private reserves (Berenty and Kaleta). Human population growth in the whole Ifotaka region has been estimated at 3.3% annually (Ferguson 2002).

Unlike the previous region to the west, much of the forest was cut prior to 1950, probably for subsistence farming and grazing. The vegetation here is mostly underlain by vast sand sheets. These sands were blown inland in past ages from coastal beaches and sand dunes by strong winds from the SE (still the

dominant wind direction). Unlike the Mahafaly Plateau these flat, sandy lands appear to support multiple crops, which only require brief fallow cycles. There are also some large patches of *Opuntia* and low-biomass secondary bush (*Acacia* and *Euphorbia*), and a species of introduced succulent vine, *Cissus quadrangularis*. Generally, to the north and east of Route Nationale #10 the vegetation is underlain by soils derived from metamorphic rocks. The climate becomes drier as one moves south and west, and the vegetation biomass decreases correspondingly. Several of the largest remnants of natural dry forest/shrubland on sandy soils remaining in this region are found north of Cap St. Marie. This dry forest/shrubland is composed of a diverse mix of deciduous hardwoods, mainly Didiereaceae species, and arboreal succulents of low height. The canopy cover and stem density are variable.

Little of the natural forest remaining throughout much of this region is currently being cut because most of the vegetation on the more fertile soils appears to have been cut long ago. However, in the few remaining forested areas, the need for fuel and construction wood - again mainly *katrafay* and also *fantiolotse* (*Allvaudia procera*) - is a major threat that, with the increasing human population, will probably increase in the future. Near the coast the continued advance of the sand dunes, reducing areas for agriculture, is also a threat to the growing human population (Ferguson 2002). Swidden agriculture here is practiced mainly on regenerating areas used in the past. Areas of sandy soil seem to support multiple rotations of crops, and the fields have been used for at least the last 50 years and probably much longer. The impact of cattle and goat grazing, its current spatial patterns, and factors controlling these patterns are likely to be important factors affecting deforestation in the Ifotaka region, as well as in the regions to the north. However, the precise impact of grazing in each area requires further investigation (Sussman *et al.* 1994; Ferguson 2002; Seddon 2000; Ratsirason *et al.* 2001). There is one relatively large river in this region, the Manambovo, which once supported gallery forest, but little appears to exist there today.

Lemur catta exists throughout the region, but is generally very widely scattered and of very low density. There is some indication that some groups here may be seasonally mobile. For example, the reserve naturalists at Cap St. Marie have observed groups migrating into the reserve to feed on seasonal fruits between October and December but none remain permanently in the reserve (Randrianananrana pers. comm.).

There may have been large numbers of ringtailed lemurs along the Manambovo River in the past, and one village bordering the river is called *Ranohira* (ringtailed lemur water), but no natural gallery forest remains. Of the diurnal lemurs, only scattered, very low-density populations of *L. catta* and *Propithecus verreauxi* exist here now. We covered approximately 415 km in this region.

Faux cap to the Mandrare River

This is a portion of the Ifotaka region and, as in the previous region, most of the natural vegetation on sandy

soils was cut before 1950. Again, the sandy soils support a rotation of crops over many years. There is some secondary growth, and to the west there is a large amount of introduced cactus (*Opuntia*). Large sisal plantations now dominate the western borders of the Mandrare River, which once supported some of the largest stretches of dense, closed-canopy gallery forest. However, a number of small patches of gallery forest still remain as private reserves, the best known of which is Berenty.

Examining Landsat image-derived products, we noticed a number of small, circular patches or “islands” of forest vegetation scattered throughout the southern portion. Unlike forest patches to the west they do not appear to be influenced by lithological boundaries. In contrast, many of these, now isolated, forest stands (of approximately 300 x 300m) appear to be protected by local human institutions. The dark patches in the southern portion of Figure 15 are forest remnants surrounded by agricultural fields and fallows (Fig. 16). This multi-temporal color composite reveals that they have not experienced any significant cutting since 1973.

According to maps based on aerial photographs taken around 1950, the boundaries of these remnant patches have remained virtually unchanged over the past 50 years. We visited six and discovered that, in each case, the local residents had maintained them as sacred areas. Interestingly, many appear to survive for spiritual rather than economic reasons, as in general they do not appear to provide harvestable products for the communities that protect them. We talked to local villagers and were told that we could not enter the forests because they protected tomb sites – they are often referred to as *fady* or taboo forests (Ferguson 2002). Lemurs that we observed and were reported in these protected forests were generally absent from the surrounding agricultural terrain.

These sacred, “island” forests are characterized by their low height (<6 m) and open canopies of deciduous and succulent trees and shrubs. Euphorbiaceae and Didiereaceae species are common. Generally, the forests are circular, three to four hundred meters in diameter (Clark *et al.* 1998). Engström (2002) found over 1400 of these forest fragments evenly distributed throughout the area but covering only 4% of the total area of analysis (which is approximately 71,000 hectares of eastern Antandroy along the southern coast, Figure 15). Prior to deforestation for agriculture, this was probably the most widespread natural habitat of the region. The spread of Christian vs. traditional beliefs is a threat to the future of these *fady* forests (Ferguson 2002).

Although some ringtailed lemurs might exist in secondary bushland and cactuslands, their densities are extremely low. The highest densities exist in the protected reserves along the Mandrare River, where the lemurs can exploit introduced fruit trees, have been provisioned in the past with food and water, and are currently provided with water and fed by tourists (Jolly *et al.* 2002). Population densities in forests where lemurs are provisioned are much higher than in other gallery forests. Ringtailed lemurs are also found in some, but not all of the “island” forests and, since we were told they

were not hunted in these forests, their distribution is probably related to the vicissitudes of history. We covered 170 km in this region.

The Mandrare River to Taolanaro

The climate becomes increasingly wetter as one moves to the east and up into the mountains near the east coast. This region supports a very different type of vegetation from the drier areas to the west. The forests take on many of the characteristics of the tall, closed-canopy, moist broadleaf evergreen forests typical of eastern Madagascar.

Three types of habitat support *Lemur catta* in this region. In the western, drier portion of the Andohahela Reserve, there are tall, dense, closed-canopy forests concentrated in a few valleys with perennial streams draining the surrounding mountains. They probably support medium-density populations of ringtailed lemurs. There are also some scattered, patchy but high-biomass forests along Route Nationale #10 toward Taolanaro and along the Ranopiso River south of this road. These forests also support local, medium-density populations of *L. catta*. Finally, the director of the Andohahela Reserve, Rasoarinana Jeanine, reported that *L. catta* is found in Petriky, the littoral forest south of Taolanaro. This may be the easternmost extension of the geographical range of ringtailed lemurs. We were unable to visit the Petriky Forest but found ringtailed lemurs in some small patches of forest just west of there, near the village of Karinaro. We surveyed 150 km in this region.

Between Isalo and Ambalavao along Route Nationale #7

There are vast areas of grassland between Route Nationale #10 to the south and Route Nationale #7 to the north, which appear to be natural and are not inhabited by lemurs. However, there are isolated forest areas along Route Nationale #7, in Isalo National Park and the southern portion of the Central Plateau south of Ambalavao, which support populations of *Lemur catta*. In each of these areas there are pockets of dense, closed-canopy forest supported by perennial streams. These forests, much like those found in the western Andohahela parcel, are in valleys within large rock massifs of both sandstone and intrusive igneous lithologies. The poor infiltration of these bare rock surfaces apparently concentrates rainwater into small areas, which then support highly mesic forests. The massifs are resistant to weathering, and supply a constant source of water in an otherwise periodically dry environment.

There are dense, but isolated, populations of ringtailed lemurs in such forests in the Isalo Massif, near the Andringitra Reserve, and in a private reserve, Anja, 20 km south of Ambalavao. There is also a population living on the rocks and low bush above the tree line on the Andringitra Massif at an elevation of more than 2500 m (Goodman and Langrand 1996). The forests are quite isolated from those along the western and southern coastal regions, and there remains a question as to the geographic origin of these ringtailed populations. We plan to examine this question in a later paper. It is

interesting to note that the forests at Isalo and Anja are both located in sacred localities that have been protected over the years by local tradition. We surveyed 675 km in this region.

Summary and Conclusions

We employed a scientific methodology that used broad-scale data sets, such as remotely sensed images, to site fine-scale data sets, such as field observations and interviews. As such, we leveraged more extensive but less costly (per area) information to more advantageously position finer detailed but costlier information. Our study first examined Landsat images and maps derived from aerial photos to construct a data set covering broad temporal and spatial scales: 50 years duration and most of southern Madagascar (from Manja to Taolanaro), and much of the natural range of *Lemur catta*.

In the field we used satellite image-derived products: a) multi-temporal color composites (derived from images acquired in 1973, 1985 and 1999/2000) which provided land cover change information and, b) multi-spectral color composites (derived from the Infrared bands of the most recent images) which provided the current land cover, as well as c) published topographic maps, which provided the location of roads and the names of villages and forests. We also employed broad survey methods to characterize the distribution of *Lemur catta*: interviews with local peoples in villages along our road route (covering over 3000 km), and direct observation of animals in specific forests identified in our image-derived map products and our interviews.

There is a great deal of variation in natural habitats found throughout southern and southwestern Madagascar. This diversity is caused by variability in climate, year-to-year climatic variability, parent material, topography, river dynamics, and past climates. Numerous biogeophysical processes control the biogeography of these dry forests - the surface drainage of rainwater, savannah burning, river migration and dune migration, inundation, weathering, and groundwater flow.

Forest boundaries in southern Madagascar are delimited by human factors as well as by solely biogeophysical factors. For example, numerous forest boundaries in 1950 are associated with lithological contacts. Savannah fires appear to have had a minor role in changing them in the last 50 years. Recent cutting can mask these preexisting forest edges.

There is also a great deal of variation in the history and intensity of forest cutting in each region, and the patterns and proximate causes for deforestation vary. The major proximate causes of deforestation in southern Madagascar are subsistence-based swidden agriculture, forest cutting to produce charcoal for larger cities, and large contiguous areas of swidden agriculture for export crop production. The past and long-term effects of rearing livestock are yet to be determined.

The spatial and temporal characteristics of these land-cover change trajectories are also very diverse. For example, deforestation for export crops is a phenomenon of the 1990s and is located near large harbors. Deforestation for charcoal began in earnest in the early 1970s, spreading rapidly in the

1980s, and is limited to areas near large urban centers and accessible from larger roads. Deforestation for subsistence agriculture is not associated with major roads but is in regions of higher population density. While present before 1950 it has expanded recently to cover large areas, such as the Mahafaly Plateau.

The ringtailed lemur occurs throughout the south and southwest, but is unevenly distributed, both geographically and in different habitats. The population densities are generally very low. They are medium to high only in gallery forests and similar higher biomass, dense-canopy, mesic forests, of which there are very few. The few remaining forests of this type have shrunk rapidly where not protected.

Most remaining high-biomass, mesic forest is in isolated areas or has been protected through government or private reserves or by local tradition. Since there are so few of these areas remaining, they should all be officially protected in some way. It is important to note that, throughout the southwest and south, many of the best forest patches still existing, with the highest ringtailed densities, are on sacred land (*fady* forests) protected by local traditions. In the southernmost region, the majority of the remaining natural dry forest areas are contained in small isolated sacred forests.

In the broadest sense the geographical distribution of ringtailed lemurs has not changed over the past 50 years and may be wider than previously thought, with small but dense populations confirmed within the Central Plateau and further east, near Taolanaro. We believe that the overall ringtailed lemur population, however, has decreased significantly in this period due to deforestation, especially due to the cutting of the forests with the highest woody plant biomass.

We believe that the populations of ringtailed lemurs in the southern portion of the Central Plateau and Isalo Massif may have originated from tributaries of the Mangoky River to the north rather than from the forests along the southern coast. We will explore this hypothesis in a later paper. In later publications, we will also examine the current distribution of ringtailed lemurs; using satellite data we will outline the present distribution of major habitats in the south and west of the island, and the history of deforestation in this region over the past 50 years; provide quantitative data on this deforestation; and estimate the density of *Lemur catta* in the major habitats and the history of the population density of ringtailed lemurs in each, and generally, over the past 50 years.

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Appendix 1. Landsat images used in this study.

Location ¹	Entity ID	Date[m/d/y]	Sensor	Sat#	Path/Row	WRS#
MXM	LM1172075007316690	6/15/73	MSS	1	172/75	1
TLE	LM1172076007316690	6/15/73	MSS	1	172/76	1
TSI	LM1172077007316690	6/15/73	MSS	1	172/77	1
BKU	LM1171076007305790	2/26/73	MSS	1	171/76	1
AMP	LM1171077007305790	2/26/73	MSS	1	171/77	1
BAR	LM1171078007305790	2/26/73	MSS	1	171/78	1
OVA	LM1170077007300290	1/02/73	MSS	1	170/77	1
CSM	LM1170078007300290	1/02/73	MSS	1	170/78	1
MXM	LT5161075008501710	1/17/85	TM	5	161/75	2
TLE	LT5161076008501710	1/17/85	TM	5	161/76	2
BKU	LT5160076008504210	2/11/85	TM	5	160/76	2
AMP	LT5160077008504210	2/11/85	TM	5	160/77	2
OVA	LT5159077008501910	1/19/85	TM	5	159/77	2
CSM	LT5159078008501910	1/19/85	TM	5	159/78	2
MXM	LE7161075000027550	10/01/00	ETM+	7	161/75	2
TLE	LE7161076000027550	10/01/00	ETM+	7	161/76	2
BKU	LE7160076000023650	8/23/00	ETM+	7	160/76	2
AMP	LE7160077000023650	8/23/00	ETM+	7	160/77	2
OVA	LE7159077009922651	8/14/99	ETM+	7	159/77	2
CSM	LE7159078009922651	8/14/99	ETM+	7	159/78	2

¹See Figure 2 for geographic coverage.

Coprophagy and Intestinal Parasites: Implications to Human-habituated Mountain Gorillas (*Gorilla gorilla beringei*) of the Virunga Mountains and Bwindi Impenetrable Forest

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Introduction

Coprophagous species

Coprophagy is the habit of eating or feeding on one's own (autocoprophagy) or other individual's (or species) excrement (allocoprophy) (Galef 1979). This phenomenon was first reported in 1882 in rabbits (Morat 1882) which form excreta (that are later ingested later) in the cecum, and the term cecotrophy refers to coprophagy practiced by rabbits and sometimes rodents (Soave and Brand 1991). Coprophagy is a normal phenomenon observed in a variety of invertebrate (Silverman *et al.* 1991) and vertebrate groups including mammals such as rodents and lagomorphs (Soave and Brand 1991). In humans, auto- and allocoprophy, or coprophilia (playing with the feces) are abnormal phenomena and practiced by those deemed mentally impaired and psychiatrically disordered, or even by normal people as a protest behavior (Zeitlin and Polivy 1995; Mason 1996; Giacometti *et al.* 1997).

As a normal phenomenon, coprophagy has nutritional importance in the provision of vitamins (mainly B-complex), proteins, amino acids, minerals (e.g., iron), and trace elements, which are excreted in the feces having not been effectively absorbed by the lower intestinal tract (Soave and Brand 1991). It aids in acquiring sufficient amounts of these nutrients in the diet of herbivorous animals, i.e., ruminants and monogastric herbivores, as plant food provides much less protein and amino acids than animal tissue (Casimir 1975). In coprophagous species, the practice is essential in providing nutrients for normal growth, development, and maturation, through increased digestibility of dry matter, organic matter, crude protein, and alfalfa (Soave and Brand 1991). In rodent pups, maternal excreta can also serve as a source of nutrients (Barnes and Fiala 1957). Prevention of this practice in coprophagous species significantly decreases weight gains (Demaux *et al.* 1980), e.g., in rabbits and rats, and significantly alters the composition of intestinal flora (Soave and Brand 1991). Rats have to constantly

re-inoculate symbionts into the gut by coprophagy to sustain a high performance of cecal microflora (Gustaffson and Fitzgerald 1960). Autocoprophagy is necessary to supply essential nutrients due to the functional construction of the digestive system of lagomorphs and rodents (Soave and Brand 1991). Rabbits separate digesta in the proximal colon by antiperistalsis-based retrograde transport of digesta back into the cecum which has high bacterial content (Soave and Brand 1991). Accumulation of bacteria in the cecum contributes to a high fermentation rate, resulting in production of fecal pellets (soft pellets) high in nitrogen content, which are ingested later on by coprophagy (Soave and Brand 1991). In rats, symbionts are trapped in the mucin which is retrogradely transported into the cecum (Soave and Brand 1991). In young monogastric herbivores and ruminants, allocoprophy facilitates the acquisition of intestinal symbionts (Soave and Brand 1991). For example, the ingestion of feces by foals is related to the normal process of "seeding" the cecum and colon with beneficial organisms essential for cellulose digestion (Crowell-Davis 1985). In young ruminants coprophagy is practiced together with ingestion of regurgitate from the parent forestomach, and serves the same purposes (Crowell-Davis, 1985). In young nonherbivorous animals, coprophagy results in the acquisition of essential nutrients otherwise missing in their diet (Soave and Brand 1991). Iron eliminated in adult swine feces is acquired by piglets through allocoprophy and prevents iron-deficiency anemia (Gleed and Sanaon 1981). In species where coprophagy normally occurs, the practice is conditioned by the morphology, functional construction, and physiology of the digestive system, and in neonates and juveniles, can be controlled by maternal pheromones e.g., rats and horses (Soave and Brand 1991). A foal will eat part of the dam's feces in response to the mare's pheromones (Soave and Brand 1991).

Coprophy, on the other hand, can produce serious medical complications if practiced by noncoprophagous animals (Widdowson 1994). Fibrous matter comprising grass, hay, and chaff in a form of a dense matt can be found in the

stomach of dogs that practice allocoprophagy on ruminant feces (Widdowson 1994). This fibrous matter prevents proper functioning of the dog's stomach (Widdowson 1994).

Non-coprophagous species

A low amino acid diet (Soave and Brand 1991), or merely behavioral problems, for example, boredom (Ralston 1986; Boyd 1986) can result in coprophagy in non-coprophagous species. It is easy to experimentally induce coprophagy in non-coprophagous species by decreasing the amount of protein in the diet (Soave and Brand 1991). While normally observed in foals between the second and fifth week after birth, it can also occur in adult horses fed low protein diets (Crowell-Davis 1985). Coprophagy has been reported in nonhuman primates (Newton 1978; Soave and Brand 1991), mostly in captive animals. It has been commonly accepted that its occurrence in nonhuman primates does not serve nutritional purposes as it does in rabbits and rodents (Soave and Brand 1991), but is due to diets deficient in proteins, amino acids, and vitamins (Flurer and Zucker 1988) or behavioral problems (Newton, 1978). Coprophagy has been reported in captive prosimians (*Lepilemurs*) and rhesus monkeys (*Macaca mulatta*), associated with re-ingestion of bacteria containing fatty acids, and vitamin B-12, respectively (Newton 1978; Soave and Brand 1991). In marmosets, coprophagy occurs with diets having a protein level lower than 6% (Flurer and Zucker 1988).

Coprophagy in Mountain Gorillas

Coprophagy has been observed in mountain gorillas (*Gorilla beringei beringei*) of the Virunga volcano chain of Eastern and Central Africa, and the Bwindi area of the Impenetrable Forest (Redmond 1983). Their range is included within the national boundaries of Rwanda, Democratic Republic of Congo (formerly Zaire) and Uganda. Adult gorillas eat some of their own feces (autocoprophagy) immediately after defecation, or old feces of other gorillas, and infants sometimes eat feces of older animals and vice versa (Redmond 1983). The practice is commonly observed, and considered to be normal (Redmond 1983) in the belief that it serves as a means of acquiring beneficial microbes; the "gut flora" (Redmond 1983), as in ruminants and other herbivorous animals. However, this only partially explains allocoprophagy in gorilla infants. In young infants, allocoprophagy usually serves to acquire nutritional elements that are missing in the diet and cannot be synthesized in the digestive system (Soave and Brand 1991). The interpretation of the meaning and importance of coprophagy in gorillas based on data derived from other great apes requires caution, because the gorilla is vegetarian (Casimir 1975). The digestive system of Virunga gorillas shows no features distinguishing it from that of humans, and there is no morphological alteration that would suggest a "ruminant type digestion" (Hokosawa and Kamiya 1961). It is assumed, therefore, that the level of gorilla digestibility of plant matter is similar to that observed in monogastric herbivores, i.e., 60-80% (Casimir 1975). As such, the lack of

a "ruminant type digestion" in gorillas would eliminate the need to "seed" the cecum and colon with symbionts. However, their monogastric herbivore type of digestion, indicates that there is a certain need to have symbionts seeded into the large intestine to digest plant material.

Nutrition of free-ranging mountain gorillas

Extensive study on the feeding ecology and nutrition of free-ranging mountain gorillas in Zaire (currently Democratic Republic of Congo) showed that the majority of plant parts eaten were richer in proteins and amino acids, than those not eaten (Casimir 1975). Past nutritional analysis of mountain gorilla diet assumed that the plants consumed contain vitamins, carbohydrates, and water (gorillas do not drink water in the field) in sufficient amounts to satisfy their complete nutritional needs (Casimir 1975). Meticulous analysis of the baselines for protein and amino acid requirements and availability demonstrated that mountain gorillas can only fulfill their requirements for these nutrients by being highly selective in their food choice, which if not maintained (i.e., if they eat one or a few plants only) is presumed to increase significantly the probability of a nutritional deficiency disease (Casimir 1975). Nutritional imbalance, for example, can be observed after 2-3 weeks of feeding exclusively on bamboo shoots in the bamboo forest (Casimir 1975). Studies have demonstrated that nonhuman primates are particularly sensitive to deficiencies in certain amino acids; the lack of a single amino acid in a diet otherwise rich in proteins causes unavoidable death in *Cercopithecus aethiops* (Casimir 1975). Considering the features of feeding ecology and nutrition of mountain gorillas, their protein amino acid requirements, and the lack of a "ruminant type digestion", coprophagy practiced by adult gorillas may serve nutritional functions, supplementing proteins and amino acids, and seeding symbionts into the large intestine to facilitate digestion of plant material.

Habituation of mountain gorillas to humans

Populations of mountain gorillas have been habituated to humans for their management and as a result of burgeoning ecotourism (Butynski *et al.* 1990; Butynski and Kalina 1993). Mountain gorillas have their own phylogenetically-specific, co-evolved, intestinal parasitofauna. The relatively close contact between gorillas and humans (including guards, poachers, tourists, veterinarians, and researchers) is believed to enhance the anthrozoönotic transmission of parasites to which gorillas may be susceptible (Ashford *et al.* 1990, 1996). Although not been demonstrated, it may also enhance the zoonotic transmission of parasites. It has been suggested that changes in the intestinal parasitofauna of mountain gorillas observed by fecal examination, provide a good means to assess the effect of habituation of gorillas to ecotourism (Ashford *et al.* 1996). Unfortunately, most information on gorilla parasites has been derived from captive specimens, housed for years under artificial conditions (Redmond 1983), and exposed to human-specific parasites, to which these nonhuman primates are susceptible (Kalter 1980). Because of the

phylogenetic closeness of human and nonhuman primates, the assemblage of intestinal metazoan parasites (macroparasites or helminths) and protozoan parasites (microparasites) in captive gorillas is an evident effect of anthrozoönotic transmission (Redmond 1983; Ashford *et al.* 1996). However, due to the limited parasitological information prior to the initiation of the habituation process, it is difficult (and methodologically incorrect) at the present time, to assess the effect of ecotourism on gorilla health based on the assemblage of their intestinal parasites.

Coprophagy and transmission of intestinal parasites

Coprophagy was discovered in 1882 and has been investigated since then as a nutritional phenomenon (Morat 1882). Some aspects of coprophagy, for example the transmission of strongylids, have been studied in veterinary parasitology (Georgi and Georgi 1990) but, being considered an abnormal phenomenon in humans (Mason 1996), coprophagy was generally neglected in medical parasitology, except in mentally retarded people with behavioral aberrations (such as coprophagy or coprophilia) requiring institutionalization (Fox and Martin 1975; Braun *et al.* 1988; Huminer *et al.* 1992; Giacometti *et al.* 1997). However, taking the subject from epidemiology and epizootiology of parasitic infections, directly transmitted parasites (through fecal ingestion, for example) as opposed to indirectly transmitted parasites (vector-borne, or requiring intermediate host[s]), take advantage of coprophagy, to propagate their own species. The potential of coprophagy, if practiced, in the epidemiology and epizootiology of parasitic infection can be enormous. Redmond (1983) identified 41 species of helminths (endoparasites) from captive and wild gorillas. Twenty-nine of them (71%) have direct life cycles and can be transmitted by coprophagy.

The results of intestinal parasitofauna investigations in free-ranging mountain gorillas of the Parc National de Volcans (Ashford *et al.* 1990, 1996; Hastings *et al.* 1992; Meader *et al.* 1997) indicate that coprophagy can be an operational force in the transmission of parasites with direct life cycles. This can be supported by the following observations:

1. Most of the intestinal helminths and protozoan parasites reported from free-ranging mountain gorillas (Ashford *et al.* 1990, 1996; Hastings *et al.* 1992; Meader *et al.* 1997) have a direct life cycle and can be transmitted via the fecal-oral route. Only one of the helminth parasites, a nematode, *Capillaria hepatica*, may not take an advantage of coprophagy for transmission (Graczyk *et al.* 1998). Another parasite is *Anoplocephala gorilla*, a cestode with an indirect life cycle transmitted via soil mites that preferentially occur on gorilla feces (Redmond 1983).
2. An extensive study of the intestinal parasitofauna of 16 social groups of mountain gorillas demonstrated remarkable uniformity of parasitism among them and among individuals within the group (Ashford *et al.*

1996), but the factor(s) generating this phenomenon were not discussed nor investigated.

3. The prevalence of infection of mountain gorillas with parasites transmitted via the fecal-oral route is high; usually over 70%, and frequently reaching 100% (Ashford *et al.* 1990, 1996; Hastings *et al.* 1992; Meader *et al.* 1997). This rate is well above the transmission thresholds. In humans, coprophagy efficiently prevents eradication of intestinal parasitic infections even when several antiparasitic agents are used simultaneously (Thacker *et al.* 1981).
4. The prevalence of entodiniomorphids (intestinal symbionts of mountain gorillas) is high, ranging from 83 to 100% (mean 86%) (Ashford *et al.* 1996). These ciliates are transmitted exclusively via the fecal-oral route with warm feces, and cannot be transmitted via contamination (Wenyon 1965).
5. Most of the nematode parasites found in mountain gorillas (Table 1) are not found in other primates, and are parasites of herbivores (Ashford *et al.* 1996), for example

Table 1. Intestinal parasites with direct life cycles reported from free-ranging human-habituated mountain gorillas (*Gorilla beringei beringei*) of the Parc National de Volcans, Rwanda, that practice coprophagy; from institutionalized mentally retarded humans with behavioral aberrations such as coprophagy and/or coprophilia; and from people who share habitats of mountain gorillas.

Parasite name	Gorillas ^a	Humans	
		Mentally retarded ^b	Sharing gorilla habitat ^c
Protozoa			
<i>Entamoeba coli</i> ^{d,e}	+	+	+
<i>E. histolytica</i> ^e	+	+	+
<i>E. hartmani</i> ^{d,e}	+	+	-
<i>Iodamoeba buetschilii</i> ^{d,e}	+	+	+
<i>Giardia lamblia</i> ^e	+	+	+
<i>Endolimax nana</i> ^{d,e}	-	+	+
<i>Rotartamonas intestinalis</i> ^e	-	+	-
<i>Chilomastix mesnili</i> ^e	-	+	-
<i>Balantidium coli</i> ^e	-	+	-
<i>Blastocystis hominis</i> ^{d,e}	-	+	-
Coccidia	+	+	-
Helminths; Nematoda			
<i>Strongyloides fuelleborni</i>	+	-	+
<i>Strongyloides</i> sp.	+	-	-
<i>Trichostrongylus</i> sp.	+	-	-
<i>Murchidius devians</i>	+	-	-
<i>Oesophagostomum</i> sp.	+	-	+
<i>O. stephanostomum</i>	+	-	-
<i>Paralibyostrongylus kalinae</i>	+	-	-
<i>Hyostrongylus kigeziensis</i>	+	-	-
<i>Strongyloides stercoralis</i>	-	+	+
<i>Ascaris</i> sp.	+	+	+
<i>Probstmayria gorillae</i> ^e	+	-	-
<i>Enterobius vermicularis</i> ^e	-	+	+
<i>Trichuris trichiura</i>	+	+	+

^a Ashford *et al.* (1990, 1996), Hastings *et al.* (1992), Meader *et al.* (1997).

^b Braun *et al.* (1988), Huminer *et al.* (1992), Giacometti *et al.* (1997).

^c Ashford *et al.* (1990).

^d Considered as "nonpathogenic parasites" in humans.

^e Immediately re-infective to host after excretion with the feces.

ungulates and paeungulates practicing coprophagy (Eden and Soest 1982).

6. A synergistic effect of coprophagy on transmission of intestinal parasites can be revealed by comparison of the intestinal parasites (and their rates of infection) in mountain gorillas and in institutionalized, mentally retarded people with behavioral aberrations who practice coprophagy and/or coprophilia (Table 1) (Braun *et al.* 1988; Ashford *et al.* 1990, 1996; Hastings *et al.* 1992; Huminer *et al.* 1992; Giacometti *et al.* 1997; Meader *et al.* 1997).

However, it must be emphasized that many parasite species that have direct life cycles and are listed in Table 1, can be also transmitted to mountain gorillas by means other than coprophagy. Many nematodes develop larvae within the egg, the egg hatches, and then the larvae leave the feces to penetrate host skin or to wait on vegetation to be eaten by the host (Parker 1982). *Trichostrongyloides* and *strongyles* develop L₃ larvae in the feces and migrate on vegetation to complete their life cycle after being eaten by mountain gorillas. Thus, development of the infective stages of these nematodes requires a minimum of several days, and coprophagy of fresh feces would not be an effective means for transmission as the parasite developmental stages are not immediately re-infective to the host (Table 1). However, gorilla territoriality and feeding and nesting habits (Casimir 1975) provide for numerous opportunities for casual fecal contamination with older stools, and consequently for the transmission of parasites with these sorts of life cycles.

Epizootiological implications of coprophagy

The habituation of mountain gorilla populations to humans is thought to enhance anthroponotic transmission of intestinal parasites (Ashford *et al.* 1990; 1996). The concept of anthroponotic transmission of parasites implies a scenario of common source epizootics, that is point, or point source, epizootics, when single or multiple exposures of gorillas to the infectious agent(s) is brief. From then on, coprophagy can serve as the vehicle for propagation and progressive epizootics. Coprophagy in free-ranging mountain gorillas may have a nutritional function; while simultaneously enhancing autoinfection and spread of the parasites among individuals in the population. A positive consequence of coprophagy related to parasite transmission and constant re-exposure (or re-inoculation) to intestinal parasites can be the generation of herd immunity and a decrease in parasite virulence.

Herd immunity is an important factor always underlying the dynamics of propagated and progressed epidemics of epizootics (Mausner and Kramer 1970). Since the parasite-exposed individuals develop immunity, as the epizootic progresses the proportion of nonsusceptibles in the population increases, and the likelihood of effective transmission to susceptibles declines (Mausner and Kramer 1970). One of the most important and well recognized features of

herd immunity is that it is not necessary to achieve 100% immunity in a population in order to halt an epidemic or epizootic (Mausner and Kramer 1970). Although coprophagy in mountain gorillas of the Parc National de Volcans was first described in 1983 (Redmond 1983), given the nutritional physiology of this species, there is little doubt that coprophagy is a quite normal phenomenon.

Coprophagy-based synergy of intestinal parasitism

The relationship between coprophagy and parasitism and its implications for gorilla health, such as immunization, has not been considered before, and is presently difficult to prove because available parasitological data have not been collected to address this issue. However, some information on coprophagy and immunity can be derived from the gorilla's closest relative; humans. Mental retardation that requires institutionalization is the major risk factor for infection with gastrointestinal parasites mainly because of coprophagy and coprophilia practiced by humans with behavioral aberrations in these institutions (Braun *et al.* 1988; Huminer *et al.* 1992; Giacometti *et al.* 1997). The parasitofauna of institutionalized, mentally retarded adults practicing coprophagy significantly differs from other adults in the same closed environments, for example, professional staff and personnel (Braun *et al.* 1988; Huminer *et al.* 1992; Giacometti *et al.* 1997). Human-to-human transmission of *Strongyloides stercoralis* in mentally retarded people is well recognized, and persistent strongyloidiasis in such populations was demonstrated to be due to autoinfection (Braun *et al.* 1988). Statistical analyses have shown that the presence of "pathogenic parasites" (Table 1) in fecal specimens of patients in mental institutions are significantly associated with coprophagy and coprophilia (Giacometti *et al.* 1977). More importantly, data analyses showed that "nonpathogenic parasites" (Table 1) were significantly more common in the institutionalized patients with these behavioral aberrations than in controls (Giacometti *et al.* 1997). Interestingly, clinical symptoms in mentally retarded patients practicing coprophagy and having parasite-positive fecal specimens were absent (or rare) irrespective of the infection with "pathogenic" or "nonpathogenic" (Table 1) parasites (Giacometti *et al.* 1997). This represents a serious public health problem in these institutions because infections with intestinal parasites among patients practicing coprophagy are asymptomatic, while the professional staff of the same facility present severe clinical symptoms upon contracting the same parasite species (Giacometti *et al.* 1997). Regarding mentally retarded people, this phenomenon has been explained by "equilibrium between host and parasite" (Giacometti *et al.* 1997).

As mentioned above, the prevalence of infection with fecal-oral transmitted parasites of mountain gorillas is usually above 70%, frequently reaching 100%, but there is not the morbidity (or mortality) that one would expect with such high infection rates (Ashford *et al.* 1990, 1996; Hastings *et al.* 1992; Meader *et al.* 1997). This may be indicative of the "host-parasite equilibrium" which operates in coprophagous,

mentally retarded people (Giacometti *et al.* 1997). However, it must be emphasized that the immune responses to intestinal parasites of humans and gorillas may be different.

Risk assessment

Epidemiologically, the risk of infection with directly transmitted (via fecal-oral route) intestinal microparasites such as *Giardia* or *Cryptosporidium* is defined by the equation;

$$P_i = 1 - \exp(-rN)$$

where r is the fraction of parasites that initiate infection (when ingested) and is directly related to the parasite infectivity (usually expressed as Infectious Dose₅₀); N represents exposure, e.g., frequency of events of parasite transmission, or amount of contaminated food (or water) consumed per time unit, (in the case of gorillas, N defines the frequency of coprophagy episodes); and P_i is the probability of infection expressed by the attack rate in common source or progressive epidemics, or by the prevalence of infection in epizootics (Rose *et al.* 1991, 1997). The infectivity of parasites varies considerably among different species; however, it is relatively stable within the species of a parasite (George and Georgi 1990). Thus, assuming a stable value of infectivity in the risk assessment equation, the prevalence with parasites transmitted via the fecal-oral route is exponentially related to the frequency of exposure, for example, the frequency of coprophagia in mountain gorillas and in mentally retarded people. This would explain why the prevalence of infection with intestinal parasites in totally isolated populations, such as mountain gorillas and institutionalized mentally retarded humans, is usually very high (Braun *et al.* 1988; Ashford *et al.* 1990, 1996; Hastings *et al.* 1992; Huminer *et al.* 1992; Giacometti *et al.* 1997; Meader *et al.* 1997). It is important to emphasize that there are several means by which exposure to intestinal parasites can occur, for example, low personal hygiene and/or low standards of hygiene (humans), or contamination (gorilla and humans). The risk assessment model described above can be applied to parasites that are immediately re-infective to mountain gorillas after excretion with the feces such as intestinal protozoans (Table 1).

Coprophagy and enteric immunization by intestinal infections

The mountain gorilla, as in all mammalian species, has its own phylogenetically-specific intestinal parasitofauna as a result of temporal and spatial host-parasite coevolution (Noble *et al.* 1989; Wolfe *et al.* 1998). Coprophagy may play an important role as a part of nutritional physiology. On an evolutionary scale, the main implication of coprophagy related to parasite transmission can be the generation of herd immunity. Coprophagy is so efficient in transmitting intestinal parasites among institutionalized, mentally retarded people that most known antiparasitic treatments fail to eradicate them (Thacker *et al.* 1981). For this reason, in the veterinary management of human-habituated popula-

tions of mountain gorillas, coprophagy could be perceived as a "two-edged sword". Due to the superior efficiency of coprophagy in the transmission of intestinal parasites, the gorilla's immune status can be maintained at a high level. However, "new" intestinal parasites introduced to gorilla populations are expected to be transmitted with an efficiency similar to the "old" ones. As demonstrated in Table 1, the list of these "new" species is not extensive: *Endolimax nana*, *Rotartamonas intestinalis*, *Chilomastix mesnili*, *Balantidium coli*, and *Blastocystis hominis*. There might be just five species of anthrozoootic "pathogenic" and "nonpathogenic" protozoan parasites that are not yet present in mountain gorillas and in the people sharing the gorilla's habitat (Table 1). Because pinworms (*Probstmayria gorillae*, and *Enterobius vermicularis*) are highly species-specific (Georgi and Georgi 1990), cross-transmission of the species listed in Table 1 is unlikely. Although pathogenicity of protozoan parasites to the mountain gorilla is unknown, considering the immune status of gorillas, it is reasonable to assume that it (and consequent morbidity) will be not higher than that currently observed due to six other anthrozoootic species infecting gorillas (Table 1). Coprophagy, through constant re-inoculation of intestinal parasites, can stimulate the intestinal immune system of gorillas, e.g., lymphoid tissue, which is the main and well-recognized mechanism of enteric (oral) immunization against intestinal infections (Deicher 1978; Newby and Stokes 1984; Brown 1996). Frequent exposure to the protozoans parasitizing intestinal mucosa increases the amount of parasite microparticles, i.e., immunogens, in that region, and enhances the uptake of these immunogens by the intestinal lymphoid tissue (Newby and Stokes 1984; Brown 1996). The lymphoid tissue, in return, stimulates production of a high amount of immunogen-specific class A immunoglobulins (IgA) secreted by the intestinal lamina propria (Newby and Stokes 1984; Brown 1996), and found as high concentrations of coproantibodies in intestinal secretions (Fubara and Freter 1972; Deicher 1978; Newby and Stokes 1984; Brown 1996). Coprophagy favors ingestion of coproantibodies, which have been demonstrated in animal models to have protective functions against intestinal infections (Fubara and Freter 1972). Also, the immunogens taken up by the lymphoid tissue trigger cell-mediated immunity processes in newly acquired intestinal infections or intensify these processes upon repeated exposure to intestinal parasites (Deicher 1978; Newby and Stokes 1984; Brown 1996). The repeated passage of a highly virulent intestinal parasite strain through susceptible hosts causes attenuation of this strain; humoral and cell-mediated protective immunity can be as effectively generated by the attenuated strains as by the virulent ones (Brown 1996). Coprophagy can enhance exposure of mountain gorillas to various strains of parasites, i.e., to a broad spectrum of immunogenic antigens, which in human and animal enteric immunization trials is achieved by genetic manipulation with infectious agents (Brown 1996). It has been demonstrated that repeated exposure to intestinal parasites via oral immunization also induces whole mono-

specific defense reaction, defined as paramunity (Raettig 1982), which cross-protects against other species of intestinal parasites (Raettig 1982).

Concluding remarks

Introduction and/or perpetuation via coprophagy (or environmental contamination) of potentially pathogenic organisms within closed populations of mountain gorillas can be potentially catastrophic, particularly when the numbers of neonates, juveniles, or naive individuals are relatively high. Although the prevalence of infection with fecal-oral transmitted parasites of mountain gorillas is high, the morbidity (or mortality) that one would expect to be associated with such high infection rates has not been observed. Why is that? The relationships between coprophagy and parasitism and its implication for gorilla health has not been elaborated before and are presently difficult to address because available parasitological data have not been collected in a manner suitable to address the issue. We provide justifications for our hypotheses related to transmission of intestinal parasites in mountain gorillas. In many instances, the empirical data to definitively conclude certain parasitological phenomena do not exist. However, it may be that the populations of human-habituated mountain gorillas are severely endangered, and it may be too late to collect such empirical evidence.

Testing of mountain gorillas for intestinal protozoa and helminths by stool examinations and the culture of recovered embryonated eggs or larvae of helminths is advantageous because it minimizes the disturbance to these great apes in their natural habitat. Although intestinal helminths and protozoans may pose a health problem in mountain gorillas, it must be emphasized that other pathogens such as filariae that infect wild gorillas (Bain *et al.* 1995), or enteric bacteria or viruses (Kalter 1980), can be even more significant for gorilla health.

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The Cross River Gorilla: The Most Endangered Gorilla Subspecies

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Introduction

The Gorillas inhabiting the Cross River watershed on the border between Nigeria and Cameroon are found in semi-deciduous and montane forests between 5°55' and 6°25'N latitude and 8°48' and 9°38'E longitude. They are distributed in and around a set of escarpments whose peaks may rise as high as 1600-1900 m (asl), above woodlands and secondary grasslands to the north, and low-lying rain forests to the southwest (Fig. 1). Today these gorillas are found in four separate populations corresponding to four separate areas (1) the Afi mountains, (2) the Mbe mountains, (3) the Boshi Extension forests of the Okwangwo division of Nigeria's Cross River National Park (CRNP), and (4) the Takamanda forest reserve of Cameroon and adjacent areas of CRNP along the Cameroon border (Fig. 1 in Oates 1998a, 1998b).

Cross River gorillas have the most northern and western distribution of all gorilla populations and appear to have been isolated for some time from the other West African gorillas. They are approximately 260 km northwest of the closest gorillas populations in the western equatorial African forests (Fig. 2).

History

Dating back to Coolidge's (1929) revision of the genus *Gorilla*, Cross River gorillas have been classified in the same subspecies as the other western gorillas *G. g. gorilla* (Savage and Wyman, 1848). Although Matschie (1904) originally considered Cross River gorillas to be sympatric with and specifically distinct from other western gorilla populations, subsequent taxonomists, including Coolidge, never tested these claims. Relying on anecdotal accounts of gorilla distribution, Coolidge believed Cross River gorillas were geographically continuous with other western gorilla populations (Coolidge 1929, 1936; Fig. 3). Groves' (1970, 1971) gorilla distribution maps were the first to demonstrate Cross River gorillas are geographically separate from other

western gorillas. Although his statistical analyses showed Cross River gorillas were the most distinctive of the West African gorilla populations, Groves (1970) reasoned that the relatively narrow cline exhibited by West African gorillas did not merit subspecific distinction for any one western gorilla population.

Taxonomic Study

Skeletal differences

Considering the systematic and evolutionary implications of geographic isolation, I decided to re-examine the taxonomy of Cross River gorillas. Because John Oates (1988) was also interested in this question, having long ago recognized the Cross River watershed, Mt. Cameroon highlands, and Bioko Island as an area of primate endemism, we decided to collaborate. For this purpose, we examined and measured 85 skulls and 72 skeletons of non-Cross River western lowland gorillas, and 60 skulls and 3 skeletons of Cross River gorillas, and compared their external features as documented from photographs and skins. We also collected data on the ecology and behavior of Cross River gorillas with the hopes of relating these to the measured skeletal differences and imparting biological objectivity to our interpretations (Sarmiento and Oates 2000).

When compared to the gorillas of the western equatorial African rainforest, Cross River gorillas have shorter skulls, shorter molar rows, narrower palates, and a relatively broader skull base. In addition, Cross River gorillas have smaller cheek-tooth surface areas, smaller gapes and much smaller braincase volumes than do the other western gorillas. Associated with their metric cranio-dental differences, Cross River gorillas exhibit a suite of characteristic non-metric cranial traits resulting in an easily recognizable and distinct skull shape. Multivariate analyses based on 11 cranial measurements were able to correctly distinguish all the male and female Cross River gorillas from all of the other male and female western gorillas (Sarmiento and Oates 2000).

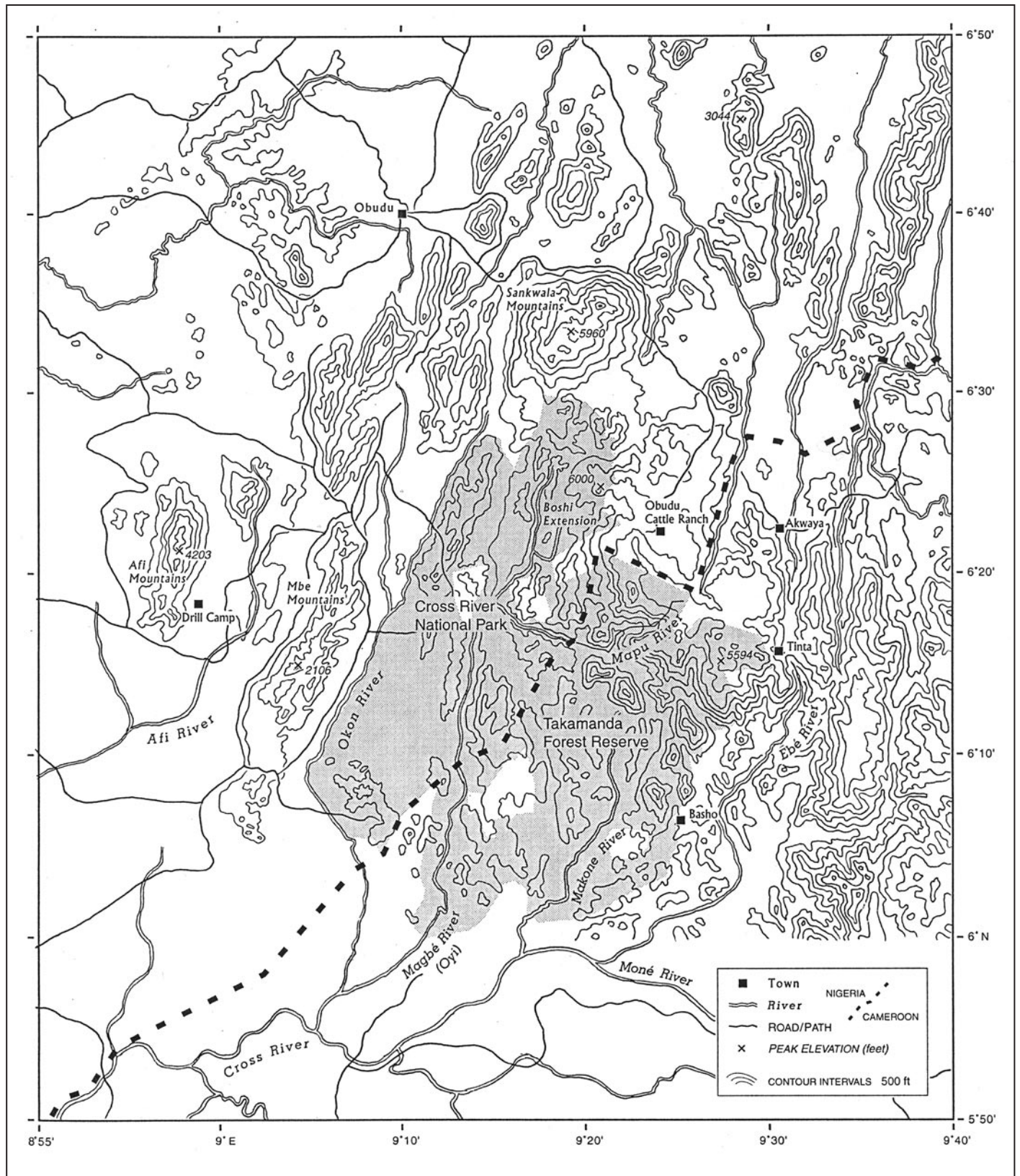


Figure 1. The areas inhabited by the Cross River gorillas. The Afi Reserve contains one group of eight gorillas. The Mbe Mountains and the Boshi extension of Cross River National Park (CRNP) at the most contain 20 animals each (J. F. Oates pers. comm.). The remaining animals are found in the Takamanda reserve and in the CRNP along the Cameroon border. Based on inhabited area and estimates of 1.5 animals per km² there is less than 150 animals living in the Takamanda reserve and adjacent areas. Groves (2002) recently estimated the number of gorillas in Takamanda and Mone forest reserves as 180.

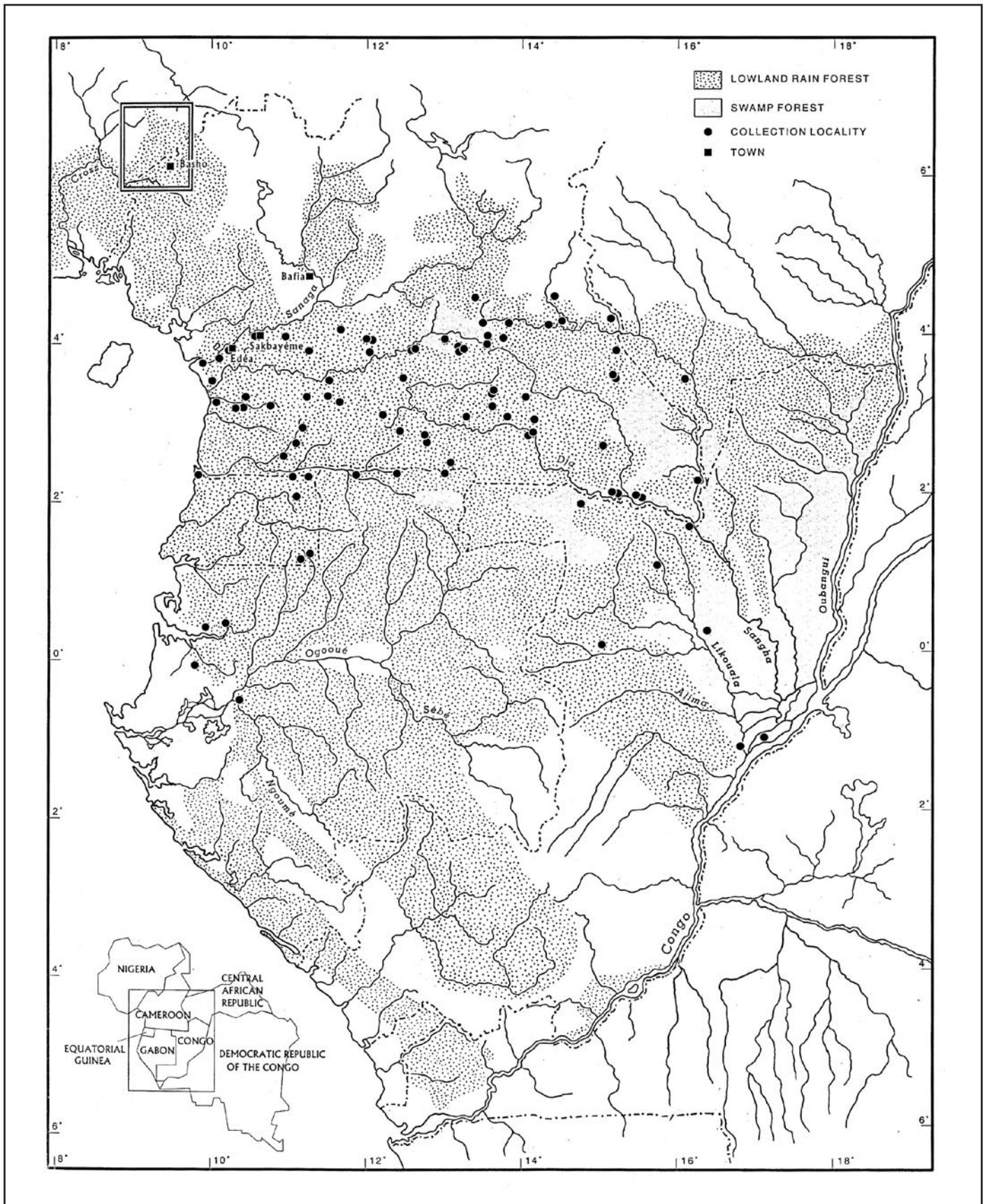


Figure 2. The West African equatorial forest with an outline of the area mapped in Figure 1, and showing the distance between the Cross River watershed and the closest non-Cross river gorilla collecting localities.

Comparisons of vertebral and long bone measurements failed to show any significant differences between Cross River gorillas and the other western gorillas (Sarmiento and Oates in press). Cross River gorillas have clavicular, brachial, crural, intermembral, and humerofemoral indices well within the range of the other western gorillas. As indicated by vertebral body measurements, they also have a body size similar to that of other western gorillas. Unfortunately, only one of the measured skeletons has complete hands and feet. Although finger and toe length was barely within the lower limits of variation seen in western gorillas, a larger sample is necessary to conclusively demonstrate if there are significant differences in hand and foot proportions (Sarmiento and Oates 2000).

The large range of variation in pelage color and facial features of western gorillas masked any seemingly unique external characteristic of Cross River gorillas. The orange-red hair on the crown, the long black hair on the limbs, the deep hollow cheeks and relatively wide face are also seen in other western gorillas.

Ecological implications of skeletal differences

Considerable differences in the habitats presently occupied by Cross River gorilla populations confound attempts to associate skeletal differences with their habitat. The Cross River gorilla habitat has a very complex topography (Fig. 1), and its climate changes both with altitude and with geographic locality. The amount of rainfall seems to decrease with increasing latitude and decreasing elevation (Table 1). The most westerly part of the gorillas' range, in the Afi Mountains, has a drier climate than the southeastern parts of Takamanda. The Obudu Plateau to the north has a three-month dry season and temperatures that range from a monthly minimum of 14-16°C to monthly maxima of 18-25°C (Table 2). The most notable feature of the Cross River gorilla habitat is the prolonged dry season, a correlate of their northern latitude.

Many of the Cross River gorilla's cranial specializations may be associated with a drier habitat and colder temperatures and a resulting diet made up of smaller, drier, and harder food items than consumed by western gorillas. A colder climate would also explain shorter hands and feet if and when these are confirmed by larger sample sizes (Sarmiento and Oates 2000).

Table 1. Average monthly and yearly rainfall (mm) for localities¹ with varying altitude and latitude in the Cross River Catchment Area.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Yearly
Obudu town ² 6°37'N, 9°08'E, alt. 396 m	4.6	14.0	45.8	116.5	254.8	244.6	240.1	238.4	356.2	260.2	30.4	2.5	1813
Obudu plateau 6°25'N, 9°20'E, alt. 1585 m													4280
Afi Base Camp 6°20'N, 9°03'E, alt. 700 m	0.4	0.1	11.8	237.2	321.0	338.0	441.8	750.3	736.7	503.7	13.1	14.7	3346
Drill Ranch Camp 6°18'N, 9°00'E, alt. 150m	14.7	0.0	78.8	220.4	293.4	462.4	449.4	697.6	482.5	544.0	55.5	5.1	3303
Ikom 5°58'N, 9°37'E, alt. 119 m													2465
Mamfe 5°31'N, 8°42'E, alt. 122 m	33	79	160	206	325	437	513	465	564	452	152	38	3424
Dikone Balue, Rumpi Hills 4°55'N, 9°25'E, alt. 270 m	113	196	374	342	307	397	757	975	801	380	231	60	4933

¹Obudu town based on monthly averages from Jan 1978 to April 1990; Obudu plateau after Hall (1981); Afi Base Camp based on monthly averages April 1996 to December 1996, and December 1997 to December 1998; Drill Ranch Camp based on monthly averages from January 1997 to September 1998; Ikom after Keay (1979); Mamfe based on monthly averages over a 32-year period after Hawkins and Brunt (1965); Dikome Balue, Rumpi hills based on monthly averages over two years after Tuegels *et al.* (1992).

²Keay (1979) reported yearly average rainfall of 1585 mm for Obudu town.

Table 2. Ambient temperature (°C) for some localities¹ in the Cross River Catchment Area.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
Ikom													
Max	32.4	32.8	33.7	33.1	32.6	32.1	30.6	30.0	31.1	31.6	32.1	31.5	32.0
Afi Base Camp													
Max	25.9	28.0	28.6	28.2	27.7	26.3	24.6	23.5	23.6	24.6	25.9	25.4	26.0
Min	17.0	18.3	20.4	20.2	19.8	19.4	19.3	18.6	18.1	18.6	18.2	17.5	18.8
Drill Ranch Camp													
Max	31.5	35.0	36.5	36.5	35.3	33.7	33.7	32.4	31.1	33.0	32.6	31.0	33.5
Min	18.5	18.5	21.5	23.5	23.5	23.0	23.0	22.9	22.9	23.0	23.0	19.0	21.9

¹Ikom based on records over a total of nine years after Teugel *et al.* (1992); Afi Base Camp based on daily averages from April 1996 to December 1996, and December 1997 to December 1998; Drill Ranch Camp based on daily averages from January 1997 to September 1998; Considering a decrease of 6.5°C per 1000 m, the expected maximum and minimum yearly average temperature at the Obudu plateau (1600 m) is 20.2°C and 13.0°C, respectively. Hall (1981) reports maximum and minimum temperatures of 18-25°C and 14-16°C, respectively, for the Obudu plateau at 1585 m.

It may be that Cross River gorillas differentiated in the woodlands and grasslands of the Cameroon highlands during an arid phase of the Pleistocene. Human cultivation, land clearing and cattle grazing in the highlands may have forced the gorillas to move to the forested slopes they presently occupy. In support of this, there are relatively recent reports (Harcourt *et al.* 1989) that gorillas ranged onto the Obudu plateau (1600 m – 1990 m asl). Regardless of where Cross River gorillas originated, placing them in the subspecies, *Gorilla gorilla diehli* [using the species *nomen* originally assigned to them by Matschie (1904)], best summarizes their distinctiveness.

Species and Subspecies Definitions, Genetics, and Distribution

Placing Cross River gorillas in a distinct subspecies *G. g. diehli* conforms with the currently used species and subspecies definitions and considers genetic factors as set out in these definitions. Principally, it emphasizes reproductive communality vs. phenotypic similarity as the most important criteria for species inclusion; the result of incorporating Mendelian genetics into synthetic evolutionary theory (Dobzhansky 1937). According to Mayr (1942, p.120), “Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups”. “A subspecies is an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species and differing taxonomically from other populations of the species” (Mayr 1969, p.41). In reference to subspecies Mayr (1969) notes “differing taxonomically” usually means “differing morphologically”, as applies to the majority of the population being compared. In all current definitions of species and subspecies (Patterson 1985; Mayr 1969, 1982; Cracraft 1987, 1989), however, reproductive communality is limited to acknowledging genetic interchange and does not indicate the magnitude of interchange associated with either species or subspecies levels.

In practice, mammalian taxonomists usually accord specific status to natural populations of like individuals (males and females) which maintain their distinctive phenotypic similarities in areas where they overlap with other such groups (Sarmiento *et al.* 2002). Maintenance of distinctiveness is taken as a sign that gene flow occurs mainly between like individuals (males and females). Populations of individuals that fail to maintain their phenotypic distinctiveness in areas of natural geographic overlap with other such populations, but otherwise are distinct may be accorded subspecific status. Physical evidence of hybridization in areas of natural overlap or of clines uniting otherwise distinct populations are interpreted as evidence of gene flow between such populations.

As is sometimes the case in primates, especially catarrhines, distinct populations that *naturally* produce hybrids or form a cline may be accorded separate specific status. This is the case when gene flow apparently occurs in one direction (male *Cercopithecus mitis* to female *C. ascanius*, see Struh-

saker *et al.* 1988), hybrids are relatively uncommon (*Papio* and *Theropithecus*, see Dunbar and Dunbar 1974; Jolly *et al.* 1997), and clines tend to be steep (i.e., occur over a narrow geographic area or parapatric zone, and include a relatively small percentage of the populations, e.g., *Hylobates pileatus* and *H. lar*, see Brockleman and Gittins 1984). Underlying this practice is the assumption that existing gene flow between species has been decreasing with time and is presently too small to overcome the inertia of genetic divergence caused by drift or selective forces (Mayr 1969, 1982; Cracraft 1989).

In cases of allopatry, without contact zones or overlap between populations, there are no biologically objective criteria for deciding whether differences between populations correspond to specific or subspecific distinctions. In these cases, species and/or subspecies distinctions are solely based on magnitude of phenotypic differences between populations and guided by consistency within the classification. The magnitude of phenotypic differences a taxonomist chooses to represent species and subspecies levels when classifying allopatric populations must be approximately equal to the magnitude of differences corresponding to objectively designated species, and subspecies, respectively. Ideally, comparisons to objectively designated species and subspecies should be made within closely related taxa, i.e., within the same genus or family group (Mayr 1969; Simpson 1961).

In practice, therefore, geographic distribution is one of the essential criteria for recognizing species and/or subspecies, specifically as it pertains to continuity and overlap of the populations in question. Direct relationships between magnitude of morphological, behavioral and/or genetic differences to species or subspecies designations do not exist. Unless a specific morphological, behavioral and/or genetic difference can predict whether or not there is genetic interchange between populations (for example, protein specific acrosomes, size and geometry of copulatory organs, and specific chromosomal inversions or translocations) no one degree of difference can be absolutely ascribed to any one taxonomic level. Considering their geographic isolation from western gorillas, there are no objective criteria for assigning Cross River gorillas to a distinct subspecies as opposed to a distinct species. Comparison of the distinguishing characters of Cross River gorillas to those distinguishing other subspecies of gorillas or the two species of chimpanzee, however, can impart some degree of objectivity (Table 3).

Species vs. Subspecies Characters in Gorillas and Chimpanzees

Similarities in body size, and long bone lengths and proportions, but marked cranio-dental differences in Cross River gorillas relative to western gorillas are significant for a number of reasons. Cheek tooth occlusal surface area has a strong genetic input and it is more or less fixed at birth. It distinguishes the two species of chimpanzee and the eastern from western gorillas (arguably two different species; Sarmiento

Table 3¹. Mean and standard deviation and range of variation of occlusal cheek tooth surface area (mm²) and palate length (mm) in Western gorilla, Cross River gorilla, five populations of Eastern Gorilla and common and pygmy chimpanzee males and females (number of specimens sampled in parentheses).

	Cheek tooth area (mm ²)	Palate length (mm)
Cross River		
Males	956.6 + 84.43 (32)	107.1 + 6.277 (36)
	1159.0-807.2	119.7-90.34
Females	838.9 + 72.38 (17)	88.48 + 4.537 (25)
	959.9-707.5	97.27-72.5
Western lowland		
Male	1098.0+ 103.2 (58)	111.2 + 7.886 (58)
	1369.0-953.5	125.0-94.65
Females	914.6 + 65.87 (28)	89.63 + 5.461 (31)
	1041.8-774.8	102.9-79.15
Virunga		
Males	1269 + 115.4 (29)	133.0 + 5.871 (25)
	1486-1101.98	143.2-117.1
Females	1088 + 59.12 (23)	103.0 + 6.61 (22)
	1198-956.4	112.3-87.84
Bwindi		
Males	1211 + 126.1 (5)	123.1 + 6.57 (5)
	1387-1034	131.4-115.6
Females	971.7 + 71.77 (3)	99.9 + 7.26 (4)
	1022-920.5	111.4-92.5
Itombwe		
Males	1278.1 + 89.70 (9)	
	1454-1108	
Females	1106 + 85.16 (8)	
	1236-933.0	
West Lake Edward		
Males	1306 + 113.9 (14)	
	1483-1125	
Females	1178 + 56.26 (16)	
	1252-1063	
Walikale Itebero-Utu		
Males	1142 + 106.1 (11)	
	1323-998.0	
Females	1085 + 60.42 (11)	
	1181-957.0	
Angumu		
Males	1267 + 51.57 (5)	126.8 + 3.945 (5)
	1351-1221	133.5-123.6
Females	1131 + 64.94 (7)	101.9 + 5.375 (9)
	1225-998.8	110.6-94.86
<i>Pan troglodytes</i>		
Males	522.1 + 57.00 (26)	82.1 + 54.7 (26)
	644.6-407.8	92.3-67.5
Females	495.2 + 2.48 (19)	74.7 + 2.48 (17)
	582.0-398.1	79.5-69.3
<i>Pan paniscus</i>		
Males	377.6 + 27.59 (17)	61.9 + 4.46 (19)
	420.0-321.5	70.2-53.8
Females	341.7 + 14.78 (10)	57.5 + 4.64 (12)
	368.0-317.9	65.0-50.8

¹Male to male and female to female comparisons of the mean cheek tooth surface area of Virunga gorillas to those of the other eastern gorilla populations showed significant difference ($t < 0.05$) only for comparisons with Walikale males and with Lake Edward females. Differences between *Pan paniscus* and *P. troglodytes*, Eastern gorillas and Western gorillas, and Cross River gorillas and Western Gorillas are all highly significant < 0.001 for cheek tooth surface area and for palate length.

and Butynski 1996), but fails to show significant differences between Virunga gorillas and the other populations of eastern gorilla (representative of at least two different subspecies; Table 1; Sarmiento *et al.* 1996). Palate length, skeletal lengths and proportions, and body size, on the other hand, have a significant environmental component, and may change ontogenetically in great apes according to lifestyle (Schultz 1942; Sarmiento 1985, 1998). Most lengths and proportions show differences between (1) the two chimpanzee species (Zihlman and Cramer 1978; Sarmiento *et al.* 1995), (2) Western and Eastern gorillas (inclusive of Virunga gorillas; Schultz 1934; Sarmiento 1985 and notes, Sarmiento *et al.* 1995, 1996) and (3) Virunga gorillas and each of the other Eastern gorilla populations (Groves and Stott 1979; Sarmiento 1985; Sarmiento *et al.* 1996).

Different cheek tooth surface areas, therefore, suggests a long period of isolation of Cross River gorillas from the other western gorillas and/or strong selection for divergent diets. On the other hand, they may also suggest body size and longbone lengths and proportions must have been under stabilizing selection in both gorilla groups. The latter justifies a subspecies as opposed to a species designation, and applies even if genetic studies show differences between Cross River gorillas and the other western gorillas are considerably greater than those existing between the different subspecies of Eastern gorilla. Because Cross River gorillas, in spite of their isolation, seem to have been under many of the same selective forces as the other western gorillas, a species distinction from the other western gorillas is not warranted.

Implications for Gorilla Conservation

The recognition of Cross River gorillas as a distinct subspecies numbering probably less than 200 individuals (Fig. 1) makes them the most endangered of all gorillas subspecies and emphasizes the need for their conservation. Unlike the other critically endangered gorilla populations, each comprising a single population (Sarmiento *et al.* 1995, 1996), Cross River gorillas are fragmented into four populations, and individuals may be unable to move between them (Oates 1998b). The majority are living in "less protected" forest reserves as opposed to national parks, and are still being actively hunted (K. McFarland and Oates pers. comm.; Groves and Maisels 1999). Much of the available habitat, especially around the perimeters of the park and reserves is badly degraded and appears to be shrinking. Very little habitat remains in the wooded highlands and most has now been degraded by human activity to secondary grasslands. Human settlements occur around the forest, and several settlements are enclaved within forest.

Current research by K. McFarland in the Afi reserve (K. McFarland and J. F. Oates pers. comm.), and Groves and Maisel (1999) in Takamanda forest reserve has built a presence in the area, but more needs to be done. A presence must be established in the Mbe mountains and Boshi extension, and a more accurate census must be undertaken, if conserva-

tion measures are to prove effective. There is a strong likelihood that the Mone forest reserve to the east also contains gorillas (Groves and Maisel 1999). Their presence or absence in this reserve must be verified and protection measures, if the animals are present, enacted. Genetic studies of the four known populations should also be done as soon as possible. This should demonstrate which populations, if any, may still remain in contact and allow the establishment and protection of corridors which will insure movement between populations. Hopefully, the recognition that Cross River gorillas are a new subspecies will stir the needed support and interest to ensure their survival.

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Primates of Guinea-Bissau, West Africa: Distribution and Conservation Status

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Introduction

Guinea-Bissau is one of the smallest countries in coastal West Africa. With an area of 36,125 km², it includes a number of small offshore islands, the Bijagos archipelago, which are almost linked to the continent by wide intertidal mud flats. The topography of the country is low-lying, rising eastwards from sea level to low altitudes (highest point at 260 m). Mangroves predominate along the coast, and penetrate inland along the six major estuaries. Closed broad-leaved forests occur on the lowland plain, and small areas of primary forest are still found in the southwest (Tombali and Quinara regions) and in the northwest (Cacheu region).

The vertebrate fauna of the country has been scarcely investigated. With regard to mammals, J. V. B. Bocage published a first list of the terrestrial species in 1892. Ten years later, during a five-month survey for the Genoa Natural History Museum, Leonardo Fea collected specimens in Bissau, Bolama, Farim, Cacheu, Cacine, and Cambec (Gestro 1904), but his (rather few) mammal records still await publication. In 1906, Maclaud published an account on the mammals and birds of West Africa, including the Portuguese Guinea. However, the first scientific expedition is that of the Swiss zoologist Albert Monard, who in 1937-38 collected specimens in a number of localities in the country (Monard 1938a, 1938b, 1940). After World War II, in 1945-46, a Portuguese zoological expedition “Missão Zoológica da Guiné”, headed by Fernando Frade, added new information on Guinea-Bissau’s fauna (Frade 1949), but no zoological expeditions were carried out in the country for the next forty years. Only in 1989 was a comprehensive wildlife inventory undertaken by the Direction Office of Forestry and Hunting of Guinea-Bissau (DGFG) and Canadian Co-operation (CECI) with financial help from the IUCN (Limoges 1989).

Many gaps still exist, however, in our knowledge of Guinea-Bissau’s biodiversity, and this greatly hampers the planning of effective conservation actions. For example, Oates (1986) listed 11 primate species for this country, two of

them only tentatively included (*Perodicticus potto* and *Galagoides demidoff*). The difficulties for determining the faunistic composition arose from a number of different reasons: in some cases, the information has to be retrieved from grey literature. Also, the fauna of adjacent countries is not well known (for the Republic of Guinea see Barnett and Prangley 1997), although, paradoxically, West African mammals have a long history as subjects of biogeographical investigation (Booth 1958; Robbins 1978; Oates 1981).

In February-March 1994, we investigated the distribution and status of the primates living in three different areas: the northwest, the Cantanhez Forest in the South and three islands of the Bijagos archipelago. In previous studies, we reviewed the status of chimpanzees in the country (Gippoliti and Dell’Omo 1995) and have also focussed on the primates living in the Cantanhez Forest (Gippoliti and Dell’Omo 1996). Here, we combine our field observations with information from the literature concerning the primate fauna of Guinea-Bissau and adjacent countries (Senegal, The Gambia, Republic of Guinea, and Sierra Leone), also providing, for each species, the synonyms most commonly used in the literature concerning the country’s primates.

Species Accounts

Galago senegalensis É. Geoffroy. Senegal bushbaby
Galago senegalensis senegalensis; Monard, 1938a: 125.

This species is widespread in the country. Records are available for Bijine and Matado-Cao (Bafatà), Cossé, Boé, Mansoa, Pitche (Gabu) (Frade and Silva, 1980). Local people confirmed the presence of one galago species in the Cantanhez Forest. The presence of another species, *Galagoides demidoff* G. Fischer in Guinea-Bissau is considered cautiously by Oates (1986, 1996), and only on the basis of its presumed occurrence in The Gambia and Senegal (Dupuy 1971). The presence of the species in these two countries, however, was based on two specimens (one of them the type specimen) of dubious origin (Grubb *et al.* 1998), and we recommend that

this high-forest species be considered absent from Senegal, The Gambia and Guinea-Bissau, at least until new evidence becomes available.

Colobus polykomos Zimmerman. Ursine colobus *Colobus polykomos polykomos*; Monard, 1938a: 127.

The north-western limit of the distribution of this species is not known. According to previous reports (Booth 1958; Dorst and Dandelot 1970; Rahm 1970; Halternorth and Diller 1980) the limit is north of the Gambia River. Oates *et al.* (1994), mapping the distribution of this species, excluded its presence in northern Guinea-Bissau, Southern Senegal and The Gambia. Published records concerning Guinea-Bissau come from Catiò, Cacine, Corubal River and Chime (Frade and Silva 1980). During the nation-wide faunistic inventory (Limoges 1989), *C. polykomos* was observed near Xitole, along the Corubal River. It also occurs in the proposed Dulombi National Park, east of Xitole (Thibault 1993). We confirmed its presence in the Cacine basin (Gippoliti and Dell’Omo 1996) and observed it, for the first time, in the extreme north-western part of the country. Small groups of 5-6 individuals were observed during two consecutive days (13 and 14 February 1994) along the São Domingos-Varela road, about 15 km west of São Domingos. The animals were presumably under hunting pressure since they fled on the ground as soon as they were sighted by us. At Susana we were informed by missionaries that local people occasionally kept white infant monkeys, which, however, never survived long in captivity. These records, 6 km from the Senegalese

border, not only confirm the presence of the species in northern Guinea-Bissau, but also indicate its presence, still not officially confirmed, in southern Senegal, and possibly in the Casamance National Park (Galat-Luong 1995).

Procolobus badius temminckii Kuhl. Temminck’s red colobus

This subspecies was widely distributed through the country in the past. Known records come from Bafatà, Bissau, Bambadinca, Boé, Cacine, Chime, Contuboeil, Crocoli Camp (c. 12°10’N, 13°55’W) Cutià, Enclé, Xitole, Cancungo, Mansoa, Sedengal, Kiu Camp (c. 12°10’N, 14°50’W), Kopulan Camp (c. 12°14’N, 13°58’W) (Frade and Silva 1980; Monard 1938a; Napier 1985). The results of the DGFC nation-wide survey (Limoges 1989) indicated an extended range in the south of the country and apparently isolated populations in the northeast, near Gabù and Farim, close to the Senegalese border. We confirmed the presence of this red colobus in the Cacine basin, while local people reported its presence in relict portions of forest between São Domingos and Susana.

The nominal *P. b. badius* and *P. b. temminckii* are usually distinguished on the basis of their colour pattern; a character that is known to be variable within populations (Monard 1938a; Struhsaker 1975). The south-eastern limits of this subspecies are unknown. It is known to occur in southern Guinea-Bissau (Monard 1938a; Frade and Silva 1980; Gippoliti and Dell’Omo 1996), and in the north-western area of the Republic of Guinea (Rode 1937; Rahm 1970), although it was not found during a recent survey in the Kounoukan

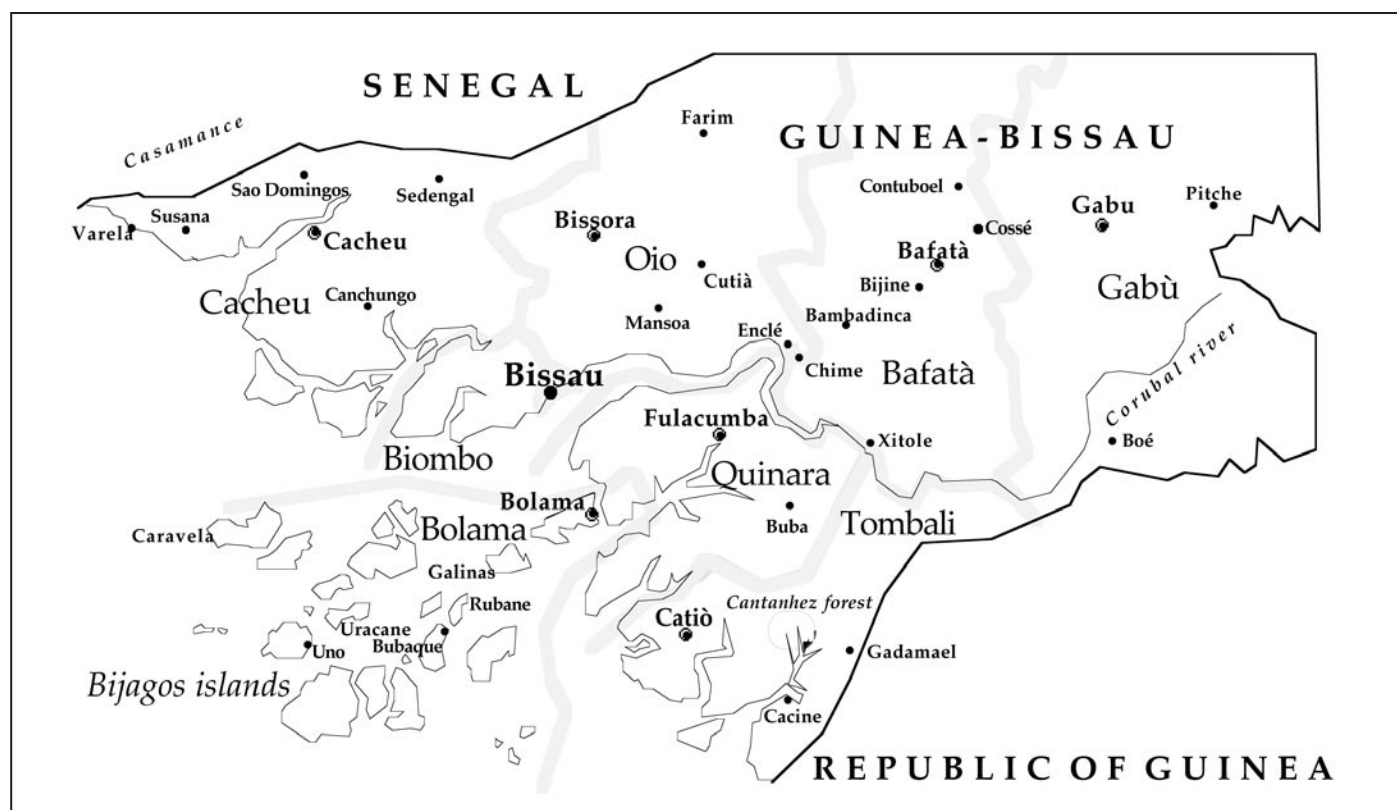


Figure 1. Map of Guinea-Bissau indicating past and actual locations of the primates, as discussed in this paper.

forest (Barnett *et al.* 1994). It has also been recorded in Sierra Leone (Roche 1971), particularly in the north-west (Harding 1984) but, more recently, Grubb and colleagues (1998) reported only *P. b. badius* in the country. The nominal subspecies certainly occurs in the high forests of Sierra Leone, but its range may be smaller than that shown in the map by Oates *et al.* (1994).

Cercopithecus sabaesus Linné. Green monkey
Cercopithecus (Chlorocebus) aethiops sabaesus; Monard, 1938a: 132

As indicated by its vernacular Creole name “Macaco de terrafe”, which means monkey of the mangroves, and the observations of Maclaud (1906), *C. sabaesus* seems particularly linked to mangrove habitat in West Africa, where its diet includes crabs and *Rhizophora* fruits, flowers, shoots and young leaves (Galat and Galat-Luong 1976). The species is widespread in Guinea-Bissau, except in the north-east (Limoges 1989). It was considered by Monard (1938a) to be the most common monkey of the country, and we observed it in the mangroves of the Cacine basin. *C. sabaesus* is commonly kept as a pet in villages and towns, and we observed several individuals in Bissau, Susana and on the Bubaque island. In the Bijagos it is present on all the islands.

Cercopithecus campbelli campbelli Waterhouse. Campbell’s guenon

Cercopithecus mona campbelli; Frade and Silva, 1980: 3

Campbell’s monkey is widespread in the country, except in the extreme north-eastern region (Limoges 1989). We observed a troop sleeping in a high tree between São Domingos and Varela, in the northwest. The species is common in the south-western region, where it can be found in association with the red and ursine colobus monkeys. It also occurs on the island of Caravela, where it is more terrestrial (probably due to the scarcity of trees and competition with the arboreal *C. petaurista*). It is probable that the species is declining due to deforestation in many parts of its range.

Cercopithecus petaurista buttikoferi Jentink. Lesser white-nosed guenon

Cercopithecus nictitans; Monard, 1938a: 137.

Cercopithecus nictitans buttikoferi; Frade and Silva, 1980: 3.

Cercopithecus petaurista petaurista; Limoges, 1989: 18.

Cercopithecus nictitans stampflii; Limoges, 1989: 18.

The presence and nomenclature of “white nosed” monkeys of Guinea-Bissau is one of the most controversial and confused issues in the study of the country’s primate fauna. Recently, both Limoges (1989) and Thibault (1993) recorded two “white nosed” monkeys; *Cercopithecus petaurista* and *C. nictitans*. We believe that the records of *C. nictitans* should be rejected, since the known eastern limit of this species is in Ivory Coast; and thus we considered only *C. petaurista* as occurring in Guinea-Bissau. This species was first recorded in the Bijagos archipelago in the Bubaque (Monard 1938), and subsequently, in the island of Rubane (Frade 1949). At the

time of our survey, it was considered present on the islands of Canabaque, Caravela, Galinhas, Uno and Uracane. We observed the species on Rubane and Caravela. On Rubane, the arboreal vegetation is limited to a few palm trees, while on Caravela high trees are found only around villages. On Caravela, *C. petaurista* was seen feeding in trees, while



Figure 2. *Cercopithecus petaurista* on Caravela Island (photo by S. Gippoliti).



Figure 3. A typical chimpanzee nest in an *Eleais guineensis* palm in the Cantanhez Forest (photo by S. Gippoliti).

sympatric *C. campbelli* was observed only on the ground. On the mainland, the species is recorded from the Cufada Lake and the proposed Dulombi National Park (Limoges 1989; Thibault 1993). These records seem to support the presence of *C. petaurista* in the Casamance (Dupuy 1972).

Erythrocebus patas Schreber. Patas monkey

This monkey is present throughout the country, except in the extreme south-east (Limoges 1989). It does not occur in the Cantanhez Forest (Gippoliti and Dell’Omo 1996), and is considered absent south of Buba. It is very common, and is the only species reported still surviving in the Bissau area.

Cercocebus atys atys Audebert. Sooty mangabey

Cercocebus torquatus atys; Frade, 1949: 169

Cercocebus aethiops; Frade and Silva, 1980: 3

The sooty mangabey is definitely known to occur in Guinea-Bissau on the basis of a unique record collected by the “Missão Zoológica da Guiné” in 1946 (Frade 1949). The record came from Gadamael, near the border with the Republic of Guinea. We were not able to confirm the presence of this species in the Cantanhez Forest, nor in the north-west, and local hunters were not aware of it. *Cercocebus atys atys* is known to occur in southern Senegal (Struhsaker, 1971), and its presence in suitable habitat in Guinea-Bissau could be expected.

Papio papio Desmarest. Guinea baboon

Papio papio papio; Monard, 1938a: 141

Guinea baboon populations in the country are declining as human pressure on habitat increases. They do not occur around Bissau or in the north-west (Limoges 1989), but it is still relatively common in the Cantanhez area and the Boé sector.

Pan troglodytes verus Schwarz. Western chimpanzee

The status of *Pan troglodytes* in Guinea-Bissau has been reviewed elsewhere (Gippoliti and Dell’Omo 1995). Subsequently, the species has been reported north of the Corubal River, in the Xitole district (Reiner and Simões 1998). Future research should be aimed at developing action plans for the conservation of this species, through the identification of protected areas at least for two viable populations, one in the Cantanhez Forest and one centered in the Boé sector. A survey was planned to estimate the number and distribution of the country’s chimpanzees (Féron and Correia 1997/1998) but the results are not yet available.

Conclusions

Studies on the ecology of cercopithecines in the mainland and on the Bijagos islands (especially where two species occur sympatrically) may offer new insights on the adaptability of these monkeys to open or disturbed habitats in West Africa. Another aspect that deserves further investigation is the habitat preference of *Cercopithecus sabaues* and its ecological relationship with other guenons, particularly *C. camp-*

belli. Studies of the westernmost chimpanzee populations in Africa could also reveal new material for students of traditional regional cultures (Wrangham *et al.* 1994), as already evidenced by previous findings on nest site selection in the Cantanhez Forest, where all observed nests were located in oil palms (Gippoliti and Dell’Omo 1995), a behaviour only occasionally observed elsewhere (de Bournonville 1967; Barnett and Prangley 1996).

Ten primate species are confirmed for the fauna of Guinea-Bissau, and *Colobus polykomos* was reported in the north for the first time. Primates, being among the most representative members of the biodiversity of Guinea-Bissau, have an important role to play as “flagships” for the conservation of some of the most remarkable natural habitats of the country. A conservation plan for the Temminck’s red colobus, which could serve as an umbrella species for forest conservation in the country, should be prepared and implemented before its status becomes critical, (Gippoliti and Carpaneto 1996). After an 11-month period of civil unrest, which began in June 1998, the country is slowly returning to civilian rule, and hopefully, the return of peace will allow an increase in interest and investment in the conservation of the rich wildlife of Guinea-Bissau.

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Distribution and Demography of the Nilgiri Langur (*Trachypithecus johnii*) in Silent Valley National Park and Adjacent Areas, Kerala, India

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Introduction

The Nilgiri langur, *Trachypithecus johnii* (Fischer, 1829), is endemic to the forests of the Western Ghats and endangered. Although it inhabits a number of different vegetation types, including montane sholas, evergreen, semi-evergreen and moist deciduous forests, populations have been dwindling, mainly due to anthropogenic pressures. Widespread destruction of its natural habitat for plantations and other agricultural needs is the main cause of its endangered status, but these black monkeys are also hunted for food and for their alleged medicinal properties. The inclusion of considerable forest habitats in the protected area network such as sanctuaries and national parks, and the implementation of the Indian Wildlife Protection Act (1972) helped to recoup the population to some extent.

Field research on the Nilgiri langur has examined its status and distribution (Pocock 1928; Poirier 1969; Daniel and Kannan 1967; Kurup 1975; Vijayan and Balakrishnan 1977; Balakrishnan 1984; Holman and Sundered 1990; KFRI 1993; Ramachandran 1995; Ramachandran, 1988; Ramachandran and Joseph 1998) and ecology and behavior in different habitats (Poirier 1968, 1970a; 1970b; Horwich 1972; Oates *et al.* 1980; Srivasthava *et al.* 1996; Ramachandran 1998). Although Poirier (1968) believed it to be a typical shola species, the middle elevation evergreen forests between 700-1800 m were identified as the ideal habitat for this folivorous primate (Ramachandran and Joseph 1997). However no detailed long-term demographic study has been attempted in undisturbed continuous evergreen forest, and it is essential to monitor such undisturbed populations in order to develop appropriate conservation and management strategies. Here we report on the status, distribution and demography of Nilgiri langur inhabiting Silent Valley National Park and adjacent areas.

Study area

Silent Valley National Park is situated in Palghat district of Kerala State and located at 11° 3'N'-11° 13' N and 76°21'-76°35'E). It is one of the core areas of the Nilgiri Biosphere Reserve. The National Park area is 90 km² and forms part of the westerly sloping Silent Valley-New Amarambalam (Fig. 1). Kunthipuzha, a tributary of Bharathapuzha, originating from the northeastern hill ranges of the National Park, drains the area. The altitude varies from 658 to 2,383 m. Silent Valley forests are one of the areas of highest rainfall in the entire Western Ghats, averaging 6000 mm per year, and the annual mean temperature lies around 20°C.

The vegetation is tropical wet evergreen. The highly diverse flora of Silent Valley includes 966 species belonging to 134 families and 559 genera (Manilal 1988). Of these 701 are dicotyledons and 265 monocotyledons. The five dominant families recorded are: Orchidaceae, Poaceae, Fabaceae, Rubiaceae, and Asteraceae. The relative abundance of certain species in specific patches has resulted in the formation of certain tree associations, which are a unique feature of the Silent Valley ecosystem. Six distinct tree associations can be distinguished in the valley (Aiyar 1932). They are: 1) *Cullenia exarillata-Palaquium ellipticum*, 2) *Palaquium ellipticum-Mesua ferrea*, 3) *Mesua ferrea-Calophyllum elatum*, 4) *Palaquium ellipticum-Poeciloneuron indicum*, 5) *Calophyllum elatum-Ochlandra* sp., and 6) *Poeciloneuron indicum-Ochlandra* sp. Of these, the first three are restricted to the southern sector, whereas the remainder are confined to the central and northern parts of the National Park.

Methods

The distribution and demography of Nilgiri langur were studied in Silent valley National Park for a period of three years from 1993 to 1996, as part of the Endangered Primate Research Project. A total of 12 major blocks were identified and stratified in the National Park and adjacent areas. The

population was estimated by total count and sweep sampling methods (NRC 1981; Whitesides *et al.* 1988). Repeat surveys were conducted on foot in each of the specific blocks to obtain an exact count of troop size, composition, and sex ratio. Individuals were classified into five classes based on the morphological differences as described by Poirier (1969). They were: adult males, adult females, subadult males, subadult females and immatures. Some adults, however, could not be sexed in the field due to visibility constraints in the forest, and were classified as unidentified. Adults could be distinguished by their fully developed body stature. Both adult and subadult females could be distinguished from males by a patch of white hair on their thighs. Subadult and adult males have elongated canine teeth. A total of 1410 Nilgiri langur troop sightings were made over the entire study period.

Distribution

The Nilgiri langur was found throughout the entire stretch of evergreen forests in the National Park, as well as semi-evergreen and moist deciduous forests in the adjacent areas (Figure 1). They occur in all the different tree associations and were observed at altitudes of up to 2150 m in montane sholas. The majority of troops were sighted between 700 m and 1600 m elevation. They were found with common langur (*Semnopithecus entellus*) troops ranging in the steep gorges with deciduous vegetation adjacent to the southwestern border of the National Park. Frequent whooping calls of Nilgiri langur were also heard from the forests of the Nilambur South Forest Division bordering the northwestern region of the Park. Eighty-five different troops were identified from the study area. Of these, 69 were ranging well inside the boundaries of the National Park, while the rest of the troops (16) were sighted in adjacent forest areas. Five troops were observed from the high altitude regions in Sispara above 2000 m elevation.

Demography

A total of 501 individuals were observed in 85 troops surveyed in the final census (Table 1). The majority of the population were in the Nilikkal and Panthanthod blocks. The numbers were lower in the Cheriawalakkad block.

Of the Nilgiri langur population, 20.2% of the individuals were adult males, and 40.1% adult females, and the sex of 5.2% of the adults was not identified. Of the subadults, there were rather more males (5.8% of the population) than females (2%). Juveniles, infants and dependant infants together formed the immature class, and they comprised 26.7% of the

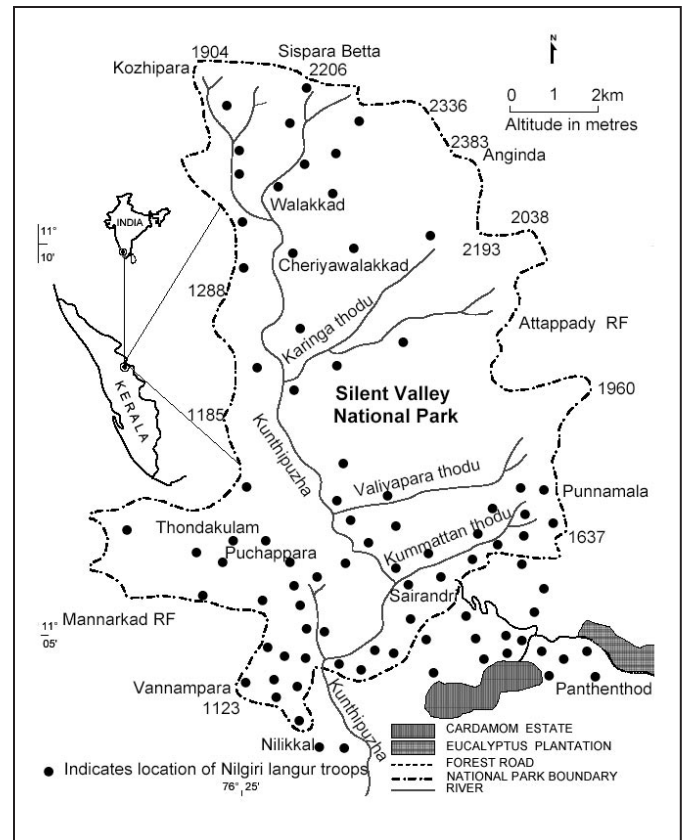


Figure 1. Distribution of Nilgiri langur (*Trachypithecus johnii*) in Silent Valley National Park and adjacent areas.

Table 1. Demography of Nilgiri langur population in Silent Valley National Park and adjacent areas.

Name of block	No of troops	Troop composition						Total
		Adult male	Adult female	Unidentified adult	Subadult male	Subadult female	Immature	
Sairandri	7	9	18	-	2	-	9	38
Aruvampara	7	7	15	9	5	1	10	47
Punnamala	8	9	19	-	2	1	14	45
Parathod	5	6	10	-	1	-	7	24
Chembotti	6	9	13	6	2	1	8	39
Nilikkal	12	15	35	4	5	-	19	78
Puchappara	7	11	24	-	4	3	17	59
Puvanchola	5	5	3	7	2	-	9	26
Cheriyawalakkad	3	3	4	-	-	-	3	10
Walakkad	7	8	15	-	2	1	13	39
Sispara	5	4	11	-	1	2	5	23
Panthanthod	13	15	34	-	3	1	20	73
Total	85	101	201	26	29	10	134	501

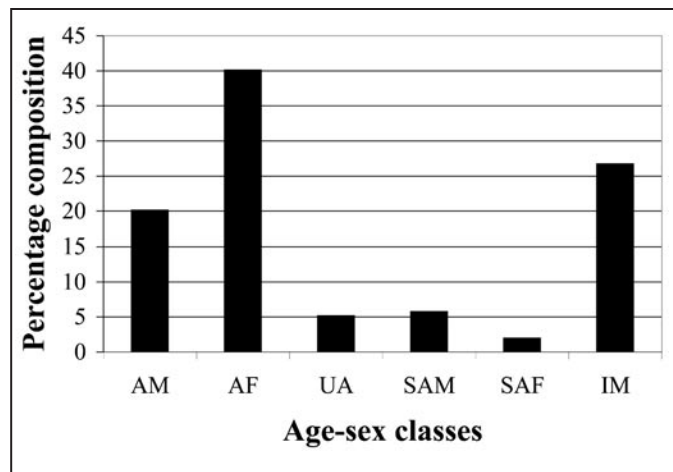


Figure 2. Troop composition of Nilgiri langur, *Trachypithecus johnii*, in Silent Valley National Park and Adjacent Areas, Kerala, India. AM=Adult male; AF=Adult female; UA=Unidentified adult; SAM=Subadult male; SAF=Subadult female; IM=Immatures.

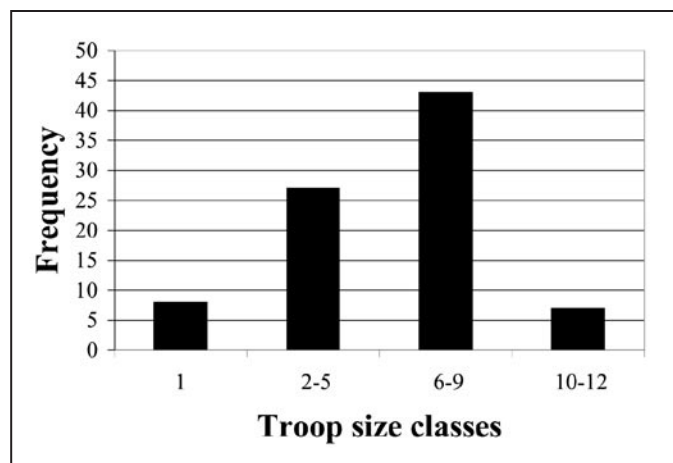


Figure 3. Troop size of Nilgiri langur, *Trachypithecus johnii*, in Silent Valley National Park and Adjacent Areas, Kerala, India.

population. (Fig. 2). Of the 302 individuals for which the sex was identified, 33% were adult males and 67% were adult females. The adult male-female ratio estimated was 1:2. The sex ratio of the subadults identified was 1:1.62.

Troop size varied from one to 12 individuals. The average of estimated troop sizes was 5.89 individuals in the Silent Valley forests. Seven troops had more than 10 individuals. Two troops, one ranging in Nilikkal section and the other in Puchappara section, each had 12 individuals. Figure 3 shows the frequency of different troop size classes. Eight solitary individuals were frequently sighted in different areas. The majority of the troops (43) were composed of six to nine individuals.

Discussion

Nilgiri langur troops were found in all of the different tree associations in the evergreen forests of the National Park, as well as the semi-evergreen and moist deciduous forests outside the Park. As this primate is largely folivorous, food

availability may be less of a limiting factor than would be the case for more frugivorous primates. Most of the Nilgiri langur troops observed in this study were found in the evergreen forests between 600 m to 1800 m and, although they appear to do well in deciduous habitat, Horwich (1972) argued evergreen forest is necessary, always forming part of the home range, for this arboreal langur.

Vijayan and Balakrishnan (1977) studied the impacts of the hydroelectric project on wildlife in Silent Valley, and described the status of Nilgiri langur population twenty years ago. They estimated about 80 troops, although they had actually sighted only 52 troops in Silent Valley and the adjacent Attappady areas, and reported that it was the most abundant primate species in the area. The results of our study clearly show the occurrence of a sustainable, healthy population still existing in the Valley. This is attributed mainly to the establishment of the National Park in 1984 and the strict monitoring of the areas under protection. In many other areas the populations have declined (Kurup 1975; KFRI, 1993).

Nilgiri langurs form smaller troops in evergreen forests, which in our study averaged 5.89 individuals. According to Poirier (1968), troops in areas where populations are high have smaller home ranges and smaller troop size when compared to other areas of lower population densities. The bigger troops have larger home ranges, probably with extensive overlap contributing to a higher rate of agonistic behavior. Hohmann and Sunderraj (1990) also described a smaller mean troop size of 4.36 individuals in evergreen forests in Mundanthurai Kalakkad, although Daniel and Kannan (1967) described the range of troop size from 1 to 30 individuals. Poirier (1969) estimated an average troop size of 8.9 individuals for Nilgiri langur troops in the sholas. Another survey (KFRI 1993) in the Kerala part of the Western Ghats revealed the existence of 348 troops with an average troop size of 11.65 individuals. Variation in troop size in different habitats may be due to the difference in the distribution, abundance and quality of the food resources in the habitat and the population density.

The size and composition of social groups is variable in a number of primate societies (Chivers and Raemakers 1980). Poirier (1969) observed a larger proportion of adults than immatures. The present study also revealed greater proportion of adults. Roonwal and Mohnot (1977) recorded the existence of all male and all female Nilgiri langur troops, whereas we found only solitary males, besides the bisexual troops. These males are probably solitary for only brief period before joining bisexual troops. Sunderraj and Johnsingh (1993) reported a higher proportion of immatures, including subadults, juveniles and infants in a Nilgiri langur population in Servalar gallery forest in Tamil Nadu. The numbers of adult females exceeded adult males in all the demographic studies (Poirier, 1969, Hohmann and Sunderraj 1990). We estimated the adult sex ratio as 1:2, which is more female-biased than the previous estimate 1:1.2 by Poirier (1969). The unequal sex ratio may be due to the existence of all-male bands and solitary males in the population.

Management strategies

1. As far as the present management strategies are concerned the entire Silent Valley National Park is treated as a 'Core Zone' and there is no separate buffer zone demarcated. There is a need for designating a suitable buffer zone for the National Park, which should include the entire stretch of adjoining rainforest and the floristically and faunistically rich Attappady Reserved Forest, particularly the Pathenthod area. Anthropogenic pressure should be minimized in the core zone.
2. The existing road through the Nilgiri langur habitat in this region should not be widened, due to its effect on canopy continuity, crucial for this arboreal species. A tourist zone should be demarcated outside the National Park, to establish an undisturbed core zone.
3. Demographic monitoring of the Nilgiri langur population in the undisturbed areas of Silent Valley National Park should be continued to allow for effective management and protection of the species.

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Pilot Study and Conservation Status of the Slender Loris (*Loris tardigradus* and *L. lydekkerianus*) in Sri Lanka

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Introduction

Slender lorises are small nocturnal prosimians endemic to Sri Lanka and India (Roonwal and Mohnot 1977). Two species and six subspecies are currently recognised (Groves 1998, 2001). Of these six taxa, two are found only in India (*Loris lydekkerianus lydekkerianus* and *L. l. malabaricus*). The Indian forms now have been the subject of long-term ecological studies (e.g., Nekaris 2001, 2002a, 2003; Rhadakrishna 2001), and their distribution and density has been mapped to some degree (Kar Gupta 1995; Nekaris 1997; Rao 1994; Singh *et al.* 1999, 2000). They are still, however, listed as “Data Deficient” in the *IUCN Red List of Threatened Species* (Hilton-Taylor 2002). Despite limited studies of the four taxa endemic to Sri Lanka (*L. tardigradus tardigradus*, *L. t. nycticeboides*, *L. lydekkerianus grandis*, and *L. l. nordicus*), severe habitat loss in that country has led to a rating of “Endangered” for Sri Lankan slender lorises (Hilton-Taylor 2002). Until now, however, only limited data have been available regarding Sri Lankan loris distribution and behaviour in the wild (Petter and Hladik 1970; Schulze and Meier 1995a).

The current study has been ongoing since 2001, and has taken place over four field trips with two major goals. First, actual surveys of lorises were deemed important to evaluate their conservation status based on real observations rather than deductions based on habitat loss alone. The results of these surveys are presented in summary below, and in more detailed form elsewhere (Nekaris and Jayewardene 2002; Nekaris and Jayewardene in review). Secondly, data on the behaviour of these species were collected to further validate the assessment of Groves (2001) regarding slender loris taxonomy, which was based mainly on the morphology of museum specimens. Further validation that the Sri Lankan taxa do indeed comprise two species, one of which is endemic to the island, has important implications for the management of these species in both the wild and captivity. These data are combined to present an updated view on the conservation status of these rare and highly specialised primates.

Materials and Methods

Study area

Surveys and behavioural observations were carried out over four periods from 27 May - 18 August 2001, 9 March - 19 April, 2002, 20 August - 19 September, 2002, and 8 December 2002 - 9 January, 2003. Research was conducted in Sri Lanka, a 66,000 km² island southeast of India across the Palk Strait and the Gulf of Mannar (5.55°-9.51°N, 79.41°-81.54°E). Sri Lanka is bordered on its western side by the Indian Ocean and on the eastern side by the Bay of Bengal. The island is characterised by three unique climatic zones: the dry zone (65% of the island), the intermediate zone, (12% of the island), and the southwestern wet zone (23% of the island). Within these zones, several forest types have been classified: desert, monsoon scrub jungle, monsoon forest and grassland, inter-monsoon forest, and rainforest interspersed with grassland. Surveys for slender lorises were conducted in each climatic zone and in each forest type. Average temperatures range from 52.5°F to 87.5°F. Rainfall averages 37-288” annually (Ashton *et al.* 1997; Esperance and Corea 2001).

Thirty-three different areas were surveyed during this study. Seven of them fell within the range of *L. t. tardigradus*, ten within the range of *L. l. nordicus*, seven within the range of *L. l. grandis*, and one within the range of *L. t. nycticeboides*. Eight additional sites were surveyed where taxonomic designation was questionable. Taxa were distinguished during this survey principally following the descriptions of Osman Hill (1933, 1953) and the distribution reviewed by Schulze and Meier (1995a).

Survey Techniques

Because of time constraints and the large area covered, broad reconnaissance survey techniques were employed to estimate the population densities at each site (White and Edwards 2000). The index used for estimating relative abundance was animal encounter rate, or “sightings” per km (National Research Council 1981; Sutherland 2002). Justifi-

cation and details of these methods are described elsewhere (Nekaris and Jayawardene in review; Nekaris *et al.* in press).

Behavioural data collection

Preliminary behavioral observations were carried out on two different taxa, *L. t. tardigradus* and *L. l. nordicus* (Figs. 1 and 2). For the Northern Ceylon or grey slender loris (*L. l. nordicus*), ten days were spent at Polonnaruwa, eight days at Minneriya-Giritale Sanctuary, and ten days were spent in Trincomalee, totalling over 190 hours of direct observation. Seven weeks were spent at Masmullah Proposed Forest Reserve, and two weeks were spent in Pitigala (Heycock Mountain Range) observing the Western Ceylon or red slender loris (*L. t. tardigradus*) for approximately 120 hours.

The preliminary data presented here were collected either *ad libitum* or at the moment of first contact. The activity budget of slender lorises at the moment of first contact has been shown to be comparable to data collected with instantaneous sample points (Nekaris 2001). Nekaris (2000, 2001) described in detail the behavioral categories used. They include: inactive (rest, sleep) vs. active (travel, feed); groom and other; position (sit, quadrupedal stand, quadrupedal walk, hang, climb, spiral, run, bridge, other); and whether or not the animal was seen by itself or with other lorises. For a detailed ethogram, see also Schulze and Meier (1995b). Information on habitat use included: substrate size, substrate angle, animal height, tree height, and tree type (when known) (Nekaris 2001).

Data analysis

Data were analyzed using Microsoft Excel and SPSS 11.0. Chi-square analyses were used to compare categorical behavioral data, whereas ANOVA tests were used to analyse ordinal data. Probability was set at the $p \leq 0.05$ level.

Results: Surveys

Approximately 766 km were walked or motored in 17 areas where no lorises were found; 192 km were walked or motored in 16 sites yielding 191 sightings of *Loris*: *L. l. nordicus* (n = 111), *L. t. tardigradus* (n = 75), *L. l. grandis* (n = 4), and *L. t. nycticeboides* (n = 1). Density estimates, based on sightings of animals per km, were: *L. t. tardigradus* (0.86-13 animals/km) and *L. l. nordicus* (0.33-50 animals/km) (Nekaris and Jayawardene 2002; Nekaris and Jayawardene in review). Sample size was too small to adequately generate any estimate for *L. l. grandis* or *L. l. nycticeboides*.

Presence of *Loris* seems to be positively associated with the presence of flying insects and heavy orthopteran leaf damage, and negatively associated with primary forest with little undergrowth. Taxa differ in their ability to thrive at the edge of human habitations, with *L. l. lydekkerianus* being the most successful. Due to deforestation, *L. t. tardigradus* was found to be absent from numerous areas from where it was known only 50 years ago, areas which are not heavily disturbed by human habitation. Human induced threats to *Loris* include

habitat loss, road kill, capture for the pet trade and use in traditional medicine, and killing due to superstitious beliefs. Electrocution on uninsulated power lines maims and kills lorises (pers. obs; V. Perera pers. comm.) (Fig. 3).

Results: Behavior and Habitat Use

Contact Data

A total of 212 data points were collected at the moment of first contact for the following taxa: *L. l. nordicus* (n = 111), *L. t. tardigradus* (n = 67), *L. l. grandis* (n = 4), and *L. t. nycticeboides* (n = 1). The moon was present and not obscured by clouds in 55% of the sightings, and was absent in the remaining 45%. Weather was clear in 68% of the sightings, cloudy in 26%, and in 6% of the sightings it was raining. Adults were seen 143 times, juveniles nine times, parked infants 12 times, and age could not be determined in the remaining 48 data points. Observations of males were obtained 40 times, of females 58 times; and the sex could not be determined in the remaining 114 observations.

The behavior and habitat use of all taxa combined upon the moment of first contact are summarized in Table 1. These results are similar to those for *L. l. lydekkerianus*, except that Sri Lankan lorises were more often active upon first contact (Nekaris 2001). The main difference between the Sri Lankan lorises and *L. l. lydekkerianus* was the use of quadrupedal running (Nekaris 2001). This category was reserved for rapid movement when only two limbs were in contact with a substrate, as opposed to the three limbs used to firmly grip branches during walking. This locomotor pattern has also been seen in captivity for *L. l. nordicus* (Schulze and Meier 1995b).

Differences between *L. t. tardigradus* and *L. l. nordicus*

No significant difference was found between these species in their behavior at first contact ($\chi^2 = 4.56$, df = 3, $p = 0.207$). No significant difference was found in positional behavior, although a trend toward significance was observed ($\chi^2 = 16.33$, df = 9, $p = 0.06$). In particular, the following postures were qualitatively different. *Loris t. tardigradus* engaged in more quadrupedal running and less quadrupedal walking. The smaller red lorises are clearly using running rather than walking whereas the larger *L. l. nordicus* is relying almost exclusively on quadrupedal walking for its most typical mode of locomotion. Percentage of sample points that animals engaged in various behaviors is summarized in Table 1.

Significant differences were found in habitat use between the two subspecies. *Loris l. nordicus* used small and medium branches significantly more than *L. t. tardigradus*, whereas *L. t. tardigradus* was spotted more often on terminal twigs and vines ($\chi^2 = 25.47$, df = 5, $p \leq 0.0001$). In terms of substrate angle, *L. t. tardigradus* used oblique substrates significantly less, and horizontal and vertical substrates significantly more than *L. l. nordicus* ($\chi^2 = 25.31$, df = 4, $p \leq 0.0001$) (Table 1). *Loris t. tardigradus* was encountered in taller trees ($F = 7.46$, df = 1, $p = 0.007$) than *L. l. nordicus*, as well as at greater heights ($F = 3.91$, df = 1, $p = 0.05$). A more detailed study of

Table 1: Summary of behaviour and habitat use for all lorises encountered, and for each subspecies, based on the moment of first contact. Significant differences are marked with an asterisk.

Parameter	All sightings (n=212)	<i>L. l. nordicus</i> (n=110)	<i>L. t. tardigradus</i> (n=95)
Height			
Tree Height	5.49 m ± 3.07	4.96 m ± 2.30*	6.11 m ± 3.70*
Animal Height	3.10 m ± 2.03	2.86 m ± 1.69*	3.36 m ± 2.35*
Minimum Animal Height	0	0	0
Maximum Animal Height	10	9	10
Behaviour			
Inactive	20.8%	19.1%	22.1%
Active	75.5%	80.0%	72.6%
Groom	1.4%	.9%	2.1%
Other/ Not seen	2.3%	0%	3.2%
Position			
Quadrupedal Walk	31.3%	39.7%	24.1%
Sit	17.9%	17.9%	18.7%
Climb Up	16.5%	15.1%	19.8%
Bridge	7.1%	10.4%	4.4%
Climb Down	7.5%	7.5%	8.8%
Quadrupedal Run	8.0%	3.8%	14.3%
Hang	2.4%	2.8%	2.2%
Spiral	0.9%	0.9%	1.1%
Quadrupedal Stand	2.8%	1.9%	4.4%
Other/Not seen	5.6%	0	2.2%
Substrate			
Terminal twig	33.3%	24.5%*	44.0%*
Small	38.7%	45.0%*	31.0%*
Medium	18.3%	25.5%*	9.5%*
Large	1.1%	2.0%	0%
Vine	5.9%	1.0%	11.9%
Ground/undergrowth/ road	2.7%	2.0%*	3.6%*
Substrate angle			
Oblique	60.4%	73.6%	43.9%
Horizontal	25.0%	18.6%	32.9%
Vertical	10.3%	2.9%*	19.5%*
Fork	1.6%	2.9%	0%
Ground/ undergrowth/ road	2.7%	2.0%	3.7%

each site is underway to determine the extent to which differences in these ecological parameters is due to availability of supports and tree types.

Social behaviour

Loris t. tardigradus was seen alone for 56.3% of contact points, and with other animals for 43.7% of contact points. *Loris l. nordicus* was seen alone for 50.5% of contact points, and with other animals for 49.5% of contact points. These figures include mothers found carrying their infants. The maximum number of animals seen together was nine, and the minimum was an animal alone; mean number of animals seen together was 1.64 ± 1.03 . Encountering animals together for nearly half of all observations once again attests to the surprisingly social nature of these nocturnal primates. Of the two *L. l. grandis* sightings made during this survey, one was of a single animal, and the other was of a pair of adults. The only sighting of *L. t. nycticeboides* was of a lone animal.

Behaviors observed when there was more than one loris together included feeding, play wrestling, and both males and females interacting with infants. Lorises of both taxa also slept communally in groups of up to four animals (Nekaris in press). No agonistic behavior was observed.

Diet

Both slender lorises were observed to eat only insect or animal prey items, including frogs, lizards and snails. They nearly always detected their prey with their eyes, and engaged in acrobatic suspensory postures to catch it (Nekaris 2002b). They grasped the prey with one or two hands; prey items were rarely caught and eaten directly with the mouth. Lorises were not observed to eat gum or drink water. The only potential non-insect item consumed by them was on a flowering *Cassia roxburghii*. Two different lactating females were observed to tug at something on the trees, and consumed several bits of whatever it was. They may have been eating the leaves, the flowers, or small insect cocoons that were woven tightly around the bases of leaves.

Morphological Differences Between *L. t. tardigradus* and *L. l. lydekkerianus*

Even to field assistants seeing lorises for the first time, the taxa appeared superficially distinct. Villagers with experience in both the north and south of the country distinguished ash-colored lorises from the dry north from the smaller red lorises of the south-west. Table 2 lists some of the differences

Table 2. Morphological variation in two taxa of slender loris. Measurements were taken according to a standard compiled by Schulze (2003). Measurements marked with an asterisk come from Schulze and Meier 1995a, from wild caught animals.

Feature	<i>L. l. nordicus</i>	<i>L. t. tardigradus</i>
Body weight – adult males	228-285g (n=4)*	172 (n=1)
Body weight – adult females	238-287g (n=5)*	118 g (n=3; 103,105,148)
Body weight – juveniles	105 g (n=2; 100, 110)	56 g (n=1)
Head Body length – adult males	227 mm (n=3)*	170 mm (n=1)
Head Body length – adult females	217 mm (n=3)*	122 mm (n=3; 116, 119, 130)
Head Body length – 2 mos infants	120 mm (n=2; 115, 125)	106 mm
General Hair Colour Dorsally	White or light buff	
General Hair Colour Ventrally	White or buff	Yellowish white
Colour of Hair Bases	Pale grey/ buff or no difference	Dark grey or black
Colour or preauricular hair	Broad white strip	No difference to rest of facial hair
Width of interocular stripe	Broad white	Narrow white to non-existent
Colour of circumocular patch	Grey/ brownish grey	Chestnut/ reddish
Shape of circumocular patch	Tear shaped	Rounded
Colour of ears	Yellow, sometimes with black rim	Yellow, sometimes mixed with pink, dark brown rim
Colour of hands and feet	Yellow	Yellow, turns pink with age
Colour of eyelids	Dark brown	Yellow

between these taxa. Aside from the great difference in color between them, the features of the facial masks are particularly striking (see Figs. 1 and 2). The circumocular patches of *L. t. tardigradus* extend almost to the ear, with the preauricular hair being the same colour. This is in contrast to both *L. l. nordicus* and *L. t. lydekkerianus*, which have a wide stripe of light preauricular hair. The ears and eyes of *L. t. tardigradus* give a much larger impression than the smaller ears and eyes of the larger grey subspecies. The diamond-like shape of the circumocular patches combined with a narrow interocular stripe in the larger grey forms also lends a distinct appearance to this subspecies.

Discussion

The data presented above allow us to form a preliminary picture of the distinctiveness of Sri Lankan slender loris taxa. In some ways, Sri Lankan slender lorises are similar to *L. l. lydekkerianus* of India. They spend a significant portion of their time in social contact with other lorises, sleep communally, and seem to be faunivorous (Bearder *et al.* 2002; Nekaris 2003; Nekaris and Rasmussen 2003). However, sig-

nificant differences between the taxa concur with the assessment of Groves that two distinct species of slender loris are found in Sri Lanka. Red lorises have a distinct locomotor pattern, move more quickly than grey lorises and, probably related to their smaller size, make more use of smaller substrates. Red lorises are much smaller than grey lorises from the dry zone; an infant grey loris is the same size as an adult female red loris. In addition to differences in body size, those in fur color and facial masks in particular may be important to species-specific mate recognition. Recent studies of African nocturnal prosimians have emphasized the importance of the facial mask in mate recognition of nocturnal species (Bearder 1999).

Data published elsewhere also lend further support to this view. Red lorises seem to have different rearing strategies from their larger grey counterparts. Mothers provide more direct contact for their offspring, whereas in grey lorises, males play a larger role (Nekaris in press). Red lorises in captivity appear to have a longer gestation period than grey lorises, and the two taxa housed together did not produce viable offspring (Goonan 1993).

Loris t. tardigradus and *L. l. nordicus* also differ in bio-acoustic patterns. Slender lorises have a vocal repertoire of approximately six audible calls (Rasmussen 1986; Schulze and Meier 1995b). The most frequently heard of these is the whistle, which can contain one to five phrases emitted in descending harmonics. Earlier on, only one whistle was recognized, which seemed to be multi-functional. Its uses include: to space individuals from different sleeping groups; to maintain affiliative contact with individuals from the same sleeping group; to call attention to an opposite sex conspecific; to indicate irritation (for example if an animal does not wish to be groomed by another); and to alert presence of a potential predator (Nekaris 2000).

A recent study has shown, however, that slender lorises emit at least five types of whistles, with differences apparent between taxa. *Loris l. nordicus* emits a significantly greater number of single phrase calls, calls more when the moon was absent, emits more of ‘call type 1 (characterised by a rise then fall in frequency),’ and never emits ‘call type 5.’ *Loris t. tardigradus* emits a greater number of multiple phrase calls, calls more when the moon is bright, predominantly makes a frequency modulated ‘call type 2,’ and produces a unique ‘call type 5’ with additional harmonics at the end of each phrase (Coults 2002; Nekaris unpubl, data). As with facial masks, calling patterns have been shown to serve as strong mate recognition systems for other species of nocturnal prosimians (e.g., Bearder *et al.* 1995; Hafen *et al.* 1998; Nietsch and Kopp 1998).

The extreme differences in body weight, in combination with differences in facial masks, and significant differences in the behavioral parameters noted above, provide strong support that these taxa should be differentiated at the species level. Coinciding with the recommendation by Groves (1998, 2001), it is important to consider red and grey lorises as independent units of conservation, even in the absence of genetic studies.

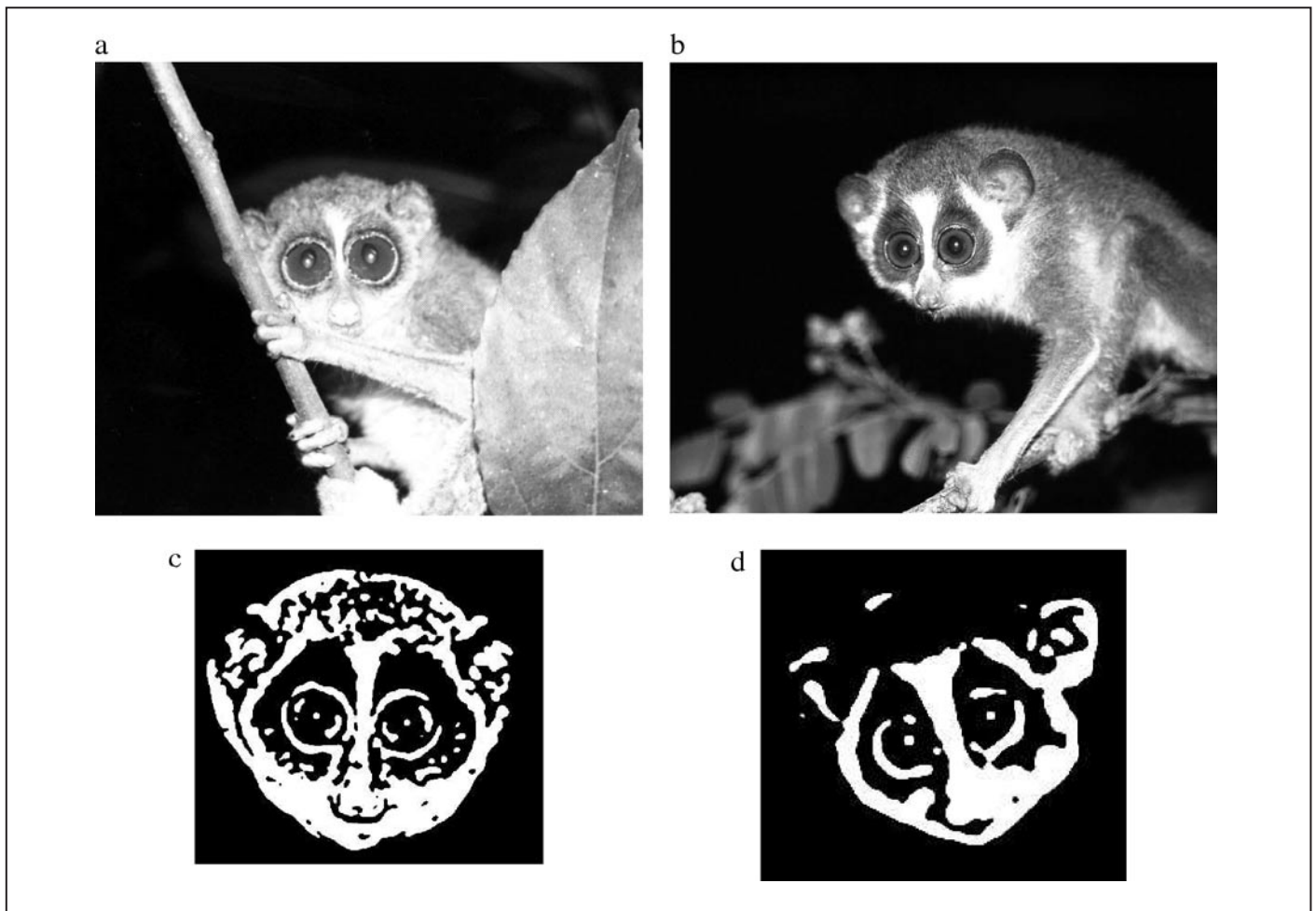


Figure 1. a. Adult male *Loris t. tardigradus* from Godakewela; b. Juvenile male *Loris l. nordicus* from Minneriya-Giritala; c. Facial mask of adult female *Loris t. tardigradus* from Pitigala; d. Facial mask of adult female *Loris l. nordicus* from Polonnaruwa.



Figure 2. Photograph of a female *Loris l. nordicus* from Trincomalee being treated after a road accident. It died shortly after. (Photo courtesy of V. B. P. Perera).

With this in mind, we make recommendations for their conservation status.

Conservation Status

Loris lydekkerianus nordicus is known to occur in at least seven distinct populations. Its presence in several areas in the northern dry zone, which are still somewhat continuous, suggests that it occurs widely there, but at relatively low densities. Its apparent ability to survive well near human habitation might also increase the overall abundance of this subspecies, though numbers are still low. However, increasing loss of habitat, such as that associated with the Mahawali Ganga Project, do not bode well for this subspecies (Erdelen 1988). We suggest that its current status as “Endangered”, criteria A1, subcategories “c” and “e”, remain: an observed, estimated, inferred or suspected reduction of at least 50% over the last 10 years or three generations, based on: a decline in area of occupancy, extent of occurrence and/or quality of habit; and the effects of introduced pathogens or pollutants (IUCN 2001). Subcategory “e” applies

mainly to the animals in the south-east, if the role of pesticides is shown to be prominent in this area.

Only preliminary suggestions can be made for *Loris lydekkerianus grandis*, as it has not been observed well enough or over enough observations to confirm its taxonomic status. Of sites visited in its known geographic distribution, only two yielded lorises at low densities. Since the same general criteria for habitat loss apply to these areas as seen for other slender loris taxa, we suggest that, as for *L. l. nordicus*, the current status of this subspecies be “Endangered”, category A1, remain, based on subcategory “c”. However, this is a very preliminary estimation, and further studies are needed.

Loris tardigradus tardigradus has now been located in only six small isolated forest patches, at both high and low densities. It was not seen in home gardens or along road sides in areas heavily disturbed by humans, and it is also subject to greater habitat loss than *L. l. nordicus*. This subspecies is also now absent from many areas where it was once known to occur, and the remaining forest patches in the south-western wet zone are not only isolated, but are also under severe encroachment (Mill 1995). Given that some authors already consider this subspecies to be a distinct species, and the mounting behavioral evidence in support of this division, its conservation status is serious. Its current status is “Endangered” category A1, but it should be ascribed the criteria B1/2abcd. That is: extent of occurrence estimated to be less than 5000 km² or area of occupancy estimated to be less than 500 km²; habitat is severely fragmented and it is known to exist at no more than five locations; and continuing decline in (a) extent of occurrence, (b) area of occupancy, (c) area, extent and quality of habitat, and (d) number of locations of subpopulations (IUCN 2001).

Though only one confirmed sighting of *L. t. nycticeboides* was made, considering the limited habitat available for this subspecies, and the numerous interviews conducted with individuals with expert knowledge of the Horton Plains, make it possible to propose the following assessment of its conservation status. *L. t. nycticeboides* falls under the category of “Critically Endangered” B1, 2abc based on the following criteria: extent of occurrence estimated to be less than 100 km²; habitat is severely fragmented; the existence of the taxa is only reported at a single location; the area of occupancy available for the taxa is continually declining (IUCN 2001; Nekaris *et al.* in press).

Plans for Future Research

This report has been generated as part of an ongoing comprehensive study of the behavior, ecology and distribution of slender lorises in Sri Lanka. Although many of the results presented in this paper are preliminary, we hope they are a first step towards better understanding this little known and unique group of primates.

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The Pig-tailed Macaque *Macaca nemestrina* in India - Status and Conservation

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Introduction

The pig-tailed macaque, *Macaca nemestrina* Linnaeus, 1766, is among the lesser-known primates of the Indian sub-continent. The species is characterized by its short tail, carried half-erect and somewhat resembling a pig's; hence the popular name. The legs and muzzle are comparatively long. The body color is brownish. The males are large, weighing up to 14.5 kg, and have 'manelike' hairs giving them a majestic look. Pig-tailed macaques range from northeastern India to southern China and Indonesia through eastern Bangladesh, Myanmar (Burma), Thailand, Laos, Cambodia and Vietnam. No comprehensive study solely on the species has been carried out in India. However, there is some information in a number of publications, including synoptic studies on primates or wildlife in general (Choudhury 1988, 1989a, 1993a, 1995a, 1995b, 1996a, 1996b, 1996c, 1996d, 1997a, 2001, 2002; McCann 1933; Mukherjee 1982; Pocock 1939, 1941; Tilson 1982). Its taxonomy and evolution have been reviewed by Fooden (1975) and Groves (2001) and it has been studied in the field in Malaya (Bernstein 1967, 1969; McClure 1964; Medway 1969). Here I present some observations concerning the distribution, habitat, status and conservation of the pig-tailed macaque.

Study Area

Northeastern India is comprised of the states of Arunachal Pradesh, Assam, Manipur, Meghalaya, Mizoram, Nagaland, and Tripura (21°58'-29°27'N, 89°42'-97°24'E). The region has very high mountains, part of the Eastern Himalaya, and hills of the Archaean plateau in Meghalaya and central Assam, and the two major plains of the Brahmaputra and Barak valleys. Habitat type ranges from tropical wet evergreen rainforest, moist deciduous, subtropical, and temperate forest to alpine vegetation and snow. Wet savanna grassland occurs in the plains.

The climate of the primate areas of the northeast are tropical monsoon and montane, with a hot and wet summer

and a cool, usually dry, winter. Average temperature generally ranges from less than 4°C (average minimum, December to early February) to 30°C (average maximum, June to August) (range 0° to above 38°C). Annual rainfall ranges from less than 1000 mm in parts of central Assam to more than 10,000 mm in parts of the southern face of the Meghalaya plateau and the foot of the Mishmi Hills. About 75% of the rain falls during the monsoon (May to September), but winter rains are not uncommon. Snow falls in winter in the higher altitudes of the Eastern Himalayas, Mishmi Hills and the Saramati Peak.

Methods

Between 1986 and 2002, I carried out field surveys in some potential habitats of the pig-tailed macaque in north-east India as part of a broader survey of primates in general. As well as travelling widely in Assam, Arunachal Pradesh, Manipur, Meghalaya, Mizoram, and Nagaland, I also visited Tripura. The presence or absence of the macaque was ascertained by direct sightings, preserved skulls in the tribal villages, and by interviewing local forest staff, villagers and hunters with the aid of photographs and drawings. Some of the skulls were identified at the Zoological Survey of India, Calcutta. Surveys were carried out by foot along existing and newly-cut paths, and trails, by vehicle along roads and tracks, by boat along nullahs and rivers, and by trained elephant along existing and newly-cut paths and trails. Observations were done with the help of naked eye, a pair of binoculars, a 10 x 50 and a 10x 46 telescope. Photographs were taken with a Canon T50 camera with 200 mm tele and a Nikon FM2.

Distribution and Habitat

In India, the pig-tailed macaque is confined to the north-east to the south of the Brahmaputra River. This mighty river (more than 8 km wide, minimum width *c.* 1.5 km) has

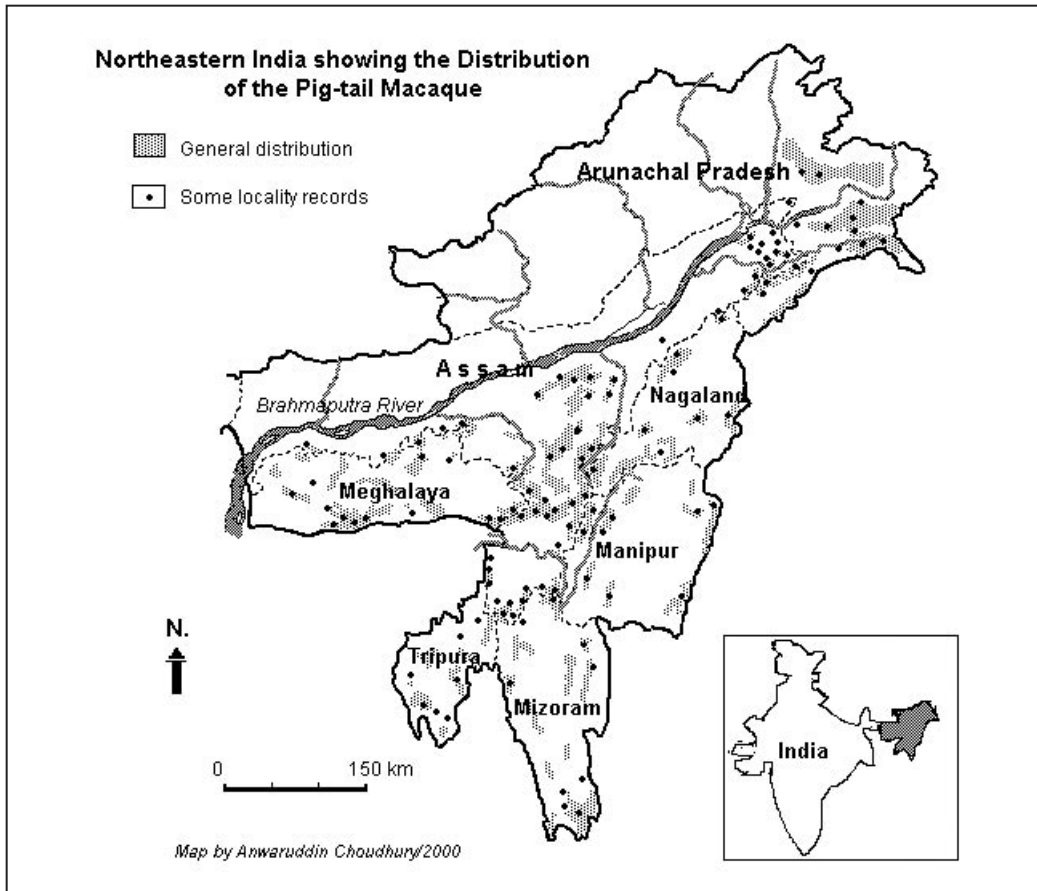


Figure 1. Northeastern India showing the distribution of the pig-tailed macaque, *Macaca nemestrina*.

acted as an effective barrier in the dispersal of the species (Choudhury 1988, 1989a). It occurs in Assam, the eastern part of Arunachal Pradesh, Manipur, Meghalaya, Mizoram, Nagaland, and Tripura (Fig. 1). Pocock (1939) described its range in India as “Eastern India (probably some districts east of the Ganges), Naga Hills, Assam”. Prater (1948) recorded the Naga Hills, Assam, and Roonwal and Mohnot (1977) India (Assam). However, the pig-tailed macaque has a relatively narrow but wider range than these authors indicated. The West Garo Hills District (90°E) in Meghalaya is the westernmost limit of its global range while Mishmi Hills (Dibang Valley District) (approx. 28°30’N) in Arunachal Pradesh is the northernmost.

Assam

In Assam, it occurs, or occurred, in most of the districts of the south bank of the Brahmaputra, as follows. *Tinsukia* (Bherjan-Borajan-Podumoni Sanctuary, Dibru-Saikhowa National Park and the following Reserved Forests - Burhi-Dihing [north and south blocks], Dangori, Digboi [west block], Dirok, Dum Duma, Kakojan, Kumsang, Mesaki, Namphai, Saleki [proposed], Tinkopani, Tirap, Torani, and Upper Dihing [east and west blocks], continued occurrence doubtful in Hahkhati and Kundil Kaliya Reserved Forests), *Dibrugarh* (Joypur Reserved Forest), *Sivasagar* (Abhoypur and Dilli Reserved Forests, perhaps extinct in Geleky

Reserved Forest), *Jorhat* (Hollongapar Reserved Forest - now Gibbon Sanctuary, Disoi, and Tiru Hill Reserved Forests, continued existence in Disoi Valley Reserved Forest is doubtful), *Golaghat* (Nambor-north block and Upper Daigurung Reserved Forests, continued existence in Lower Daigurung Reserved Forest is not known, extinct in Nambor-south block, Diphu, Doyang and Rengma Reserved Forests), *Karbi Anglong* (many localities including Garampani, East Karbi Anglong, Karbi Anglong and Nambor Sanctuaries, near Jirikinding, Singhason area, the Reserved Forests of Amreng, Balasor [proposed], Daldali, Dhansiri, Disama, Jungthung, Kaki, Kaliyoni, Langlokso [proposed], Lungnit, Nambor-north block, Nambor-west block, Patradisa, Umjakini [proposed], and West Mikir Hills [proposed], and in some unclassified forest areas), *Nagaon* (Bagser, Borpani, Doboka, and Lumding Reserved Forests), *Morigaon* (Kholahat and Sonaikuchi Reserved Forests), southern *Kamrup* (Gorbhanga, Rani, Bogaikhas, Apricola, and Apricola East [proposed] Reserved Forests; continued existence in Amcheng, South Amcheng and Khanapara Reserved Forests is not known), *Goalpara* (near the Garo Hills border), *North Cachar Hills* (Barail, Krungming, and Langting-Mupa Reserved Forests, and unclassified forests in the Barails, Simleng river area, and the proposed Khorongma Sanctuary), *Cachar* (Barail, Barak, Innerline, Lower Jiri, North Cachar, Sonai, and Upper Jiri Reserved Forests), *Hailakandi* (Innerline, and Katakhal

Reserved Forests, and in unclassified forests towards the north of the Innerline, for example in the areas of Baldaboldi, Kartikchara, and Garodpunji), and *Karimganj* (Badshahitilla, Longai, Patharia Hill, and Shingla Reserved Forests, its continued occurrence in Dohalia and Tilbhum Reserved Forests is doubtful).

Arunachal Pradesh

In Arunachal Pradesh, the pig-tailed macaque is found towards the east of the Dibang River. It occurs in the *Dibang Valley* (recorded in Mehao Sanctuary), *Lohit* (mainly in Digaru, Kamlang, Manabum, Tengapani, and Turung Reserved Forests, and Kamlang Sanctuary), *Changlang* (Namdapha National Park and Diyun, Honkap, Miao, Namchik, Namdang, Namphuk, Pangsau, and Rima Reserved Forests), and *Tirap* (Namsang and Borduria “Village Reserve Forests”, as well as unclassified forests on the main Patkai Range), all in eastern part of the state. It has vanished from the forested areas on the plains in Roing-Santipur (Dibang Valley district) Namsai-Bordumsa (Lohit and Changlang districts) areas.

Nagaland and Manipur

In Nagaland, it has been recorded in all the districts, i.e., *Kohima*, *Mokokchung*, *Mon*, *Phek*, *Wokha*, *Tuensang*, and *Zunheboto* (mainly in the Satoi area; Choudhury 1997b). The sale of meat of a pig-tailed macaque in Kohima market in 1997 suggested that a few can still be found in the neighbourhood of Kohima township. In Manipur, the species is thinly distributed in all the hill districts - *Churachandpur* (mainly Keilam Hill Sanctuary, and Tolbung Reserved Forest), *Ukhrul* (mainly in Shiroy and Anko Range areas), *Tamenglong* (Jiri-Makru and Bunning Sanctuaries, Irangmukh Reserved Forest, and unclassified forests towards the north), *Chandel* (Yangoupokpi Lokchao Sanctuary, Moreh Reserved Forest [proposed] and some unclassified forests), and *Senapati* (mainly in the Barail Range).

Mizoram, Tripura and Meghalaya

In Mizoram, as well as Tripura and Meghalaya it is patchily and thinly distributed in all the districts. Mizoram - *Aizawl* and *Kolasib* (especially in Innerline Reserved Forest), *Mamit* (especially in Dampa Sanctuary), *Champhai* (especially in Murlen National Park and Lengteng Sanctuary), *Lunglei*, *Lawngtlai* (especially in Ngengpui Sanctuary), and *Saiha* (especially in Phawngpui National Park and near Palak Dil). Tripura – *Dholai* (especially in Gumti Sanctuary), *West* (especially in Sepahijala Sanctuary), *North* and *South* Districts (scattered). Meghalaya – *Jaintia Hills* (especially in Narpuh and Saipung Reserved Forests), *East Khasi Hills* (especially in the south-facing gorges and canyons), *West Khasi Hills* (scattered in private and community forests), *Ri-Bhoi* (especially in Nongkhylllem Sanctuary and Reserved Forest), *East Garo Hills* (especially in Songsak Reserved Forest), *West Garo Hills* (scattered) and *South Garo Hills* (especially in Balpakram National Park).

Further information on the distribution of the species in these states can be found in McCann (1933, for Nagaland), Mukherjee (1982, for Tripura), and Biswas and Diengdoh (1977) and Choudhury (1998c) for Meghalaya. Throughout its range in north-east India, the pig-tailed macaque is sympatric with other primates such as the Assamese macaque *M. assamensis*, stump-tailed macaque *M. arctoides*, rhesus macaque *Macaca mulatta*, capped langur *Presbytis pileatus*, hoolock gibbon *Hylobates hoolock*, and slow loris *Nycticebus coucang*. In southern Assam, Mizoram and Tripura, it is also sympatric with Phayre’s leaf monkey *Presbytis phayrei*.

Like the stump-tailed macaque, the pig-tailed macaque is basically a dweller of dense forest, both evergreen and semievergreen, in the plains, foothills and hills. It has been recorded from altitudes of less than 50 m in Karimganj (edge of Patharia Hill Reserved Forest) to above 2000 m in Nagaland (Barail Range). All the recorded sites were in evergreen or semievergreen forest, both tropical and sub-tropical. Within the evergreen biotope it also occurs in deciduous dominated forests such as Dhansiri and Lumding Reserved Forests of Assam, but is not restricted to them. There are evergreen and semievergreen patches in all such deciduous habitats of north-east India. In some small forest pockets such as Bherjan, Borajan and Podumoni in Assam, it also occasionally enters tea plantations and can be seen in the vicinity of human settlements. While the extent of occurrence of the species is still large, almost the entire north-east of India south of the Brahmaputra River and east of the Dibang River (about 150,000 km²), the total potential habitat, i.e., dense forest, is only about 35,000 km². Of this area, the known “area of occupancy” (as per IUCN criteria; IUCN 1996) is even smaller: less than 16,000 km².

Status

The pig-tailed macaque is a rare primate of the Indian sub-continent. Sightings and field observations are few and far between in most of its range within India. However, in some very small forest patches in the District of Tinsukia, eastern Assam (especially Bherjan-Borajan-Podumoni Sanctuary) it is commonly seen and is not even shy. During more than one and a half decades of fieldwork, I have found it to be scarce with a low encounter rate. It is extremely shy in areas where poaching is rampant, for example, the Assam-Mizoram border. In the Barail Range of Assam, one of its major haunts, it restricts itself to the denser parts of the forests.

It is difficult to make a population estimate of such a shy and thinly distributed species as the pig-tailed macaque, but a general idea of population abundance is essential for conservation action. The population density can be estimated for three areas only: Bherjan, Borajan and Podumoni. The ecological density in a 1992-94 survey was 8.6/km² in Borajan, 33.3/km² in Bherjan and 8/km² in Podumoni (including the sanctuary and adjacent areas, which are used by the macaques). The figures for Podumoni and Borajan may be underestimated. However, such high densities are unlikely to



Figure 2. The pig-tailed macaque, *Macaca nemestrina*. In India, it is confined to the forests in the northeast to south of the Brahmaputra River only.

be found in other areas of north-east India. In Hollongapar Reserved Forest (now the Gibbon Sanctuary) the crude density is about 2.5/km². Choudhury (1989a), basing his information largely on Mackinnon and Mackinnon (1987), estimated an overall density of 1.5/km² for Assam. If this density is used then there may be around 24,000 of these macaques left in India (taking the area occupancy as less than 16,000 km²). For Assam, 7500-9000 macaques were estimated in the late eighties using the same density (Choudhury 1989a).

Conservation Problems

Habitat destruction

Destruction of forests by felling, encroachment, *jhum* (slash-and-burn shifting cultivation of the hill tribes), and monoculture tree plantation is a major threat to the survival of the pig-tailed macaque with all other forest-dwelling primates. The forest cover in north-east India is disappearing at an alarming rate. More than 1,000 km² of forest were destroyed annually in the 1970s and 1980s (derived from data of the National Remote Sensing Agency). This alarming rate of loss is evident from examples such as Manipur where the dense forest cover has declined from 50.5% in 1980-82 to 23.8% in 1995. During the same period, the decrease in Meghalaya was from 33.1% to 18.0%, and in Tripura, from 43.4% to 17.3% (source: National Remote Sensing Agency for 1980-82 and State of Forest Report, Government of India for 1995).

Encroachment is a major problem in the reserved forests. Almost the entire population of primates, including the pig-tailed macaque, has vanished from the 900 km² rain forest tract comprising Nambor (south block), Diphu, and Rengma Reserved Forests in Golaghat district (Assam) because of border problems with Nagaland in the 1970s and 1980s, and consequent felling, poaching and encroachment (Choudhury 1999).



Figure 3. Habitat destruction for slash-and-burn shifting cultivation and illegal felling is a major threat to the pig-tailed macaque in its entire range.

In the hilly areas throughout the north-east, *jhum* cultivation is an important driver of forest destruction. For instance, in a small state such as Manipur (total area: 22,327 km²), *jhum* currently covers more than 1,800 km² or 8.2 %. Even in the hilly areas of Assam, the area currently under *jhum* is more than 2,600 km². Forest cutting is not only reducing the habitat and the numbers of primates but also resulting in fragmentation. The pig-tailed macaque is a forest-dweller and its survival depends upon the continued existence of large expanses of forest. The ultimate cause of habitat destruction is, however, the very rapid growth of the human population. Every year more than five *lakhs* (half a million) of new faces are being added to the population of north-east India.

Poaching

Like most other primates, the pig-tailed macaque is also killed for food by many of the hill tribes of north-east India. Poaching is severe in Nagaland, Tripura, the hills of Manipur, Mizoram, Tirap and Dibang Valley districts of Arunachal Pradesh, as well as North Cachar Hills and parts of Cachar districts of Assam. Poaching also occurs in the Meghalaya, Changlang and Lohit districts of Arunachal Pradesh, and other parts of Assam. The species is almost extirpated for this reason in the Assam-Nagaland border, especially in the Golaghat and Jorhat sectors. Hunting is the main reason for their extreme shyness in most of their range except for some areas of Tinsukia district, Nambor (north block) Reserved Forest and the Gibbon Sanctuary (Hollongapar). While in the past, traditional weapons, including snares and self-made muzzle-loaders, were used, the easy availability of automatic firearms has aggravated this threat over the last two decades. There are also instances of well-organized hunting trips from Nagaland and Mizoram to parts of Assam (Choudhury 1986). Various hill tribes such as the Nagas, Kukis (including Hmar, Paite, Biate), Mizos, Chakmas, and Tipperas relish primate meat and hunt regularly. Tangsas, Garos, Khasis, Lais (Pawis), Maras (Lakhers) and Reangs also frequently kill primates for food.

Trade

Although there is no significant trade in pig-tailed macaques, any young animal within easy reach is usually captured as a pet. Small numbers are also taken (illegally) for supply to zoos. There were records of poaching in the Garo Hills of Meghalaya to supply zoos in the 1980s (the late Mohammed Moosa, animal dealer, pers. comm.).

Crop-raiding

Crop raiding by pig-tailed macaques in the cultivations and orchards is rare. I have obtained occasional reports from the Barail Range, Garo and Khasi Hills. Near Borajan in the Tinsukia district of Assam, the macaques were observed feeding in the paddyfield after the harvest. They also enter tea plantations (without causing any damage) and orchards near Bherjan in the same district. The macaques sometimes take maize and other crops in the *jhum* cultivations.

Other problems

Unsustainable bamboo harvesting for large paper mills (at Jagiroad, Panchgram, and Jogighopa in Assam, and Tuli in Nagaland), oil mining and exploration (eastern Assam and adjacent areas of Arunachal Pradesh), and open-cast coal mining (eastern Assam and parts of Meghalaya) which destroy the habitat, besides causing pollution and disturbance, are some of the other conservation issues. In Dibru-Saikhowa National Park, the great earthquake of 1950 resulted in some major geomorphological changes, which included the sinking of large parts of the present national park, while huge amounts of silt brought down by the Brahmaputra and the Lohit rivers has accumulated on the riverbeds. Since then the area has begun to suffer regular flooding (and water logging) during the monsoon which is resulting in a change of the vegetation types (Choudhury 1998a). Evergreen trees are being replaced by deciduous species, while the low-lying areas are being colonized by *Salix tetrasperma*. This has greatly reduced the potential habitat of the macaque in the park (only about a quarter is suitable now).



Figure 4. Pig-tailed macaques feeding in a paddyfield in Borajan forests, Tinsukia district of Assam. Crop raiding by this species is a very rare sight.

Conservation Measures Taken

Legal protection

The pig-tailed macaque is protected under Schedule-II (part I) of the Wild Life (Protection) Act of India, which prohibits its killing or capture, dead or alive. However, enforcement is virtually nonexistent except in some of the protected areas. Most local people are also unaware of its legal status. The 2000 IUCN Red List of Threatened Species (Hilton-Taylor 2002) listed it as “Vulnerable”.

Habitat protection

The pig-tailed macaque is found in about 30 protected areas, while its presence is doubtful in a further five. Namdapha National Park and the contiguous Kamlang Wildlife Sanctuary of Arunachal Pradesh seem to be the best-secured and largest protected zone for the species. Security is more due to sheer size and inaccessibility of large parts of this combined wilderness rather than actual enforcement. The populations in Balpakram, and Nokrek National Parks of Meghalaya, the Gibbon and Bherjan-Borajan-Podumoni Sanctuaries of Assam, and Dampa Sanctuary of Mizoram are also reasonably well protected, but their protection in Intanki Sanctuary of Nagaland is poor. The protected areas having the pig-tailed macaque are listed in Table 1, and about a third of the known area of occupancy is under protected status (some areas of Namdapha and Kamlang are unsuitable for the species due to snowfall).

Recommendations

1. The creation of new protected areas in Assam. The important known habitats include Dhansiri Reserved Forest and adjacent forests (recommended as Dhansiri Tiger Reserve; Choudhury 1998b), Nambor (north block; Golaghat portion) and Upper and Lower Dairgung Reserved Forests (recommended as an extension of Garampani Sanctuary; Choudhury 1993a), Upper Dihing (west block), Dirok, Joypur and Dilli Reserved Forests (all recommended as Upper Dihing National Park; Choudhury 1996c), the Barail Range (recommended as a national park as well as a biosphere reserve; Choudhury 1989b, 1993b), and Innerline Reserved Forest and adjacent forests (recommended as a sanctuary/national park as well as a biosphere reserve; Choudhury 1983, 1993b).
2. Further protected areas. The Satoi and Saramati areas in Nagaland, and the Anko Range in Manipur should be given protected status. In Meghalaya, the area of Nongkhylliem Sanctuary should be extended to include the entire reserved forest area and parts of Narpuh, (blocks I and II), and Saipung Reserved Forest should be declared as a sanctuary. In Mizoram, the Innerline Reserved Forest should also be accorded sanctuary status.

3. Existing protected areas such as Intanki, Garampani, East Karbi Anglong, Nambor and Yangoupokpi Lokchao should be provided with adequate protection and management protocols.
4. Measures should be taken to control *jhum* cultivation, as well as poaching for meat.
5. The pig-tailed macaque should be brought under Schedule I of the Indian Wild Life (Protection) Act, which gives highest protection and completely bans the killing or capture dead or alive.

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Table 1. Protected areas in north-east India with the pig-tailed macaque, *Macaca nemestrina* (Yes = presence confirmed; ? = presence doubtful).

Protected area	Area km ²	Pig-tailed macaque	Remarks
Assam			
Bherjan-Borajan-Podumoni Wildlife Sanctuary	7.22	Yes	
Dibru-Saikhowa National Park	340.00	Yes	
East Karbi Anglong Wildlife Sanctuary	221.81	Yes	
Garampani Wildlife Sanctuary	6.05	Yes	Contiguous with Nambor (north block) Reserved Forest and Nambor Sanctuary
Gibbon Wildlife Sanctuary	20.98	Yes	
Kaziranga National Park	472.50	?	Possible only in Kanchanjuri area
Karbi Anglong Wildlife Sanctuary	96.00	Yes	
Nambor Wildlife Sanctuary	37.00	Yes	Contiguous with Garampani Sanctuary
Arunachal Pradesh			
Dibang Wildlife Sanctuary	4149.00	?	
Kamlang Wildlife Sanctuary	783.00	Yes	Contiguous with Namdapha National Park
Mehao Wildlife Sanctuary	281.50	Yes	
Namdapha National Park	1985.00	Yes	Contiguous with Kamlang Wildlife Sanctuary
Manipur			
Bunning Wildlife Sanctuary	115.00	Yes	
Jiri-Makru Wildlife Sanctuary	198.00	Yes	
Keilam Hill Wildlife Sanctuary	187.00	Yes	
Yangoupokpi Lokchao Wildlife Sanctuary	184.80	Yes	
Zeilad Lake Wildlife Sanctuary	21.00	Yes	
Meghalaya			
Balpakram National Park	312.00	Yes	The area is less than 200 km ² as there was some anomaly in computing.
Nokrek National Park	68.01	Yes	
Nongkhylliem Wildlife Sanctuary	29.00	Yes	
Siju Wildlife Sanctuary	5.20	Yes	Contiguous with Balpakram National Park
Mizoram			
Dampa Wildlife Sanctuary	500.00	Yes	
Khawnglung Wildlife Sanctuary	41.00	?	
Lengteng Wildlife Sanctuary	120.00	Yes	
Murlen National Park	200.00	Yes	
Ngengpui Wildlife Sanctuary	110.00	Yes	
Palak Dil Sanctuary	15.30	Yes	
Phawngpui National Park	50.00	Yes	
Thorang Wildlife Sanctuary	50.00	?	
Nagaland			
Fakim Wildlife Sanctuary	6.42	Yes	
Intanki Wildlife Sanctuary	202.02	Yes	
Pulie-Badge Wildlife Sanctuary	9.23	?	
Rangapahar Wildlife Sanctuary	4.70	Extinct	
Tripura			
Gumti Wildlife Sanctuary	389.50	Yes	
Rowa Wildlife Sanctuary	8.58	Extinct	
Sepahijala Wildlife Sanctuary	18.53	Yes	
Trishna Wildlife Sanctuary	170.60	Yes	
Total protected areas		30(35)	

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Assamese Macaques (*Macaca assamensis*) in Nepal

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Introduction

Three species of monkeys have been reported from Nepal; the Rhesus macaque *Macaca mulatta* (Zimmermann, 1780), Hanuman Langur *Semnopithecus entellus* (Dufresne, 1797), and the Assamese macaque *Macaca assamensis* (McClelland, 1839). Information on the distributions, behavioral ecology and conservation status of these species is provided by Bishop (1979), Southwick *et al.* (1982), Johnson *et al.* (1988), Jackson (1990), Chalise (1995, 1997, 1998, 1999, 2000, 2000a, 2000b) and Chalise *et al.* (2001). Here I report on Assamese monkey populations in Nepal, including some aspects of their behavior, and the comparative morphological characters of those studied to date in Nepal and other countries. *Macaca assamensis* inhabits the foothills of the Himalayas and adjoining mountain chains of South-east Asia, from central Nepal eastward through Bhutan, north-eastern India, northern and eastern Burma, southern China, northern and western Thailand, Laos, and northern Vietnam, besides an isolated record in south-western Bangladesh. This species – together with *M. sinica*, *M. radiata*, and *M. thibetana* – is assigned to the *sinica* group of macaques, defined by the shared-derived characters of male and female reproductive anatomy.

Study Sites

Nepal has numerous distinct ecological zones and vegetation types, with some of the last pristine mountain ecosystems on earth, and harbors, as such, a highly diverse fauna and flora. Natural landscapes are categorized into three major regions. The northernmost high snow-capped area above 5,000 m; the Himalayan range running east to west. The central region of the country with an average altitude of 2,000 m known as the mid-hills, comprising highland valleys at elevations of 600 to 3,500 m, which occasionally receive snow in winter. The southern part of the country consists of Siwalik (the Churiya range) and Tarai plain in the subtropical zone (NBAP, 2000). Of some 186 mammals listed for the country,

27 have been declared “protected” by the Wildlife Act, 2045 of His Majesty’s Government (Chalise 1995a), and the Assamese monkey is one of them. Nepalese primate populations, however, have yet to be systematically surveyed. Here we report on our studies in four separate areas, encompassing an east-west range of over 200 km, and an altitudinal range of about 1100 m (Fig. 1).

Makalu-Barun National Park and buffer zone (27°28’N, 87°10’E)

Makalu-Barun National Park (MBCNP) is in the east of Kathmandu valley, near Mt. Everest and on the foothills of Mt. Makalu, the world’s fifth highest peak. The phytogeography of the Arun basin is unique amongst the protected areas of Nepal, showing affinities to both Oriental and Palearctic regions. As a result, the western part of this area was declared as the Makalu-Barun National Park and Conservation Area. Around 32,000 Rai and Sherpa ethnic people live in the buffer zone of the park. Three primates, Rhesus macaque, Hanuman langur, and the Assamese macaque, have been reported in the Makalu-Barun area (Jackson 1990; Chalise 1997a). They are considered crop pests in the Conservation Area of the Arun basin (Giri and Shah 1992). (Local people report that while attacking the crops, some of the Assamese macaques stay on the periphery of the fields as guards, and are called ‘Pahare Bandar’ or guarding monkeys.) Groups occupy mainly the steep, rocky areas in the higher elevations (‘Pahara’ means steep rocky area in Nepali language).

Langtang National Park and buffer zone (85°15’-86°0’E and 28°20’N)

Langtang National Park (LNP) is in the central Himalayan region of Nepal, 132 km north of the capital, Kathmandu, bordering, in the northeast, the Nepal-Tibet autonomous region of China. Langtang Lirung (7,245 m) is the highest point in the park, and Dorje Lhakpa (6,988 m) lies to the east. The lowest elevations drop to about 1,000 m on the banks of the Bhote Koshi-Trisuli River. Langtang National

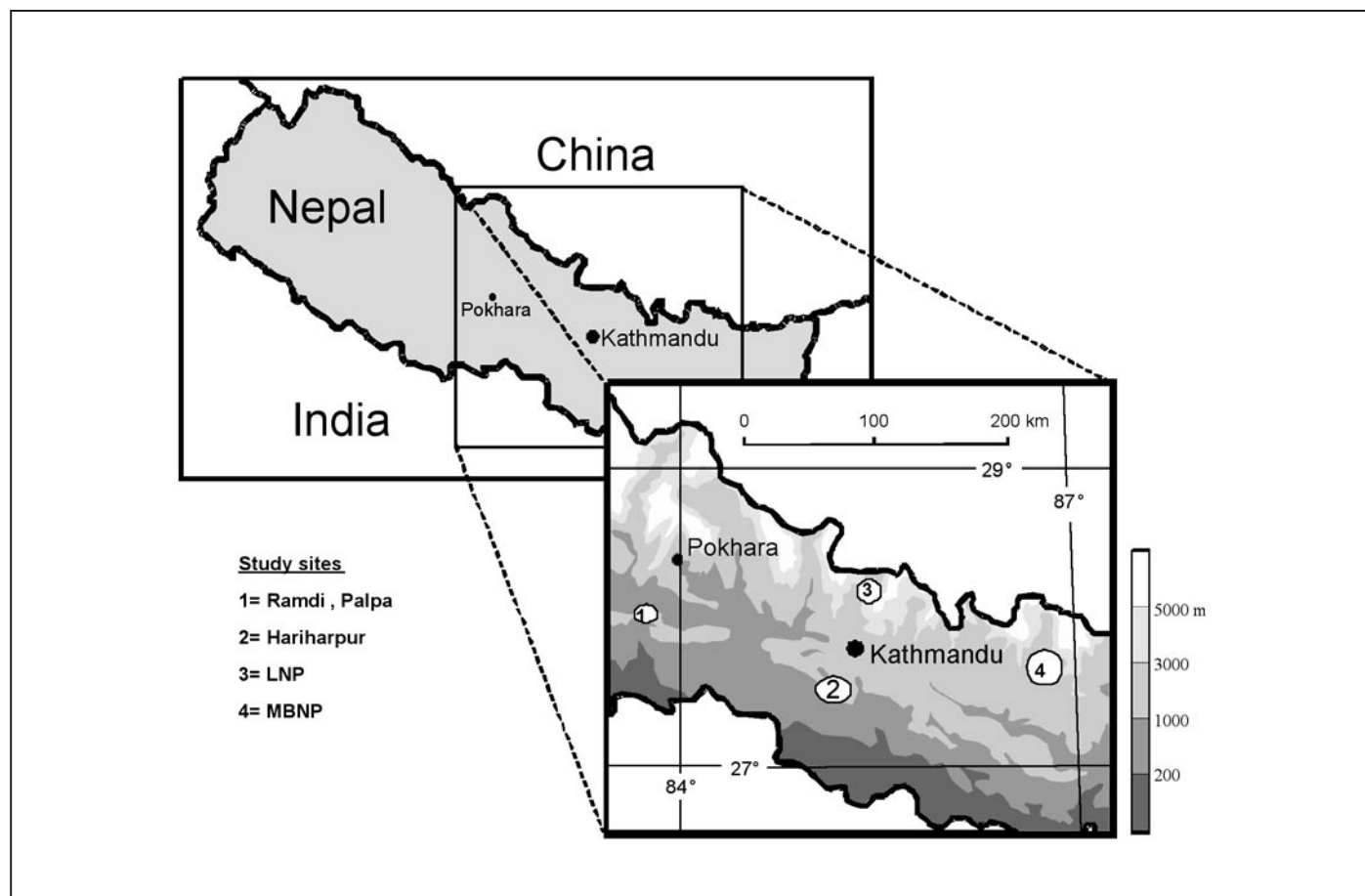


Figure 1. The four study sites in Nepal for the Assamese macaque.

Park covers 1,710 km² in three districts: Rasuwa, Nuwakot and Sindhupalchok of Bagmati zone in Nepal. Forty-five indigenous village settlements inside the park are being managed according to the Himalayan National Park Regulation 2036 (1979). Forty-six species of mammals occur there, including those typical of the area, such as pika, Himalayan black bear, Himalayan thar, leopard, ghoral, serow, snow leopard (*Uncia uncia*), Clouded leopard (*Pardofelis nebulosa*), musk deer (*Moschus chrysogaster*), red panda (*Ailu-*rus fulgens**), and three species of monkeys; Rhesus monkeys, Hanuman Langur and Assamese monkeys. Surveys have located *M. assamensis* in Helambu, Dahalghedi, Ghattekhola, Melung, Rimiche, and Sebrubesi, mostly around fields and plantations.

Ramdi, Palpa Area, 27°45'N, 83°55'E

Ramdi is a small highway settlement in Palpa District along the Kaligandaki River, in west Nepal. It is contiguous with the temperate forest to the north and subtropical hill Sal forest (*Shorea robusta*) and riparian forest in the south. Elevations are quite low (around 420 m asl), however, due to the area's location in the mid-hills, mountains in central Nepal, running east to west along the Himalayas, and lying north of Siwalik and the Churiya range of Nepal. Floristically it shows an affinity with the Palaearctic. It is very accessible and Assamese monkeys are easily observed there.

Hariharpur Area, 27°18'N, 85°30'E

Hariharpur is an ancient settlement in the Makawanpur District of Nepal. It lies in the south-west of the Kathmandu valley, and can be reached by bus as far as Chaughada-Het-*auda* but then requires a 5-hour walk along the mountains. Assamese monkeys were observed along the Bagmati River near Phaparbari village.

Methods

The procedures and equipment used during the field-work, and the food items and plants eaten by the Assamese monkeys have been described elsewhere (Chalise 1998; Chalise *et al.* 2001). Tree densities and the composition of the forests in MBNP and LNP (but not in the Ramdi, Palpa Area nor in the Hariharpur Area) were determined in four quadrates of 900 m² (30 m x 30 m) within the home range of the focal groups. The quadrates covered nearly 0.36 ha in each research site. Different topographic types (river edge, slopes and flat areas) and altitudes (from 1000 m to 1500 m asl in MBNP and 1000 m to 2000 m asl in LNP) were selected so that the total topographic, phytogeographic and ecological patterns could be represented adequately. All the plants inside the quadrates which had trunks equal to or greater than 12 cm in DBH (diameter at breast height) were marked and identified. The ground vegetation was also recorded to examine the

food plants and diversity on the forest floor. Human impacts and the condition of the trees were recorded. As such, the quadrates revealed the abundance of tree species, their condition and density, and it was possible to obtain a picture of the existing plant communities, the degree of disturbance and the composition of the forests.

The behaviors of monkeys were recorded by scan sampling for one minute at intervals of 10 minutes (Martin and Bateson 1993). Daily observation lasted up to eight hours. Other events and interesting behaviors of any group members were recorded whenever they were seen (all occurrences). Counts of group size and composition were carried out repeatedly during observations. Besides the general survey of this species in the area, for comparative purposes, data were obtained regularly from two groups from MBNP and LNP.

Habitats

Observations of Assamese monkeys were carried out in a number of localities in Nepal. While the results presented here are combined, differences between populations are mentioned whenever relevant.

Habitat in the Makalu-Barun National Park and buffer zone

Schima wallichii was found to be dominant. It is a species used by the local people as fodder for livestock and pigs, and was second in rank as a food item for the monkeys (21.74% of feeding time). It also ranked second in dominance in the study group's home range. Unidentified climbers and herbs were first ranked in the diet (25.75% of feeding time). Many of the plants are used as fodder by the local people for their livestock. Including *S. wallichii*, 23 fodder plants comprised 70%, and non-fodder plants 30%, of the total plant species recorded in the quadrates. Among the non-fodder plants *Elaeocarpus robustus* (23.4%) was the dominant species recorded (Chalise 1999). Many of the non-fodder plants were used either for commercial or household purposes by local people. The habitat of the Assamese macaques was found to be steep slopes and rocky areas with patchy forest. They also frequently used open bushy and shrubby land to forage. They were more scarce in the remoter parts of the forest interior.

Habitat in the Langtang National Park and buffer zone

The botanical quadrates were set up at different elevations. A preliminary investigation indicated 18 species of plants in the home range of the Assamese macaques. *Lyonia ovalifolia* was the dominant species, the leaves of which are

eaten by the monkeys. Commonly eaten are the fruits of *Pyrus pasia* which was third-ranking in the study area. Of the 18 species, only three were not seen to be used by the monkeys during the observations. However, more detailed studies will undoubtedly reveal higher plant diversity for the area. An interesting finding was that the monkeys eat young pine needles, generally ignored by domestic cattle (Chalise *et al.* 2001).

Assamese Macaque Groups

Makalu-Barun National Park and buffer zone

We recorded a total of 142 Assamese macaques in seven groups in the area of Lakuwa in 1997. Group size ranged from seven to 50 individuals, including adult males and females, young adults, juveniles, and infants of different ages. A few lone adult males and all-male groups (with larger body sizes than group dwelling males) were also observed. There were relatively few young adults of both sexes (5%), which predictably will affect the adult population in the immediate future. The population of juveniles and infants combined (35%) was reasonable (Table 1), although it may be that their survival (reflected in the numbers of young adults) is low. The immature to mature ratio was 1:1.7, and the adult sex ratio was 1:1.6.

A survey in the same area and season in the following year, 1998, recorded 72 individuals in four groups. The young adult population increased to 11% of the total, while the proportion of adult females was lower (31.9%). The numbers of other age/sex groups were similar to the previous year. The population of juveniles and infants combined (40%) was higher than in the previous year, however, indicating that survival had increased to 11%. The mature/immature ratio was reversed (0.9:1), while the adult sex ratio was 1:1.9. Lone males or all male groups were not recorded during this survey. Group sizes ranged from 13 to 27 individuals, similar to the previous year. The number of monkeys in Lakuwa was evidently lower in 1998, when I focused specifically on the area in and around Lakuwa village.

Three further areas in and around the Makalu-Barun National Park were surveyed in 1999: Dankhila, Sintup, and Apsuwa, and resulted in the observation of a further 202 monkeys (Table 1). The mature/immature ratio in these areas combined was 1:1.7. Juveniles and infants considered together accounted for 37.5% of the individuals seen. Young adult males and females were considerably reduced in numbers: only one young female at Sintup, and five sub-adult males at Dankhila and Apsuwa (2.9% of the population considered).

Table 1. Size and composition of Assamese monkeys populations in the different localities surveyed in the area of Makalu-Barun.

Locality	Adult male	Adult female	Sub Adult male	Sub-adult female	Juvenile	Infants	Total	Year
Lakuwa	33	53	4	2	20	30	142	1997
Lakuwa	12	23	4	4	12	17	72	1998
Dankhila	24	38	3	-	19	20	104	1999
Sintup	6	13	-	1	3	8	31	1999
Apsuwa	11	23	2	-	15	16	67	1999

The situation was more encouraging in the numbers of juveniles and infants, especially at Apsuwa where they accounted for 46% of the monkeys seen.

Another locality surveyed, outside the protected area, about 100 km south of Makalu-Barun National Park, was Mulghat along the Tamor River. Thirty individuals were sighted at the lowest altitude recorded for this species (380 m asl).

Langtang National Park and buffer zone

Surveys in seven localities in the Langtang National Park and buffer zone revealed a different pattern (Table 2) indicating a population structure distinct from that observed in Makalu-Barun. The young population was 8.3% (8+4 individuals in 145), which is more favorable than in the Makalu population. Adult sex ratio was 1:2, and the immature to mature ratio was 1:1.9 (145/76). Juveniles and infants comprised 39% of the population (Table 2). A separate population was located around the Doring area of Helambu; a group of 12 individuals north of Timbu village.

Ramdi, Palpa Area

During the survey of the mid-hills of Nepal in October 2000, we observed a group of 30 individuals along the Kaligandaki River, by the Sunauli-Pokhara highway near Tansen, Palpa, at an elevation of 420 m asl. The group was much more habituated to people and traffic than was the case for Assamese macaques in other areas.

Hariharpur Area

In May 1998, we saw a group of 11 individuals along the Bagmati River in Tapke Danda in the Hariharpur area,

Makawanpur district of central Nepal. The Assamese macaques we observed there were smaller and more shy than those of Makalu-Barun and Langtang.

Body size

As in other members of the genus, male Assamese macaques are larger than females. Measurements of a female found dead in the Lakuwa area were as follows. Head to rump was 24 inches (600 mm). The tail was 14 inches (350 mm) long. The sole of the foot was 7 inches long. Body weight was estimated at 12-15 kg (unfortunately the weighing machine was not functioning at the time). It is my impression that Assamese macaques in Nepal are larger and heavy than elsewhere (Table 3).

Pelage

The fur coloration of Assamese monkeys observed in Nepal varies from dark-brown to blackish-brown on the back, and whitish blond to ashy white on the abdomen. In the adult female, the cheeks and around the eyes are mostly crimson-red to pinkish red. These colors are absent in adult males, which are mostly whitish-yellow on the face, but dark violet around the nose. One or two adults seen in each group had overall darker and ashy fur coloration. The pelage coloration of infants and juveniles also varied, but they are generally more blond than the older individuals. The palm, sole and nails are dirty brown, while their off-white ischial callosities are conspicuous from a distance, especially in darker individuals. Female juveniles have more pinkish ear tips and faces than male juveniles. The animals described here are from

Table 2. Composition of Assamese monkey populations in different localities surveyed in Langtang National Park (2000-01).

Locality in Langtang National Park	Adult male	Adult female	Sub-adult male	Sub-adult female	Juvenile	Infant	Total
Ghatte Khola	4	6	2	-	3	5	20
Sole-Brabal	7	13	3	1	8	4	36
Shyafu Besi	5	11	2	1	7	6	32
Rimiche	2	4	-	-	2	2	10
Melung	4	10	1	2	5	8	30
Dahal Phedi	1	2	-	-	1	1	5
Pranjal	2	5	-	-	2	3	12
Total	25	51	8	4	28	29	145

Table 3. External measurements of specimens of Assamese monkey, *Macaca assamensis*.

Reference	Head & Body HB (mm)	Tail length T (mm)	T/HB Ratio	Weight (kg)	Species / Locality
Roonwal and Mohnot (1977)	440-527	178-386	0.35-0.52	4.6-6.8	<i>M. assamensis</i>
Fooden (1988)	530-587	236-293	0.44-0.55	7.0-8.6	<i>M. a. pelops</i>
Fooden (1988)	437-555	170-225	0.31-0.47	4.86-8.75	<i>M. a. assamensis</i>
Prater (1993)	<600	c. 200	NA (0.33)	12 (male)	<i>M. assamensis</i>
Rowe (1996)	431-587	204-292	0.47-0.49	4.9-8.6	<i>M. assamensis</i>
Chalise (1998)	600	350	0.58	12-15 (female)	Makalu-Barun National Park
Chalise (1998)	558.5	305	0.55	8 (young female)	Makalu-Barun National Park
Srivastava (1999)	538-730	140-460	0.26-0.63	7.9-15	<i>M. assamensis</i>
Chalise (2000)	585	334	0.57	9.5 (young female)	Ilam, east Nepal
Chalise et. al. (2001)	650	350	0.54	10.4 (male)	Langtang National Park

Note: References of Chalise = Unpublished data and papers.

groups ranging from 980 m to 1500 m asl. Assamese macaque groups observed in areas 2200 m to 2500 m asl were too shy to obtain detailed observations, but are bigger and darker than those at lower elevations.

Local people call Assamese macaques rock, or cliff, monkeys. In Makulu, they call them ‘Thoro’, after their vocalizations (see below). They reported that they seldom raid crop fields, and recognized their closeness to the Tibetan macaques.

Behavioral Observations

Vocalizations

Observations of the mountain populations of Assamese macaques were limited. They give “Thruuu” alarm vocalizations on seeing people, and a “Pio” call is produced when they see deer. At lower elevations, however, we were able to observe a number of different vocalizations. When harassed or displaced by an adult male, the sub adults produce a “Quinch” vocalization. As in the mountain groups we observed, they produce a “Pio” sound in the presence of barking deer (*Muntiacus muntjak*) but also when they saw a Himalayan yellow throated martin (*Martes flavigula*). “Chrkhayak” and “Khio”, are hiccup sounds they give when approached by the observers. Sometimes it is accompanied by lip-smacking. The macaques give a “Chianck” alarm call when people throw stones at them, as well as on sighting raptors, such as the mountain eagle, kites and goshawk (*Accipiter* sp.). On one occasion we observed a drongo (*Dicrurus* sp.) chasing a young adult that produced the “pio” alarm several times while hiding. Roonwal and Mohnot (1977) and Prater (1993) provide further information on vocalizations in this species.

Interactions with langurs

On one occasion we observed a group of Assamese macaques resting very close to some langurs, *Semnopithecus entellus*, on a steep cliff; a common sleeping site. For about two hours both groups were exchanging places, taking turns foraging on the same food. However, when they were close to each other, the langurs would move up to the canopy or

middle crowns of the food trees, while the macaques would feed on the shrubs or ground vegetation below. The macaques were not seen to climb up into the canopy, even when feeding on the same trees which had been used just previously by the langurs. This behavior, therefore, clearly indicated distinct feeding habits, even when the same trees were exploited. That night, both species remained on the cliff in their separate subgroups, sometimes as little as 5 m apart. Adult langurs were sometimes disturbed by a threat from a larger juvenile Assamese macaque and would move away. The langurs were evidently very cautious and vigilant towards the macaques, which, on the other hand, were observed grooming each other and seemingly ignored them.

Other behaviors

During our observations in MBNP in 1997 (March and April with 140 contact hours) and 1998 (around March and April with 124 contact hours), we recorded four major behavior categories: feeding, walking, grooming and resting. The results in each year were very similar, differing by only 3 to 4%. The 1997/1998 percentage times invested in: feeding were 47/44; walking - 29/25; grooming - 9/13 and resting - 15/18 (Fig. 2). Chalise (1998) reported on the daily activities and details of their behavior. Geophagy was recorded in 1997 (see Chalise 1997a, 1997b). In general, it would seem that this species is less quarrelsome, more sluggish and very shy; quite distinct from other macaques such as the Rhesus macaque.

Individuals would often hang by their legs during play, and also to reach items that interested them. Once an adult male pulled a juvenile toward him to groom him, and the unwilling juvenile kicked him. Females would commonly slap juvenile males as they went past. Body contact and huddling between adult males and between male juveniles and infants was common.

We also carried out observations on a macaque group in Langtang National Park in October-November 2000 and April-May 2001. Differences in time budgets were noticeable (Fig. 3). In 2000 the macaques foraged less (20% as

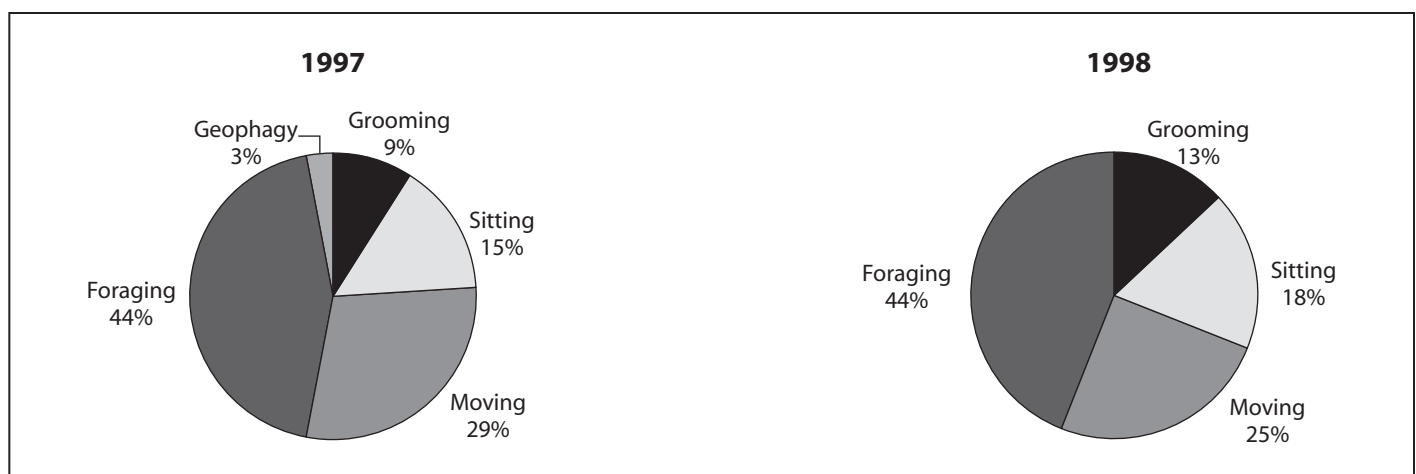


Figure 2. Major behaviors of Assamese macaques, *Macaca assamensis*, recorded in Lakuwa, Makalu-Barun Conservation Area in 1997 (left) and 1998 (right).

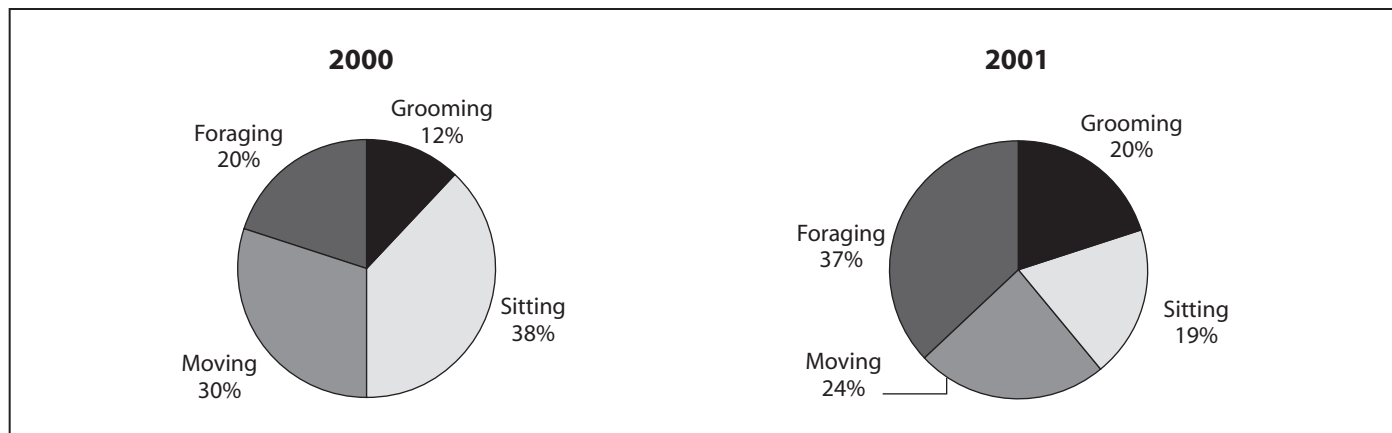


Figure 3. Major behaviors of Assamese macaque, *Macaca assamensis*, recorded in Langtang National Park in 2000 (left) and 2001 (right).

opposed to 37% in 2001) and moved more (30% compared to 24% of their daily activity) than in 2001. They also groomed less (12% compared to 20% in 2001) and rested (sitting) more (38% compared to 19% in 2001). Feeding behavior, food items and the plants and plant parts eaten were identified (see Chalise *et al.* 2001). Assamese macaques are predominantly leaf eaters; but will eat fruits and flowers whenever they are available. Due to the clumped distribution and seasonality in availability of fruits and flowers, the mainstay of the diet is leaves, young shoots, and petioles and, on occasion, agricultural crops (see below). Chalise *et al.* (2001) reported on the daily activities and details of their behavior.

Reproductive Behavior

We observed females “presenting” to passing males. Juvenile males who attempted to mount were driven away with a slap. When presenting, the female would shake her head and raise her hindquarters. Males were seen to pull out and eat vaginal plugs. Once, following an unsuccessful copulation, an individual pulled out nearly 20 inches of sticky sperm and eat it. Copulations between high-ranking males and estrus females were followed by prolonged periods of grooming. Considering the observed ages of infants, we estimated that their breeding seasons would be around November to December.

Sleeping sites

Sleeping sites are typically rocky cliffs, usually along the steep banks of streams and rivers. More than five such sites were recorded for one of the study groups. They evidently provide some security against carnivores. Each site is used regularly: a study group used one site for five nights in a row, but mostly they are used on alternate nights. They climb up nearly an hour before sunset, grooming and moving around before settling down. The sites are usually devoid of trees and shrubs. In the evening and early morning they separate out into their larger subgroups of up to 10 individuals, including adult males, females, juveniles and infants of different ages. Adult males were seen hugging the juveniles and grooming them briefly on cold mornings.

Crop-Raiding

Crop-raiding is commonly reported for these monkeys, and is considered to have a significant economic impact on farmers in the highlands. We used a questionnaire to examine the perceived extent and frequency of crop-raiding, including estimates by local villagers of the loss to their harvest. All three species, Rhesus macaque, Hanuman Langur, and the Assamese macaque, are reported to raid the crops of local farmers.

Rhesus and Assamese macaques were reported to be the most frequent crop raiders, but villagers indicated that the latter cause the most damage. There are fewer Rhesus than Assamese macaques in the MBNP study area. Eighty villagers were interviewed during 1997/98 in the MBNP. The agricultural production lost due to crop-raiding by wildlife in general was estimated at 39,696.65 kg; averaging 496.21 kg for each household; 67% of the loss being cereals and 33% tubers and fruits. More than half (55%) was due to monkeys. Of this portion of damage caused by monkeys, maize fields were targeted most (29% of total loss), then potatoes and tubers - 23%, rice - 13%, fruits - 12% and kodo - 12% (Chalise 1999). The tubers and fruits accounted for 35% of the total loss caused by the monkeys, and the cereals combined comprised 65% of the loss in Lakuwa village.

Further surveys (56 households) in 2001 indicated a slightly different picture. The total crop loss was estimate at 10,081.35 kg, averaging 180 kg per house. Maize fields were the most frequently raided (41% of total loss assessed), followed by fruit crops (18%), rice (14%), millet (13%), and potatoes and yams (11%). Wheat, buckwheat and beans were not widely cultivated, and crop-raiding was insignificant (Fig. 4a).

Farmers faced a similar problem of crop-raiding by langurs and Assamese and rhesus macaques at Langtang National Park (LNP). In the upper LNP area, crop-raiding by Assamese macaques and langurs was more common than by rhesus macaques, which are fewer in number. Assamese macaques are less common than Rhesus macaques in the lower elevations. The monkeys uproot the new maize seedlings to eat the seed, and eat the entire stalks of the

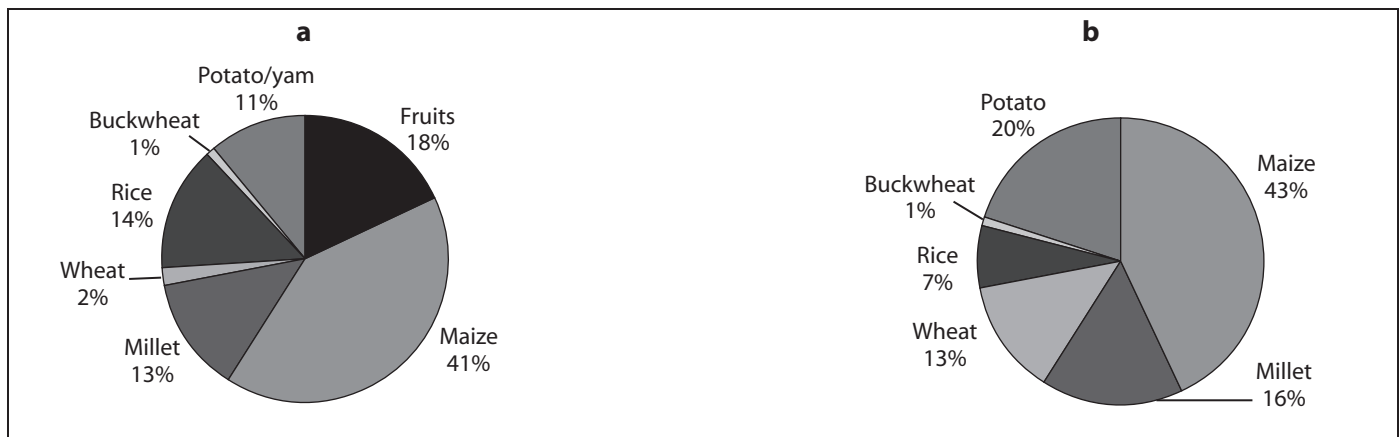


Figure 4. Crop-raiding by Rhesus macaque, Hanuman Langur, and the Assamese macaque in the Makalu-Barun National Park in 2001 (a) and Langtang National Park (2000/01) (b).

small-seeded millet. Crop damage is acute in the lower part of Langtang where the three species are found. Crop-raiding data were collected from 76 households from upper Langtang to the buffer zone at lower altitudes. Each household was estimated to have lost 391.67 kg of their crop yields. Of 29,767.16 kg of total food lost, maize accounted for 43%, potato 20%, millet 16%, wheat 13%, rice 7%, and buckwheat 1% (Fig. 4b). At higher elevations crop-raiding was reduced due to the absence of rhesus monkeys in the colder areas.

Some Comparisons with Other Studies

Group size

Southwick *et al.* (1964) reported on two groups of Assamese monkeys in Darjeeling, and estimated group sizes of 10-25, with an adult sex ratio of 1:1.7. In Thailand, Carpenter (1942) noted that undisturbed groups typically consisted of about 12-26 individuals. Fooden (1971) recorded 11 Assamese macaque groups in Kanchanaburi, Thailand, with group sizes ranging from 10 to 50 individuals. Aggimarangsee (1992) observed two semi-tame groups of this species in Wat Tham Pla, Chiang Rai, Thailand, with 36 and 56 individuals. As found by Southwick *et al.* (1964), the adult sex ratio was about 1:1.7.

Body size and external characters

Roonwal and Mohnot (1977) reported an average head-body length for males of 476 to 680 mm and for females 440 to 527 mm. Tail length ranged from 178 to 386 mm, being 0.35 to 0.52 of the body length. The weights of males were 6.1 to 13.0 kg and of females were 4.6 to 6.8 kg. Prater (1993) reported the weight of an old male as around 12 kg.

Fa (1989) summarized the external characters of *M. assamensis* as described by a number of authors. He described pelage color as varying from deep rust to lighter yellowish brown, anterior dorsal fur almost invariably more yellowed than posterior, and skin of the muzzle darker, brown to purplish. In some individuals the face appears purple. There is variation in tail length, some tails reaching to only just above

the knee, and in others the tail extends to below the knee (Fa 1989, p. 57). The side-whiskers and beard are moderately developed in Assamese macaques. Facial skin color in the *sinica* group adults is buffy in adult males and variably buffy to pinkish to red in adult females (Fooden 1988). As described by Fooden, (1980), in the Assamese macaques the dorsal surface is golden brown to reddish brown and drab brown posteriorly, contrasting with reddish posterior dorsal pelage of *M. mulatta*.

Behavior

In a study of a group in Wat Tham Pla, Chiang Rai, Thailand, Aggimarangsee (1992) categorized the behaviors recorded for all age/sex classes of Assamese macaque into seven activities. The time budget estimated by Aggimarangsee was as follows: 31% in rest, 27% travel, 17% feeding, 15% playing, 8% grooming, 1% aggression and 0.3% sexual activities. The diet contained a high proportion of fruits, leaves, and flowers, but very little bark and insects (Aggimarangsee 1992). In Bangladesh, however, Ahsan (1994) recorded a diet of mostly leaves (46%), flowers (31%) and fruits (23%). According to Roonwal and Mohnot (1977), they also consume insects and probably some vertebrates such as lizards (Fooden 1971).

Studying a provisioned group of free-ranging Assamese monkeys in Golpara, India, Sarkar and Bhattacharjee (1996) reported that during 182 hours of focal animal sampling the monkeys used 36% of their total time for feeding, 30% for resting, 20% grooming and 15% locomotion. At the same site and in the same year (1998), Subba (1998) carried out a study based on 10-minute scans, which resulted in a similar pattern (foraging 43%, 22% walking, 18% resting and 17% grooming). Slight differences are probably due only to methodology and the natural range of variation. Larvae and insects supplement protein in the primate's diet, and soil related materials counteract phenolic substances in their foods (Chalise 1995). Prater (1993) reported maize crop-raiding by Assamese macaques at Tarkhola, Darjeeling, India. There the local Lepcha tribe hunted them for food and medicinal purposes.

Conclusion

Although Assamese macaques have been studied in India, Thailand and other parts of south-east Asia (e.g., Fa 1989; Fooden 1980, 1988, 1989, 1991; Aggimarngsee 1992; Sarkar and Bhattacharjee 1996), the Nepal populations are still poorly known, and detailed long-term behavioral-ecological research programs are needed, besides further studies of population structure and demographics and their geographic distribution, in order to provide a better understanding of their conservation status. External measurements of the Assamese macaques in the Makalu-Barun area have indicated some differences from those so far described from south-east Asia (Table 3). It is uncertain whether the Nepalese populations are of the subspecies *Macaca assamensis pelops* (Hodgson, 1840) or whether they may need to be considered a new subspecies. Molecular genetic studies would be helpful in resolving their taxonomic status.

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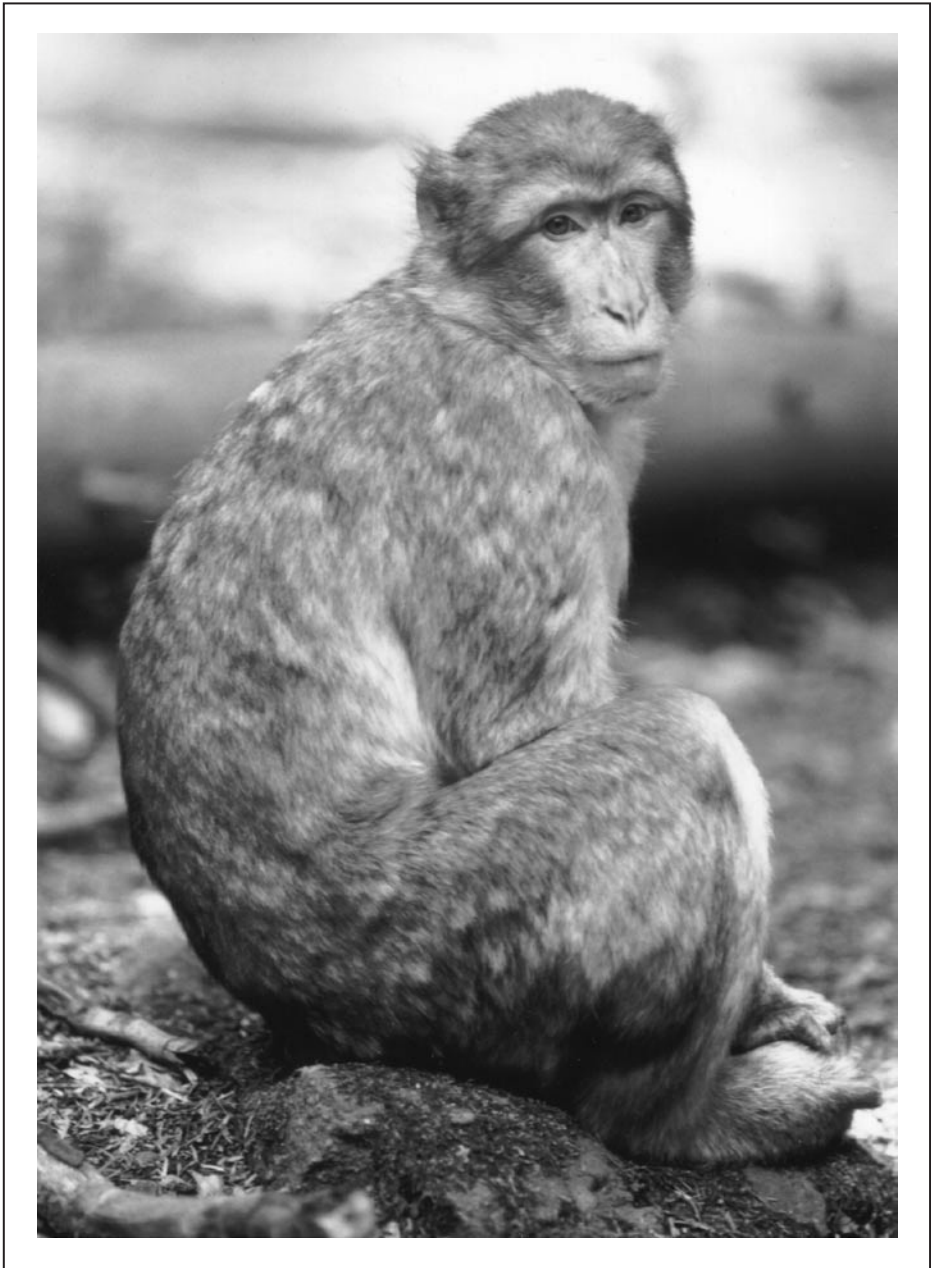
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